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

4
5 [Dataset quality, *Chinlestegophis* and origin of caecilians]

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35 **Abstract**

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

55 **Keywords**

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

58 **Introduction**

59 *Chinlestegophis jenkinsi* was named and described by Pardo et al. (2017a) as a Late Triassic
60 stem-caecilian. Although we agree that *C. jenkinsi* presents an interesting mix of characters,
61 we wish to respond to claims Pardo et al. (2017a) made about *Chinlestegophis* that were
62 incompletely tested, and are in some cases weakened by underlying problems with character
63 construction and taxon sampling. Taken together, those basic issues raise doubts about the
64 main claim of Pardo et al. (2017a)—that *Chinlestegophis* is a stem-caecilian.

65 Caecilians have a scanty fossil record (Santos et al. 2020; Kligman et al. 2023), with the
66 earliest well-supported stem members, *Funcusvermis gilmorei* Kligman et al., 2023, and
67 *Eocaecilia micropodia* Jenkins and Walsh, 1993 (Jenkins and Walsh 1993), dating from the
68 Late Triassic and the Early Jurassic. *Eocaecilia* retains limbs and some cranial bones that are
69 absent in the caecilian crown group (Gymnophiona; see Wake 2020); partial femora were
70 also assigned to *Funcusvermis* and the Early Cretaceous or, more likely, Late Jurassic
71 (Lasseron et al. 2019) *Rubricacaecilia monbaroni* Evans and Sigogneau-Russell, 2001
72 (Evans and Sigogneau-Russell 2001; Kligman et al. 2023). Since *Eocaecilia* was named, a
73 more thorough anatomical study (Jenkins et al. 2007) and many phylogenetic analyses
74 confirmed its position along the caecilian stem (Laurin 1998; Vallin and Laurin 2004;
75 Maddin et al. 2012a; Pardo et al. 2017a: fig. S6). However, despite the absence of serious
76 doubts about the status of *Eocaecilia* in the literature (Evans and Sigogneau-Russell 2001;
77 Carroll 2007: 54; Sigurdson and Bolt 2010: 1373; further corroborated by Kligman et al.
78 2023), Pardo et al. (2017a: abstract) stated: “The position of *Eocaecilia* within tetrapod
79 phylogeny is controversial, as it already acquired the specialized morphology that
80 characterizes modern caecilians by the Jurassic.” That statement is misleading: all
81 phylogenetic analyses that included *Eocaecilia* support its placement as a stem-caecilian; it is
82 the position of caecilians as a group in the context of its ancestry among extinct tetrapods that
83 remained controversial.

84 In contrast, the interpretation of *Chinlestegophis jenkinsi* (slightly younger than
85 *Funcusvermis*: Kligman et al. 2023) as a stem-caecilian (Pardo et al. 2017a) has less
86 anatomical and phylogenetic support. Without a more comprehensive analysis based on a
87 substantially revised matrix, *Chinlestegophis* currently cannot be supported as a stem-
88 caecilian and should not be treated as one in secondary analyses, such as molecular estimates
89 of divergence times (as previously stated by Santos et al. 2020 and Kligman et al. 2023). The
90 problem is not merely one of narrow paleontological interest, but also carries broader
91 implications for understanding the tempo and sequence of amphibian evolution. The analyses
92 by Pardo et al. (2017a) surprisingly appeared to anchor the caecilians (through
93 *Chinlestegophis*) within the stereospondyl temnospondyls, whereas frogs and salamanders
94 (i.e., batrachians) remained in a more common placement as dissorophoid temnospondyls,
95 producing a novel and immediately controversial hypothesis of lissamphibian origins.
96 Therefore, reassessing the position of *Chinlestegophis* among other tetrapods (including
97 *Eocaecilia*) may have major implications for understanding the ancestry of all extant

98 amphibians. Indeed, the captivating notion of the problem of amphibian origins and the
99 evolution of specialized caecilian traits having been “solved” with the discovery of
100 *Chinlestegophis* has already permeated popular zoology textbooks (Pough et al. 2022, figs.
101 9.2 and 9.5).

102 Here we show that the original phylogenetic analyses (Pardo et al. 2017a) fall short in
103 supporting the placement of *Chinlestegophis* as a stem-caecilian because of 1) problems with
104 the matrices used, including narrow taxon sampling, errors and oversights in character
105 construction and modification, and incorrect scores within the original data sets underpinning
106 the resulting matrices; 2) a suboptimal methodology, including reliance on a majority-rule
107 consensus tree and incomplete reporting of tree statistics; and 3) qualitative problems with
108 the diagnostic features linking *Chinlestegophis* (and in some cases *Rileymillerus*) to
109 caecilians. Our objective is to review and evaluate the problematic aspects of the original
110 analyses in order to facilitate future emendations and expansions, so that a clearer picture of
111 the affinities of *Chinlestegophis* may emerge.

112 Although Kligman et al. (2023: supplementary information parts 3–4) published their
113 reevaluation of one of the matrices and the characters that Pardo et al. (2017a) had used to tie
114 caecilians to *Chinlestegophis* and other stereospondyls while our work was still in progress,
115 their work complements ours, as we expand upon the matrix corrections, character treatments
116 and parameters used for analyses, and discussion of character construction.

117 *Nomenclature*

118 Our usage of the clade names Gymnophiona, Amphibia and Lissamphibia follows Wake
119 (2020) and Laurin et al. (2020a, b); temnospondyl nomenclature follows Schoch (2013,
120 2018), except for the name Temnospondyli, whose definition by Schoch (2013) excludes
121 important groups of animals universally considered temnospondyls when applied to our trees;
122 instead, we use the definition by Yates and Warren (2000). Whenever possible we applied the
123 same set of names to all figures. Junior synonyms are shown in parentheses, and names that
124 cannot be applied to a particular tree (because of qualifying clauses or definitions that restrict
125 their applicability to certain phylogenetic contexts) are not shown on that tree; by chance,
126 Schoch’s (2013) Eutemnospondyli cannot be applied in any of our figures. Schoch (2013)
127 gave identical definitions for Stereospondyli and Stereospondylomorpha; it is obvious that
128 that is an accident and that the intended definition for Stereospondyli can be recovered by

129 replacing “most” by “least”. Misspellings of genus and species names in the matrices and
130 figures of Pardo et al. (2017a) were silently corrected by us. See Marjanovič and Laurin
131 (2019: 13) for discussion of the correction of “Albanerpetontidae” to Albanerpetidae.

132 We use “caecilians” for crown-group caecilians (Gymnophiona: Wake 2020) and their
133 uncontroversial relatives like *Eocaecilia* and *Funcusvermis*. This may be, depending on the
134 phylogenetic hypothesis, a smaller grouping than Gymnophionomorpha under either the
135 original definition of that name (Marjanovič and Laurin 2008) or the potentially much wider
136 one by Kligman et al. (2023). The problem of how best to define Gymnophionomorpha is
137 beyond the scope of this paper.

138 The names Lepospondyli and Microsauria are used here informally for traditional groupings
139 of taxa; the likely para- or polyphyly of these groupings (see Marjanovič and Laurin [2019]
140 for discussion and references, especially but not only Pardo et al. [2017b]) is beyond the
141 scope of this work. For simplicity we present these names without quotation marks
142 throughout.

143 *Abbreviations*

144 AMNH FARB: Collection of Fossil Amphibians, Reptiles and Birds at the American
145 Museum of Natural History (New York).

146 app.: appendix (of cited works).

147 CI: consistency index.

148 MPT: most parsimonious tree.

149 MRC: majority-rule consensus.

150 OTU: operational taxonomic unit (a line in a data matrix).

151 RC: rescaled consistency index.

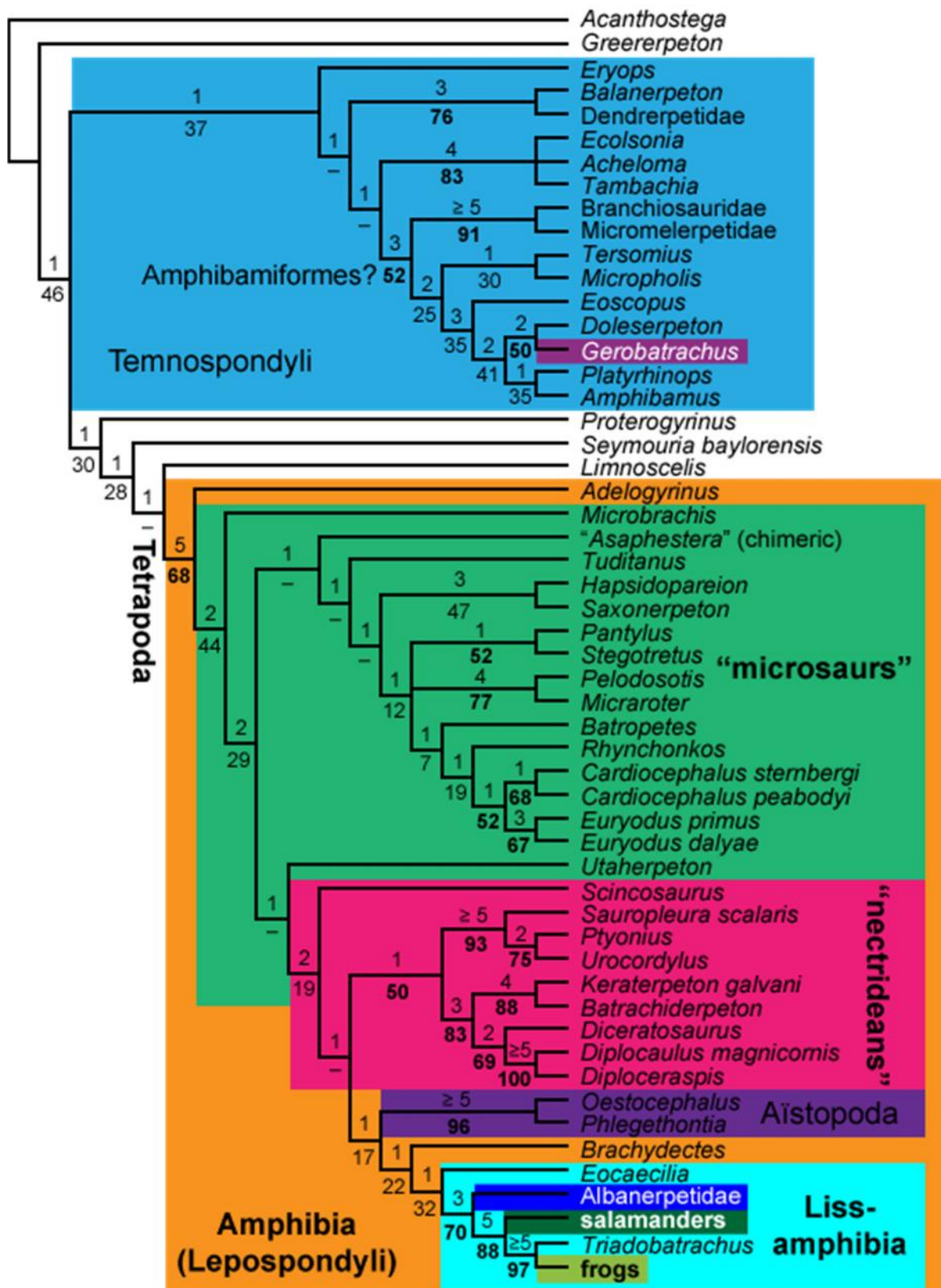
152 RI: retention index.

153 supp. inf.: supplementary information (of cited works).

154 **Matrices, Methodologies, and Missteps**

156 Pardo et al. (2017a) analyzed two matrices: a taxonomically broader, unpublished dataset,
157 and an expanded, published matrix focused on the position of *Chinlestegophis* and
158 *Rileymillerus* within temnospondyls. The originally unpublished matrix (see Supplementary
159 File 1 for a NEXUS file), which generated the trees shown in Pardo et al. (2017a: fig. S6),
160 contains 319 characters (27 of them parsimony-uninformative, including five constant ones)
161 and 71 OTUs; it is based on the matrix of Maddin et al. (2012a), with additions of characters
162 and taxa from Huttenlocker et al. (2013) and several new ones. Those earlier matrices are
163 based on that of Anderson et al. (2008a), but subsequently proposed corrections to that matrix
164 (Marjanovič and Laurin 2009; Skutschas and Martin 2011; Sigurdson and Green 2011) were
165 neither included in the resulting composite matrix nor addressed in the text by Pardo et al.
166 (2017a) or any of the references therein. Those changes have considerable influence on the
167 resulting tree topology, as exemplified in Figure 1.

168 **Figure 1. Strict consensus of the four MPTs obtained by Marjanovič & Laurin (2009:**
169 **electronic supplementary material 2) from their modified version of the matrix of**
170 **Anderson et al. (2008a) with ordering of clinal characters.** Note that contrary to Anderson
171 et al. (2008a), who had found extant amphibians to be diphyletic, with the stem-caecilian
172 *Eocaecilia* among lepospondyls but Albanerpetidae, Caudata, *Triadobatrachus* and Anura
173 among temnospondyls, Lissamphibia (cyan rectangle) is recovered and placed among
174 “lepospondyls” (orange rectangle). The temnospondyl *Gerobatrachus*, interpreted as a
175 member of the batrachian stem by Anderson et al. (2008a (Anderson et al. 2008b); i.e.,
176 closest to frogs and salamanders), is marked with a purple rectangle and white font. The
177 names of extant taxa are in boldface; “frogs” and “salamanders” are composites. The
178 application of the name Amphibamiformes is unclear due to the absence of *Dissorophus*.
179 Numbers below internodes are bootstrap percentages (in bold if 50 or higher; “–” indicates
180 clades contradicted by the bootstrap tree, always by clades with bootstrap percentages of 40
181 or less), numbers above internodes are Bremer values. Some or all of the Bremer values
182 shown as “ 5” might actually be 5, because Marjanovič and Laurin (2009 (Marjanovič and
183 Laurin 2009)) were unable to find all trees that were up to 5 steps longer than the MPTs,
184 although the fact that an earlier iteration of this analysis, with a dataset that differed only in
185 two cells, found the same results makes this possibility unlikely. Note that “*Asaphestera*” as
186 used here is a chimera of the amniote *Asaphestera*, the “microsaur” *Steenerpeton* and an
187 indeterminate lower jaw; most of the material belongs to *Steenerpeton*, however (Mann et al.
188 2020). The Dendrerpetidae OTU was originally called “*Dendrerpeton*” but is mostly based
189 on its apparently close relative *Dendrysekos*.



190

191 The published matrix (Pardo et al. 2017a: supporting information part D), which generated
 192 the trees shown in Pardo et al. (2017a: fig. 2, 3, S7), has 345 characters (23 parsimony-
 193 uninformative) and 76 OTUs. It is built on the unpublished matrix by the addition of

194 characters and taxa taken primarily from Schoch (2013)—see Gee (2022) for a thorough
195 discussion of that lineage of matrices.

196 It is of course common practice to modify and expand existing data sets, and underlying
197 errors are frequently perpetuated into later generations of matrices when first-hand
198 reassessment of specimens is infeasible, detailed comparison to the literature is deemed too
199 time-consuming, or the full history of characters becomes obscured over time, leading to
200 different meanings of the same character for different taxa that were added or revised at
201 different times (Marjanovič and Laurin 2019; Gee 2021, 2022). In those cases, conservative
202 practice is to accept that preexisting descriptions and scores are reliable. However, over many
203 iterations of matrices, substantial errors can and do accumulate—this is a known and
204 pervasive problem with large data matrices that are recycled in consecutive studies (Simões
205 et al. 2017; Laurin and Piñeiro 2018; Marjanovič and Laurin 2019; Gee 2021, 2022; Kligman
206 et al. 2023: supp. inf. part 4; and see our Discussion section).

207 The merging of existing matrices also can generate additional problems related to redundant
208 characters and states. As an example, multiple characters related to the lower jaw in the
209 published matrix of Pardo et al. (2017a) carry redundancy (in particular characters 147, 148,
210 146, 272, 273, 322, 344; see full evaluation below), and because each is strongly associated
211 with specialized morphologies mainly observed in caecilians, even when correctly scored,
212 these may generate bias by inflating support for the purported relationship between
213 *Chinlestegophis* and caecilians. Moreover, as characters are merged, moved, modified, and
214 added, it becomes increasingly easy to overlook simple mechanical errors, such as state 26(2)
215 being mentioned neither in the list of state labels within the matrix file nor in the character
216 list despite all three states being scored for numerous taxa in the matrix (Pardo et al. 2017a:
217 SI appendix parts C, D).

218 Robust analyses also may be thwarted by constraints related to the original taxon sampling of
219 the underlying matrices; in other words, matrices compiled by other authors were (implicitly
220 or explicitly) constructed with the intent to apply them to specific problems, and thus any
221 clade may be densely or sparsely sampled depending on the question that was originally
222 addressed, rather than on questions of later interest. Inserting new taxa may be difficult if
223 additional variation is not easily accommodated without major character revisions, and this
224 may limit which taxa can be speedily added. The matrix of Anderson et al. (2008a) is slightly
225 modified from that of Anderson (2007), which is a merger of a matrix that sampled

226 lepospondyls (Anderson 2001) and a matrix that sampled amphibamiform temnospondyls
227 (Anderson et al. 2008b). As a result, all descendants of the matrix of Anderson et al. (2008a),
228 including the unpublished matrix of Pardo et al. (2017a), sample lepospondyls,
229 amphibamiforms, and very little in between; in the case of Pardo et al. (2017a: fig. S6), other
230 than the amphibamiforms and the added taxa *Chinlestegophis* and *Rileymillerus*, taxa include
231 only seven other temnospondyl OTUs (some composite), the colosteid *Greererpeton*,
232 lepospondyls, the diadectomorph pan-amniote *Limnoscelis*, the seymouriamorph *Seymouria*
233 and the anthracosaur *Proterogyrinus*. The taxon sample is completed by the designated
234 outgroup *Acanthostega*, the earliest well-understood limbed vertebrate.

235 The more narrowly focused published matrix of Pardo et al. (2017a) omits almost all taxa not
236 sampled by Schoch (2013), retaining only temnospondyls, lissamphibians, and the same two
237 outgroups as Schoch (2013), *Proterogyrinus* and *Greererpeton*. The stated reason for this
238 drastic omission of taxa, which eliminated all lepospondyls, *Seymouria* and *Limnoscelis*, was
239 to reduce calculation time for the Bayesian analysis (Pardo et al. 2017a: E5394), after
240 analysis of the unpublished matrix suggested that *Chinlestegophis* and lissamphibians nested
241 within Temnospondyli.

242 In short, Pardo et al. (2017a) first tested the phylogenetic position of *Chinlestegophis* and the
243 similar *Rileymillerus* (Bolt and Chatterjee 2000) “coarsely” by adding them to a matrix that
244 sampled lepospondyls, amphibamiforms, a few other extinct taxa, and lissamphibians.
245 *Chinlestegophis* and *Rileymillerus* were found as temnospondyls close to, but outside,
246 Amphibamiformes (Pardo et al. 2017a: fig. S6). Accepting the result that *Chinlestegophis*,
247 *Rileymillerus* and lissamphibians were temnospondyls, Pardo et al. (2017a) zoomed in by
248 adding them to a matrix that sampled temnospondyls (and temnospondyl-related characters)
249 more broadly, but omitted most other extinct clades. The question of whether caecilians are
250 lepospondyls or stereospondyl temnospondyls was never adequately tested; the unpublished
251 matrix lacks stereospondyls and uses unrevised scores for lepospondyls that were previously
252 criticized (Marjanović and Laurin 2009; Skutschas and Martin 2011; Sigurdson and Green
253 2011), whereas the published one lacks lepospondyls altogether.

254 The published matrix further lacks representation of Albanerpetidae (a member or the sister
255 group of Lissamphibia), despite their presence in the unpublished matrix and their undoubted
256 affinities with lissamphibians (see below). Daza et al. (2020) added Albanerpetidae (as a
257 composite taxon with new data) back into the published matrix of Pardo et al. (2017a) and

258 analyzed the result by implied weighting. They found caecilians and batrachians as sister
259 taxa, followed by Karauridae as the next more distant relative, then Albanerpetidae, then the
260 branchiosaurid *Apateon* and then the rest of Amphibamiformes. *Chinlestegophis* and
261 *Rileymillerus* instead formed the sister-group of Brachyopoidea within Stereospondyli (Daza
262 et al. 2020: fig. 4E, S14). Clearly, omitting even the poorly known Albanerpetidae had a
263 large effect on the resulting relationships among extinct taxa and living amphibians.

264 *Phylogeny inferred from parsimony*

265 The original parsimony analysis of the published matrix yielded 882 shortest trees (Pardo et
266 al. 2017a; and see below). As often occurs, the strict consensus was poorly resolved. To
267 remedy this, Pardo et al. (2017a: fig. S7B) produced a majority-rule consensus (MRC) tree
268 and used it as the basis for comparison with the tree resulting from a Bayesian analysis of the
269 same matrix (their fig. 2C = S7A). Both the MRC and Bayesian trees showed batrachians as
270 amphibamiforms, but caecilians as stereospondyls closest to *Chinlestegophis*, and
271 *Rileymillerus* as sister to caecilians + *Chinlestegophis*. However, none of the 28 nodes that
272 separate caecilians and (batrachians + karaurids) have 50% or higher bootstrap support, and
273 none (even the basal caecilian node) occur in 100% of the shortest trees (Pardo et al. 2017a:
274 fig. S7B). We stress that the percentage of MPTs in which a given node occurs, as long as it
275 is not 0 or 100, is not a support measure in a parsimony analysis (references in Serra Silva
276 and Wilkinson 2021; also stressed by Kligman et al. [2023] in a longer discussion: supp. inf.
277 part 3); all MPTs are equally most parsimonious, and therefore equally optimal by the sole
278 criterion the analysis used. Therefore, the MRC tree provides an incomplete picture of the
279 results of any parsimony analysis, even if there is only a single island of MPTs (see below).
280 Indeed, a fully resolved MRC is not even necessarily identical to any MPT (J. Felsenstein,
281 pers. comm. to D. M. 2017).

282 Investigating that problem specifically, Serra Silva and Wilkinson (2021) reevaluated the full
283 diversity of MPTs supported by the published matrix of Pardo et al. (2017a), noting in their
284 introductory paragraph that “[d]espite concerns that summarizing MPTs with the majority-
285 rule consensus is potentially misleading [...], some workers still use the majority-rule method
286 as if it were unproblematic (e.g. [...] Pardo et al. 2017[a]).” After briefly describing
287 reanalysis by Marjanovič and Laurin (2018: 57–58; 2019: 144, fig. 30I–K), they
288 demonstrated why the MRC is misleading in the specific case of Pardo et al. (2017a), and
289 why it is important to inspect individual trees when the strict consensus is unsatisfactorily

290 resolved: the 882 trees form islands which are each highly congruent internally, but very
291 different from each other. Over half of the MPTs belong to a single island; therefore, the
292 overall MRC (Pardo et al. 2017a: fig. S7B) is almost entirely identical (Serra Silva and
293 Wilkinson 2021: fig. 2) to the MRC of that one island and fails to represent the MPTs on the
294 other islands.

295 Of the other islands, one (figured by Marjanovič and Laurin, 2019: fig. 30I; Serra Silva and
296 Wilkinson 2021: fig. 3c) agrees with the most popular hypothesis of lissamphibian origins,
297 which is also supported by the previously unpublished matrix of Pardo et al. (2017a: fig. S6):
298 that Lissamphibia (including *Eocaecilia* but excluding *Chinlestegophis* and *Rileymillerus*)
299 nests inside Amphibamiformes, close to *Gerobatrachus* (Atkins et al. 2019; Schoch et al.
300 2020; Daza et al. 2020: fig. 4D/S13; Kligman et al. 2023). It further differs from the largest
301 island in that the karaurids occupy their usual position as stem-salamanders (corroborated by
302 Jones et al. 2022), not the entirely novel one as stem-batrachians found on the largest island.
303 Moreover, on the stereospondyl side of the tree, *Chinlestegophis* and *Rileymillerus* form the
304 sister-group of Brachyopoidea, rather than being nested in it as on the largest island.

305 Another island (Marjanovič and Laurin 2019: fig. 30K; Serra Silva and Wilkinson 2021: fig.
306 3b) shows Lissamphibia as the sister-group of *Chinlestegophis* + *Rileymillerus*. Together,
307 they are nested within Stereospondyli, next to Brachyopoidea. Within Lissamphibia,
308 Karauridae and Batrachia are sister-groups as on the largest island.

309 Yet another island (Marjanovič and Laurin 2019: fig. 30I; Serra Silva and Wilkinson 2021:
310 fig. 3a) positions Lissamphibia next to *Gerobatrachus* within Amphibamiformes, and
311 *Chinlestegophis* is nested within the caecilians as the sister-group of *Eocaecilia*, while
312 *Rileymillerus* is placed among the stereospondyls as the sister-group of Brachyopoidea.

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

316 *Bayesian inference of phylogeny*

317 With the result of the parsimony analysis of the published matrix wholly inconclusive, any
318 argument from that matrix that the topology shown in fig. S7B of Pardo et al. (2017a) should
319 be preferred over the equally parsimonious alternatives must come from the congruence of

320 that topology with the result of the Bayesian analysis of the same matrix, which is the only
321 result figured in the main paper (Pardo et al. 2017a: figs. 2B, C, 3, S7A). However, we do not
322 think that Bayesian inference is automatically superior to parsimony as a method of
323 phylogenetic analysis of paleontological matrices.

324 The supposed problem of common branch lengths for all characters in previous simulations,
325 pointed out by Goloboff et al. (2017, 2018) and given great weight by Marjanovič and Laurin
326 (2019: 98), was fully accounted for by the two latest treatments of the question of how best to
327 analyze morphological data (Puttick et al. 2018; Keating et al. 2020) and found to be
328 irrelevant. Yet, those two studies did not simulate any missing data, and the misuse of the
329 MRC to represent the results of parsimony analyses by Puttick et al. (2018) will overestimate
330 the precision but underestimate the accuracy of parsimony, as Keating et al. (2020: fig. 5)
331 demonstrated. Furthermore, the homoplasy distributions in the matrices simulated by Puttick
332 et al. (2018), and probably Keating et al. (2020) as well, do not encompass cases like the
333 matrix of Marjanovič and Laurin (2019) at the very least, and evidently not the matrix of
334 Pardo et al. (2017a) either—given the multiple starkly different topologies that it supports as
335 equally parsimonious.

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

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

352 that case, right for the wrong reasons, and is likely to be wrong for the same reasons in other
353 circumstances.

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

366 **Material and Methods**

367 As noted above, Pardo et al. (2017a) performed analyses of two matrices (one published, one
368 unpublished) with similar character samples but different taxon samples. The originally
369 unpublished matrix was kindly shared with us by J. Pardo and A. Huttenlocker, and we
370 publish it here: Supplementary File 1 contains the unaltered matrix in a NEXUS file, with an
371 added PAUP command block that replicates our analyses of it (called a1 and a2 below) when
372 the file is executed in PAUP*. All of our analyses (Table 1) were run in PAUP* 4.0a169
373 (Swofford 2021) for Windows. This includes bootstrap analyses to test the results of selected
374 phylogenetic analyses for robustness; we have relied on not only the bootstrap trees, which
375 we present as figures, but also on the lists of bipartitions in the PAUP* output
376 (Supplementary Tables 1–4, contained in Supplementary File 2). The published matrix was
377 modified in Mesquite versions up to 3.70 (Maddison and Maddison 2021). The
378 Kishino/Hasegawa, Templeton and winning-sites tests were employed to assess whether
379 constrained and unconstrained trees resulting from the previously unpublished matrix are
380 significantly different; all three tests are available in PAUP*.

381 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	Marjanovi & 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: SF 1	none	no	292	1450	as in Pardo et al. (2017a: fig. S6B)
a2	3	unpublished: SF 1	constraint for LH	no	292	1454	LH; Lissamphibia contains <i>Gerobatrachus</i> , positions of <i>Chinlestegophis</i> + <i>Rileymillerus</i> as in a1
b	–	published: SF 3	none	no	322	1514	five islands: caecilians next to batrachians, 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 Marjanovi & Laurin (2019: fig. 30I–K), only one island figured by Pardo et al. (2017a: fig. S7B)
bootstrap of b	4	published: SF 3	none	no	322	n/a	Diphyly of modern amphibians: Karauridae + Batrachia next to <i>Gerobatrachus</i> (43%), caecilians next to <i>Chinlestegophis</i> (52%) in Stereospondyli
c	5	published: SF 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: SF 4	none	yes	324	1563	Lissamphibia next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli

bootstrap of d1	7	published: SF 4	none	yes	324	n/a	Lissamphibia (55%) next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> (35%); <i>Chinlestegophis</i> as gymnophionomorph not compatible with bootstrap tree (39%)
d2	8, 9	published: SF 4	Albanerpetidae	yes	329	1616	four islands: Lissamphibia always in Amphibamiformes (closer to <i>Apateon</i> than <i>Doleserpeton</i> or <i>Gerobatrachus</i>), <i>Chinlestegophis</i> and <i>Rileymillerus</i> either on the caecilian stem or in Stereospondyli
bootstrap of d2	10	published: SF 4	Albanerpetidae	yes	329	n/a	Lissamphibia (45%) next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> (27%); <i>Chinlestegophis</i> as gymnophionomorph not compatible with bootstrap tree (44%)
e1	11–13	published: SF 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	14	published: SF 6	corrections of characters and scores	yes	321	1567	Lissamphibia next to <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
e3	15	published: SF 5	corrections; Albanerpetidae	no	326	1564	(Albanerpetidae (Karauridae, Lissamphibia)) in Amphibamiformes, <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli
e4	16, 17	published: SF 6	corrections; Albanerpetidae	yes	326	1619	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: SF 6	corrections; Albanerpetidae	yes	326	n/a	Lissamphibia (71%) in Amphibamiformes (Dissorophoidea: 36%), <i>Chinlestegophis</i> + <i>Rileymillerus</i> in Stereospondyli (35%); <i>Chinlestegophis</i> + <i>Rileymillerus</i> as gymnophionomorphs (18%) or next to Lissamphibia (23%), let alone Lissamphibia in Stereospondyli (9%), not compatible with bootstrap tree

382 inf. char. = number of parsimony-informative characters; LH = “lepospondyl hypothesis” on lissamphibian origins (*Eocaecilia* closer to *Carrolla*
383 than to *Doleserpeton*); SF = Supplementary File that contains the matrix and the settings for the analysis in question.

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

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

392 We reanalyzed the originally unpublished matrix (associated with figure S6 of Pardo et al.
393 2017a) to determine how many steps are needed to change the results. Two analyses were
394 performed: one (a1) unconstrained, to replicate the original results, and one (a2) constrained
395 to find *Eocaecilia* closer to the lepospondyl *Carrolla* than to the temnospondyl *Doleserpeton*,
396 *de facto* enforcing the “lepospondyl hypothesis” of lissamphibian origins (but not any
397 particular version of it) to enable us to compare the number of necessary extra steps. (The
398 constraint also allows the “polyphyly hypothesis” that was supported by earlier versions of
399 that matrix, most recently Huttenlocker et al. [2013].)

400 In both analyses, all characters were unordered, and no changes were made to the matrix. The
401 search parameters were as follows: 10,000 random addition sequence replicates (far more
402 than proved necessary) were performed holding one tree at each step, followed by branch
403 swapping using TBR (tree bisection and reconnection) with a reconnection limit of 8 and a
404 limit of 50 million rearrangements per replicate (which was never hit); steepest descent was
405 not in effect; unlimited automatic increases on the Maxtrees setting; branches collapsed if
406 maximum branch length was 0.

407 *Analyses of the unmodified previously published matrix*

408 We reanalyzed (analysis b) an unrevised version of the published matrix of Pardo et al.
409 (2017a: supporting information part D; basis for their figures 2, 3 and S7) to verify its
410 replicability and to further inspect the results. We computed consensus trees for each island,
411 rather than for the entire sample of MPTs; unlike Serra Silva and Wilkinson (2021), who
412 computed the MRC of each island, we used the strict consensus. The search settings were as
413 above, except for the use of only 1000 unlimited replicates.

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

420 *Addition of Albanerpetidae to the previously published matrix*

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

437 Instead of publishing matrix files, Daza et al. (2020) published only the scores of the
438 albanerpetid OTUs they revised in, or added to, the previously published matrix files they
439 used. They confused the scores they added to the matrix of Pardo et al. (2017a; their
440 reference 22) with the scores of Albanerpetidae they revised in the matrix of Pardo et al.
441 (2017b; their reference 21) and presented these scores for the wrong matrix on pp. 16 and 17
442 of their supplementary text; this is easy to determine because the matrix of Pardo et al.
443 (2017a) has 345 characters whereas that of Pardo et al. (2017b) has 370. Unable to add a
444 string of 370 scores to a matrix of 345 characters, we added the string of 345 scores to the
445 matrix of Pardo et al. (2017a) without any changes. The resulting NEXUS file, including a

446 PAUP block that repeats analysis c when executed, is published here as Supplementary File
447 3. The search settings were as above.

448 *Ordering continuous characters*

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

459 In the process of ordering all such clines in the unmodified published matrix, we discovered
460 (like Kligman et al., 2023: supp. inf. part 4) that state 2 of character 9 is missing from the
461 character list of Pardo et al. (2017a: part C of the supplementary text). In the
462 “charstatelabels” block of the NEXUS file published as part D of the supplementary text,
463 state 2 does occur, but in the matrix it is scored exclusively for *Ichthyophis*. J. Pardo (pers.
464 comm. 2021) explained that state 2, absent from Schoch’s (2013) matrix, was intended to be
465 introduced into the matrix, but this was implemented incompletely and accidentally omitted
466 from the published character list. For characters 3, 26 and 201, the implementation of state 2
467 as published in part D seems complete even though it is likewise missing from part C in all
468 three cases. Conversely, character 292 has three states in part C, of which state 1 does not
469 occur in the matrix. Characters 301 and 318 have three states in part C as well, of which the
470 matrix lacks state 2.

471 We performed two parsimony and two bootstrap analyses—without (d1) and with (d2)
472 Albanerpetidae as in analyses b and c—ordering the following clinal characters of the
473 published matrix: 9, 67, 75, 110, 143, 145, 158, 163, 170, 182, 187, 191, 201, 205, 209, 213,
474 214, 221, 226, 229, 242, 243, 262, 264, 266, 269, 271, 273, 279, 298, 300, 302, 304, 327,
475 328, and 334 (36 ordered out of 345 total characters; 10.4%). We first reordered the states of
476 characters 9, 205, 221, 327 and 328 to allow linear ordering because the original order did not

477 follow the cline. The states of character 9 (preorbital region length) originally were: 0, less
478 than twice the length of posterior skull table; 1, more; 2, equal in length. That character
479 discretizes a continuous variable, so we ordered the character after changing the numbering
480 of the states to: 0, less than twice the length of posterior skull table; 1, equal in length; 2,
481 more (longer). Likewise, states 0 and 1 of characters 205 and 221 had to be exchanged, as
482 well as states 1 and 2 of characters 327 and 328. The resulting data matrix (and PAUP block)
483 is available as Supplementary File 4.

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

488 *Evaluation of potential synapomorphies and revisions to the published matrix*

489 Throughout the main text and the supplementary material, Pardo et al. (2017a) suggested
490 various features as synapomorphies of caecilians with either *Chinlestegophis* alone or
491 *Chinlestegophis* and other stereospondyls. Many correspond to characters in the published
492 matrix. Here we evaluate all proposed synapomorphies and explain, where applicable, our
493 revisions of scores in the matrix. To facilitate retrieval and ensure nothing is overlooked, we
494 quote and discuss them below in the order in which they appeared in Pardo et al. (2017a).
495 Our intention is not to fully revise the matrix (see Gee 2022), but to demonstrate the strong
496 influence exerted by incorrect scores and compounding errors.

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

503 The diagnosis of *Chinlestegophis* (which is repeated in part B of the supplementary
504 information of Pardo et al. 2017a) states on p. E5389: “A shared feature with stereospondyls
505 and caecilians is opisthotics fused to exoccipitals.” As pointed out by Santos et al. (2020),
506 that feature is universal among lissamphibians except larval and some neotenic salamanders
507 (e.g., Duellman and Trueb 1994; Jones et al. 2022). It further occurs in the amphibamiform

508 temnospondyl *Doleserpeton* (Sigurdson and Bolt 2010), a few lepospondyls (e.g., Pardo et al.
509 2015) and some (Maddin et al. 2013; Daza et al. 2020) though apparently not all
510 albanerpetids (Matsumoto and Evans 2018). Among stereospondyls, conversely, it seems to
511 be limited to extremely large and correspondingly unusually highly ossified adults of
512 *Mastodonsaurus giganteus* (Jaeger, 1828) (Kligman et al. 2023: supp. inf. part 3). There is no
513 corresponding character in the published matrix of Pardo et al. (2017a).

514 “Shared features with brachyopoids and caecilians” were proposed to (p. E5389) “include
515 lacrimal fused to maxilla”. This hypothesis is difficult to evaluate. The maxillopalatine of
516 *Funcusvermis* does not contain the nasolacrimal duct, so there is no evidence that it contains
517 the lacrimal bone (Kligman et al. 2023). In *Chinlestegophis*, a separate lacrimal is absent, and
518 the nasolacrimal duct lies entirely in what would otherwise be called the maxilla (Pardo et al.
519 2017a); however, the maxilla is dorsoventrally much narrower than what is expected for a
520 fusion product. (The maxilla is taller, but not conspicuously so, in the closely related
521 *Rileymillerus* [Bolt and Chatterjee 2000: fig. 1.3]; however, Kligman et al. [2023: supp. inf.
522 part 3] suggested quite plausibly that the fragmentary supposed nasal of *Rileymillerus* is
523 actually a separate lacrimal.) As a result, fusion of the lacrimal to the maxilla cannot be
524 distinguished from wholesale absence of the lacrimal in the currently known material of
525 *Chinlestegophis*. Similarly, the cause of the absence of a separate lacrimal (loss or fusion) in
526 most brachyopoids and a few other stereospondyls is unknown; even the nasolacrimal canal
527 has not been traced in any of them (see Kligman et al. 2023: supp. inf. part 3 for details).
528 Only in a few gymnophionans, as pointed out by Santos et al. (2020) and discussed by
529 Theska et al. (2018), is ontogenetic fusion of the lacrimal to the maxilla documented
530 (*Hypogeophis rostratus* [Cuvier, 1829]: Müller 2006; *Gegeneophis ramaswamii* Taylor,
531 1964: Müller et al. 2005; probably *Idiocranium russeli* Parker, 1936: Theska et al. 2018;
532 possibly the “prefrontal” of *Dermophis mexicanus* [Duméril and Bibron, 1841]: Wake and
533 Hanken 1982), although it has generally been hard in gymnophionans to tell the prefrontal,
534 the lacrimal, and even the septomaxilla apart, and it is not clear whether the lacrimal ever
535 forms in most gymnophionans (Theska et al. 2018). It is wholly unknown if the two extant
536 species scored in the matrix, *Epicrionops bicolor* Boulenger, 1883, and *Ichthyophis*
537 *bannanicus* Yang, 1984, let alone the Early Jurassic *Eocaecilia*, possess(ed) a discrete
538 lacrimal bone during development or not. However, character 21 of the published matrix only
539 describes presence or absence of the lacrimal, without mentioning the causes of such absence
540 (such as fusion to the maxilla). We interpret this as describing the observed presence or

541 absence of a separate bone in adults and have therefore not changed the scores of these taxa
542 (all “absent”, state 1).

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

563 On the same page, “[s]hared features with *Rileymillerus* and caecilians include the following:
564 orbits small and laterally directed.” Orbit size, not coded in the published matrix, should be
565 quantified before it can be evaluated, but is expected to be convergent among animals that
566 live in low-light conditions. Indeed the orbits of *Funcusvermis* appear to have been
567 considerably larger than those of other caecilians, *Chinlestegophis* or *Rileymillerus* (Kligman
568 et al. 2023). Orbit location was included as character 26: “Orbit location. Medial, framed by
569 wide jugals laterally (0), or lateral emplacement, framed by very slender jugals (1).” Dilkes
570 (2015) revised the definition of character 26, but focused on the width of the jugal in his
571 modifications. We interpret the intention of character 26 to be the location of the orbit and
572 instead suggest rewording this character. Additionally, although three states are scored in the

573 original matrix, only two are given in the character definition. The third state refers to
574 particularly large orbits framed by relatively slender jugals and slender frontals (J. Pardo
575 pers. comm. 2021; Kligman et al. 2023: supp. inf. part 4), but it is scored for batrachians that
576 lack jugals. In order to keep the scores, we have reinterpreted it as referring to the size of the
577 orbit or orbitotemporal fenestra rather than the jugal explicitly. Therefore, like Kligman et al.
578 (2023), we have only changed the score of *Eocaecilia* from 2 to 1. We have further followed
579 Kligman et al. (2023) in changing the scores of two amphibamiforms: *Platyrhinops* from 2 to
580 1, *Apateon* from 0 to 2.

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

584 Character 146 reads: “Symphyseal teeth. No accessory teeth posterior to symphyseal tusks
585 (0), or a transverse row of such teeth (1).” State 1 is found in some stereospondyl taxa.
586 Despite the absence of symphyseal tusks, state 1 also was scored for *Chinlestegophis*,
587 *Eocaecilia* and the two extant caecilians (Pardo et al., 2017a). We changed the score of
588 *Chinlestegophis* to 0 because the lingual toothrow of the holotype and the referred specimens
589 is restricted to the coronoids, and the coronoids do not participate in the symphyseal region of
590 this animal (Pardo et al. 2017: fig. S3, movies S4 and S7). The lingual toothrow of
591 *Eocaecilia*, *Epicrionops* and *Ichthyophis* does reach all the way to the symphysis, so we
592 retained a score of 1 for those, but caution that this likely duplicates character scores for the
593 coronoid dentition characters as explained in the Discussion (contra Kligman et al. 2023).

594 Characters 147 and 148 describe presence/absence of teeth on specific coronoids and are thus
595 redundant with character 272, which describes presence/absence of coronoid teeth in general
596 (Pardo et al. 2017a). Characters 147 and 148 contain potentially important, non-overlapping
597 variation, so we opted to keep that variation over retaining the more general variation
598 captured by character 272, which we have excluded from our analyses. Because it is difficult
599 to identify which coronoid is tooth-bearing in some taxa (i.e., where fewer than three
600 distinguishable coronoids are present), *Doleserpeton* and caecilians in particular, we have,
601 unlike Kligman et al. (2023: supp. inf. part 4), modified the definition of characters 147 and
602 148 as follows, which allowed us to keep all of the original scores:

603 147. Dentition lingual of distal half of labial tooththrow. Present (0), or absent
604 (1).

605 148. Dentition lingual of mesial half of labial tooththrow. Present (0), or absent
606 (1).

607 Character 322, “Splential teeth. Present (0), absent (1)”, was scored 0 exclusively for
608 *Ichthyophis*, *Epicrionops* and the dvinosaurian temnospondyl *Trimerorhachis insignis* Cope,
609 1878. The scores for the former two refer to the fact that the lingual tooththrow of caecilians
610 has historically been thought to be borne on the splential (references in Müller 2006;
611 “splential” was still used in quotation marks by Wilkinson et al. 2021). However, the bone
612 that bears this tooththrow is not in the ventral position of a splential, but the dorsolingual one of
613 a coronoid, in the three extant caecilians whose development is well enough understood to
614 tell (Müller et al. 2005; Müller 2006; Theska et al. 2018); a splential has never been positively
615 identified in any caecilian—or any other lissamphibian. In other words, the scores of 1 for
616 *Triadobatrachus*, *Cryptobranchus*, *Hynobius*, *Ambystoma* and *Leptodactylus* are not correct
617 either; we have followed Gee (2022) in changing the scores of all lissamphibians that were
618 not already scored as unknown to inapplicable (-). Moreover, the existence of teeth (including
619 “denticles”: Gee et al. 2017) on the splential of any species of *Trimerorhachis* has never been
620 claimed or illustrated in the literature (most recently Milner and Schoch 2013), and D. M.
621 found teeth to be absent there in personal observation of AMNH FARB 4565 (type specimen
622 of *T. insignis*) and AMNH FARB 4572 (referred to the same species). We changed this score
623 to 1. Only one certain and one possible case of tooth-bearing splentials are known in all of
624 Tetrapodomorpha, if not Gnathostomata, and neither is sampled in any of the matrices we
625 mention here: *Caerorhachis*, in which a “denticle” field extends from the coronoids and the
626 prearticular onto the splential (Ruta et al. 2002), and the unnamed “Parrsboro jaw”, where the
627 same may or may not be the case (Sookias et al. 2014). In short, state 0 does not occur in the
628 revised matrix at all; the character is constant and therefore useless in a parsimony analysis.
629 Finally, *Chinlestegophis* was scored as unknown; we have corrected this to 1 because Pardo
630 et al. (2017a: fig. S3) depicted the absence of teeth on the splential.

631 It is worth mention that Pardo et al. (2017a) agreed on the absence of splentials in caecilians:
632 all three were scored in the published matrix as lacking splentials (state 2 of character 264).
633 This is contrary to the main text, in which they erroneously (Müller 2006, Theska et al. 2018)

634 described the pseudodentary as “comprising the dentary, coronoid, splenial, and anterior
635 Meckel’s cartilage” (p. E5391).

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

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

650 The next feature listed as shared between *Chinlestegophis* and caecilians is “quadrate
651 completely anterior to ear”, possibly meaning the otic capsules. If so, this character state—
652 which is not coded in the matrix—is standard among brachystelechid and lysorophian
653 lepospondyls (Maddin et al. 2011; Glienke 2013, 2015; Pardo et al. 2015; Pardo and
654 Anderson 2016) and widespread among lissamphibians as well. For present purposes it is
655 only interesting if caecilians are temnospondyls, which this matrix cannot test.

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

664 Character 112 is presented in the character list as having two states: “Cultriform process
665 (width). Base not wider than rest, clearly set off from basal plate (0), or merging continuously
666 into plate (1)” (Pardo et al. 2017a: part C of the supplementary text). In the matrix, however,
667 three states are scored; the first two are as given in the list, and the third (state 2) is called
668 “flaring anteriorly” in the “charstatelabels” block, as in Schoch (2013). We followed Gee
669 (2022) and Kligman et al. (2023) in transferring state 2 to character 343, which originally
670 described whether the cultriform process is “[n]arrow, tapering anteriorly (0)” or “spatulate
671 and parallel-sided (1)”. In other words, character 112 now describes the shape of the caudal
672 end of the cultriform process in two states, and character 343 now describes the shape of the
673 rostral end in three states that form a continuum of widths; character 343 is therefore ordered
674 in our analyses with ordered characters (e2, e4). Our scores for both characters follow those
675 of Gee (2022), which represents an update on Kligman et al. (2023). In addition, we scored
676 *Chinlestegophis* as unknown for character 343; it was reconstructed as having state 1 (Pardo
677 et al. 2017a: fig. 1H) and scored accordingly, but the entire rostral half of the cultriform
678 process appears to be unknown (Pardo et al. 2017a: fig. 1B).

679 Character 114 is: “Cultriform process (outline). Of similar width throughout (0), or
680 posteriorly expanding abruptly to about twice the width (1).” State 1 was scored only for the
681 two extant caecilian OTUs and for the temnospondyls *Rileymillerus*, *Eryops* and *Onchiodon*.
682 We are not sure if the conditions of those taxa should be considered homologous; the two
683 eryopids have a bulbous expansion near the base of the cultriform process, followed caudally
684 by a constriction and then the basal plate along with its contacts to the pterygoids (Sawin
685 1941; Boy 1990); *Rileymillerus* has a strongly biconcave cultriform process that gradually
686 expands caudally until it reaches five times its narrowest width where it merges into the basal
687 plate (Bolt and Chatterjee 2000: fig. 1.2, 2.2); *Epicrionops* and *Ichthyophis* have rostrally
688 pointed cultriform processes that widen rather suddenly at the caudal ends of their contacts
689 with the (maxillo)palatines (Jenkins et al. 2007: fig. 6B, D). But, in any case, *Chinlestegophis*
690 and *Eocaecilia* were correctly scored 0, so (like Gee 2022 and Kligman et al. 2023) we have
691 not modified this character or its scores.

692 “[O]ccipital condyles extend far beyond posterior edge of skull roof” is the next character
693 state proposed to be shared by *Chinlestegophis* and caecilians (Pardo et al. 2017a: E5390). It
694 is coded in the published matrix as character 137: “Exoccipital condyles. Short and broad
695 base, projecting only with their posterior half behind the rim of the skull table (0), or almost

696 the complete element posterior to level of occipital flange (1)”. State 1 was scored
697 exclusively for most trematosauroids and brachyopoids, *Rileymillerus*, *Chinlestegophis*,
698 *Eocaecilia*, *Cryptobranchus* and *Ambystoma*. However, that state (which appears to be more
699 widespread among stereospondyl and dvinosaurian temnospondyls: Kligman et al. 2023:
700 supp. inf. part 3) can be reached by elongating the condyles, reducing the caudal extent of the
701 skull roof, extending the braincase caudally, or a combination of two or all three factors. The
702 stalked occipital condyles of *Chinlestegophis* (and *Rileymillerus*: Bolt and Chatterjee 2000)
703 are standard for stereospondyls, but are not found in any caecilians; this was beautifully
704 illustrated by Pardo et al. (2017a: fig. 3). Rather, lissamphibians (and albanerpetids: Daza et
705 al. 2020) generally expose large parts of the otic capsules in dorsal view, resulting in the
706 occipital condyles lying entirely far beyond the posterior edge of the skull roof. The condyles
707 themselves are weakly elongated in some caecilians and not at all in others, as again shown
708 by Pardo et al. (2017a: fig. 3) and described and illustrated by Jenkins et al. (2007: fig. 1–4,
709 6). This includes *Eocaecilia*, despite its retention of postparietal and probable tabular bones
710 (Pardo et al. 2017a: fig. 3; Jenkins et al. 2007). Conversely, milder examples of the
711 stereospondyl condition exist in various lepospondyls (Santos et al. 2020, and references
712 therein). Therefore, *Eocaecilia* should not receive the same score as *Chinlestegophis*; we
713 reinterpreted the character as referring to condyle elongation instead of the skull table,
714 limiting state 1 to condyles with a stalked base, and consequently revised the scores of
715 *Eocaecilia*, *Cryptobranchus* and *Ambystoma* to 0.

716 The last character state proposed to be shared by *Chinlestegophis* and caecilians (Pardo et al.
717 2017a: E5390) is presence of a “pterygoquadrate”, referring to fusion of the pterygoid and the
718 quadrate bones (as observed in the ontogeny of some extant caecilians: Wake and Hanken
719 1982; Müller et al. 2005; Müller 2006; Theska et al. 2018: fig. 1c). On the next page,
720 however, *Chinlestegophis* is more cautiously stated to possess, “perhaps, an incipient
721 pterygoquadrate based on the structure of the suspensorium and apparent absence of the
722 quadratojugal.” The full description of the skull (Pardo et al. 2017a: part B of the
723 supplementary text) states the matter in a similarly limited way: “A separate quadrate is not
724 evident in either side of the skull, but it is likely that the saddle-shaped posterolateral face of
725 the pterygoid represents the articular glenoid, and we hypothesize that this therefore
726 represents a fused pterygoid-quadrate element (pterygoquadrate).” Thus, a pterygoquadrate is
727 not observed in *Chinlestegophis*, and cannot be used to link it to caecilians. The issue is
728 further complicated by *Eocaecilia*, in which the quadrate appears to be fused to the stapes

729 and not to the pterygoid (Jenkins et al. 2007). Additionally, a pterygoquadrate is not universal
730 in Gymnophiona, being absent in non-teresomatans like *Ichthyophis*, *Epicrionops* and
731 *Amazops* (Jenkins et al. 2007: fig. 6B, D; Wilkinson et al. 2021: fig. 3) and the teresomatan
732 *Chikila* (“pterygoid process of the quadrate”, separated from the quadrate by a suture and
733 meeting the maxillopalatine, in Kamei et al. 2012: fig. S2(b)). If the fused pterygoquadrate is
734 not only real in *Chinlestegophis*, but also homologous between *Chinlestegophis* and
735 Teresomata or a subset thereof, it must have been independently lost three successive times in
736 *Eocaecilia*, Rhinatrematidae and Ichthyophiidae, and at least once more in *Chikila*.

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

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

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

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

769 In their Discussion section, Pardo et al. (2017a: E5393) made a far-reaching claim: “a sulcus
770 associated with the opening of the nasolacrimal duct in the orbit is present in both
771 *Chinlestegophis* and *Eocaecilia* in a similar position to the tentacular sulcus of the basal
772 caecilian *Epicrionops petersi*”, citing Jenkins et al. (2007: fig. 10), which indeed shows the
773 tentacular foramen inside the orbit of the extant *Epicrionops* and a “tentacular sulcus” on the
774 orbital margin of the maxilla of *Eocaecilia*. Evidence of the caecilian tentacle, a body part
775 composed mostly of the nasolacrimal duct and eye musculature and associated with
776 chemosensation in extant caecilians, has not been reported from any vertebrates other than
777 Gymnophiona and *Eocaecilia*. In *Chinlestegophis*, the maxilla does not reach the orbit, being
778 excluded by a contact of the prefrontal and the lateral exposure of the palatine (Pardo et al.
779 2017a: fig. 1, S4). The nasolacrimal duct is housed in the maxilla and meets the orbit in two
780 pores well medial of the skull surface (Pardo et al. 2017a: fig. S4C). Although the sulcus is
781 stated to be in the orbital margin in part F of the supplementary material, it was not
782 reconstructed in fig. 1J, which instead shows an elliptical orbit devoid of any corners; the
783 reconstruction in fig. 1I shows a more angular orbit, fitting the μ CT images in fig. 1E–G, but
784 these corners are very wide, obtuse and rounded, offering no evidence of a tentacular sulcus.
785 A nasolacrimal duct that is separated from the surface of the head would not function in
786 sensory reception, and seems unlikely to explain the evolution of the caecilian tentacle.
787 *Fucusvermis* also lacked a tentacular sulcus unless the sulcus had an unusually far dorsal
788 position, i.e., at the dorsoventral midpoint of the rostral orbit margin at minimum (Kligman et
789 al. 2023: fig. 1a, g–i). In any case, no feature relating to the nasolacrimal duct or the shape of
790 the orbit is coded in the published matrix.

791

792 **Results**

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

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

795 Our unconstrained analysis (a1; Fig. 2) found 12 MPTs of 1450 steps, as reported in Part G of
796 the supplementary information of Pardo et al. (2017a); their previously unreported indices
797 are: CI excluding uninformative characters = 0.2668, RI = 0.6532, RC = 0.1815. The
798 resulting strict consensus is identical to that of Pardo et al. (2017a: fig. S6B), with
799 *Chinlestegophis* and *Rileymillerus* positioned as the sister-group to all other amphibamiform
800 temnospondyls including Lissamphibia, which in turn contains *Eocaecilia* and Gymnophiona.
801 Of the 319 characters, 292 are parsimony-informative.

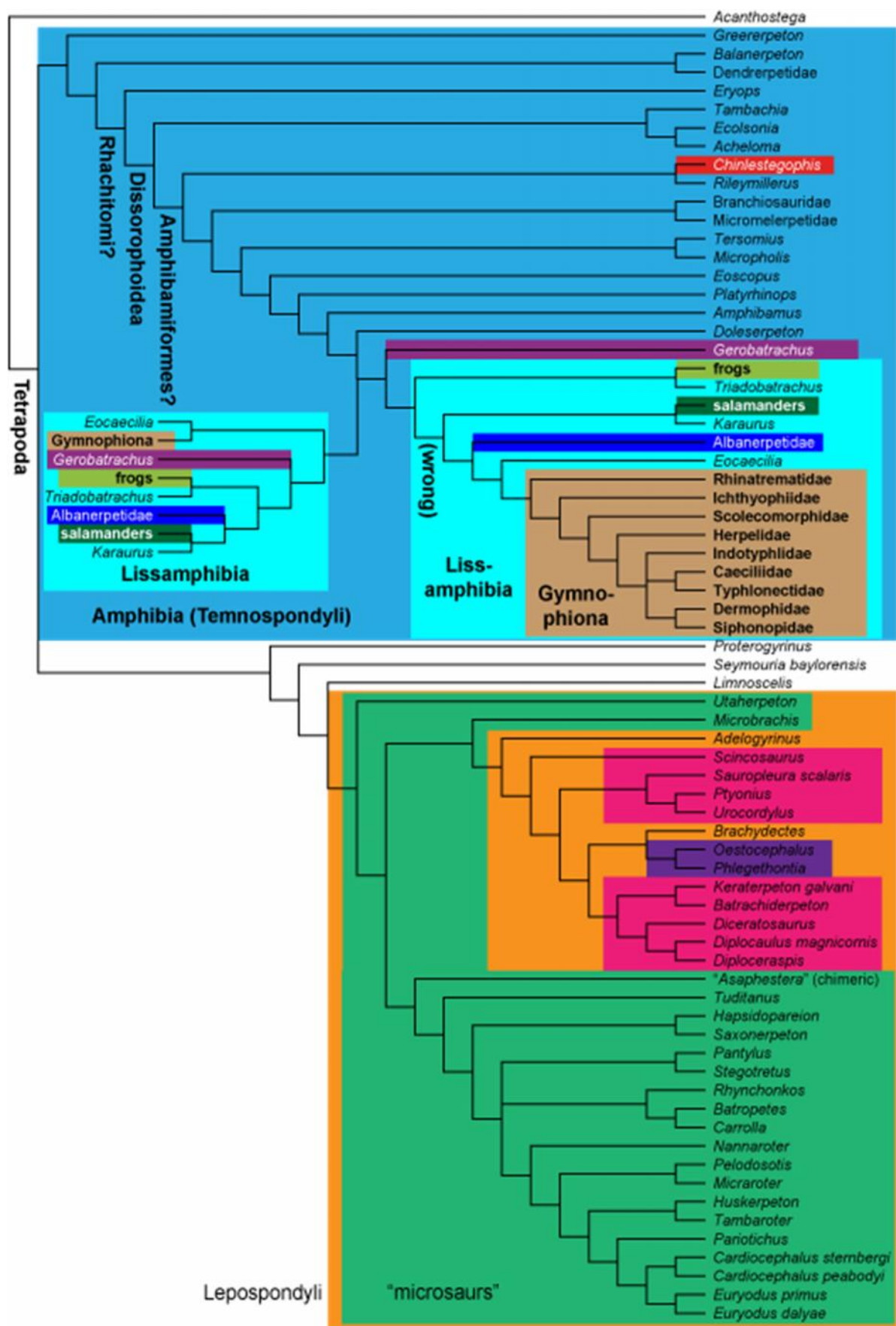
802 The MPTs form two islands that differ in their resolution of Lissamphibia: (1) *Gerobatrachus*
803 as the sister-group of Lissamphibia, within which “frogs” + *Triadobatrachus* is the sister-
804 group of a clade formed by “salamanders” + *Karaurus* on one side and Albanerpetidae +
805 *Eocaecilia*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

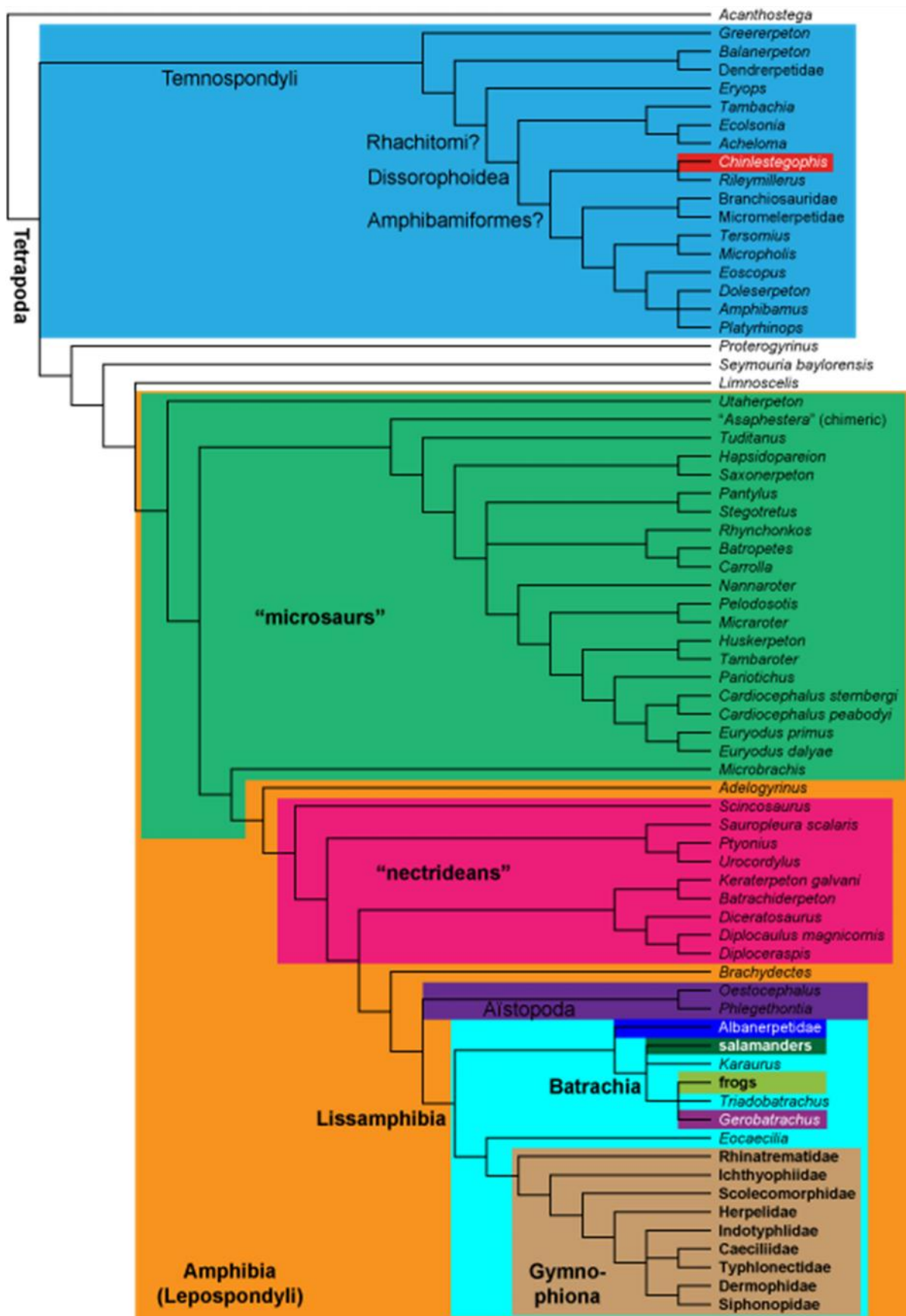
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812 **Figure 2. Strict consensus of the 12 MPTs obtained from our analysis a1 (see Table 1),**
813 **using the unpublished matrix used by Pardo et al. (2017a: fig. S6B).** The two islands are
814 represented by the duplication of Lissamphibia and its sister-group (on one island) or member
815 (on the other island) *Gerobatrachus*. The branch marked “(wrong)” contradicts the molecular
816 consensus (Hime et al. 2020). The application of the name Rhachitomi as defined by Schoch
817 (2013) is unclear due to the absence of *Mastodonsaurus* from the matrix, the application of
818 the name Amphibamiformes as defined by Schoch (2018) is unclear due to the absence of
819 *Dissorophus*. Colored rectangles and boldface, as well as “*Asaphestera*” and Dendrerpetidae,
820 as in Fig. 1; red rectangle for *Chinlestegophis*, brown rectangle for crown-group caecilians
821 (Gymnophiona).

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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

827 **“temnospondyl hypothesis” of lissamphibian origins**; a version of the “lepospondyl
828 hypothesis” results. Colors, boldface, “*Asaphestera*” and Dendrerpetidae as in Fig. 2.

829 Constraining *Eocaecilia* to be closer to the lepospondyl *Carrolla* (analysis a2; Fig. 3) than to
830 the temnospondyl *Doleserpeton* produced 48 MPTs of a very similar length (1454 steps) and
831 very similar indices (CI excluding uninformative characters = 0.2661, RI = 0.6519, RC =
832 0.1807). The positions of *Chinlestegophis* and *Rileymillerus* remain unchanged compared to
833 Pardo et al. (2017a: fig. S6). Although the “lepospondyl hypothesis” is supported in this
834 experiment, Lissamphibia contains *Gerobatrachus*, and it nests far from *Carrolla*, indeed on
835 the other side of the lepospondyl tree—next to the limbless aistopods, followed by the limb-
836 reduced *Brachydectes*, much as in Marjanovi and Laurin (2009; Fig. 1) whose matrix has a
837 common ancestor with this one (Anderson et al. 2008a). The strict consensus shows a less
838 well resolved version of the abovementioned topology (2).

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

842 *Analyses of the unmodified previously published matrix*

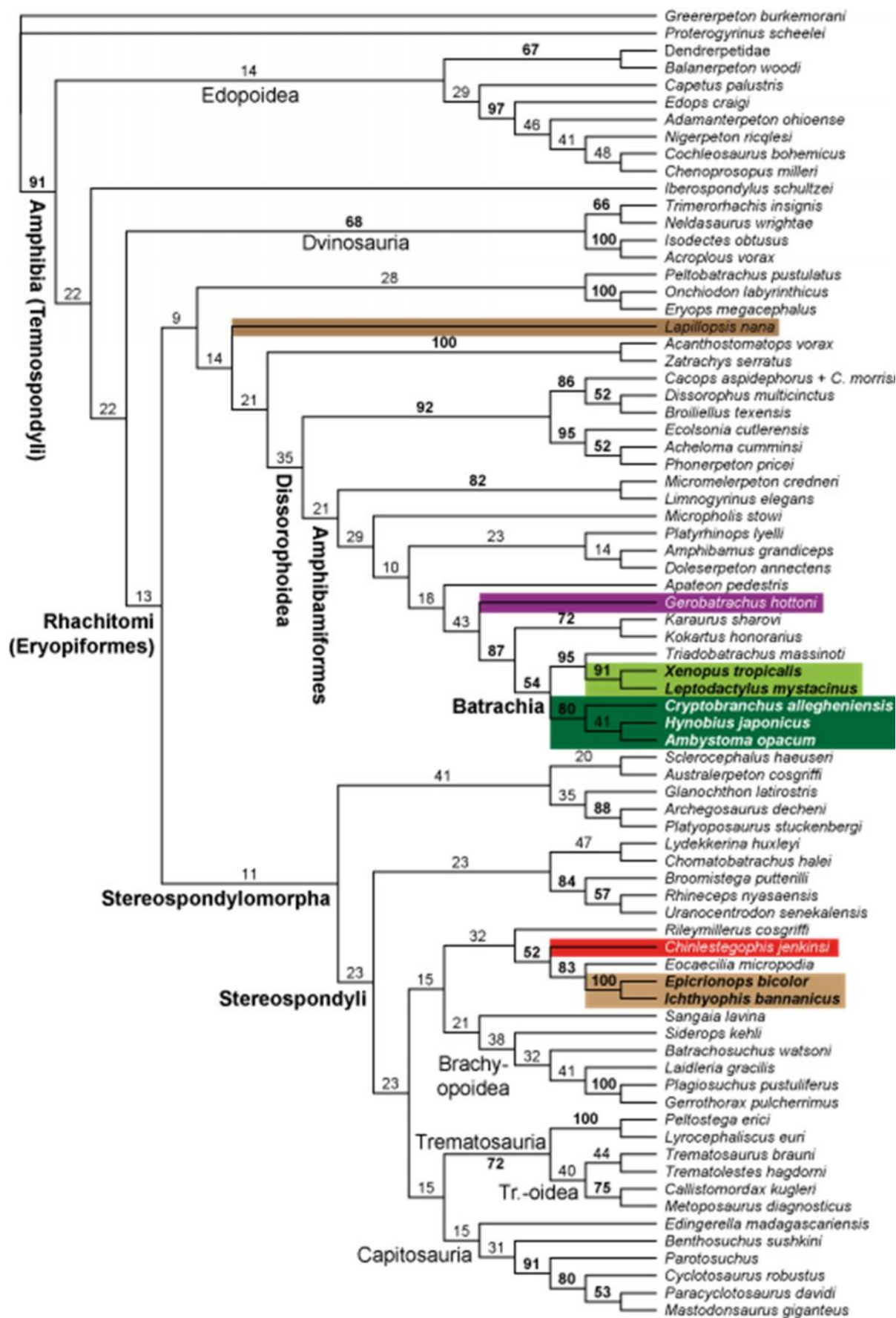
843 Reanalysis of the published matrix (analysis b) yielded identical results to those of Pardo et
844 al. (2017a), Marjanovi and Laurin (2019: fig. 30I–K), Serra Silva and Wilkinson (2021) and
845 Gee (2022), returning 882 MPTs each with a length of 1,514 steps, CI excluding
846 uninformative characters = 0.2548, RI = 0.6858, RC = 0.1812. Of the 345 characters, 322 are
847 parsimony-informative. The MPTs are spread across the five islands found and described by
848 Serra Silva and Wilkinson (2021). The strict consensus trees of two islands (illustrated by
849 Marjanovi and Laurin 2019: fig. 30I; Serra Silva and Wilkinson 2021: fig. 3a, c) both
850 retrieve a monophyletic Lissamphibia nested within the amphibamiform dissorophoids. In
851 one of them (Serra Silva and Wilkinson 2021: fig. 3a), *Chinlestegophis* is the sister taxon to
852 *Eocaecilia*, while in the other it is a stereospondyl that lies next to *Rileymillerus*. The strict
853 consensus trees of two other islands (Marjanovi and Laurin 2019: fig. 30J; Serra Silva and
854 Wilkinson 2021: fig. 2b, 3d) retrieve Batrachia within amphibamiforms, whereas caecilians
855 (including *Eocaecilia*) are the sister taxon to *Chinlestegophis* within Stereospondyli, as
856 presented by Pardo et al. (2017a). The strict consensus of the remaining island (Marjanovi
857 and Laurin 2019: fig. 30K; Serra Silva and Wilkinson 2021: fig. 3b) retrieves Lissamphibia
858 as the sister taxon to *Chinlestegophis* + *Rileymillerus* within Stereospondyli. Thus, in only

859 three of the five islands of optimal trees is the configuration of *Chinlestegophis* as a stem-
860 caecilian obtained, and in one of them it is a lissamphibian nested within Amphibamiformes
861 rather than Stereospondyli.

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

871 Inspection of the list of bipartitions in the output of PAUP* (Supplementary Table 1),
872 including those that are incompatible with the bootstrap tree, shows that Lissamphibia was
873 found in 37% of the bootstrap replicates—support comparable to that for Dissorophoidea
874 including Batrachia (35%), which is shown in the bootstrap tree (Fig. 4). An exclusive clade
875 of all lissamphibians and *Chinlestegophis* occurs in 21% of the replicates and combines with
876 *Rileymillerus* in 20%; all lissamphibians and any or all dissorophoids form an exclusive clade
877 in no more than 16% of the replicates. Stereospondyli excluding *Chinlestegophis* and
878 optionally *Rileymillerus* appears in only 9%, as often as, e.g., an improbable clade of all
879 lissamphibians except *Eocaecilia*. Only 8% group all lissamphibians, *Chinlestegophis* and
880 *Gerobatrachus* exclusively.

881 **Figure 4. Bootstrap tree obtained from the published matrix used by Pardo et al.**
882 **(2017a) when all characters are unordered (analysis b).** The bootstrap tree shows
883 moderate support (52%) for the diphyly of extant amphibians. Colors and boldface as in Fig.
884 3, bootstrap values > 50% also in boldface; darker brown rectangle for *Lapillopsis*, a small
885 temnospondyl thought to be a stereospondyl convergent to dissorophoids. The blue rectangle
886 for Temnospondyli is omitted because all OTUs except *Greererpeton* and *Proterogyrinus* are
887 (inferred to be) temnospondyls; the cyan rectangle for Lissamphibia is omitted because the
888 name Lissamphibia does not apply on this tree. Tr.-oidea = Trematosauroidea. The
889 Dendrerpetidae OTU was called “*Dendrerpeton acadianum*” by Pardo et al. (2017a) but is
890 mostly based on its apparently close relative *Dendrysekos*. In this and the following figures
891 we have also corrected spelling mistakes in taxon names compared to the matrix and the
892 figures of Pardo et al. (2017a).



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895 *Addition of Albanerpetidae to the previously published matrix*

896 The matrix of Daza et al. (2020: fig. 4E, S14), i.e., the published matrix of Pardo et al.
897 (2017a) with Albanerpetidae added, yielded a single island of 45 MPTs (analysis c; length =
898 1565 steps, CI excluding uninformative characters = 0.2510, RI = 0.6795, RC = 0.1741).
899 Their strict consensus (Fig. 5) is topologically identical to that of Daza et al. (2020: fig. S14),
900 except for slightly lower resolution: Dissorophidae, Trematopidae, and a node supporting
901 *Edingerella*, *Benthosuchus*, Capitosauroidea and Trematosauroidea + Brachyopoidea are
902 unresolved. Interestingly, all nodes marked “95” in the MRC of Daza et al. (2020: fig. S14)
903 are present in the strict consensus of our analysis, whereas a few of those marked “100” are
904 not. Amphibamiformes, including Lissamphibia, is resolved exactly as in Daza et al. (2020:
905 fig. 4E, S14): there is a clade (*Apateon* (Albanerpetidae (Karauridae, Lissamphibia))) which
906 is the sister-group of (*Micropholis* (*Platyrhinops* (*Amphibamus* (*Doleserpeton*,
907 *Gerobatrachus*)))) within Dissorophoidea. Likewise, *Chinlestegophis* and *Rileymillerus* are
908 positioned as in Daza et al. (2020: fig. S14), as the sister-group to Brachyopoidea within
909 Stereospondyli.

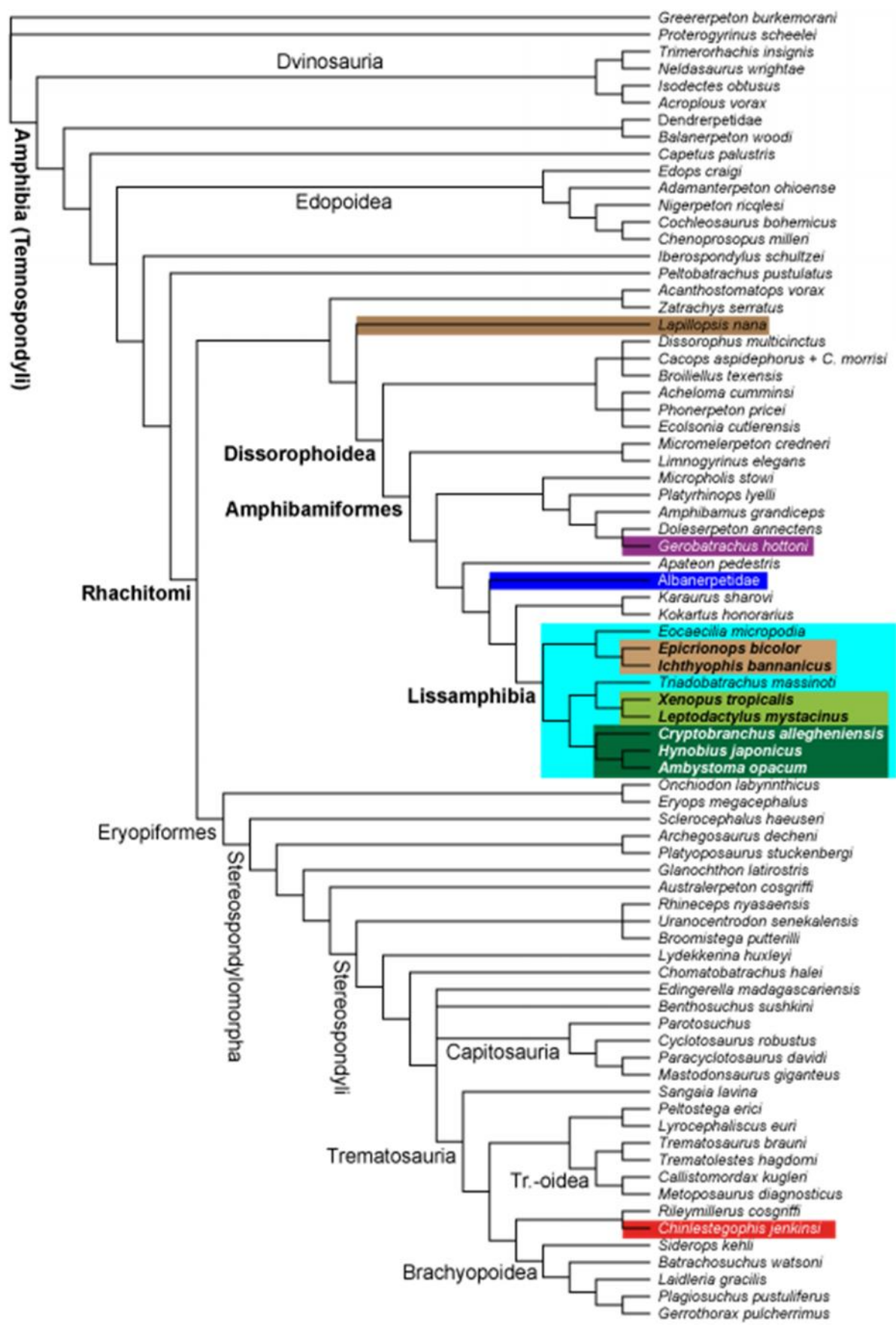
910 The addition of Albanerpetidae renders seven characters parsimony-informative, so that 329
911 of the total of 345 now have this status.

912

913

914 **Figure 5. Strict consensus of the 45 MPTs obtained from the published matrix of**
915 **Pardo et al. (2017a) with addition of Albanerpetidae from Daza et al. (2020); all**
916 **characters are unordered (analysis c).** The resolution differs slightly from Daza et al.
917 (2020: fig. S14) because we used parsimony with equal rather than implied weights. Colors,
918 boldface and Dendrerpidae as in Fig. 3 and 4 here and in all following figures; Tr.-oidea =
919 Trematosauroidea.

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921

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923 *Ordering continuous characters*

924 Ordering of clinal characters (analysis d1) in the otherwise unmodified published matrix of
925 Pardo et al. (2017a) rendered two characters parsimony-informative (for a total of 324 of the
926 345 characters in the matrix) and resulted in a single island of 14 MPTs (length = 1563 steps,
927 CI excluding uninformative characters = 0.2500, RI = 0.6882, RC = 0.1770). The strict
928 consensus is almost completely resolved (Fig. 6) and shows Lissamphibia as the sister-group
929 of the clade formed by *Chinlestegophis* and *Rileymillerus*, nested within the brachyopoid
930 stereospondyls.

931 The bootstrap tree of analysis d1 (Fig. 7) recovers a moderately supported (55% frequency)
932 Lissamphibia with the same sister-group, and the *Chinlestegophis-Rileymillerus* clade is
933 again less supported (41%). Affinities between the *Chinlestegophis-Rileymillerus* clade and
934 Lissamphibia are slightly better supported than with unordered states, but at 35%, this clade
935 is still weak. The position of *Chinlestegophis* as a stem-caecilian, incompatible with the
936 bootstrap tree, occurs with a frequency of 39% (Supplementary Table 2). Lissamphibia is
937 separated from *Doleserpeton* or *Gerobatrachus* by bootstrap values no higher than 36%, but
938 an exclusive clade of frogs, salamanders, karaurids and *Gerobatrachus* has only 31% support
939 (even less if any other dissorophoids are added) and an exclusive Lissamphibia-
940 *Gerobatrachus* clade only 18% (likewise less if others are added; Supplementary Table 2).

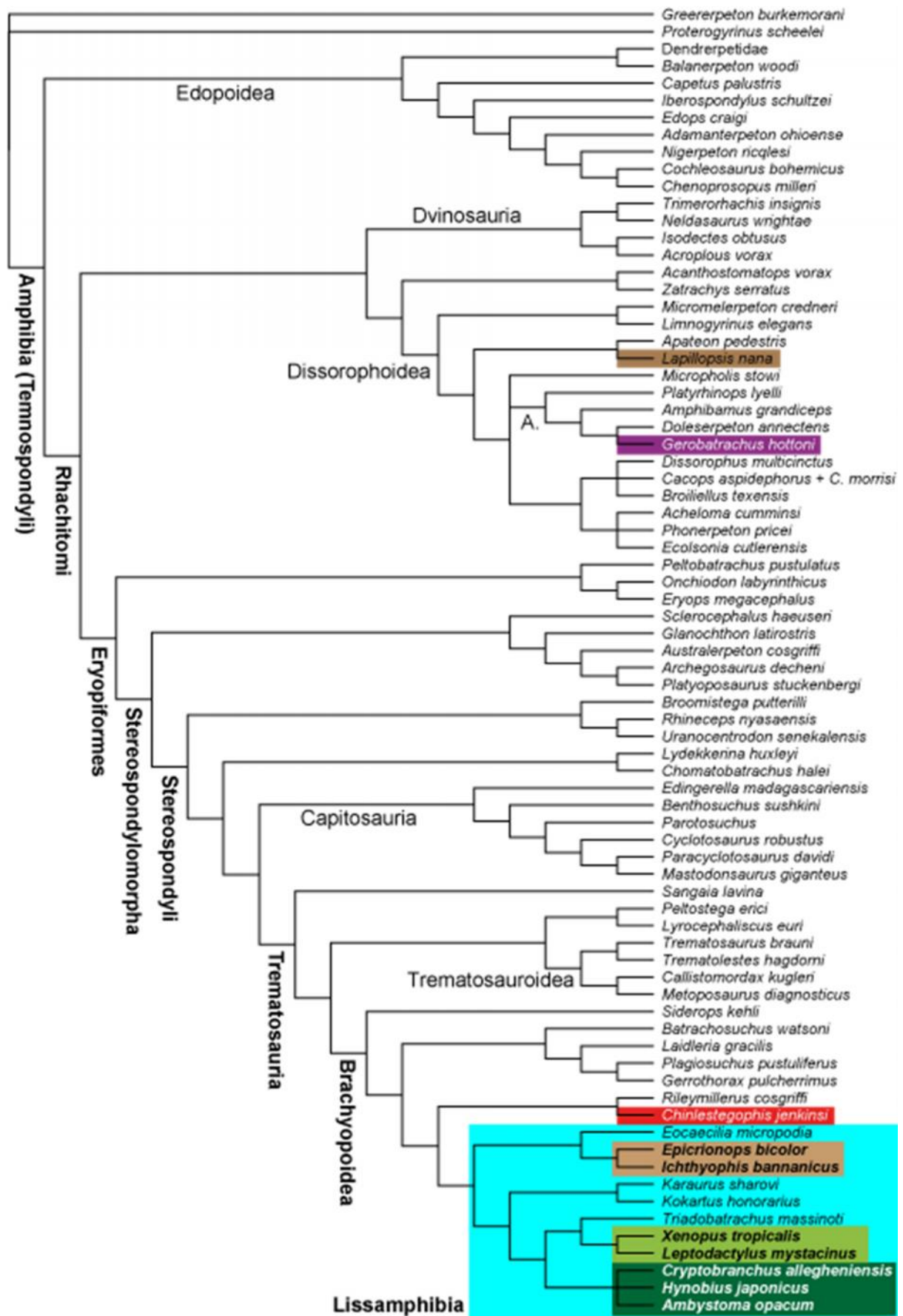
941

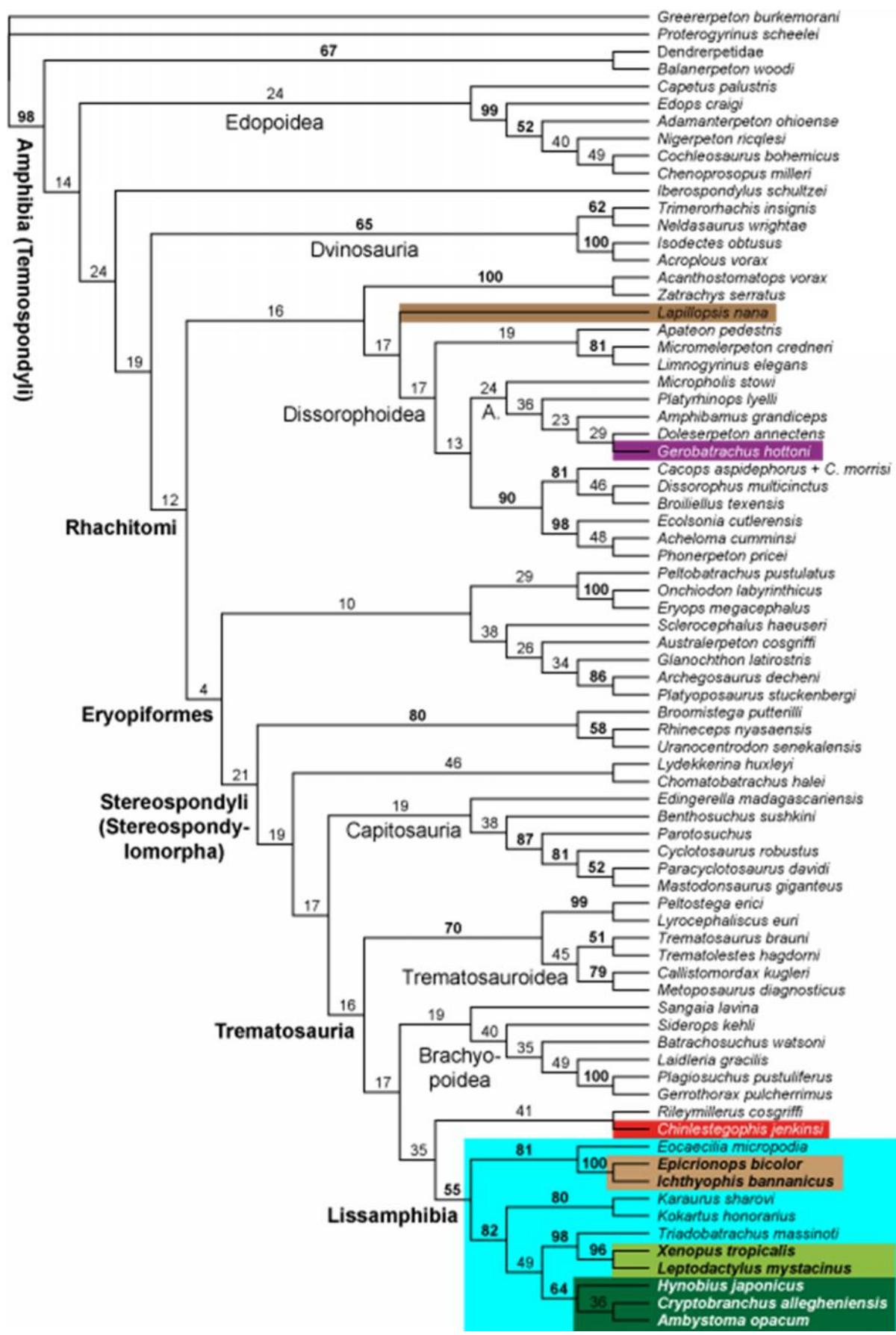
942

943 **Figure 6. Strict consensus of the 14 MPTs obtained from the published matrix of**
944 **Pardo et al. (2017a) with clinal characters ordered (analysis d1). A. = Amphibamiformes.**

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

948





951 When the clinal characters are ordered and Albanerpetidae is added (analysis d2), 329
952 characters are parsimony-informative, and the published matrix yields 195 MPTs (1616 steps,
953 CI excluding uninformative characters = 0.2442, RI = 0.6823, RC = 0.1702). They are
954 distributed over four islands, which are shown in Figures 8 and 9. In all MPTs, Lissamphibia
955 is nested in Amphibamiformes, closer to the branchiosaurid *Apateon* than to *Doleserpeton* or
956 *Gerobatrachus*. In one island (Fig. 8), *Chinlestegophis* and *Rileymillerus* lie inside
957 Lissamphibia on the caecilian stem while Albanerpetidae and Karauridae form the batrachian
958 stem; the other three (Fig. 9) have (*Apateon* (Albanerpetidae (Karauridae, Lissamphibia)))
959 next to Amphibamiformes while the *Chinlestegophis-Rileymillerus* clade lies next to or inside
960 the brachyopoid stereospondyls.

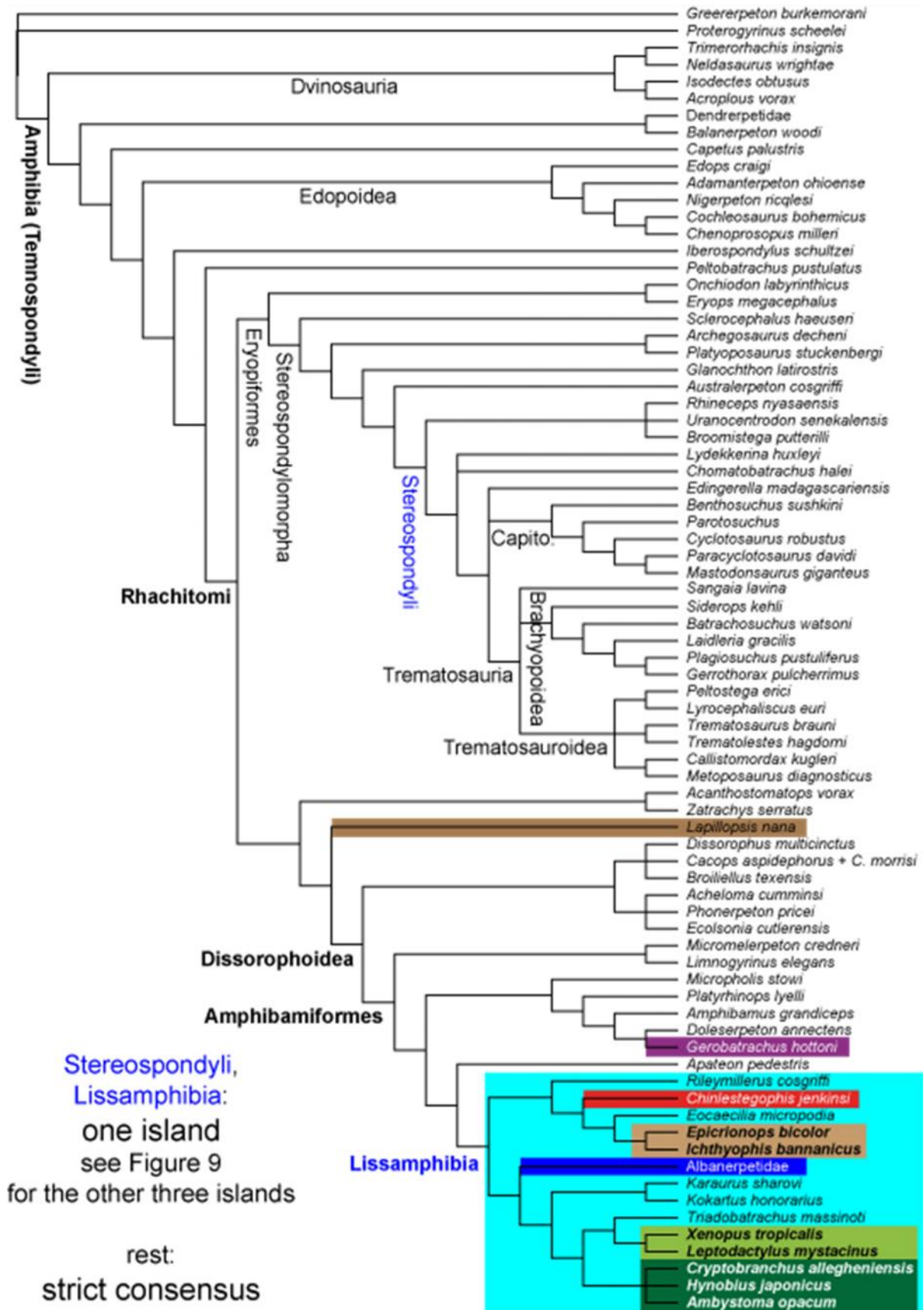
961

962

963 **Figure 8. Strict consensus of all (except in Stereospondyli and Lissamphibia) or some**
964 **(in Stereospondyli and Lissamphibia) of the 195 MPTs obtained from the published**
965 **matrix of Pardo et al. (2017a) with clinal characters ordered and Albanerpetidae added**
966 **(analysis d2). For the other MPTs, see Fig. 9. Capito. = Capitosauria.**

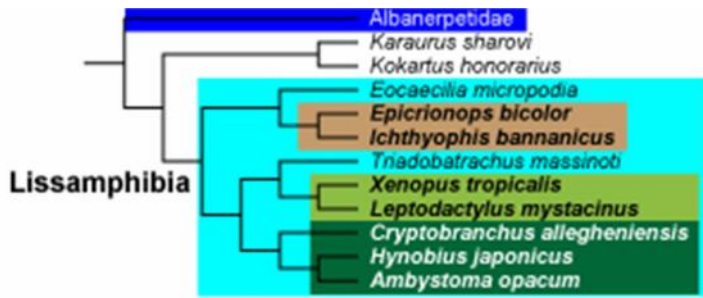
967 **Figure 9. Strict consensus of each of the remaining three islands of MPTs from**
968 **analysis d2.** Lissamphibia is identical in all three; two islands differ only in that *Edingerella*
969 and *Benthosuchus* switch places. The remainder of the tree is identical in all four islands and
970 not repeated here; see Fig. 8. Tr.-oidea = Trematosauroidea.

971

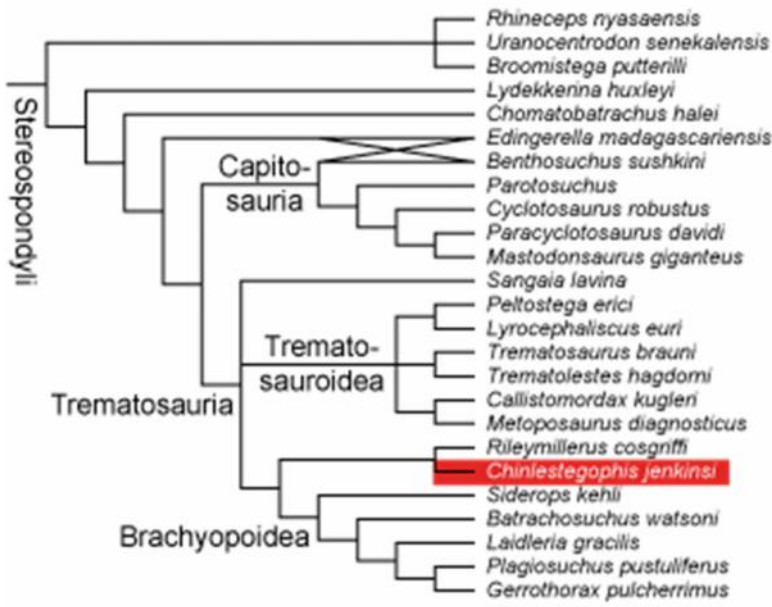


Stereospondyli,
 Lissamphibia:
 one island
 see Figure 9
 for the other three islands

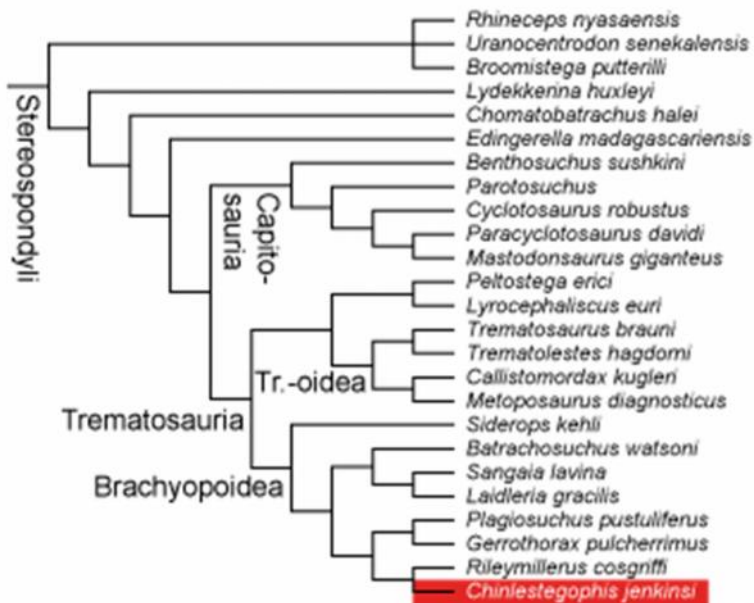
rest:
 strict consensus



three islands
see Figure 8
for the remaining island
and the rest of the tree



two islands



one island

973

974 Bootstrapping analysis d2 (Fig. 10) shows weaker support for Lissamphibia (45%) than
 975 without ordering and without Albanerpetidae (see above under analysis b). Lissamphibia and
 976 a clade formed by *Chinlestegophis* and *Rileymillerus* are found as sister groups with low
 977 support (27%). Interestingly, both clades together form the sister-group of Dissorophoidea
 978 rather than being nested in Stereospondyli; the support for exclusion from a position close to

979 *Gerobatrachus* or *Doleserpeton* is comparatively high (62%), but the support for exclusion
980 from Trematosauria within Stereospondyli is low (26%). Noteworthy, on the other hand, is
981 the support (72%) for excluding Karauridae (*Karaurus* and *Kokartus*), universally considered
982 a clade of stem-salamanders (Jones et al. 2022, and references therein), from Batrachia (frogs
983 + salamanders). An exclusive clade of Albanerpetidae, Karauridae and Batrachia has 63%
984 support, contradicting Matsumoto & Evans (2018) and Daza et al. (2020); this may be due to
985 character sampling.

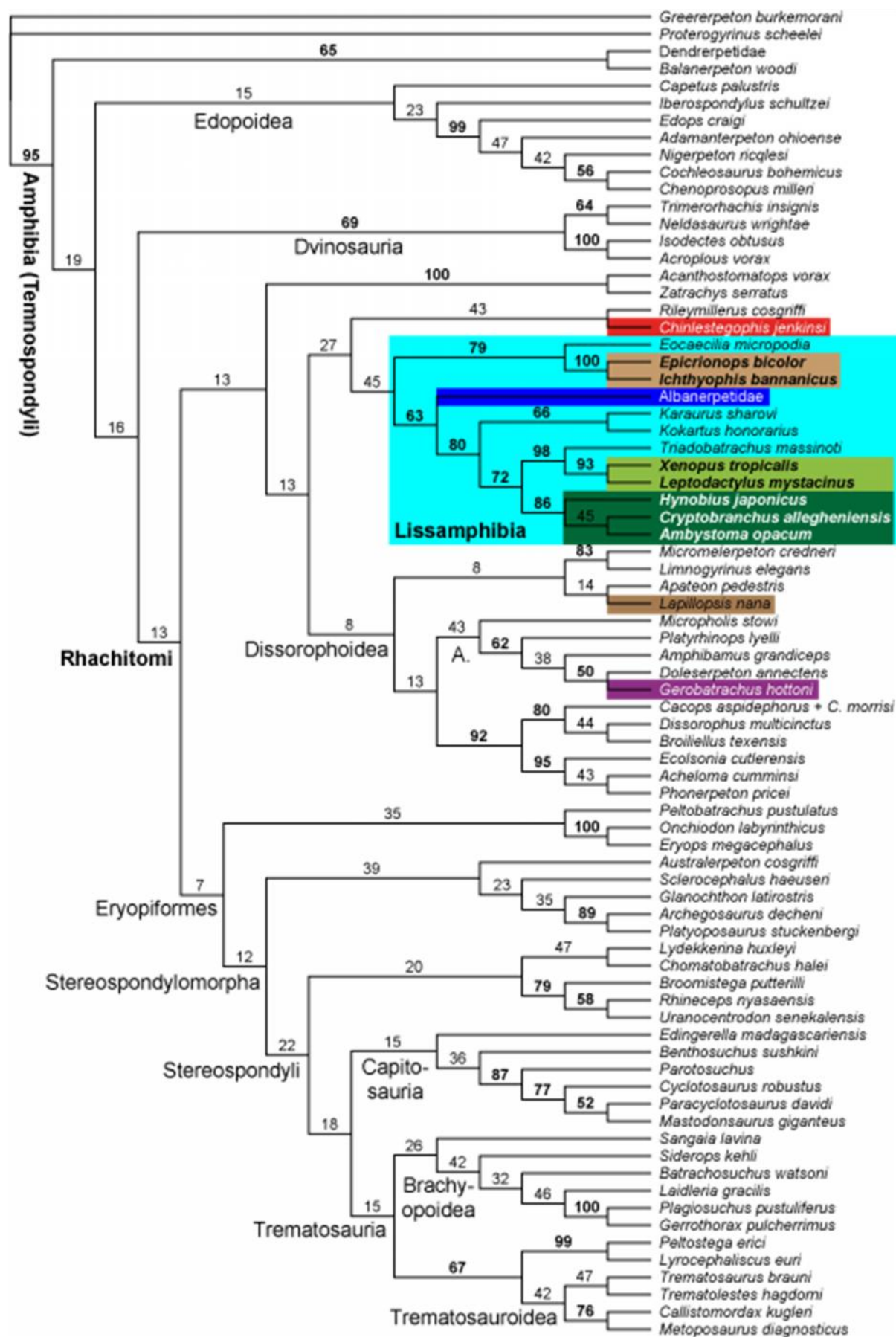
986 The list of bipartitions not compatible with the bootstrap tree (Supplementary Table 3)
987 reveals 44% bootstrap support for a clade of *Chinlestegophis* and the three caecilians (slightly
988 more than the 38% without ordering and without Albanerpetidae) and 30% for a clade that
989 includes these four and *Rileymillerus*. *Chinlestegophis* and *Rileymillerus* are excluded from
990 Dissorophoidea + Lissamphibia in 21% of the bootstrap replicates. The support for exclusion
991 of Albanerpetidae from Lissamphibia (17%) is lower than it could be given the 63% for a
992 specific placement in Lissamphibia mentioned above; 13% of the replicates find all
993 dissorophoids, all batrachians, the karaurids and Albanerpetidae in an exclusive clade, 7%
994 group the caecilians with Albanerpetidae, 6% group all lissamphibians with *Chinlestegophis*
995 to the exclusion of Albanerpetidae.

996

997

998 **Figure 10. Bootstrap tree obtained from the published matrix of Pardo et al. (2017a)**
999 **with clinal characters ordered and Albanerpetidae added (analysis d2).** Bootstrap values
1000 50% in boldface. A. = Amphibamiformes.

1001



1003 *Revised published matrix*

1004 The matrix including the changes we proposed was run both with all characters unordered, as
1005 they were in Pardo et al. (2017a), and with the herein proposed characters that form
1006 morphological clines ordered; both of these options were used both without and with the
1007 addition of Albanerpetidae from Daza et al. (2020). The analysis with all characters
1008 unordered and Albanerpetidae excluded (e1) resulted in 1341 MPTs, each with a length of
1009 1514 steps (CI excluding uninformative characters = 0.2535, RI = 0.6849, RC = 0.1801),
1010 distributed over seven islands of optimal trees. Of the 344 characters, only 319 are
1011 parsimony-informative. In all seven islands, Lissamphibia is recovered and excludes
1012 *Chinlestegophis* (as well as *Rileymillerus*). One island (Fig. 11) places (Brachyopoidea
1013 (Lissamphibia (*Chinlestegophis*, *Rileymillerus*))) in Stereospondyli, and Karauridae on the
1014 batrachian stem; the others recover Lissamphibia next to *Gerobatrachus* in
1015 Amphibamiformes while the *Chinlestegophis*-*Rileymillerus* clade remains nested in
1016 Stereospondyli next to or inside Brachyopoidea, and Lissamphibia is either (frogs (karaurids
1017 (caecilians, salamanders))) (Fig. 12), contradicting the molecular consensus (Hime et al.
1018 2020), or (caecilians (frogs (karaurids, salamanders))) (Fig. 13).

1019

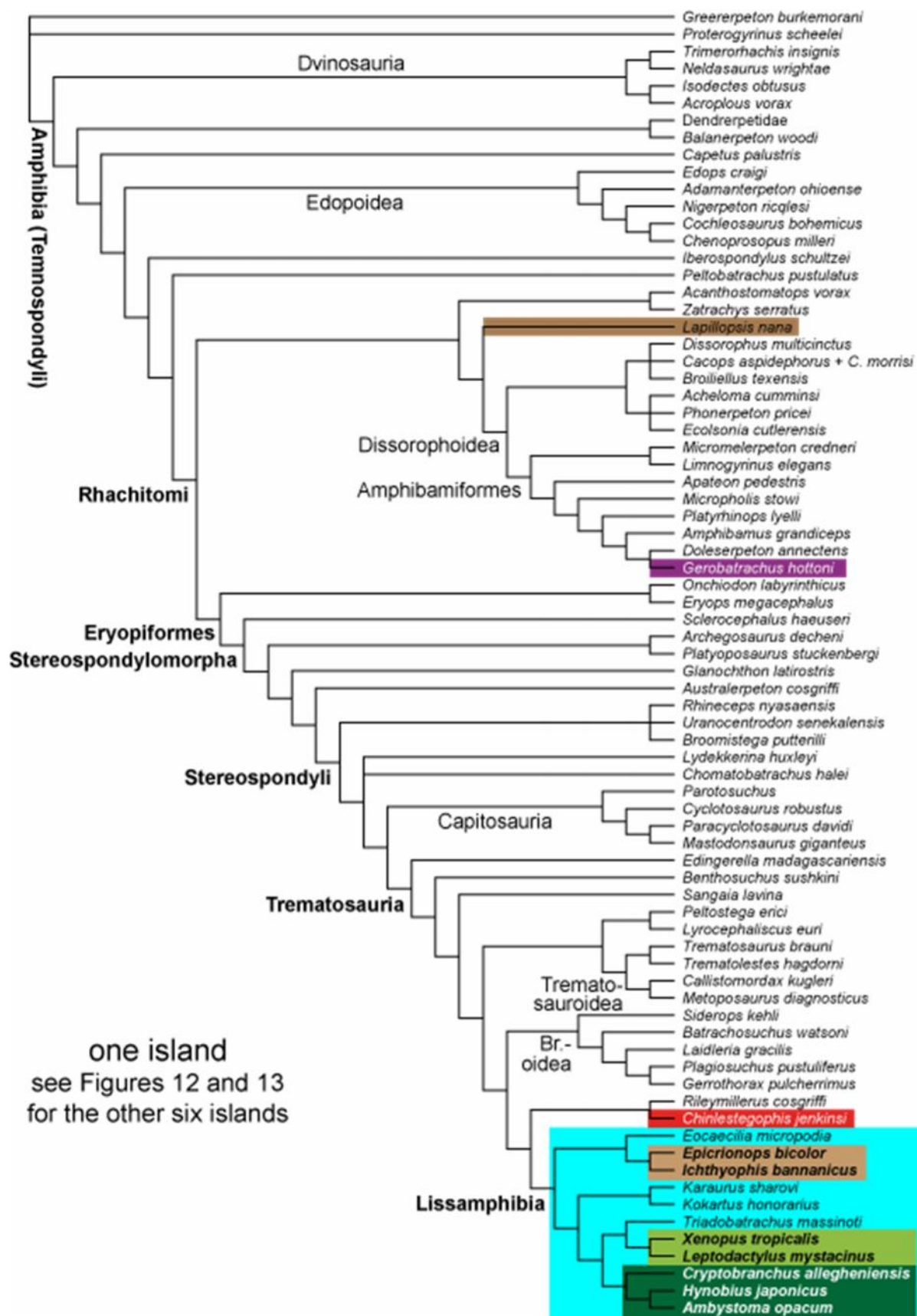
1020

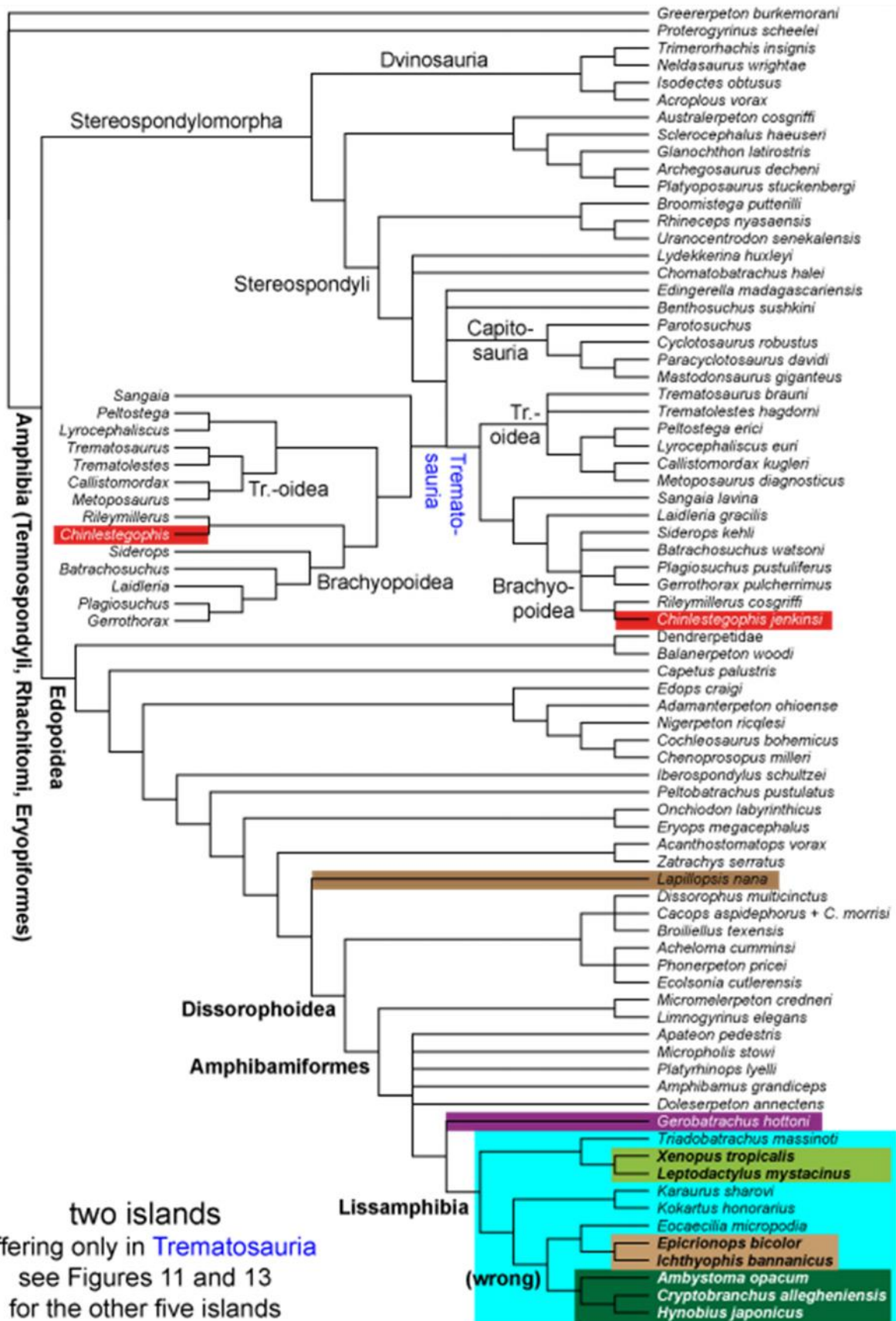
1021 **Figure 11. Strict consensus tree of some of the 1341 MPTs recovered in analysis e1**
1022 (published matrix of Pardo et al. [2017a] after revision, all characters unordered). For the
1023 other MPTs, see Figs. 12 and 13. Br.-oidea = Brachyopoidea.

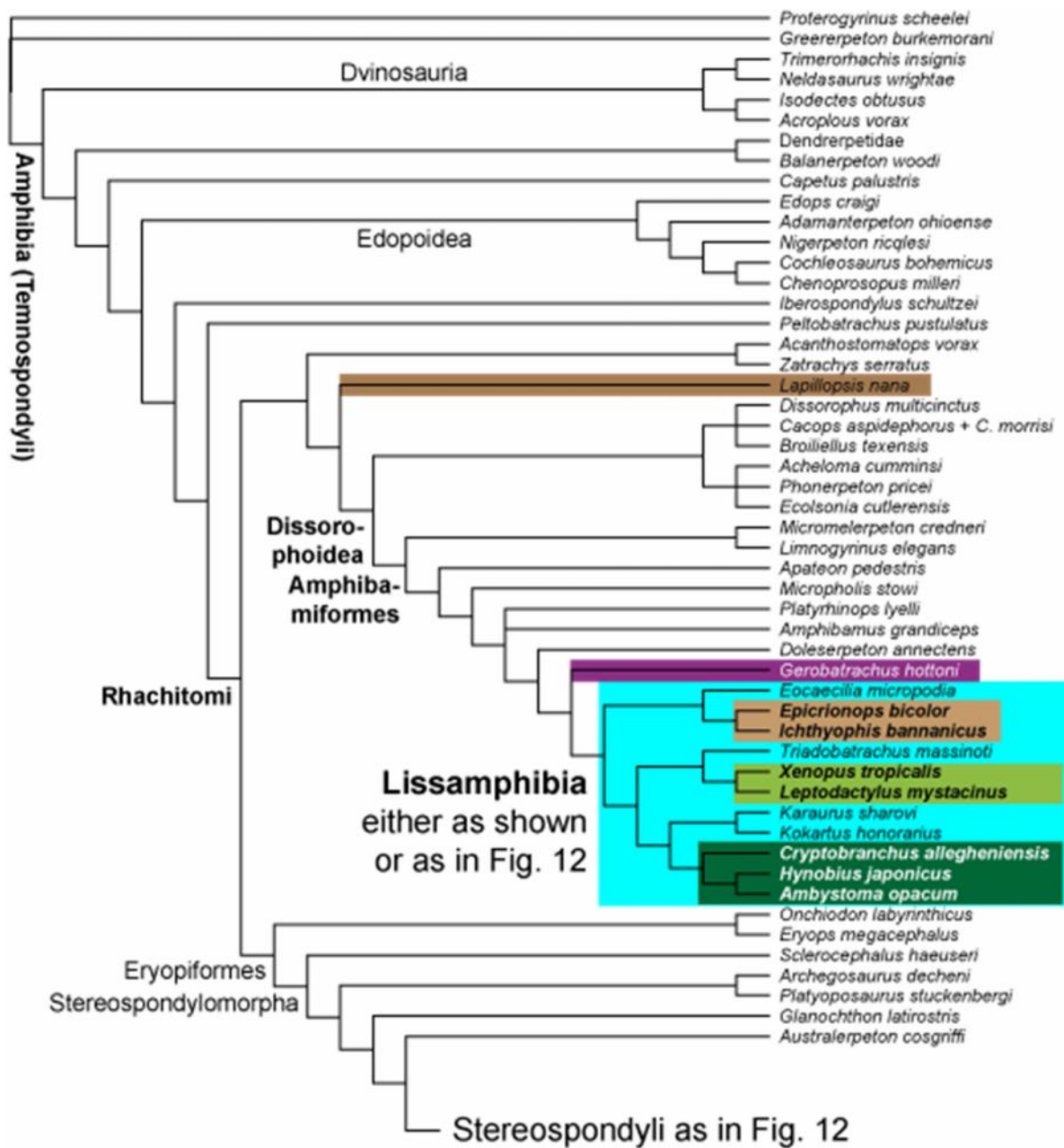
1024 **Figure 12. Strict consensus of each of two further islands of MPTs from analysis e1.**
1025 For space reasons, one of the two resolutions of Trematosauria is mirrored and presented
1026 without species names. Tr.-oidea = Trematosauroida. The branch marked “(wrong)”
1027 contradicts the molecular consensus (Hime et al. 2020).

1028 **Figure 13. Strict consensus of each of the remaining four islands of MPTs from**
1029 **analysis e1.** Except for Lissamphibia, the part depicted here is identical in all four islands;
1030 Lissamphibia is resolved either as shown or as in Fig. 12, Stereospondyli is resolved as in
1031 Fig. 12 (with both options shown there for Trematosauria).

1032







four islands
 (both combinations of both
 resolutions of Lissamphibia
 and Stereospondyli occur)
 see Figures 11 and 12
 for the other six islands

1035

1036 The second analysis, using ordered characters (e2), resulted in a single island of only six
 1037 MPTs (1567 steps; CI excluding parsimony-uninformative characters = 0.2553, RI = 0.6868,
 1038 RC = 0.1753). 321 characters were parsimony-informative. The well-resolved strict
 1039 consensus is shown in Figure 14. Lissamphibia is recovered and placed next to a

1040 *Rileymillerus* + *Chinlestegophis* clade, which lies next to Plagiosauridae within the
1041 brachyopoid stereospondyls; Karauridae lies on the batrachian stem. *Gerobatrachus* remains
1042 next to *Doleserpeton* inside an internally rearranged Dissorophoidea.

1043 The third and fourth analyses differ from the first and second by the addition of
1044 Albanerpetidae (from Daza et al. 2020) as in analysis c. In both, 326 of the 344 characters
1045 were parsimony-informative. The unordered analysis e3 yielded 297 MPTs (1564 steps, CI
1046 excluding uninformative characters = 0.2498, RI = 0.6790, RC = 0.1732); PAUP* groups
1047 them as two islands, but these are similar enough that we present the overall strict consensus
1048 in Figure 15. Dissorophoidea including Lissamphibia is resolved as in analysis c; the
1049 *Rileymillerus* + *Chinlestegophis* clade is grouped with the poorly resolved brachyopoid
1050 stereospondyls.

1051

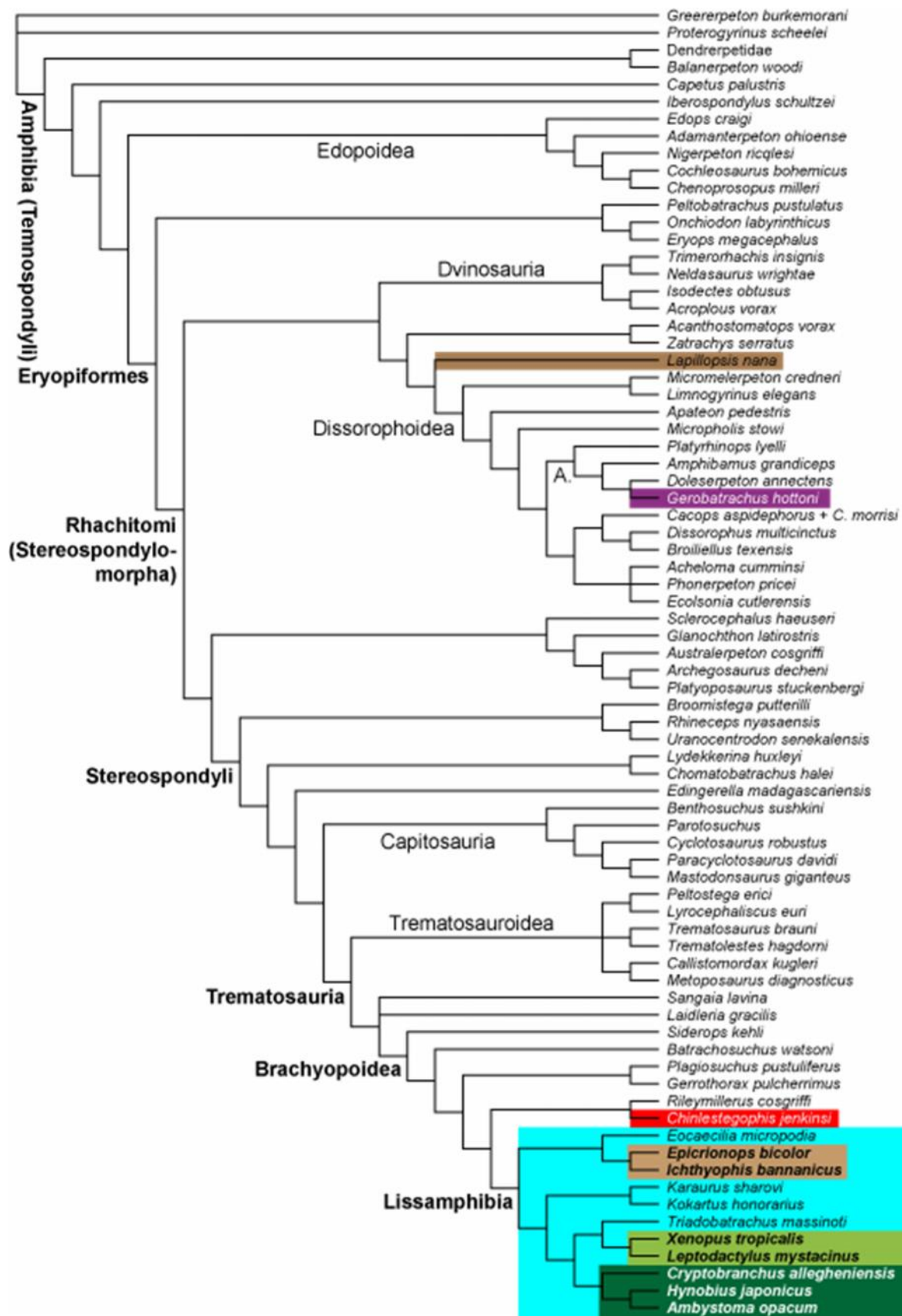
1052

1053

1054 **Figure 14. Strict consensus tree of the six MPTs recovered in analysis e2** (published
1055 matrix of Pardo et al. [2017a] after revision, clinal characters ordered). A. =
1056 Amphibamiformes.

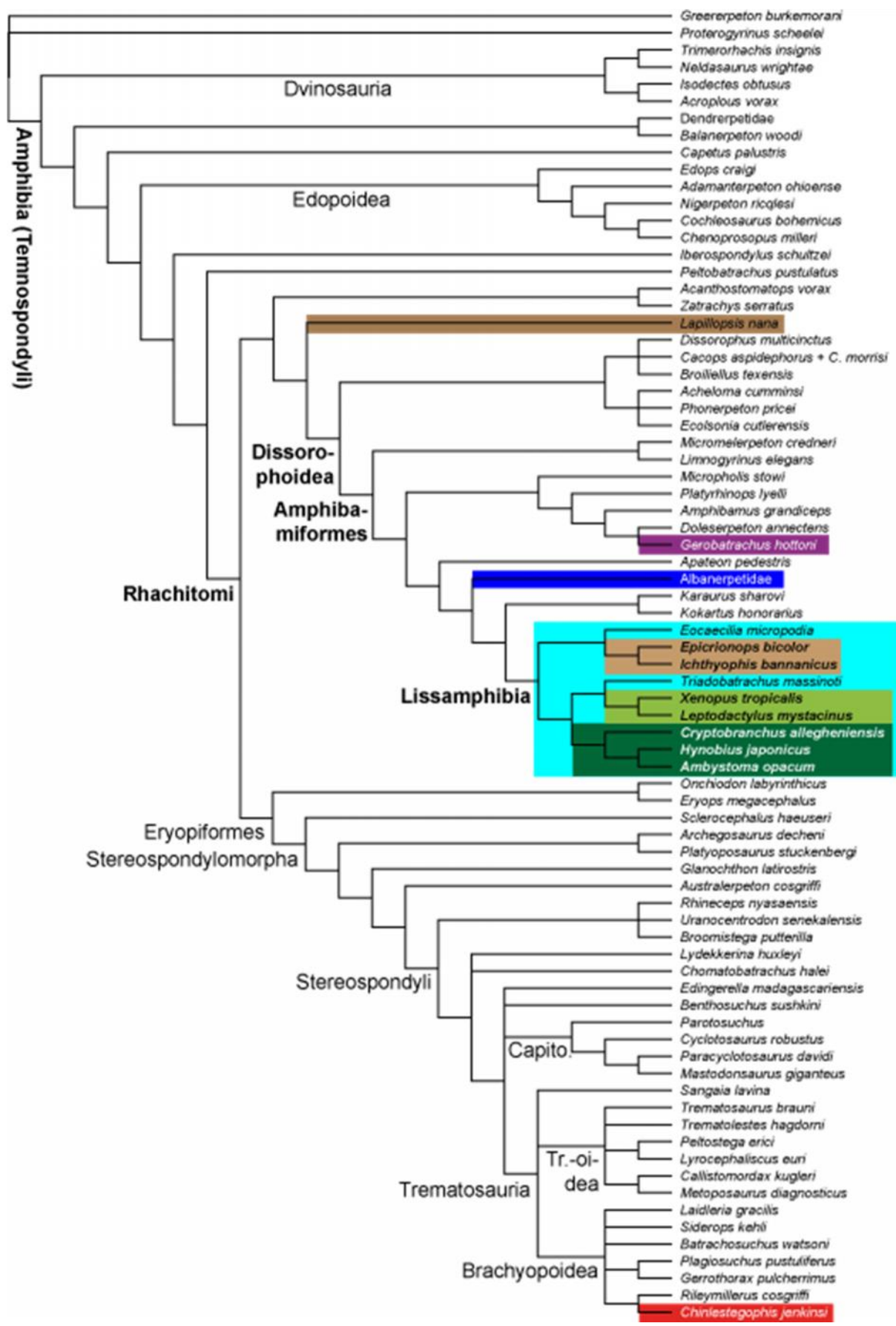
1057 **Figure 15. Strict consensus of the 297 MPTs recovered in analysis e3** (published
1058 matrix of Pardo et al. [2017a] after revision, Albanerpetidae added from Daza et al. [2020],
1059 all characters unordered). Capito. = Capitosauria; Tr.-oidea = Trematosauroidea.

1060



1061

1062



1064 In the ordered analysis e4, 36 MPTs are recovered (1619 steps, CI without uninformative
1065 characters = 0.2425, RI = 0.6812, RC = 0.1687). They all group the *Rileymillerus* +
1066 *Chinlestegophis* clade with Brachyopoidea as in analysis e3, while Lissamphibia is nested
1067 among the amphibamiform dissorophoids, closer to *Apateon* than to *Gerobatrachus* or
1068 *Doleserpeton*. PAUP* groups the MPTs into three islands depending on how they resolve
1069 amphibamiform phylogeny: one island (Fig. 16) has (*Doleserpeton* (*Gerobatrachus*
1070 (*Apateon*, Lissamphibia))) inside Amphibamidae, Albanerpetidae on the caecilian stem and
1071 Karauridae on the batrachian stem; the other two (Fig. 17) have (*Apateon* (Albanerpetidae
1072 (Karauridae, Lissamphibia))) close to but outside Amphibamidae, which contains
1073 *Gerobatrachus*; the Early Triassic amphibamiform *Micropholis* is either on the amphibamid
1074 or on the lissamphibian side.

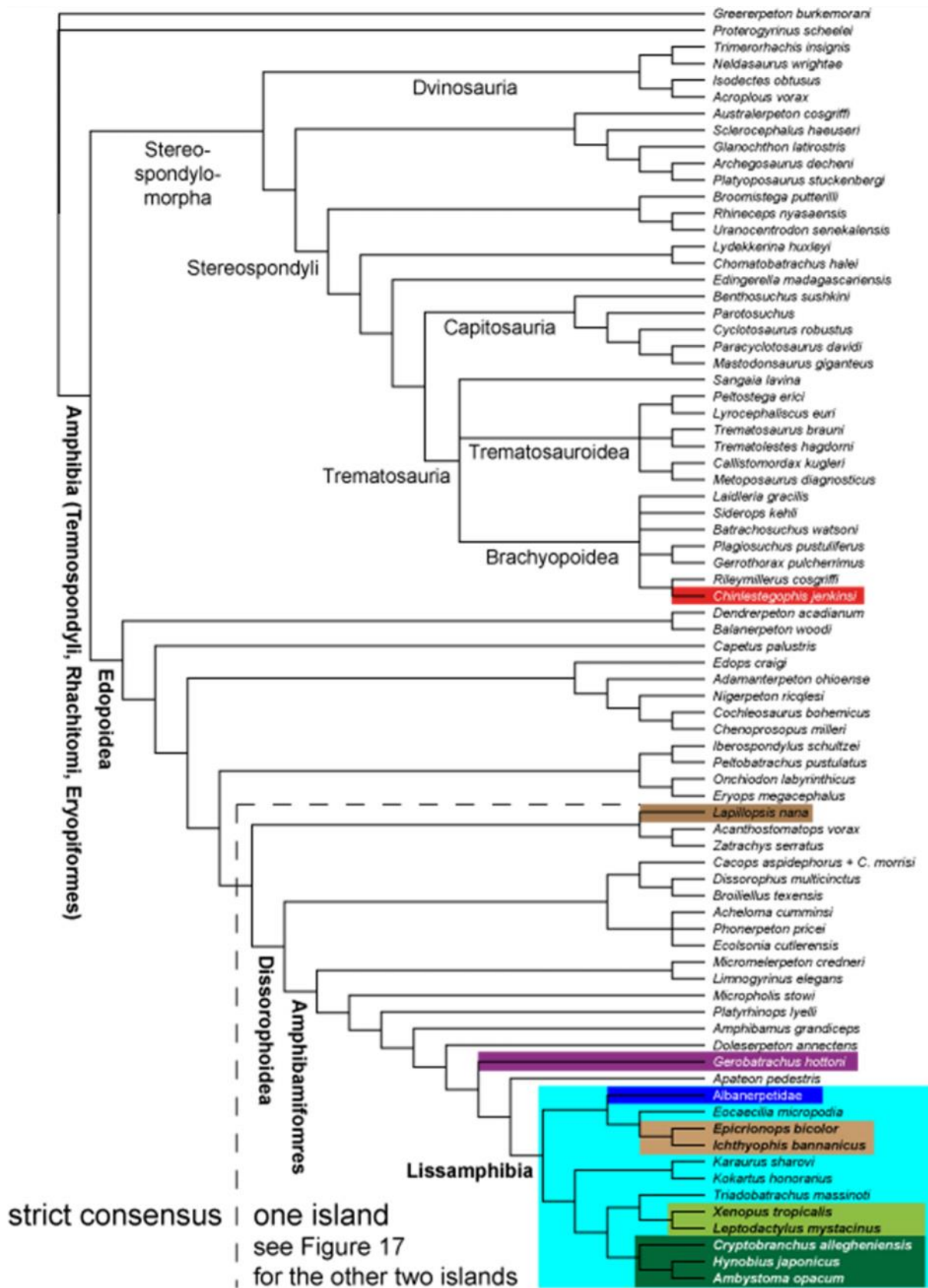
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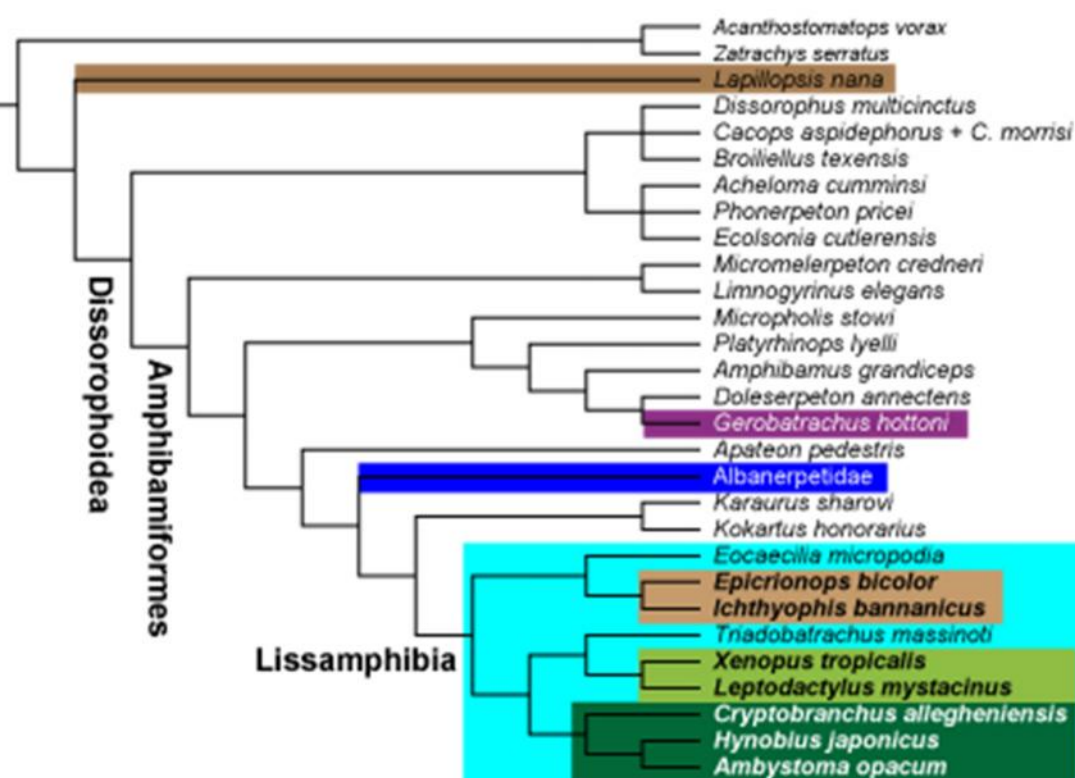
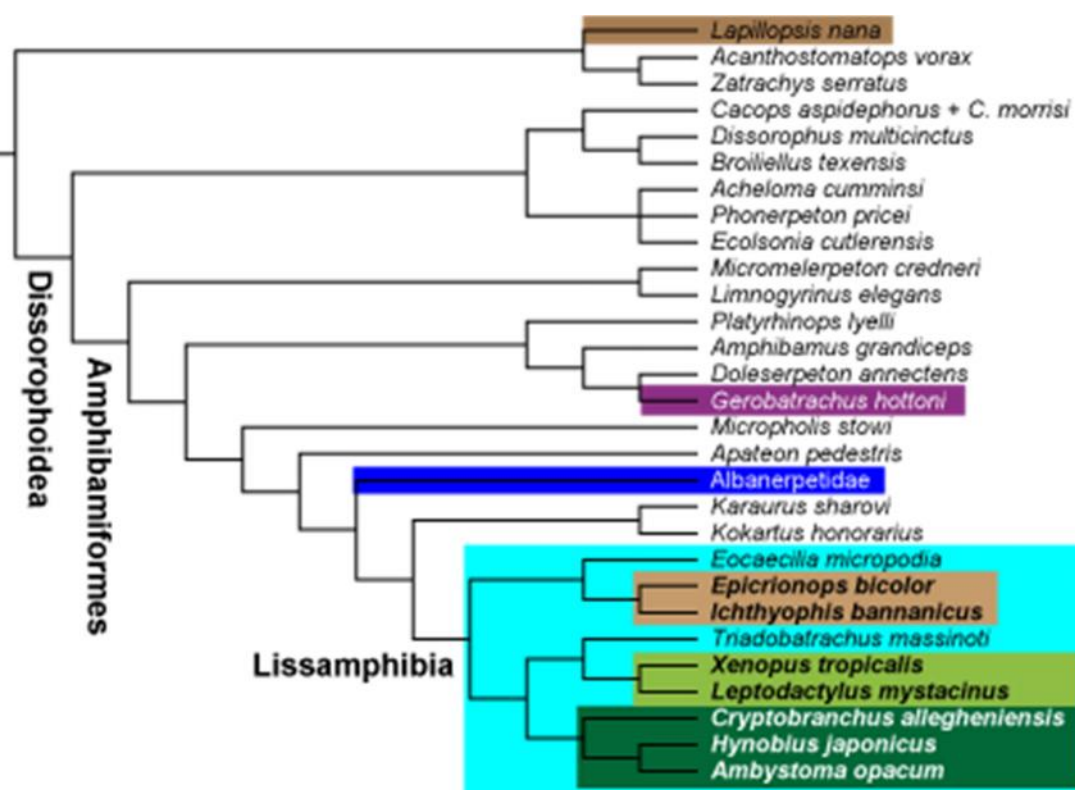
1077 **Figure 16. Strict consensus of all (to the left and above the stippled line) or some (to**
1078 **the right and below the stippled line) of the 36 MPTs recovered in analysis e4** (published
1079 matrix of Pardo et al. [2017a] after revision, Albanerpetidae added from Daza et al. [2020],
1080 clinal characters ordered). For the other MPTs, see Fig. 17.

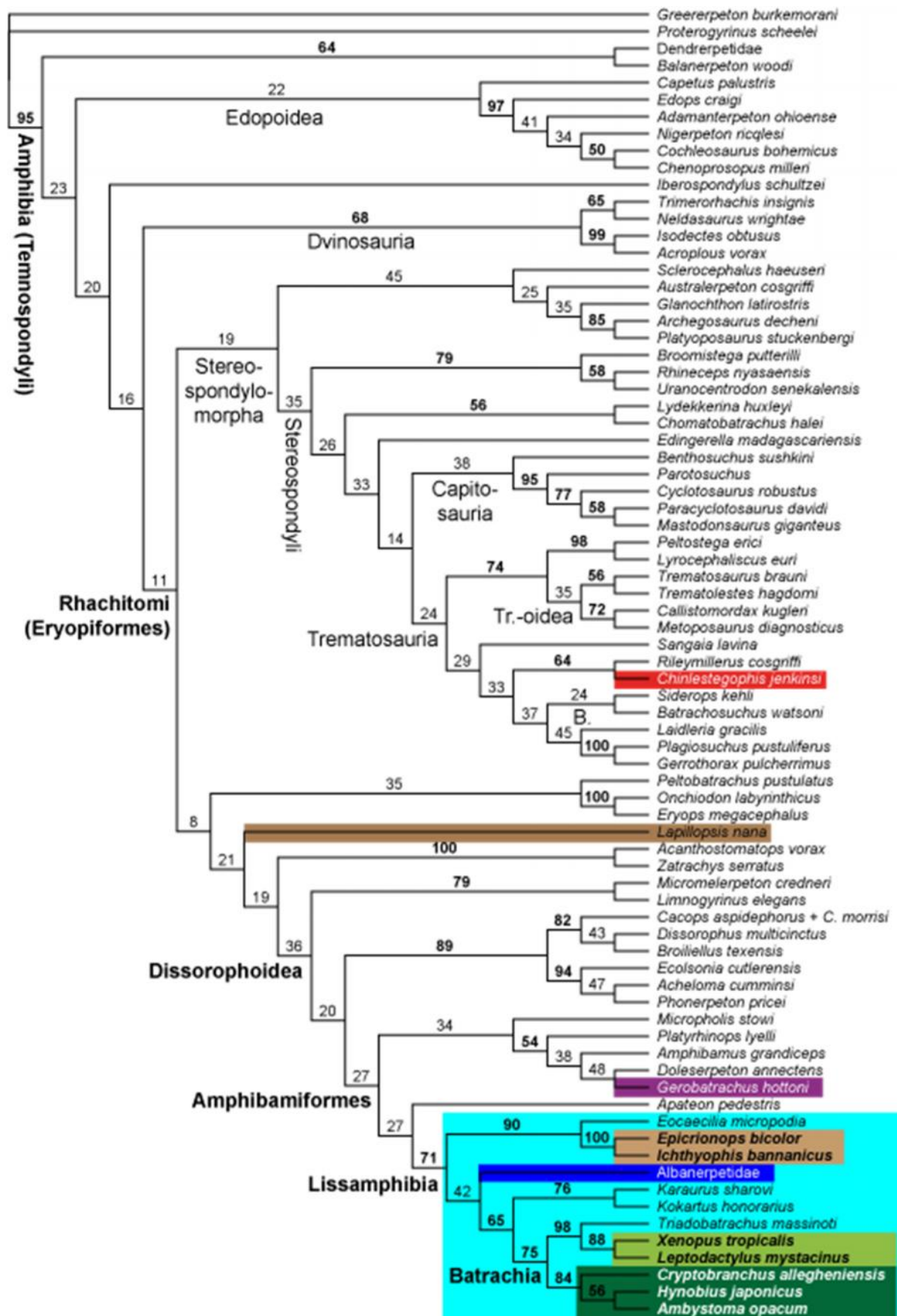
1081 **Figure 17. Strict consensus of each of the remaining two islands of MPTs from**
1082 **analysis e4.** The remainder of the tree is identical in all three islands and not repeated here;
1083 see Fig. 16.

1084



rest of tree identical to overall strict consensus in Figure 16





1088 **Figure 18. Bootstrap tree of analysis e4** (published matrix of Pardo et al. [2017a] after
1089 revision, Albanerpetidae added from Daza et al. [2020], clinal characters ordered). Bootstrap
1090 values 50% in boldface. B. = Brachyopoidea; Tr.-oidea = Trematosauroidea.

1091 Bootstrapping analysis e4 reveals (Fig. 18) considerable support for Lissamphibia (71%),
1092 within which Albanerpetidae (42%) and Karauridae (65%) lie on the batrachian stem but not
1093 in Batrachia (75%). Lissamphibia is, with limited support, placed next to *Apateon* (27%) in
1094 Dissorophoidea (36%); similar support is recovered for placing *Chinlestegophis* (and
1095 *Rileymillerus*) close to brachyopoids and plagiosaurids (33%) in Stereospondyli (35%).

1096 Groupings not compatible with the bootstrap tree (Supplementary Table 4) include
1097 *Chinlestegophis* + *Rileymillerus* as gymnophionomorphs (18%) or in an exclusive clade with
1098 Lissamphibia (23%); comparable support exists for Lissamphibia without Albanerpetidae
1099 (26%) or Lissamphibia without Karauridae or Albanerpetidae (20%), both of which are also
1100 incompatible with the bootstrap tree. An exclusive clade of lissamphibians and
1101 stereospondyls occurs in only 9% of the bootstrap replicates.

1102 **Discussion**

1103 *Support for alternative topologies*

1104 Our work corroborates some of the results of the analyses performed by Pardo et al. (2017a),
1105 but also highlights weaknesses in the phylogenetic signal that was claimed to support
1106 caecilian affinities of *Chinlestegophis*. Indeed, Pardo et al. (2017a: abstract) claimed: “Our
1107 results place the taxon confidently within lissamphibians.” On the contrary, our results
1108 demonstrate that the affinities of *Chinlestegophis* cannot be ascertained with confidence
1109 based on either of the two matrices of Pardo et al. (2017a).

1110 First, we stress that the unpublished matrix (our analysis a1, see Table 1; Fig. 2; Pardo et al.
1111 2017a: fig. S6) yielded a commonly recovered Lissamphibia, nested within dissorophoids and
1112 optionally containing *Gerobatrachus* but never *Chinlestegophis*. Forcing a version of the
1113 “lepospondyl hypothesis” of amphibian ancestry by constraining *Eocaecilia* to nest among
1114 lepospondyls (analysis a2; Fig. 3) results in only slightly longer trees (4 steps added to the
1115 1450 of the unconstrained trees) that are not significantly different from the unconstrained
1116 trees (p between 0.62 and 0.72 according to the three usual tests). This is important because it
1117 suggests that when a broader sample of extinct tetrapods is included, a more mainstream
1118 hypothesis of both lissamphibian ancestry and Paleozoic tetrapod relationships is produced,

1119 and the stereospondyls represented in this matrix, *Rileymillerus* and *Chinlestegophis*, are
1120 distanced from lissamphibian origins.

1121 All of our remaining analyses focused on the published matrix of Pardo et al. (2017a).
1122 Unsurprisingly, we confirmed (analysis b) the results of Marjanovič and Laurin (2019: fig.
1123 30I–K), Serra Silva and Wilkinson (2021) and Gee (2022) that Pardo et al. (2017a) found all
1124 MPTs that fit this matrix, that the MRC tree they reported is accurate as such, and that the
1125 MRC tree is a highly incomplete representation of the MPTs: it is equally parsimonious for
1126 Batrachia and Gymnophiona to lie in Stereospondyli or Amphibamiformes, and for them to
1127 form Lissamphibia or not, which may or may not contain *Chinlestegophis*. We further
1128 contribute the first fully published bootstrap analysis of this matrix (Fig. 4, Supplementary
1129 Table 1); contrary to Pardo et al. (2017a: fig. S7B), it supports diphyly of extant amphibians,
1130 although the support is not strong (52% for grouping *Chinlestegophis* with the caecilians;
1131 43% for grouping *Gerobatrachus* with the batrachians; only 35% for grouping all
1132 dissorophoids with the batrachians to the exclusion of any caecilians).

1133 Pardo et al. (2017a: fig. S7B) found no bootstrap values of 50% or higher on any node that
1134 separates caecilians and batrachians (they did not publish values below 50%). Although we
1135 used 200 bootstrap replicates of 500 addition-sequence replicates each, Pardo et al. (2017a)
1136 used 1000 bootstrap replicates of 100 addition-sequence replicates each (J. Pardo pers.
1137 comm. 2023; the settings were not published); this may explain the different result. It is
1138 possible and indeed likely that the differences are slight, e.g., where we found 52% support
1139 for caecilians + *Chinlestegophis*, they probably found support between 40% and 49%.

1140 However, adding Albanerpetidae to the matrix (analysis c; Fig. 5) confirms the result of Daza
1141 et al. (2020): Lissamphibia is found in Amphibamiformes in all MPTs, while *Chinlestegophis*
1142 is always a stereospondyl. The omission of albanerpetids from the original matrix was clearly
1143 a suboptimal choice, given that all studies published since their discovery over half a century
1144 ago support close affinities between albanerpetids and lissamphibians, if not a position
1145 among lissamphibians (e.g., Estes 1969; Estes and Hoffstetter 1976; Fox and Naylor 1982;
1146 McGowan and Evans 1995; Maddin et al. 2013; Daza et al. 2020; Kligman et al. 2023). Even
1147 the most unorthodox analysis of albanerpetid affinities that we know of suggests close
1148 affinities to batrachians (McGowan 2002).

1149 The effect of ordering characters within the original published matrix (i.e., without
1150 Albanerpetidae and without corrections other than renumbering the states of some ordered
1151 characters) (analysis d1; Fig. 6) narrowed down the five islands to one: Lissamphibia (which
1152 has 55% bootstrap support) forms the sister group of the stereospondyls *Chinlestegophis* and
1153 *Rileymillerus*. This arrangement only occurs in 35% of the bootstrap replicates, however (Fig.
1154 7; Supplementary Table 2). Adding Albanerpetidae (analysis d2) moved Lissamphibia into
1155 the amphibamiform dissorophoids; it is equally parsimonious for *Chinlestegophis* and
1156 *Rileymillerus* to be stem-caecilians (Fig. 8) or brachyopoid stereospondyls (Fig. 9).
1157 Bootstrapping this analysis (Fig. 10; Supplementary Table 3) revealed modest support for
1158 Lissamphibia (45%) and weak support for any position of that clade, but comparatively
1159 strong support against a position close to *Gerobatrachus* or *Doleserpeton* (62%).

1160 A modest revision of the published matrix, without Albanerpetidae, replicated the basic
1161 results of analyses c and d1 as equally parsimonious when all characters were unordered
1162 (analysis e1; Figs. 11–13). Ordering (analysis e2; Fig. 14) restricted Lissamphibia to
1163 Stereospondyli as in analysis d1 (unmodified matrix, likewise ordered, likewise without
1164 Albanerpetidae). Adding Albanerpetidae without ordering (analysis e3; Fig. 15) essentially
1165 replicated analysis c, ordering (analysis e4; Fig. 16, 17) introduced variation within
1166 Lissamphibia but kept it in the same place as in analysis c—with strong bootstrap support: a
1167 lissamphibian-stereospondyl clade is not compatible with the bootstrap tree (Fig. 18) and
1168 only occurs in 9% of the replicates (Supplementary Table 4). The 71% support for
1169 Lissamphibia (with Albanerpetidae) excluding *Chinlestegophis* (or *Rileymillerus*,
1170 *Gerobatrachus* or any other traditional non-member) is worth highlighting.

1171 In all four cases, ordering increased the resolution of the results. We interpret this as an
1172 example of ordering bringing out phylogenetic signal in data, congruent with results from
1173 simulations and some empirical examples (Marjanovič and Laurin 2008, 2019; Grand et al.
1174 2013; Rineau et al. 2015, 2018; and references therein). As the same references show,
1175 ordering does not automatically increase the net resolution; in matrices that already contain
1176 one or more sufficiently strong false signals, revealing the phylogenetic signal introduces
1177 conflict and decreases the total resolution.

1178 Strikingly, none of our trees from analyses c, d1 or e (most parsimonious or bootstrap)
1179 support affinities between *Chinlestegophis* and caecilians to the exclusion of other
1180 lissamphibians, and in analysis d2 it is only one of two equally parsimonious options and

1181 only occurs in 44% of the bootstrap replicates (Supplementary Table 3). Although the
1182 bootstrap analysis of the original matrix under original conditions (analysis b; Fig. 4,
1183 Supplementary Table 1) does support diphyly of extant amphibians and an exclusive clade of
1184 *Chinlestegophis* and the three caecilians, this clade only occurs in 52% of the replicates, and
1185 an exclusive clade of frogs, salamanders, karaurids and *Gerobatrachus* to the exclusion of
1186 *Chinlestegophis* is found in only 43%. Our highly restricted revisions to the published matrix
1187 (analyses e1, e2; see Gee 2022 for a much more thorough, if cautious, revision), as well as
1188 the addition of Albanerpetidae to the taxon sample (analysis c) or the combination of both
1189 (analyses e3, e4), resulted in an exclusive clade comprising lissamphibians nested among
1190 dissorophoids (analyses c, e1, e3, e4 and its bootstrap analysis), or Lissamphibia as sister to
1191 *Chinlestegophis + Rileymillerus* within Stereospondyli (analyses e1, e2). The former is the
1192 currently most widespread hypothesis on the origin of the extant amphibian clades; the latter
1193 is new, but considerably less novel than extant amphibian diphyly as proposed by Pardo et al.
1194 (2017a).

1195 It is worth noting again that the matrix contains evidence for a sister relationship between
1196 Lissamphibia and the *Chinlestegophis + Rileymillerus* clade, always within Stereospondyli,
1197 as recovered in analyses b (as one of several equal options), d1 (if only with 35% bootstrap
1198 support), d2 (as one of several equal options, with 27% bootstrap support), e1 (as one of two
1199 options) and e2. Although weakly supported, the fact that this result occurred in the original
1200 (analyses b–d) and the revised matrix (analyses e1, 2) suggests that *Chinlestegophis* may
1201 contribute important information about amphibian evolution in the context of the
1202 “temnospondyl hypothesis”, even if it cannot be supported specifically as a stem-caecilian.
1203 More likely, however, it may highlight convergence between the *Chinlestegophis +*
1204 *Rileymillerus* clade and lissamphibians in general or caecilians in particular; this is,
1205 moderately, supported by our bootstrap of analysis e4 (Fig. 18; Supplementary Table 4),
1206 where *Chinlestegophis + Rileymillerus* were recovered next to Lissamphibia in only 23% and
1207 as gymnophionomorphs in only 18% of the bootstrap replicates while a lissamphibian-
1208 stereospondyl clade only has 9% bootstrap support (all three groupings are incompatible with
1209 the bootstrap tree: Fig. 18), as well as by the bootstrap analysis conducted by Kligman et al.
1210 (2023: extended data figure 6), where Lissamphibia excluding *Chinlestegophis* and
1211 *Rileymillerus* occurred in 55% of the replicates and Stereospondyli including a
1212 *Chinlestegophis + Rileymillerus* clade in 57%. Minimally, our results highlight the
1213 importance of albanerpetids for understanding lissamphibian relationships. Note that the first

1214 known complete and undistorted albanerpetid skull (Daza et al. 2020) was not used by
1215 Kligman et al. (2023), who preferred using *Celtdens ibericus*—known from complete
1216 skeletons which are, however, thoroughly flattened and split through the bone, making
1217 certain parts very hard to interpret (McGowan 2002)—over a composite Albanerpetidae
1218 OTU. Using more than one albanerpetid OTU would probably require adding albanerpetid-
1219 related characters to the matrix.

1220 Pardo et al. (2017a) emphasized that the topology they presented was supported by Bayesian
1221 inference. As discussed above (Matrices, Methodologies, and Missteps: Bayesian inference
1222 of phylogeny), missing data have unpredictable, sometimes very strong, effects on parametric
1223 methods of phylogenetics such as Bayesian inference, while the non-parametric method
1224 called parsimony is unaffected by this particular issue and therefore safer for paleontological
1225 data. Matrix quality remains more important than the method of analysis (Simões et al. 2017;
1226 Marjanovi and Laurin 2019; Gee 2021, 2022; and references therein).

1227 *Assessment of qualitative arguments*

1228 As further support for a close relationship between *Chinlestegophis* and caecilians, Pardo et
1229 al. (2017a) proposed a number of features supposedly shared between both taxa, and in some
1230 cases with other stereospondyls. Most of them are coded in the matrix in some form. We
1231 have reviewed them all above (Materials and Methods: Evaluation of potential
1232 synapomorphies and revisions to the published matrix) and find serious problems in all of
1233 them; none supports placing caecilians as the sister taxon of *Chinlestegophis* (or
1234 *Chinlestegophis* + *Rileymillerus*), or in stereospondyls in general. In many ways, the original
1235 discussion of features proposed to link *Chinlestegophis* and caecilians (Pardo et al. 2017a)
1236 described transformations that would be required for brachyopoids to give rise to caecilians,
1237 not what is actually visible in the preserved material.

1238 Outside of characters addressed directly in Pardo et al. (2017a) we noted several other
1239 features by which *Chinlestegophis* resembles other stereospondyls but differs starkly from
1240 caecilians. The elongate nature of the basicranial articulation in *Chinlestegophis* superficially
1241 resembles that of *Eocaecilia* and Gymnophiona. However, in *Chinlestegophis*, the basicranial
1242 joint forms a strong girder, tightly sutured (Pardo et al. 2017a), similar to the condition seen
1243 in other stereospondyls. In caecilians, the basicranial joint is instead elongate, with a loosely
1244 constructed connection and thick cartilage covering the bony joint surfaces of both the *os*

1245 *basale* and the (epi)pterygoid or pterygoquadrate (Maddin et al. 2012b). Furthermore, the
1246 occipital morphology of *Chinlestegophis* is unlike that of any caecilian—or any other
1247 lissamphibian—in its possession of well-developed posttemporal fenestrae. In that respect,
1248 *Chinlestegophis* is very similar to brachyopoid stereospondyls, and loss of those fenestrae in
1249 caecilians and other lissamphibians is convergent under the topology advocated by Pardo et
1250 al. (2017a: fig. 2C).

1251 What little is known and described of the postcranial skeleton (Pardo et al. 2017a: fig. S5)
1252 also resembles other stereospondyls but starkly differs from caecilians. The interclavicle of
1253 *Chinlestegophis* is a large plate, as usual for stereospondyls; in lissamphibians and
1254 albanerpetids, no trace of an interclavicle is known. Similarly, the clavicles consist mostly of
1255 a large plate and look unremarkable for a stereospondyl in all details of their shape; clavicles
1256 are absent in albanerpetids, caecilians (including *Eocaecilia*) and salamanders, and those of
1257 frogs are robust curved struts without any plate-like component, more similar to those of
1258 extant amniotes. A few neural arches are preserved in *Chinlestegophis*, but centra are not;
1259 this is standard for morphologically immature temnospondyls, but only observable (as
1260 presence or absence of ossification) in a very short phase in the ontogeny of frogs and
1261 hynobiid salamanders, and not known in caecilians—in *Gegeneophis* and in *Caecilia*
1262 *orientalis* Taylor, 1968, the centra ossify before the neural arches (Müller 2006; Pérez et al.
1263 2009)—or albanerpetids (though albanerpetid ontogeny is virtually unknown). Indeed, early
1264 ossification of the centra (earlier than the neural arches or not long after them), quickly
1265 followed by suturing or even fusion to the neural arches, is a synapomorphy of
1266 lissamphibians and probably a few amphibamiforms (notably *Doleserpeton* and
1267 *Gerobatrachus*) under the “temnospondyl hypothesis”, or of Seymouriamorpha,
1268 Chroniosuchia and Tetrapoda under the “lepospondyl hypothesis” (Laurin and Reisz 1997;
1269 Danto et al. 2019). It should be stressed that full neurocentral fusion is not found outside
1270 these clades (and Albanerpetidae), but is found in all known vertebrae of *Eocaecilia* (Jenkins
1271 et al. 2007) and the lone vertebra referred to *Funcusvermis* (Kligman et al. 2023). The ribs of
1272 *Chinlestegophis* are, plesiomorphically, longer than three successive vertebrae; they are
1273 shorter in amphibamiforms and a few select lepospondyls (Marjanović and Laurin 2008,
1274 2019), and much shorter, about as long as one vertebra, in albanerpetids and all
1275 lissamphibians except a few peramorphic salamandrids (Marjanović and Witzmann 2015, and
1276 references therein). The only known similarity of the postcranium of *Chinlestegophis* to that

1277 of caecilians is body elongation; the massive dermal shoulder girdle does not suggest limb
1278 reduction, and indeed the presumed ulna has an unremarkable size.

1279 *Homoplastic rather than stepwise evolution*

1280 Interpretations of functional biology and evolutionary trends rely on our perspective of
1281 phylogenetic relationships. In the original description of *Chinlestegophis*, once a consensus
1282 tree was selected and reported, a number of the characteristics used in the matrices and
1283 discussed above were used to infer a stepwise evolution of traits toward the specialized
1284 fossorial and head-first burrowing lifestyle of caecilians. Those features include fusion of the
1285 lacrimal + maxilla and exoccipital + opisthotic (interpreted to represent stages in the
1286 consolidation of the skull), repositioning of the jaw suspension, small and laterally oriented
1287 eyes, etc. However, as we demonstrate above, most of those features have a wider
1288 distribution across Paleozoic tetrapods or present confounding problems of homoplasy across
1289 many disparate clades, extinct and extant.

1290 When taxa exhibit traces of “specialized” morphology, care should be taken to avoid circular
1291 arguments based on functional considerations. In the case of potentially fossorial or
1292 burrowing vertebrates, in which selective pressures lead to a narrow range of morphologies
1293 regardless of ancestry (e.g., Barros et al. 2011, Sherratt et al. 2014, Da Silva et al. 2018,
1294 Evans et al. 2022), it is particularly important that matrices be constructed to minimize
1295 redundant characters, and that characters sample anatomy broadly to avoid inadvertently
1296 “stacking the deck” and focusing on a heavily modified region. Through the use of tree
1297 statistics, character partitions and other methods to ascertain robustness, resulting topologies
1298 should be explored for potentially misleading signals. As mentioned above, tree statistics
1299 were mostly lacking from the original report of *Chinlestegophis* as a stem-caecilian, and
1300 Pardo et al. (2017a) did not discuss whether the specific characters uniting that taxon and
1301 caecilians might be correlated homoplasies associated with burrowing.

1302 A related problem in this regard was the aforementioned removal of all lepospondyls from
1303 the unpublished matrix to create the published matrix after the initial recovery of
1304 *Chinlestegophis* as a temnospondyl by Pardo et al. (2017a). Lepospondyls have presented
1305 various challenges to reaching a consensus on lissamphibian origins (Anderson 2001;
1306 Marjanovi and Laurin 2008, 2009, 2013, 2019; Laurin et al. 2022; Jansen and Marjanovi
1307 2022; Mann et al. 2022; and references therein). Thus, including lepospondyls in tests of the

1308 origins of extant amphibians is critical to represent the full range of morphology during the
1309 Paleozoic and reveal potential homoplasy. Removing those taxa from analyses, and thus
1310 removing many different pathways and anatomical combinations, could make it more likely
1311 that any elongate, fossorial, or burrowing taxa be placed together incorrectly in the
1312 phylogeny, such as *Chinlestegophis* clustering with caecilians in some tree islands produced
1313 from the published matrix.

1314 Schoch et al. (2020) added three lepospondyls to the published matrix of Pardo et al. (2017a),
1315 but they did not add any characters that would help resolve their phylogeny or their
1316 relationship to lissamphibians. This was not changed by Kligman et al. (2023), in which those
1317 three lepospondyls form the sister-group of *Greererpeton* (Kligman et al. 2023: extended data
1318 fig. 5–7), an Early Carboniferous colosteid that is a more appropriate outgroup than the
1319 anthracosaur *Proterogyrinus* that was used as such.

1320 Considering that alternative hypotheses of relationships are equally supported by the
1321 published matrix, even without broader taxonomic sampling to include lepospondyls, the
1322 proposed stepwise evolution of caecilian features falls apart. Rather than traits linking
1323 *Chinlestegophis* and caecilians, those same characteristics appear to represent homoplasy, as
1324 shown in trees that place *Chinlestegophis* close to but outside Lissamphibia (our analyses a,
1325 d, e2 and some MPTs plus the bootstrap tree of b), or far away (our analyses c, e1 and some
1326 MPTs of b).

1327 *The adsymphysial bone and the lingual tooththrow*

1328 Kligman et al. (2023) made the novel argument that the lingual tooththrow in the lower jaw of
1329 caecilians is borne not on a coronoid, but on the adsymphysial, a bone that is
1330 plesiomorphically present between coronoid 1 and the symphysis in tetrapodomorphs but
1331 generally thought to be absent in all lissamphibians, all lepo- and all temnospondyls among
1332 others. Where present, it usually bears teeth, often including a tooththrow. Kligman et al.
1333 (2023) proposed to equate this tooththrow with the short lingual tooththrow seen at the
1334 symphysis of at least some *Doleserpeton* specimens and with the lingual tooththrow of
1335 caecilians, including *Funcusvermis*, noting the absence of teeth in this region in
1336 *Chinlestegophis*. To populate the long branch between the non-temnospondyl *Greererpeton*
1337 and *Doleserpeton* in their fig. 3, they relied on isolated reports of an adsymphysial bone (also

1338 called “parasymphysial bone” or “parasymphysial plate”) in other temnospondyls, listed in
1339 part 3 of their supplementary information. We find all of them questionable.

1340 The most recent report of an adsymphysial in a temnospondyl concerns *Cacops aspidophorus*
1341 Williston, 1910 (Anderson et al. 2020), a reasonably close relative of *Doleserpeton* as shown
1342 in Kligman et al. (2023: fig. 3). Despite its novelty, Anderson et al. (2020: 9–10) did not
1343 argue for the interpretation they proposed, but merely briefly presented it as an
1344 uncontroversial fact; it is not mentioned in their Discussion section. The photos in their fig. 8
1345 are not clear enough to demonstrate the suture between the adsymphysial and the dentary. In
1346 the photo in lingual view, we can see the line that is drawn solid as part of the suture in the
1347 interpretative drawing; but we cannot see the part that is drawn stippled, and we can see
1348 several other lines in the supposed adsymphysial and even in the supposed dentary that could
1349 be sutures or fractures. The photo in ventral view is even less clear. The proposed
1350 adsymphysial would bear the “tusks”/“fangs” that lie lingual of the (dentary) toothrow
1351 (Anderson et al. 2020: fig. 8; Kligman et al. 2023: fig. 3); it should be noted that this
1352 combination of a toothrow on the dentary with “tusks” on the adsymphysial but no other teeth
1353 in this region has not been documented elsewhere. In numerous non-temnospondyls with an
1354 uncontroversial adsymphysial bone, there are “tusks” on the dentary, followed labially by the
1355 dentary toothrow and lingually sometimes by an adsymphysial toothrow and/or, yet further
1356 lingually, adsymphysial “tusks” (e.g., Ahlberg and Clack 1998; Lombard and Bolt 2006). Not
1357 having studied the *C. aspidophorus* specimen, we will not argue for or against either
1358 interpretation any further, but we reiterate that the published case is insufficient to decide the
1359 question.

1360 An adsymphysial was previously reported in *Cacops morrisoni* Reisz, Schoch and Anderson,
1361 2009, in a single sentence and not illustrated (Reisz et al. 2009: 794). Sutures around the
1362 putative adsymphysial are not present in the remarkably few published specimens of
1363 *Doleserpeton* (e.g., Sigurdsen and Bolt 2010: fig. 6A; Kligman et al. 2023: fig. 3). In
1364 *Georgenthalia*, a close relative of *Doleserpeton*, the usual expansion of the dentary at the
1365 symphysis (compare *Salamandra*: Kligman et al. 2023: fig. 3) was suggested to be an
1366 adsymphysial in what seems to be an overedited paragraph that is not quite clear (Anderson
1367 et al. 2008b: 67). No sutures were reported or illustrated, and the preservation in ventral view
1368 obscures any teeth.

1369 The evidence for an adsymphysial in the stereospondyl *Parotosuchus* (Shishkin and Sulej
1370 2009: 52–53, 69) consists of nothing but a notch in the occlusal face of the mesial end of the
1371 dentary of early juveniles, between the toothrow and the tusks, that was identified in that
1372 paper as marking the mesial end of Meckel’s cartilage, with the dentary growing around it in
1373 later documented ontogenetic stages. The unspoken assumption that every notch must be a
1374 marker of fusion of two separate bones was routinely used in the 1930s to infer about three
1375 times as many bones in the skulls of immature caecilians as have actually been observed
1376 (Müller 2006: 983); it should not be perpetuated.

1377 In two specimens of the stereospondyl *Plagiosuchus*, “there is evidence for the presence of an
1378 additional small, toothless, dorsal symphyseal ossification” which “probably represents an
1379 adsymphyseal” according to Damiani et al. (2009: 363). The photo of one these specimens
1380 (fig. 4A), and probably the preservation as well, is insufficient to determine if the
1381 “ossification” is surrounded by sutures or, for example, continuous with the ossified
1382 Meckelian part of the symphysis.

1383 Finally, in one of the four partial lower jaws referred to the stereospondyl *Qantas*, “the
1384 symphyseal plate contains not only the dentary, but also an additional bone, the dorsal
1385 surface of which has symphyseal canines. This additional ossification is probably
1386 homologous to the adsymphyseal” (Novikov 2012: 183). There is no further description or
1387 illustration; the line drawings of the holotype, another lower-jaw ramus, lack any indication
1388 of such an extra bone (fig. 1(b), (c)).

1389 We conclude that the evidence to equate the lingual toothrow of caecilians to that of
1390 *Doleserpeton*, or the bone which bears it to the adsymphysial, is at present very weak even if
1391 caecilians are assumed to be temnospondyls. Admittedly, coronoids that reach the symphysis
1392 have not been documented either (the gap is smaller in the lepospondyls *Pantylus* and
1393 *Euryodus* than in *Chinlestegophis*, but still clear: Romer 1969; Gee et al. 2020); the best
1394 candidates are *Platyrhinops*, a close relative of *Doleserpeton* and *Georgenthalia*, in which the
1395 denticle-bearing lingual surface of the lower jaw extends to the symphysis or nearly so, but
1396 the denticles obscure any sutures (Clack and Milner 2010), and *Acheloma*, where the dentary
1397 bears “tusks” lingual of the toothrow and is lingually followed by a separate bone which
1398 carries a denticle field and participates in the symphysis, but the jaw fragments illustrated by
1399 Polley and Reisz (2011: fig. 9, 10) are too short to clarify the identity of this bone.

1400 *Evolutionary ecology*

1401 The grooves for the lateral-line organ identified by Pardo et al. (2017a) on the skull of
1402 *Chinlestegophis* indicate an animal that was strictly aquatic for at least part of its adult life. In
1403 contrast, there is no evidence of lateral-line grooves or other aquatic features in *Eocaecilia* or
1404 the admittedly fragmentary *Funcusvermis*, and among extant caecilians aquatic lifestyles are
1405 restricted to larvae (of those few taxa that have them) and the highly nested clade
1406 Typhlonectidae. The inference of an aquatic lifestyle in *Chinlestegophis* is further supported
1407 by its poorly ossified vertebral column and probably also by its craniocaudally elongate plate-
1408 like clavicles. Perhaps aquatic vs. terrestrial lifestyles explain why *Chinlestegophis* was able
1409 to coexist with caecilians like the slightly older *Funcusvermis*; the wide, flat vertebra referred
1410 to the latter lacks a neural spine, interpreted as a fossorial adaptation by Kligman et al.
1411 (2023).

1412 *Matrix quality, taxon sampling and character sampling*

1413 The discussion above takes at face value both the coding and scoring of the two matrices, and
1414 their character and taxon samples, apart from our limited modifications in analyses c, d2 and
1415 e; but these issues deserve comments. We have not scrutinized the matrices in full (see Gee
1416 [2022] for a cautious but comprehensive treatment of the published matrix of Pardo et al.
1417 [2017a]), as we wished only to test whether alternative topologies can be equally (or better)
1418 supported by the original matrices, and to show the impact of a few scoring changes that were
1419 obviously needed. The absence of lepospondyls in the matrix published by Pardo et al.
1420 (2017a) prevents us from looking into how many extra steps an origin of lissamphibians
1421 among them would imply, compared to an origin among temnospondyls. Similarly, the
1422 removal of characters that are variable only among lepospondyls prevents using the published
1423 matrix as a starting point for such comparisons; unfortunately, this was not changed by
1424 Schoch et al. (2020) or Kligman et al. (2023) despite the former's addition of three
1425 lepospondyl taxa which the latter then retained. The heretofore unpublished precursor matrix
1426 remains available for this purpose, but it would need to be updated and greatly enlarged; in its
1427 present form, only four extra steps need to be added to the original 1450 to make an odd
1428 version of the lepospondyl hypothesis possible.

1429

1430

1431 **Conclusions**

1432 Published in one of the most prestigious journals, the description of *Chinlestegophis* (Pardo
1433 et al. 2017a) resulted in a new hypothesis about the origins of the extant amphibian clades
1434 and a new scenario for the origin of caecilians and their fossorial lifestyle that has attracted
1435 attention far beyond that of specialist researchers (Pough et al. 2022). We show that these
1436 exciting proposals are poorly supported by the original datasets and the original methods of
1437 analysis, as well as by limited revisions to one of the datasets aimed at eliminating the most
1438 conspicuous cases of character redundancy and a few questionable anatomical interpretations
1439 of *Chinlestegophis* and other taxa. The question of lissamphibian origins remains unsolved,
1440 although our revisions to the matrix reveal further support for Lissamphibia excluding
1441 *Chinlestegophis* and any Paleozoic taxa. In any case, we join Kligman et al. (2023) in
1442 cautioning against calibrating the divergence of caecilians and batrachians according to the
1443 phylogenetic hypothesis of Pardo et al. (2017a), i.e., by using the Late Carboniferous age of
1444 certain dissorophoid temnospondyls as the calibration date.

1445 Concerning phylogenetics, we reiterate that the majority-rule consensus is not a useful
1446 representation of the result of a parsimony analysis, and that not all issues with Bayesian
1447 analysis of matrices with missing data have been solved; but most importantly, matrix quality
1448 remains paramount in phylogenetic analysis. This concerns typographic errors,
1449 misinterpretations of published literature, redundant characters (in the dataset we revised, the
1450 double toothrow in the lower jaw of caecilians was coded as seven characters that an analysis
1451 could only treat as independent), characters that represent two or more independently varying
1452 features, and inconsistencies in scoring.

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1948 **List of supplements:**

1949 Supplementary File 1: Mesquite NEXUS file of Pardo et al. (2017a: fig. S6), previously
1950 unpublished. We have added a PAUP block that repeats our unconstrained and constrained
1951 analyses (a1, a2) if the file is executed in PAUP*, and a TREES block that contains one tree
1952 resulting from each analysis; before conducting the analyses, the PAUP block performs the
1953 statistical tests comparing the trees in the TREES block. Otherwise the file remains as
1954 provided by J. Pardo and A. Huttenlocker.

1955 Supplementary File 2: Supplementary Tables 1–4, showing the bootstrap bipartitions
1956 corresponding to analyses b, d1, d2 and e4.

1957 Supplementary File 3: Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the
1958 albanerpetid OTU of Daza et al. (2020) added. No scores are changed, all characters are
1959 unordered. We have also added a PAUP block and deleted the CHARSTATELABELS block
1960 because Mesquite could not deal with it correctly. If the file is executed in PAUP*, it repeats
1961 our analysis b (without Albanerpetidae), bootstraps it, and repeats analysis c (with
1962 Albanerpetidae).

1963 Supplementary File 4: Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the
1964 clinal characters ordered and the albanerpetid OTU of Daza et al. (2020) added. For
1965 characters 9, 205, 221, 327 and 328, the states had to be reordered to allow for linear ordering
1966 as described in the text. If executed in PAUP*, the file repeats our analysis d1 (without
1967 Albanerpetidae), bootstraps it, repeats analysis d2 (with Albanerpetidae) and bootstraps it as
1968 well.

1969 Supplementary File 5: Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the
1970 modifications to characters and individual scores described in the text and the albanerpetid
1971 OTU of Daza et al. (2020) added. If executed in PAUP*, the file repeats our analyses e1
1972 (without Albanerpetidae) and e3 (with Albanerpetidae).

1973 Supplementary File 6: Mesquite NEXUS file of Pardo et al. (2017a: fig. 2, 3, S7) with the
1974 modifications to characters and individual scores described in the text, the albanerpetid OTU
1975 of Daza et al. (2020) added and the clinal characters ordered. If executed in PAUP*, the file
1976 performs our analyses e2 (without Albanerpetidae) and e4 (with Albanerpetidae) and then
1977 bootstraps e4.