

# 1 **The scratch-digging lifestyle of the Permian “microsauro”** 2 ***Batropetes* as a model for the exaptive origin of jumping** 3 **locomotion in frogs**

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11

## 12 **Abstract**

13 Recent studies have shown that the Triassic stem-frog *Triadobatrachus* lacked the ability to  
14 jump off, but nonetheless had the forelimb strength to withstand the impact of landing from a  
15 jump. We propose a hypothesis to resolve this pseudoparadox: the strengthened forelimbs are  
16 former adaptations to forelimb-based digging that later made jumping possible by exaptation.

17 Micro-CT data from a skeleton of *Batropetes palatinus* reveal thin cortical bone,  
18 confirming *Batropetes* as terrestrial. Combining adaptations to walking and digging,  
19 confirmed by statistical analyses, *Batropetes* is thought to have searched for food in leaf litter  
20 or topsoil. We interpret *Batropetes* as having used one forelimb at a time to shove leaf litter  
21 aside. *Batropetes* may thus represent an analog or possibly a homolog of the digging stage  
22 that preceded the origin of Salientia.

23 We discuss the possibility of homology with the digging lifestyles of other  
24 “microsauro” and other amphibians.

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26 *Batropetes*; *Triadobatrachus*; “Microsauria”; Salientia; Anura; digging; jumping

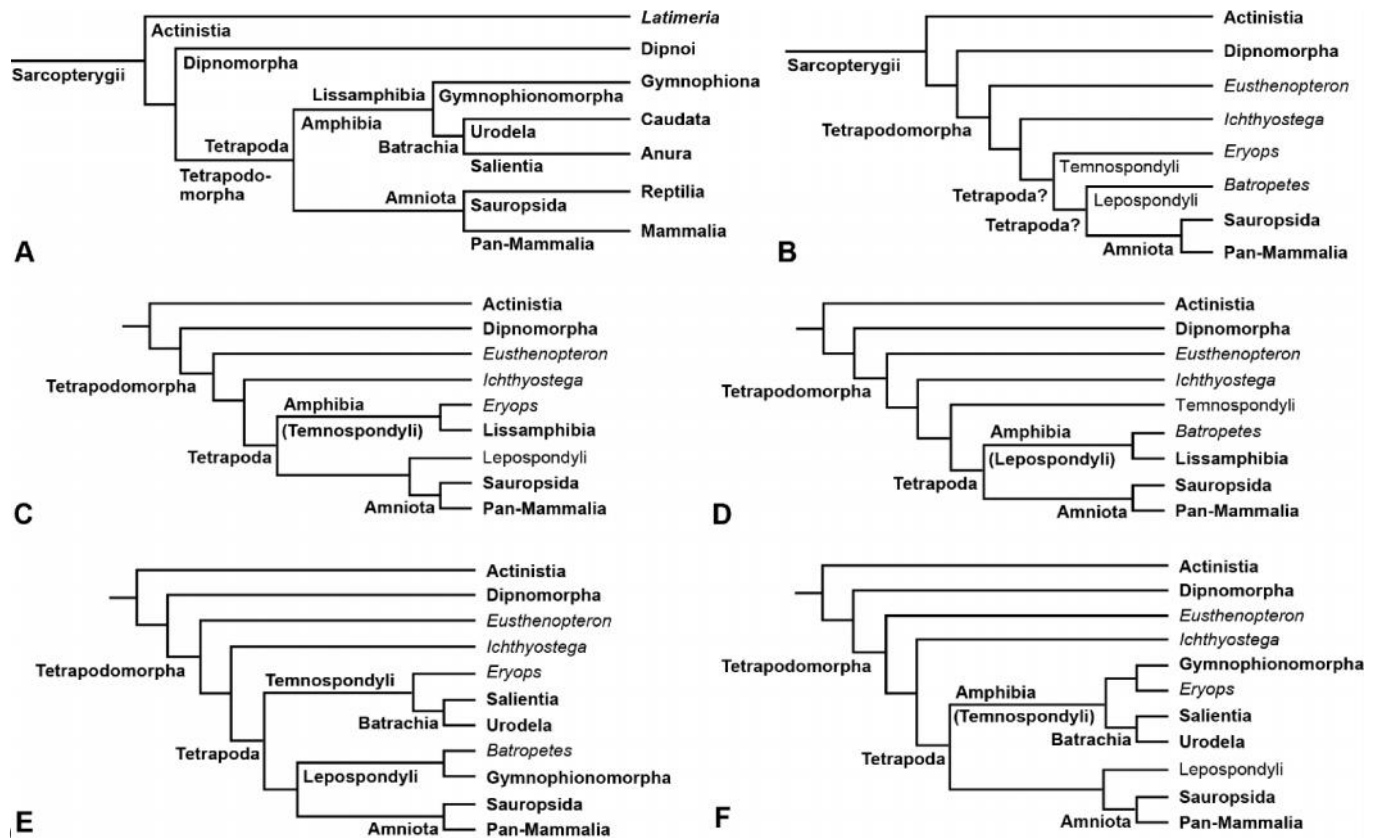
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## 28 **1. Introduction**

29 The origin of frogs (total group: Salientia) is the subject of two major questions. While there  
30 is now a consensus about the phylogenetic position of Salientia as the sister-group of Urodela  
31 (the total group of salamanders) according to molecular (Irisarri et al., 2017; Hime et al.,  
32 2020; and references therein) and morphological data alike (Pardo et al., 2017a; Marjanovi &

33 Laurin, 2019; Daza et al., 2020; and references therein; contradicted by Mann et al., 2019a,  
34 with < 50% bootstrap support), the phylogenetic position of Salientia + Urodela (together  
35 Batrachia), as well as that of the third extant amphibian clade (the caecilians: total or near-  
36 total group Gymnophionomorpha Marjanovi & Laurin, 2008), remains an unsolved problem  
37 (Marjanovi & Laurin, 2019; Danto et al., 2019; Laurin et al., 2019; Daza et al., 2020; Fig. 1).  
38 For well over a century, three groups of hypotheses persisted in the literature: the  
39 “temnospondyl hypothesis” (Fig. 1C), which unites the extant amphibian clades as a clade  
40 Lissamphibia and nests this clade within the Paleozoic temnospondyls, most recently  
41 supported by the phylogenetic analyses of Pardo et al. (2017a: fig. S6; 2017b), and Mann et  
42 al. (2019a) and Daza et al. (2020: fig. S13); the “lepospondyl hypothesis” (Fig. 1D) which  
43 nests Lissamphibia within or close to the Paleozoic “microsaurs” (e.g. Vallin & Laurin, 2004;  
44 Pawley, 2006: appendix 16; Marjanovi & Laurin, 2013, 2019; Daza et al., 2020: fig. S12,  
45 S15); and the “polyphyly hypothesis” (Fig. 1E), according to which the batrachians are  
46 temnospondyls while the caecilians are “microsaurs”. Unlike the other two, the polyphyly  
47 hypothesis, last proposed by Anderson et al. (2008), appears not to be preferred by any  
48 colleagues anymore; however, it has been replaced by a similar hypothesis (Pardo et al.,  
49 2017a) according to which batrachians and caecilians are nested within two different clades of  
50 temnospondyls (Fig. 1F), although a minimal update to that matrix restored Lissamphibia  
51 (Daza et al., 2020: fig. S14). Of these four hypotheses, the “classic” polyphyly hypothesis  
52 (Fig. 1E) is the only one that is not compatible with the molecular consensus, which strongly  
53 supports reciprocal monophyly of Lissamphibia and Amniota (Fig. 1A). At least the 21<sup>st</sup>-  
54 century versions of all four are compatible with the current paleontological consensus (Fig.  
55 1B). Soft anatomy not preserved in fossils has not so far been able to advance the debate  
56 either, because the soft-tissue features shared by extant amphibians could all be either  
57 tetrapod symplesiomorphies lost in amniotes or lissamphibian autapomorphies. Additionally,  
58 the discovery of the fourth group of “modern amphibians”, the Middle Jurassic to Pleistocene  
59 albanerpetids with their unexpected combination of character states (Estes & Hoffstetter,  
60 1976; McGowan, 2002; Maddin et al., 2013; Matsumoto & Evans, 2018; Daza et al., 2020),  
61 has complicated this situation further (Marjanovi & Laurin, 2013, 2019; Daza et al., 2020).

62 Equally unsolved remains the evolution of the unique jumping locomotion,  
63 accompanied by diagnostic skeletal peculiarities (Sigurdsen et al., 2012), that has  
64 characterized crown-group frogs (usually called Anura) and their closest relatives at least  
65 since the Early Jurassic *Prosalirus* (Jenkins & Shubin, 1998; Roek, 2013; Herrel et al., 2016;  
66 and references therein; see also the Late Triassic ilium described by Stocker et al., 2019). The



68 **Fig. 1.** Modified from Marjanovi & Laurin (2019: fig. 2). Names of extant taxa in boldface,  
 69 names of junior synonyms on a given topology in parentheses. (A) Molecular consensus:  
 70 Lissamphibia monophyletic with respect to Amniota (e.g. Irisarri et al., 2017; Hime et al.,  
 71 2020). (B) Paleontological consensus: Lepospondyli closer to Amniota than Temnospondyli.  
 72 (In Pardo et al., 2017b, and some trees found in the update by Daza et al., 2020: fig. S13, at  
 73 least some lepospondyls were even found within Amniota, as sauropsids.) (C)  
 74 “Temnospondyl hypothesis”: lissamphibians as a clade of temnospondyls (e.g. Pardo et al.,  
 75 2017b; Mann et al., 2019a; Daza et al., 2020: fig. S13); compatible with A and B. (D)  
 76 “Lepospondyl hypothesis”: lissamphibians as a clade of lepospondyls very close to *Batropetes*  
 77 (e.g. Vallin & Laurin, 2004; Pawley, 2006: appendix 16; Marjanovi & Laurin, 2019; Daza et  
 78 al., 2020: fig. S12, S15); compatible with A and B. (E) “Polyphyly hypothesis”: frogs and  
 79 salamanders as temnospondyls, caecilians as lepospondyls (e.g. Anderson et al., 2008);  
 80 compatible with B but not A. (F) Hypothesis of Pardo et al. (2017a): extant amphibians as  
 81 two separate clades of temnospondyls; compatible with A and B.

82

83 Early Triassic *Triadobatrachus* (Rage & Roček, 1989; Roček & Rage, 2000; Ascarrunz et al.,  
 84 2016), the sister-group to all other salientians (probably including the fragmentary coeval  
 85 *Czatkobatrachus*: Evans & Borsuk-Białynicka, 2009), was not capable of frog-like jumping  
 86 (Ascarrunz et al., 2016; Lires et al., 2016; and references therein). The same inference is

87 suggested by sacral vertebrae referred to *Czatkobatrachus* (Evans & Borsuk-Białynicka,  
88 2009: 99). This indicates that jumping evolved within the early history of Salientia –  
89 specifically during the latter half of Carroll’s Gap, a period poor in fossils of lissamphibians  
90 and ecologically comparable animals (Marjanovi & Laurin, 2013; not noted there is the  
91 coeval scarcity of pan-squamates highlighted e.g. by Simões et al., 2018). Mainly due to this  
92 lack of potentially informative fossils, the question of how this novel mode of locomotion  
93 evolved has received disproportionately little attention.

94 Although *Triadobatrachus* did not locomote by jumping, and although its poorly  
95 known shoulder girdle may not have been modified into the shock absorber required by the  
96 extremely short trunks of anurans (Ascarrunz et al., 2016), its forelimbs were already able to  
97 withstand the stresses of landing from a jump, judging from their size and the laterally  
98 (instead of medially) deflected deltopectoral crest on the humerus (Sigurdson et al., 2012;  
99 Ascarrunz et al., 2016). This suggests an exaptation: the forelimbs were reinforced, and their  
100 posture modified (Jenkins & Shubin, 1998; Sigurdson et al., 2012), as an adaptation to  
101 something else that required a long reach and powerful abduction, and were then available to  
102 enable the evolution of sustained jumping.

103 We propose below that this preceding lifestyle was a terrestrial one that involved  
104 forelimb-based digging, but not outright burrowing – most likely a search for food in leaf  
105 litter and/or topsoil. Further, we report that several lines of evidence indicate the presence of  
106 such a lifestyle in the Early Permian “microsauro” *Batropetes palatinus*; some of them can also  
107 be applied to other “microsaurs” and suggest the same lifestyle for some of them.

108 Although a phylogenetic analysis is beyond the scope of this paper, we note that the  
109 “lepospondyl hypothesis” opens the possibility, discussed in section 4.5, that the ecological  
110 niches of *Batropetes* and the earliest salientians were homologous. However, should that turn  
111 out not to be the case, *Batropetes* would remain useful as an analog to the origin of frogs.

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115 **Fig. 2.** *Batropetes palatinus* (MB.Am.1232) in dorsal view of (A) the original fossil specimen  
116 with parts of the skeleton preserved as a natural mold, and (B) a composite cast of the  
117 specimen in dorsal view.

118





## 120 **2. Material and Methods**

### 121 *2.1 Computed microtomography*

122 The specimen MB.Am.1232 (Museum für Naturkunde, Berlin), referred to *Batropetes*  
123 *palatinus* by Glienke (2015) and shown in Figure 2, was scanned at the MB as a 2×3-part  
124 multiscan using computed X-ray microtomography (phoenix|xraynanotom s) at 130 kV and  
125 230 μA with an effective voxel size of 0.01785 mm and 1800 images/360° with a timing of  
126 750 ms. Cone beam reconstruction was performed using datos|x-reconstruction software (GE  
127 Sensing & Inspection Technologies GmbH phoenix|x-ray). The multiscan of two parts was  
128 visualized, merged and segmented in VG Studio Max 3.0. The posterior part of the specimen  
129 was scanned separately to segment the hindlimb.

130 Slight mechanical artefacts occurred on the scans, especially on the scan of the  
131 hindlimb. These are caused by the thin slices and represent a technical issue that cannot be  
132 completely avoided. An additional complication is the small size of the specimen, adding  
133 noise to the resolution of the CT scan.

134

### 135 *2.2 Statistical analyses of limb proportions*

136 We have performed two statistical analyses of limb proportions, based on a dataset expanded  
137 from that of Lires et al. (2016), to classify the locomotor style of all four species (Glienke,  
138 2015) of *Batropetes*, as well as a few other “microsaurs”, temnospondyls and  
139 *Triadobatrachus*, by independent means. Our new measurements are shown in Table 1, their  
140 sources are listed in Table 2; the entire dataset constitutes Table S1, including the previously  
141 unpublished raw measurements of Lires et al. (2016), provided by Andrés Lires.

142 Lires et al. (2016) measured the lengths of the humerus, radius/ulna, femur,  
143 fibula/tibia and the proximal tarsus. Due to the rarity of sufficiently complete skeletons of our  
144 added taxa, we had to exclude the proximal tarsus from the analysis and considered only the  
145 remaining four linear measurements of the long bones. This change only had a moderate  
146 effect on the results as the different locomotor modes still separated comparably well (Tables  
147 3, S1; Fig. S1).

148 Apart from *Triadobatrachus*, the dataset of Lires et al. (2016) contains extant  
149 batrachians and squamates, which are assigned to locomotor categories: foot-propelled  
150 swimmers (Sw), jumpers (J), hoppers/walkers not using lateral undulation (HW) and  
151 swimmers as well as walkers making use of lateral undulation (LU). We divided the latter  
152 category by the presence (LUD) or absence (LU) of digging, scratching or burrowing  
153 behavior based on the data published in Oliveira et al. (2017a, b). Aquatic, amphibious or

154 terrestrial animals within the LU (or the LUD) category cannot be distinguished by their limb  
155 proportions (Lires et al., 2016, and reference therein); LU and LUD can, however, be  
156 distinguished as described below.

157 To this dataset, we added extinct taxa without assigning them to one of the established  
158 locomotor modes: the albanerpetid near-lissamphibian (Daza et al., 2020) *Celtesdens ibericus*  
159 (two individuals); the “microsaurs” *Tuditonus punctulatus*, *Pantylus cordatus* and *Diabloroter*  
160 *bolti*, as well as individuals (left and right sides measured separately in two cases) belonging  
161 to all four species (Glienke, 2015) of *Batropetes*, including MB.Am.1232; and the  
162 amphibamiform (Schoch, 2018 “2019”) temnospondyls *Platyrrhinops lyelli*, *Micropholis stowi*  
163 (two individuals), and *Doleserpeton annectens* (composite of several individuals scaled to the  
164 same size). Despite its importance in recent studies on lissamphibian origins (Anderson et al.,  
165 2008; Marjanovi & Laurin, 2009, 2019; Pardo et al., 2017a; Mann et al., 2019a, and  
166 references therein), the amphibamiform *Gerobatrachus hottoni* had to be excluded from the  
167 linear discriminant analysis (LDA) because the preserved limbs of the only known specimen  
168 are not complete enough.

169 Measurements of MB.Am.1232 (*Batropetes palatinus*) were taken from our CT scan;  
170 humerus, radius-ulna, femur and fibula-tibia were compared to the left and right side of the  
171 specimen as measured in Glienke (2015), and the measurement of the tarsus was taken from  
172 the negative imprint of the specimen itself (negative slab).

173 In a first step, a (non-phylogenetic) LDA was performed to recover the separation  
174 among locomotor categories and to predict in which of those categories the included fossil  
175 specimens should belong, based on linear measurements of the preserved limb bones divided  
176 by their geometric mean.

177 In a second step, a multivariate analysis of variance (a-posteriori MANOVA)  
178 including the fossil specimens, split by locomotion mode (Sw, J, HW, LU, LUD), was  
179 conducted, using the four measurements as the dependent variables and the locomotor modes  
180 as the independent one. The MANOVA was used to test whether morphometric variables  
181 differed between the locomotor modes in our dataset. The classification accuracy was  
182 estimated using 10-fold cross-validation (Mostellar & Tukey, 1968; Stone, 1974). After 1000  
183 trials it gave 66.7% accuracy for the extant taxa, whose lifestyles are known.

184 Both of these analyses do not take phylogeny into account. We have not performed a  
185 phylogenetic Flexible Discriminant Analysis (pFDA; Motani & Schmitz, 2011) because time-  
186 calibrated phylogenies are not available for squamates and batrachians at the required  
187 phylogenetic resolution; we would need to interpolate the divergence dates for a large number



188 of nodes. Additionally, divergence times of extinct taxa can only be dated by paleontological  
189 means. To compose a “supertimetre” including divergences dated by both paleontological  
190 and molecular means (for extant taxa without a fossil record) would be well beyond the scope  
191 of this paper.

192 Additionally, given that our sample of extant taxa is identical to that of Lires et al.  
193 (2016), we accept their finding that the correlation between limb proportions and locomotor  
194 modes shows a much stronger ( $p < 0.001$ ) ecological than phylogenetic signal. Our results  
195 from both the LDA and the MANOVA are congruent with this: the extant HW taxa and the  
196 two extinct taxa our analyses classify as HW form at least three separate clades as discussed  
197 below; although Lires et al. (2016) did not distinguish LU (plesiomorphic for tetrapods) from  
198 LUD, both of these categories are broadly distributed across squamates and caudates and are  
199 inferred for most of the extinct taxa, which are widely distributed on the tree (under all  
200 phylogenetic hypotheses).

201

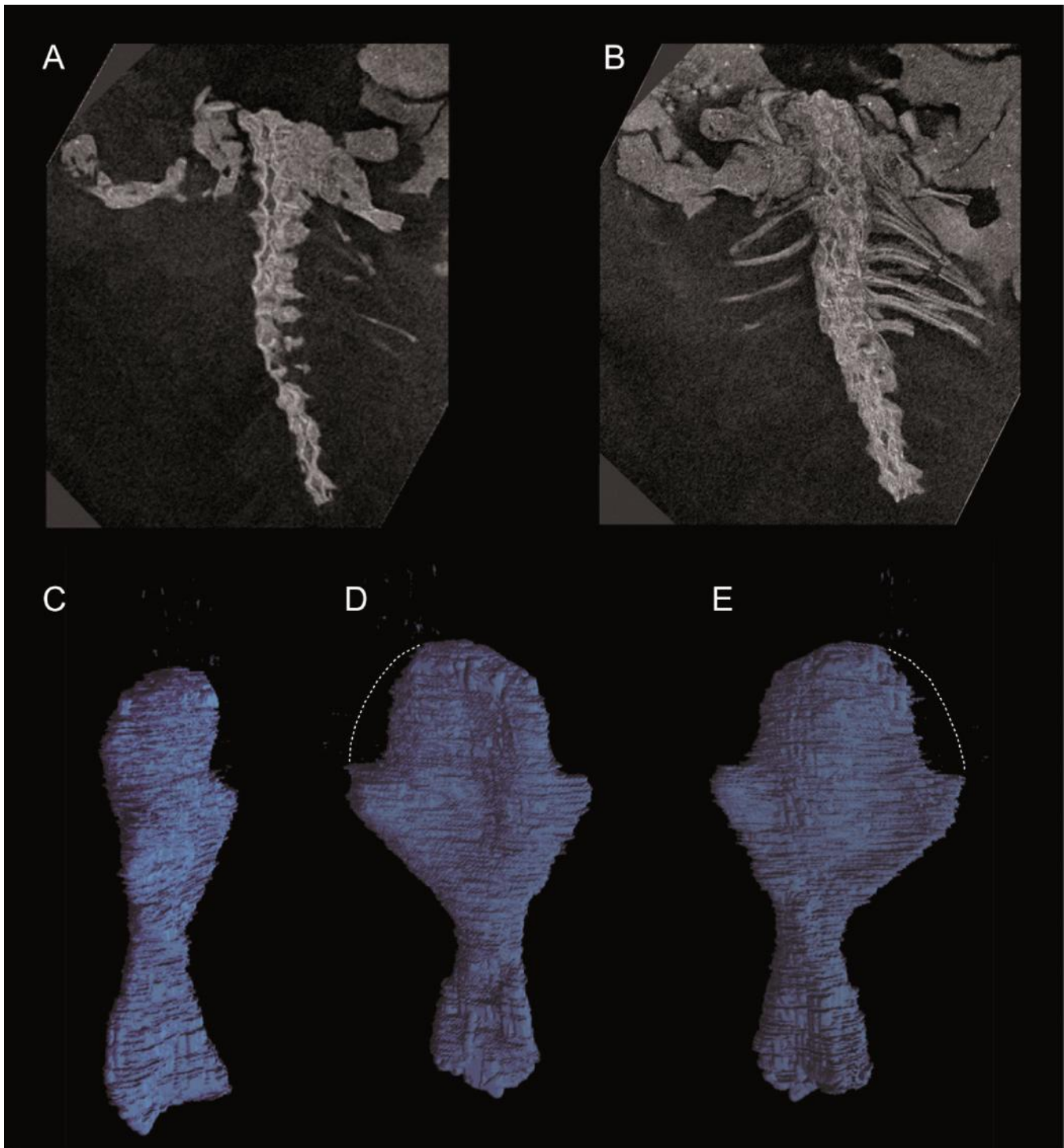
## 202 **3. Results**

### 203 *3.1 Bone microanatomy, proportions and lifestyle of Batropetes*

204 Micro-CT data from MB.Am.1232, a postcranial skeleton of an adult *Batropetes palatinus*,  
205 reveal a thin, solid cortex throughout the proximal and distal limb bones, the girdles and the  
206 vertebrae (Fig. 3). In the humerus, the cortex makes up less than half of the diameter at mid-  
207 diaphysis; elsewhere in the humerus, and everywhere in the femur, it is much less. All ribs are  
208 split throughout their length, which is visible both on the outside (Fig. 2) and in the scan  
209 images (Fig. 3); this indicates collapse of an extensive marrow cavity under diagenetic  
210 pressure. These observations confirm (e.g. de Buffrénil & Rage, 1993; Laurin et al., 2004,  
211 2011; Cubo et al., 2005; Germain & Laurin, 2005; Krilloff et al., 2008; Canoville & Laurin,  
212 2009, 2010; de Buffrénil et al., 2010; Cooper et al., 2011 “2012”; Dumont et al., 2013;  
213 Quémeneur et al., 2013) previous interpretations of *Batropetes* as terrestrial (Gliénke, 2013,  
214 2015; contra Carroll, 1991; Mann & Maddin, 2019), even though the resolution of the scan  
215 does not permit us to distinguish spongiosa from the infill of the marrow cavity.

216 The  $\mu$ CT data allow us to reconstruct the humerus of MB.Am.1232 in three  
217 dimensions (Fig. 3C–E). We find a dorsal process (accentuated by breakage) as reported in  
218 various lissamphibians, “microsaurs” and amphibamiforms, and a triangular deltopectoral  
219 crest that is not deflected medially as it is in salamanders (e.g. *Ambystoma*: Sigurdson et al.,  
220 2012: fig. 3A) or to a lesser degree in *Eocaecilia* (Jenkins et al., 2007: fig. 42; Sigurdson et



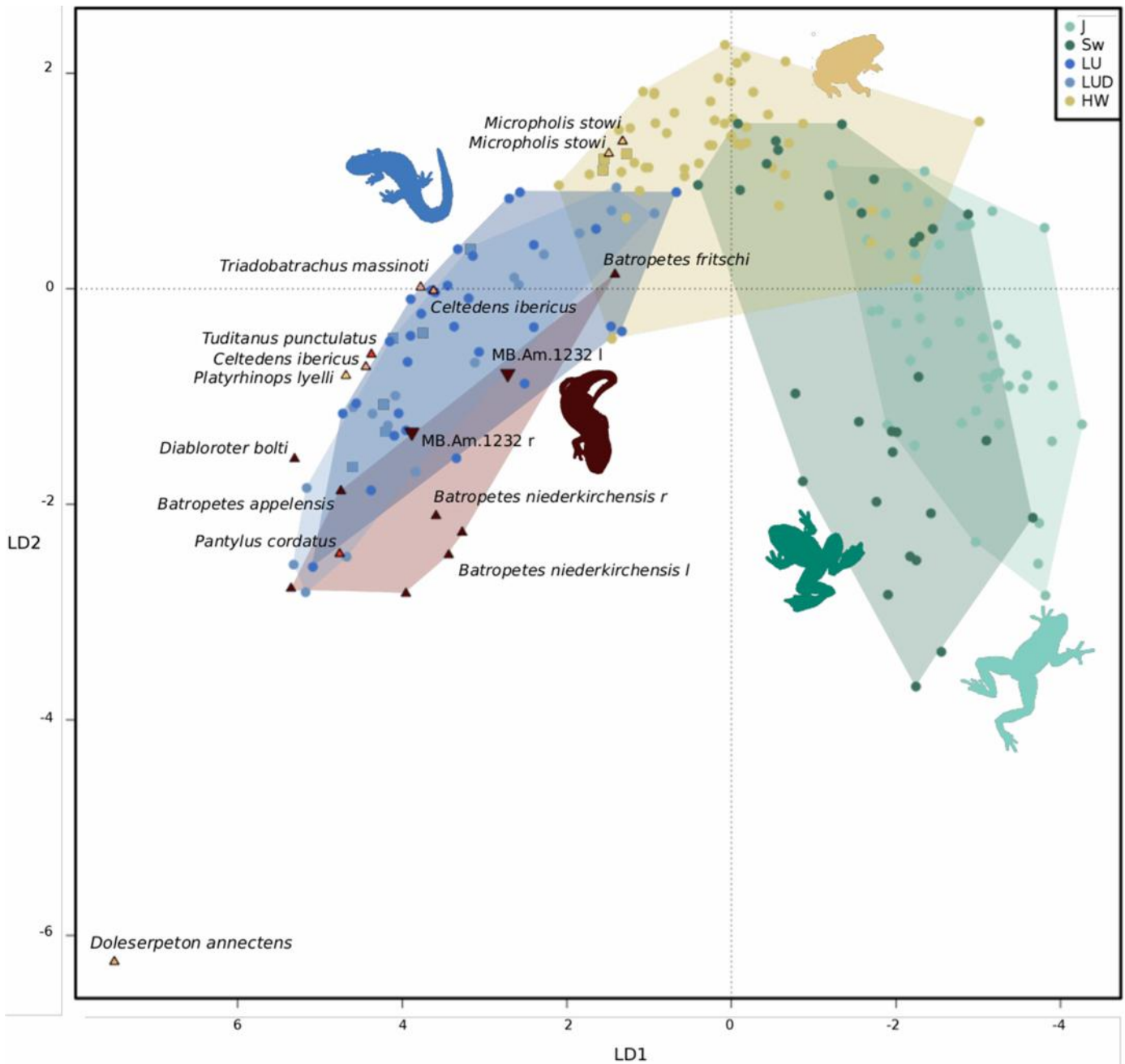


222 **Fig. 3.** (A, B) CT images showing thin cortex in the craniodorsal part of the vertebral column  
223 and the humerus of *Batropetes palatinus* (MB.Am.1232). (C–E) Right humerus in anterior  
224 (C), dorsal (D) and ventral views (E); the stippled line indicates a broken portion of the dorsal  
225 process (not shown in (C)) opposite the deltopectoral process.

226

227 al., 2012), but slightly laterally, producing a shallow concavity lateral of it (Fig. 3D), similar  
228 to the less extreme cases among salientians (Sigurdsen et al., 2012).

229



231 **Fig. 4.** First two canonical axes of the discriminant function analysis (LDA) of corrected  
 232 morphometric variables and the five defined locomotor categories. The different locomotor  
 233 categories are plotted in different colors. Brachystelechids are shown as dark red triangles  
 234 (always *Batropetes palatinus* if unlabeled); the two larger ones that point downward mark the  
 235 left and the right side of MB.Am.1232. Bright red triangles: other “microsaurs”; yellowish  
 236 triangles: amphibamiform temnospondyls; pale red triangles: lissamphibians. Squares indicate  
 237 *Ambystoma tigrinum* (in light blue for LUD) and *Bufo bufo* (in yellow-green for HW); for a  
 238 version with every extant taxon labeled, see Fig. S2. All extinct taxa plot within or closest to  
 239 the LU/LUD cluster. Extant taxa from Lires et al. (2016), distinction of LU and LUD from  
 240 Oliveira et al. (2017a, b). **Abbreviations:** HW = hopping/walking; J = jumping; LU =

241 laterally undulating, not digging; LUD = laterally undulating, digging to some degree; l = left  
242 side; r = right side; Sw = swimming.

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243

### 244 3.2 Comparative limb proportions and lifestyles

245 The morphometric variability of the limbs of the sampled taxa, both extant and extinct,  
246 reflects different locomotor functions, which we categorize for the extant species following  
247 Lires et al. (2016), Oliveira et al. (2017a, b) and references therein. In our LDA (Fig. 4–6, S1–  
248 S3; Table 3), the fossil individuals mostly plot with caudates and squamates (which retain  
249 much of the ancestral tetrapod body shape) in a wider cluster including the lateral undulator  
250 (LU) cluster of extant species and the separately categorized cluster of extant individuals  
251 known to routinely engage in digging behavior (LUD).

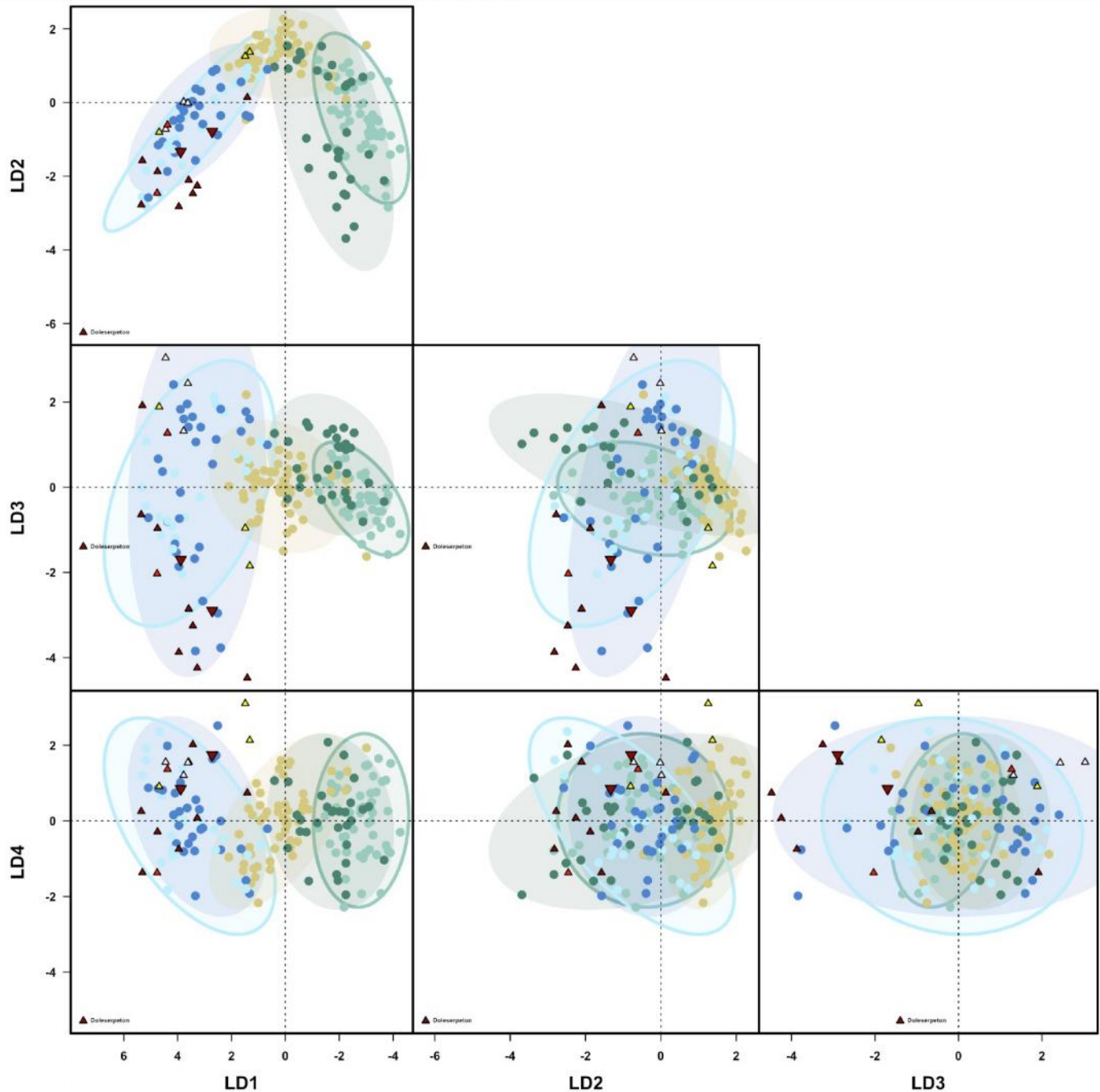
252 In the LDA, the LU and LUD clusters do not separate well in most comparisons (Fig.  
253 4–6, S1–S3). Indeed, the right side of MB.Am.1232 is classified as LU, the left side as LUD  
254 (Table 3). Only the comparison of canonical variant 1 to canonical variant 4 (Fig. 5, S1) shifts  
255 the digging individuals further away from all other locomotor categories, but they still retain a  
256 large overlap. This is in part due to the wide definition of “digging” in the analysis, and in  
257 part to the facts that LU is the plesiomorphic state and that LUD is directly derived from it  
258 (while e.g. Sw is evolutionarily derived from J, not directly from LU). Nonetheless,  
259 MANOVA finds all five locomotor categories to be clearly distinct ( $F = 50.037$ ,  $df = 16$  and  
260  $p\text{-value} = 9.28 \times 10^{-109}$ , well below the detection threshold of  $2.2 \times 10^{-16}$ ).

261 The LDA prediction of the added extinct taxa using Bayesian posterior probability  
262 (Table 3) recovers most of them as digging and plots them outside the overlap area of LU and  
263 LUD (Fig. 5; compare Fig. 4), but classifies one of the *Batropetes* specimens (the only one  
264 included of *B. fritschi*) as a toad-like hopper/walker (HW). The other *Batropetes* specimens  
265 are classified as LUD, except for the right side of MB.Am.1232 as mentioned.

266 A direct comparison of the ranges of the four used limb measurements reveals that  
267 *Batropetes* generally falls within the range recovered as LU/LUD. The relative lengths of  
268 radius and ulna, however, also overlap with the HW category (Fig. 6), revealing a more  
269 elongated distal forelimb.

270 *Triadobatrachus* also still falls within the LU/LUD cluster, as it did in Lires et al.  
271 (2016). Specifically, *Triadobatrachus* is classified as LU (Table 3), agreeing with the idea  
272 that limb morphology is generally plesiomorphic for most taxa falling within LU and LUD.

273 *Doleserpeton* is the only taxon that does not cluster with any of the defined groups  
274 representing locomotor categories in Fig. 4 and 5. It plots as a distant outlier in the LDA (Fig.



276 **Fig. 5.** Comparisons of all linear discriminants, with 95% confidence intervals for all tested  
277 locomotor groups. Red triangles indicate fossil specimens; the two that point downwards are  
278 the left and the right side of MB.Am.1232. The comparison (top left) of linear discriminant  
279 (LD) 1 and LD2 is identical to Fig. 4 and S2, the comparison of LD1 and LD4 (bottom left) is  
280 identical to S1 and S3. Abbreviations of locomotor modes as in Fig. 4.

281

282 4–6), because once the measurements are divided by the geometric mean, the femur length  
283 appears to be smaller than in all other specimens used in this analysis, while the radius-ulna  
284 length appears to be greater. Because sufficiently articulated or associated skeletons are not



285 known (Bolt, 1969; Sigurdson et al., 2010; Gee et al., 2020), the measurements were taken  
286 from different specimens, corrected for size, as well as from the skeletal reconstruction by  
287 Sigurdson et al. (2010), and both linear measurements (from the figured bones as well as from  
288 the reconstruction) show the same relation once they are divided by the geometric mean.  
289 However, we cannot exclude a measurement error in the literature at this point. Nor can we  
290 exclude the possibility that some of the measured material comes from other amphibamiform  
291 taxa, of which two are known from skulls found at the same site (Fröbisch & Reisz, 2008;  
292 Anderson & Bolt, 2013; Atkins et al., 2020), as discussed in detail by Gee et al. (2020).

293         Of the other two amphibamiform temnospondyls that we were able to sample,  
294 *Platyrrhinops* is classified as a lateral undulator as expected, with absence of digging behavior  
295 (LU) weakly favored (BPP = 59%) over its presence (LUD; BPP = 41%), while *Micropholis*,  
296 with its particularly short trunk and long limbs (Schoch & Rubidge, 2005), emerges  
297 unambiguously as a hopper/walker (90% and 95% for the two specimens) – more froglike in  
298 this respect than *Triadobatrachus* (BPP = 71% for LU, < 0.1% for HW). The LDA reveals  
299 that *Micropholis* is particularly close to *Bufo bufo* in linear discriminants 1 and 2, though  
300 widely separated by linear discriminant 4 (Fig. 4, 5, S1).

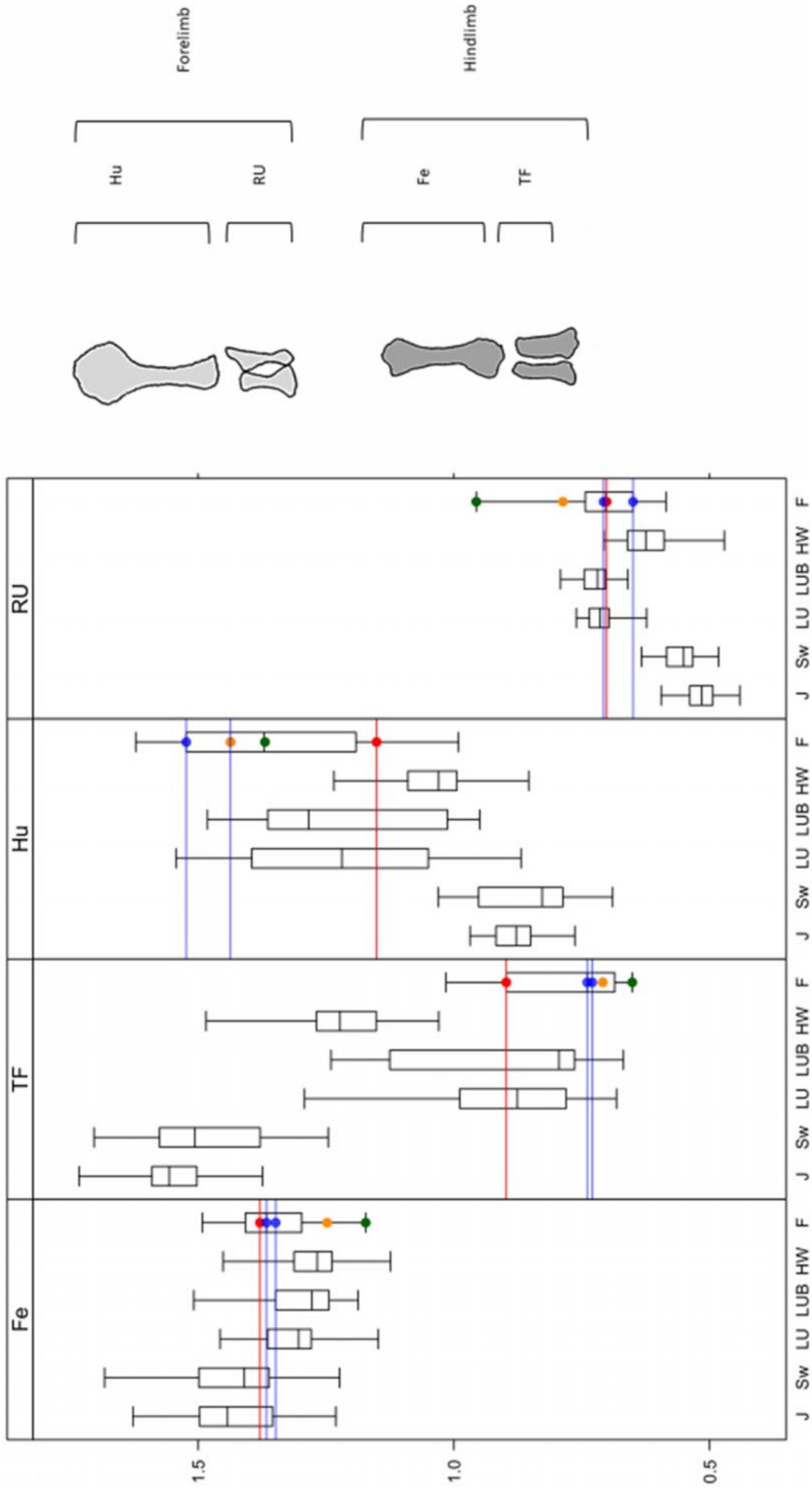
301         The three “microsaurs” other than *Batropetes* are classified as lateral undulators, in  
302 agreement with their interpretations as terrestrial in the literature. For *Tuditonus*, with its  
303 particularly lizardlike proportions (very similar to those of contemporary early amniotes of  
304 the same size), LU is favored (64%) over LUD (36%), while the opposite is the case for the  
305 early brachystelechid *Diabloroter* (34% vs. 66%) and for the particularly stocky *Pantylus*  
306 (20% vs. 80%).

307         The two specimens of the albanerpetid near-lissamphibian *Celtdens ibericus* are  
308 classified as LU (78% and 81% respectively) over LUD (22% and 19%). While this is  
309 evidence against limb-based digging (see also Daza et al., 2020), it may not contradict head-  
310 based digging in leaf litter (Wiechmann et al., 2000; Gardner, 2001; and references therein).

311         It is noteworthy that *Triadobatrachus*, which has a considerably longer tarsus than all  
312 non-salientians in our sample, remains in LU even though we ignore its tarsus, and does not  
313 join HW. As in Lires et al. (2016), no other salientian is found in LU or LUD.

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316

317 **Fig. 6.** The different locomotor categories (HW = hopping/walking; J = jumping; LU =  
318 laterally undulating, not digging; LUD = laterally undulating, digging to some degree; Sw =  
319 swimming) and selected fossil specimens (“F”; not assigned to a locomotor category) are  
320 plotted against the linear measurements of the long bones (in mm; left to right: femur, tibia +  
321 fibula, humerus, radius + ulna) of all included taxa. Box plots show the variation in length.  
322 Red dots and lines: *Triadobatrachus*; blue: left and right sides of MB.Am.1232 (*Batropetes*  
323 *palatinus*); orange: *Pantylus*; green: *Doleserpeton*. The drawings at the right show the  
324 holotype of *Batropetes palatinus* (after Glienke, 2015: fig. 1A).

325

## 326 4. Discussion

### 327 4.1 The locomotion and foraging mode of *Batropetes* and other brachystelechids

328 Its large, robust limbs and girdles (e.g. Fig. 3) and absence of evidence for lateral-line grooves  
329 suggest that all species of *Batropetes* were terrestrial walkers (Glienke, 2013, 2015), a  
330 hypothesis further bolstered by the bone microanatomy and the statistical analyses of limb  
331 proportions presented here.

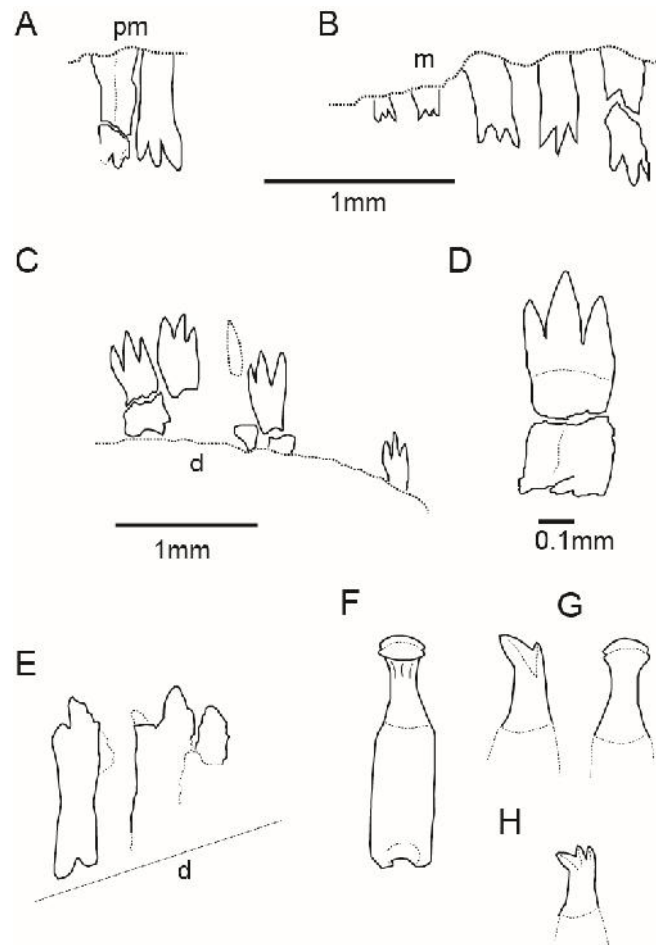
332 The same is suggested by the general proportions of all species of *Batropetes* (Fig. 3).  
333 As noted in previous works (Carroll, 1991; Glienke, 2013, 2015), *Batropetes* has an unusually  
334 short vertebral column for a “microsauro”: depending on the species (Glienke, 2015), there are  
335 only 17 to 19 vertebrae in the presacral region. Carroll (1998) stated that this number is the  
336 smallest known for presacral vertebrae in any “microsauro”, a statement that is – apart from the  
337 17 presacral vertebrae of its fellow brachystelechid *Diabloroter* (Mann & Maddin, 2019) –  
338 still valid by a considerable margin (the next smallest number is 24, for *Pantylus*: Carroll,  
339 1998) but has to be considered carefully. For many of the known “microsauros”, particularly  
340 the other described brachystelechids, only fragmentary postcrania (*Carrollia*) or none  
341 (*Quasicaecilia*) are known, though there is evidence that *Carrollia* had *Batropetes*-like  
342 proportions (Mann et al., 2019b). (*Brachystelechus* is a junior synonym of *Batropetes* [see  
343 Carroll, 1991]. Further brachystelechids have not been described.) Similar numbers of  
344 presacral vertebrae are found in the very stoutest amphibamiform temnospondyls  
345 (*Gerobatrachus* has 17, various “branchiosaurids” have 19 or more, *Micropholis* has 20 to 21  
346 [Broili & Schröder, 1937; Boy, 1985; Schoch & Rubidge, 2005: fig. 5]) and in early crown-  
347 group salamanders.

348 Within this general locomotor mode, the unusually large forelimbs and the very large,  
349 thoroughly ossified shoulder girdle of *Batropetes* indicate large muscle attachment sites, as

350 Glienke (2013, 2015) also inferred from the expanded ends of the limb bones; the robust first  
351 metacarpals and first manual digits further suggest some kind of digging behavior. The  
352 clawlike terminal phalanges may specifically fit scratch-digging, as does the fact that the  
353 hands are not broadened into shovels, but instead quite narrow. (Of the four metacarpals, the  
354 fourth is the shortest and narrowest, and bears only a single phalanx, which has, however, the  
355 same clawlike shape and almost the same size as the other terminal phalanges.) However, the  
356 large and robust humerus is not further reinforced by a thickened cortex as often occurs in  
357 limb-based diggers.

358 Glienke (2015: 23) interpreted the distinctive pits on the frontals of *Batropetes*, as well  
359 as similar but less distinct sculpture on the frontals of *Carrolla* and *Quasicaecilia*, as  
360 suggesting that the overlying “skin was considerably thickened, similar to burrowing animals  
361 such as [certain] microhylid frogs or moles”. Pits very similar to those of *Batropetes* have  
362 since been found on the frontals and postfrontals of *Diabloroter* (Mann & Maddin, 2019). In  
363 all described brachystelechids (*Batropetes*; *Carrolla*: Maddin et al., 2011; *Quasicaecilia*:  
364 Pardo et al., 2015; *Diabloroter*: Mann & Maddin, 2019), the head was short and robust, and –  
365 unlike in most other “microsaurs” – the occipital joint was a hinge that only allowed  
366 dorsoventral movement; thus, thickened skin on the roof of the head could have been used to  
367 compact the roof of a burrow or more generally to move material out of the way upwards.  
368 Yet, the skull especially of *Batropetes* was not (Glienke, 2013) as chisel-like as reconstructed  
369 earlier (Carroll, 1991), the mouth being barely subterminal. This is quite distinct from the  
370 shovel- or spade-like, more pointed and more elongated heads of burrowing “microsaurs” like  
371 gymnarthrids or ostodolepidids (e.g. Anderson et al., 2009). The orbits are oriented  
372 dorsolaterally and quite large in all brachystelechids (further enlarged into teardrop-shaped  
373 orbitotemporal fenestrae in *Batropetes*: Glienke, 2013, 2015), arguing against a subterranean  
374 existence and against head-based digging in resistant soil that could damage the eyes (Maddin  
375 et al., 2011). Although the strongly interdigitated transverse sutures of the skull roof of, at  
376 least, the largest and skeletally most mature known specimen of *Batropetes* (*B.*  
377 *niederkirchensis*: Glienke, 2013: fig. 2, 3) suggest that the skull roof was often under  
378 mechanical stress, especially compression (reviewed in Anderson et al., 2009; Bright, 2012;  
379 Porro et al., 2015), this condition is not found in *Carrolla* (Maddin et al., 2011) or apparently  
380 *Quasicaecilia* (Pardo et al., 2015), and seemingly only weakly in *Diabloroter* (Mann &  
381 Maddin, 2019).





382

383 **Fig. 7.** Illustration of teeth of several “microsaurs” and salamanders. (A) *Batropetes*  
384 *palatinus*, MNHM PW 2001/309, left premaxilla. (B) *B. palatinus*, MNHM PW 2001/307,  
385 right maxilla. (C) *B. palatinus*, MNHM PW 2001/307, right dentary. (D) *B. palatinus*,  
386 MNHM PW 2001/307, isolated dentary tooth. (E) *Carrolla craddocki*, TMM 40031-54, left  
387 dentary (left side), not to scale. (F, G, H) models: general organisation of adult caudate tooth  
388 in lingual and mesial or distal views, similar to *Ambystoma* tooth morphology; (H) shows a  
389 tricuspid tooth as found in *A. mabeei*. (A–D) after Glienke (2015), (E) based on Mann et al.  
390 (2019b), (F–H) summarized from Beneski & Larsen (1989).

391

392 Finally, the teeth of *Batropetes* and *Carrolla* (Glienke, 2015; Mann et al., 2019b;  
393 unknown in *Quasicaecilia*) each have three cusps arranged in a mesiodistal line (Fig. 7); as  
394 reviewed by Glienke (2015), this is suggestive of very small fast-moving prey. We postulate  
395 that *Batropetes* supplemented the lateral movements of the forelimbs by dorsal movements of  
396 the head to remove leaf litter or soil, and used ventral movements of the head to snap up soil  
397 insects.

398

399

400 *4.2 An extant model?*

401 The extant species of *Ambystoma*, or at least their terrestrial forms, are called mole  
402 salamanders because they are often found under logs, in leaf litter, or in crevices in the  
403 ground. Many occupy burrows dug by other animals. Although they often enlarge existing  
404 hollows, most species neither use a systematic method to do so, nor do most of them initiate  
405 burrows; of the five species that Semlitsch (1983) observed in an experimental setting, three  
406 (*A. opacum*, *A. annulatum*, *A. maculatum*) did not dig into a moist sandy soil even when their  
407 life was threatened by desiccation, and one (*A. talpoideum*) only did in half of the cases. “Its  
408 snout appeared to ‘plow’ a hole into the soil with little use of its forelimbs to dig. *Ambystoma*  
409 *talpoideum* were never found more than 10 cm inside the entrance of a burrow.” (Semlitsch,  
410 1983: 617) *A. tigrinum*, however, routinely dug burrows in the experiment, “sometimes  
411 initially making a slight depression with its snout and then alternately using both forelimbs to  
412 dig”, and ending up “10–70 cm from the burrow entrance” (Semlitsch, 1983: 617).

413 Semlitsch (1983: 618) pointed out that *A. tigrinum* “lacks specialized digging  
414 anatomy” after noting that “*Ambystoma talpoideum* and *A. tigrinum* had significantly wider  
415 heads and thicker forelimbs than *A. annulatum*, *A. maculatum*, and *A. opacum*.” *A. tigrinum*  
416 does have large limbs for a salamander; but the humerus, radius and ulna are much more  
417 slender than in *Batropetes* (notably excepting the only known individual of *B. appelensis*,  
418 which is markedly immature), the phalanges are somewhat more elongate, and the ventral  
419 curvature of the tapered terminal phalanges, weakly expressed in *Batropetes*, is barely  
420 noticeable in *A. tigrinum* (DigiMorph Staff, 2008a). The shoulder girdle of *A. tigrinum*, on the  
421 other hand, is unremarkable for a salamander, consisting of small, slender scapulae and  
422 separate triangular coracoids; not only is the interclavicle absent as in all lissamphibians, but  
423 the left and right shoulders are set far apart from each other (DigiMorph Staff, 2008a). This  
424 contrasts sharply with the large and wide scapulocoracoids of *Batropetes* that are comparable  
425 in size to the humeri (Fig. 2, 3; Glienke 2013, 2015). Any motion between the left and the  
426 right scapulocoracoid of *Batropetes* appears to have been blocked by the large interclavicle  
427 which overlapped them (the plesiomorphic condition); this would largely prevent shoulder  
428 movements from increasing the reach of the forelimbs, but would have made the shoulder  
429 girdle a much more stable anchor for musculature. Although *A. tigrinum* has only 16 presacral  
430 vertebrae, the individual vertebrae are more elongate than in *Batropetes*, slightly  
431 overcompensating for the latter’s greater numbers of presacrals and giving it proportions  
432 between those of *B. palatinus* (17 presacrals) and *B. niederkirchensis* (19). The skull of *A.*  
433 *tigrinum* is not more robust than in other salamanders, retaining many loose sutures and a flat

434 shape with large, rostr dorsally facing nares and very large, lateroventrally open  
435 orbitotemporal fenestrae (DigiMorph Staff, 2008b).

436 *Ambystoma maculatum*, *A. mexicanum* (the neotenic axolotl) and *A. tigrinum* are  
437 included in our LDA. In Figure 4, which compares the first two linear discriminants, *A.*  
438 *tigrinum* (as well as the other *Ambystoma* species included) fills the space between the extinct  
439 taxa classified as LUD by the MANOVA (brachystelechids and *Pantylus*: Table 3) and those  
440 classified as LU; in Figure S1, which compares the first and the fourth linear discriminant, it  
441 overlaps entirely with the former cluster.

442 The postmetamorphic teeth of *Ambystoma* are small, numerous, pedicellate and  
443 linguolabially bicuspid, as usual for salamanders or indeed lissamphibians generally and not  
444 particularly like the condition seen in *Batropetes* or *Carrolla*. Indeed, *Ambystoma* spp. are  
445 rather generalist predators not limited to tiny prey (AmphibiaWeb, 2021). However,  
446 *Ambystoma* dentitions often show adaptations that prevent the teeth from penetrating prey so  
447 deeply that the prey would get stuck. These may include mesiodistally expanded, blade-  
448 shaped cusps, inflated cusps with corrugated surfaces, dense arrangements of teeth in up to  
449 five rows on one bone, or the third cusp on the dentary teeth of *A. mabeei* (Beneski & Larsen,  
450 1989; Fig. 7H). The small-sized *A. mabeei* is known to eat earthworms (AmphibiaWeb,  
451 2021). Possibly, then, the mesiodistally tricuspid teeth of *Batropetes* and *Carrolla* and the  
452 linguolabially tricuspid dentary teeth of *A. mabeei* are adaptations to relatively large rather  
453 than relatively small prey. However, these possibilities need not be mutually exclusive.  
454 Indeed, at the same time as drawing attention to the cusps of *Batropetes*, Glienke (2015)  
455 pointed out that only the cusps bear enamel, while the stalk of each tooth crown consists of  
456 dentine only; this may have rendered the teeth somewhat flexible and avoided damage in  
457 attacks on much larger, struggling prey, not unlike the weakly mineralized or unmineralized  
458 hinge zone of the pedicellate teeth widely found in lissamphibians.

459 Linguolabially tricuspid teeth (with blade-shaped cusps in all cases) have also been  
460 reported in five extant anuran species (the alytid *Alytes obstetricans*, the rhacophorid  
461 *Polypedates maculatus*, the hyperoliid *Heterixalus madagascariensis* and the hylids  
462 *Agalychnis callidryas* and *Phyllomedusa bicolor*: Greven & Ritz, 2009). Unfortunately, the  
463 function of such teeth, in anurans as well as in *Ambystoma mabeei*, remains very poorly  
464 understood; diets of anurans are generally understudied and insufficiently documented.  
465 However, *Al. obstetricans* – coincidentally a forelimb-based burrower (Nomura et al., 2009) –  
466 preys on large arthropods, earthworms and slugs, as well as ants (Glandt, 2018: 161); and *Po.*  
467 *maculatus* is known to have an unusually wide prey size range that includes insect larvae as

468 well as large arthropods and small vertebrates (Das & Coe, 1994). Tricuspid teeth therefore  
469 seem to be compatible with both small and very large prey relative to the predator's own size.

470 The three similarly tall, mesiodistally arranged cusps of the teeth of *Batropetes* have  
471 invited comparison (Mann & Maddin, 2019) to those of the extant marine iguanas  
472 (*Amblyrhynchus*), which scrape algae off rocks in the sea, and to the mesial teeth of the Early  
473 Triassic amphibamiform temnospondyl *Tungussogyrinus*, all known individuals of which  
474 seem to have been aquatic (larval or possibly neotenic). A lifestyle as aquatic or amphibious  
475 herbivores, however, is contradicted not only by the lack of unambiguous adaptations for  
476 swimming or diving – notably osteosclerosis – in *Batropetes*, but also by the shapes of the  
477 teeth themselves: the apical part of the crown, measured across all three cusps, is much wider  
478 mesiodistally in *Amblyrhynchus* than the basal stalk part, and the apical parts of successive  
479 teeth more or less touch or overlap, forming a largely continuous cutting surface (e.g. Miralles  
480 et al., 2017: fig. 9D, 10A), while there is scarcely any, and on average no, such apical  
481 widening in *Batropetes*, where the noticeable gaps between the teeth extend for the entire  
482 height of the teeth (Glienke, 2013: fig. 3A, B; 2015: fig. 10K–O; contra Carroll, 1991). We  
483 prefer to compare the teeth of *Amblyrhynchus* to the quite similar teeth of its terrestrial sister-  
484 group, the herbivorous Galápagos land iguanas (*Conolophus* spp.), which are identical except  
485 for more prominent central cusps and, in the more distal teeth, an additional mesial fourth  
486 cusp (Melstrom, 2017: fig. 1D). This shape seems to be a special case of the leaf-shaped,  
487 coarsely denticulated tooth crowns of other herbivorous and omnivorous squamates (e.g.  
488 Melstrom, 2017: fig. 10A, B, 11D) and indeed most herbivores among toothed non-  
489 mammalian amniotes – not to mention certain Permian aquatic seymouriamorphs (Bulanov,  
490 2003) among non-amniotes. The combination of three cusps with a lack of apical widening of  
491 the crown in *Batropetes* and *Carrollia* is instead shared with many insectivorous squamates  
492 (e.g. Melstrom, 2017: fig. 1B, 3, 9B, D). Apart from the size of the cusps, this shape is also  
493 found in the albanerpetid near-lissamphibians. The teeth of *Batropetes palatinus* and the  
494 albanerpetids *Albanerpeton* and *Anoualerpeton*, and the mesial teeth of *Tungussogyrinus*, are  
495 compared in Werneburg (2009: fig. 10).

496

#### 497 *4.3 Digging in brachystelechids in phylogenetic context*

498 Recently, four phylogenetic analyses based on two very different large datasets (Pardo et al.,  
499 2017b: ext. data fig. 7; Marjanovi & Laurin, 2019; Mann & Maddin, 2019; Mann et al.,  
500 2019a) found Brachystelechidae and Lysorophia as sister-groups. In some ways, this is an odd  
501 pair. The lysorophians, in all four analyses represented by *Brachydectes* (Pardo & Anderson,



502 2016) and in the fourth also by *Infernovenator* (Mann et al., 2019a), are very elongate animals  
503 (with up to 97 presacral vertebrae) whose limbs are correspondingly small (though the digits  
504 are not reduced in number). Their skulls show some adaptations to head-first digging (Pardo  
505 & Anderson, 2016). Daza et al. (2020: fig. S15) updated the scores of Albanerpetidae in  
506 Marjanovi & Laurin (2019), applied implied weighting, and found Brachystelechidae and  
507 Lysorophia as successively closer relatives of Albanerpetidae + Lissamphibia.

508 The further relationships of this grouping remain unclear. The two very different  
509 datasets of Vallin & Laurin (2004) and Marjanovi & Laurin (2019: fig. 14) found  
510 *Rhynchonkos* to be closely related, which seems to have been a head-first burrower (only the  
511 skull is known). However, this position of *Rhynchonkos* appears to depend on the  
512 lissamphibians: when some or all lissamphibians are constrained to be temnospondyls,  
513 *Rhynchonkos* groups next to a clade formed by the head-first burrowing Gymnarthridae and  
514 Ostodolepididae in Marjanovi & Laurin (2019: fig. 15, 17). Such a clade was also found by  
515 Daza et al. (2020: fig. S15) despite the lack of a constraint. Postcranial material is known  
516 from *Aletrimyti*, a taxon found as a close relative of *Rhynchonkos* by Pardo et al. (2017b),  
517 Mann & Maddin (2019) and Mann et al. (2019a), and indeed included in *Rhynchonkos* until  
518 the taxonomic revision by Szostakiwskyj et al. (2015). (Marjanovi & Laurin [2019] preferred  
519 not to include it in their phylogenetic analysis to avoid straining the character sample.)  
520 *Aletrimyti* is moderately elongate and has limbs similar to those of *Brachydectes*.  
521 Rhynchonkidae, Gymnarthridae and Ostodolepididae also formed a clade in Pardo et al.  
522 (2017b), where, however, very few other “microsaurs” were included in the sample, as well as  
523 in the unconstrained exploratory Bayesian analysis of Marjanovi & Laurin (2019: fig. 20).  
524 Adding “microsaurs” to the matrix of Pardo et al. (2017b), Mann & Maddin (2019) found a  
525 clade of gymnarthrids and rhynchonkids but not necessarily ostodolepidids; Mann et al.  
526 (2019a) found a clade of gymnarthrids, rhynchonkids and brachystelechids + lysorophians as  
527 the sister-group of Ostodolepididae. Gymnarthridae and Ostodolepididae did not approach  
528 Brachystelechidae + *Brachydectes* in any analyses of Marjanovi & Laurin (2019).

529 The hapsidopareiid “microsaurs” may be similarly close to Brachystelechidae +  
530 Lysorophia (Marjanovi & Laurin, 2019: fig. 14; Gee et al., 2019; Daza et al., 2020: fig. S15).  
531 One of them, *Llistrofus*, was recently redescribed as having cranial adaptations for digging,  
532 though not as strongly developed as in the brachystelechid *Carrolla* (Gee et al., 2019); this  
533 was interpreted as indicating that *Llistrofus* lived in leaf litter, in crevices or in burrows dug  
534 by other animals, and was compared to the abovementioned *Ambystoma*.

535 In the unconstrained parsimony analysis of the full dataset of Marjanovič & Laurin  
536 (2019: fig. 14), and similarly in Daza et al. (2020: fig. S15), Lissamphibia is even closer to  
537 Brachystelechidae + *Brachydectes* than *Rhynchonkos* or Hapsidopareiidae. It is likely that  
538 some amount of digging behavior is plesiomorphic for Lissamphibia: except for the extant,  
539 highly nested typhlonectids, all known total-group caecilians (Gymnophionomorpha) are  
540 fossorial (Jenkins et al., 2007), and a lesser degree of head-based digging is inferred  
541 (Wiechmann et al., 2000; Gardner, 2001; and references therein) for Albanerpetidae, a clade  
542 extinct since the early Pleistocene that appears to be the sister-group of Lissamphibia (Daza et  
543 al., 2020). Daza et al. (2020), followed by Skutschas et al. (2021), briefly argued for an  
544 arboreal lifestyle in at least some albanerpetids, based mostly on the ballistic tongue and the  
545 curved terminal phalanges. The smallest chameleons live in leaf litter, however, and  
546 plethodontid salamanders with ballistic tongues span about the same range of lifestyles.  
547 Clawlike terminal phalanges are shared, as it happens, with *Batropetes*.

548 There is no evidence of digging behavior in early urodeles or salientians. However,  
549 almost all early (i.e. Triassic or Jurassic) urodeles known to date are only known from  
550 skeletally immature individuals, prompting Skutschas (2018) to suggest that neoteny is  
551 plesiomorphic for urodeles and that metamorphic life-history strategies are derived within the  
552 clade; in that case, some of the morphology of postmetamorphic urodeles may not be  
553 homologous with that of other animals, and their lifestyles evidently would not be.

554 Although digging or burrowing by various means (usually the hindlimbs, without  
555 involving the forelimbs or the head; reviewed by Nomura et al., 2009) evolved several times  
556 within the salientian crown-group, it is clearly not plesiomorphic for the total group, being  
557 absent in the entire stem-group as currently understood. We propose nonetheless that the  
558 jumping locomotor mode that is plesiomorphic for Jurassic and later salientians, from  
559 *Prosalirus* on crownwards (Jenkins & Shubin, 1998), was made possible by adaptations to an  
560 earlier forelimb-based surface-digging lifestyle.

561

#### 562 *4.4 The origin of jumping and landing in salientians*

563 In order to be able to evolve jumping as a mode of locomotion, the animals in question first  
564 have to be able to land safely. This predicts the former existence of animals that were able to  
565 land safely, but not to jump routinely. It also predicts that the ability to land safely is either  
566 trivial or an exaptation, i.e. an adaptation to a very different selection pressure that may no  
567 longer apply.

568           The ability to land safely on dry land is clearly not trivial, judging from the many  
569 shock-absorbing adaptations found in the forelimbs and shoulder girdles of anurans (Emerson,  
570 1984; Havelková & Rošek, 2006; Essner et al., 2010; Sigurdson et al., 2012; Herrel et al.,  
571 2016). But that leaves other options.

572           Gans & Parsons (1965) reviewed the then current hypotheses on the origin of jumping  
573 as a basic locomotor mode in salientians. In that time, no Jurassic salientians (or other modern  
574 amphibians) were yet known, both the anatomy of *Triadobatrachus* (cited under its  
575 preoccupied name *Protobatrachus*) and its relevance to early salientian evolution were poorly  
576 understood, other Triassic salientians were unknown, and even the behavior of the extant  
577 amphicoelan frogs (*Ascaphus* and *Leiopelma*) that has figured so prominently in the most  
578 recent works on this topic (Essner et al., 2010; Sigurdson et al., 2012; Herrel et al., 2016) had  
579 yet to be observed in detail. Under these limitations, Gans & Parsons (1965) made two  
580 important postulates: 1) “Pre-frogs” were, at first, fundamentally aquatic animals that climbed  
581 the shore to search for food, but escaped predators by fleeing into the water. Jumping was an  
582 escape mechanism from land into water before it also became a mode of locomotion on land;  
583 as jumping abilities gradually improved, the pre-frogs were gradually able to increase their  
584 radius of activity on land without losing the ability to escape into the water. Thus, the ability  
585 to land was trivial, because it was the ability of small animals to land in water after a brief  
586 fall. Only the ability to land on dry land would have had to evolve after the ability to jump. 2)  
587 The very origin of jumping was to be found in sit-and-wait predation, as pre-frogs would keep  
588 their heads well above the ground by propping themselves up with their forelimbs, then, when  
589 prey approached, pivot over their hands by extending one hindlimb or two; the simultaneous  
590 use of both hindlimbs emerged as the better solution and was favored by natural selection. We  
591 think both of these hypotheses are now testable.

592           In support of hypothesis 1, Essner et al. (2010) and Herrel et al. (2016) pointed out  
593 that the extant amphicoelans, the sister-group to the rest of the anuran crown-group, generally  
594 do not use their forelimbs to decelerate when they land from a jump; amphicoelans are small,  
595 do not jump often, and mostly jump into water. Both Essner et al. (2010) and Herrel et al.  
596 (2016) followed Gans & Parsons (1965) in suggesting that this lifestyle was ancestral for the  
597 anuran crown-group and beyond, so that the use of the forelimbs as shock absorbers would  
598 only have evolved in the sister-group of Amphicoela. This hypothesis does not, however,  
599 seem to explain how the forelimbs became adapted to providing this function in the other half  
600 of the crown-group. Furthermore, Sigurdson et al. (2012) pointed out two interesting facts:  
601 *Leiopelma* pronates the forearms before landing, despite not usually landing on its hands; and

602 both *Ascaphus* and *Leiopelma* have features that are considered related to this use of the  
603 forelimbs, such as the fusion of radius and ulna, which is not only present throughout the  
604 crown-group without exception, but also found outside the crown-group in the Jurassic stem-  
605 salientians *Notobatrachus*, *Vieraella* and *Prosalirus* (Báez & Basso, 1996; Jenkins & Shubin,  
606 1998; Báez & Nicoli, 2004; Sigurdson et al., 2012). We therefore follow Sigurdson et al.  
607 (2012) in regarding the lifestyle and locomotion of Amphicoela in general and *Ascaphus* in  
608 particular as autapomorphic, and conversely the use of the forelimbs to absorb the impact of  
609 jumping as plesiomorphic for the anuran crown-group.

610 This interpretation is further bolstered by the shoulder girdle. The contact between the  
611 left and the right shoulder girdle is formed by soft tissue (mostly cartilage) that is elastic to  
612 compression in extant anurans, amphicoelans included, and thus functions as a shock absorber  
613 (Emerson, 1984; Havelková & Roček, 2006). Only the ossified parts are known in extinct  
614 taxa, but their shape suggests that this additional shock absorber was in place not only in the  
615 Cretaceous *Liaobatrachus* (Dong et al., 2013: fig. 7) which may belong just inside or just  
616 outside the crown-group, but even in the Jurassic stem-salientian *Notobatrachus* (Báez &  
617 Nicoli, 2004), though probably not in *Triadobatrachus* (Ascarrunz et al., 2016).

618 Thus, we postulate that jumping evolved instead among mostly or entirely terrestrial  
619 walkers that escaped predators by hiding or perhaps running on land rather than by jumping  
620 into water. Terrestrial walking has a long history among the potential relatives of jumping  
621 salientians. Lires et al. (2016) found, and we confirm (Fig. 4–6; Table 3), that  
622 *Triadobatrachus* locomoted by lateral undulation, agreeing with its latest redescription  
623 (Ascarrunz et al., 2016) as not a habitual or good jumper; although lateral undulation is  
624 equally compatible with walking and swimming, the highly reduced tail in combination with  
625 the short trunk argues strongly against the latter option. The numerous isolated bones  
626 described as *Czatkobatrachus* (Evans & Borsuk-Białynicka, 2009), among them long, gracile,  
627 but very well ossified limb bones, are at the very least compatible with an ecologically  
628 *Triadobatrachus*-like animal. Outside Salientia, the presence of very short trunks in all  
629 Triassic (Schoch et al., 2020) to Early Cretaceous urodeles argues at least for a terrestrial  
630 walking ancestry of these animals (most of which are only known from individuals that had  
631 not undergone metamorphosis and were therefore aquatic); there is no evidence for a water-  
632 bound adult lifestyle in early gymnophionomorphs or albanerpetids. Beyond the modern  
633 amphibians, we have to turn both to the amphibamiform temnospondyls (Fig. 1C–F) and to  
634 the brachystelechid “microsaurs” (Fig. 1D, E) to cover the phylogenetic possibilities. Bone  
635 microanatomy suggests a terrestrial lifestyle both in the amphibamiform *Doleserpeton* (more



636 or less: Laurin et al., 2004; see also Gee et al., 2020) and, as we report here, the  
637 brachystelechid *Batropetes palatinus*; the amphibamiform *Micropholis* has also been  
638 qualitatively described as terrestrial (McHugh, 2015), though the very thick cortex reported  
639 there suggests the possibility that *Micropholis* was actually amphibious. Interestingly, our  
640 analyses of limb proportions find (Fig. 4–6; Table 3) that both *Micropholis* and *Batropetes*  
641 *fritschi* cluster with toads and other hopping or walking anurans that are not habitual long-  
642 distance jumpers, but do not make use of lateral undulation either. In sum, no matter whether  
643 salientians are temnospondyls or “microsaurs”, they are nested in a group with a mostly  
644 terrestrial history that reaches back to the Early Permian (if not earlier), and jumping most  
645 likely evolved in a terrestrial context together with one of three independent reductions of  
646 lateral undulation.

647         Having cast great doubt on hypothesis 1, we need to predict animals that were able to  
648 land safely on dry land but not to jump. We think that Sigurdsen et al. (2012) found one, and  
649 that we can offer another.  
650 Sigurdsen et al. (2012) reviewed the anatomical adaptations to the use of the forelimbs as  
651 shock absorbers in landing. One of them, the apomorphic lateral deflection of the  
652 deltopectoral crest (or at least a shallow concavity lateral to the crest), was to varying degrees  
653 found in all investigated extant anurans (including *Leiopelma*), except for the more or less  
654 straight ventral orientation of the crest (without a simple concavity) in *Ascaphus*. Lateral  
655 deflection was likewise found in the Jurassic stem-salientians *Notobatrachus* and *Vieraella* as  
656 well as, if it is not due to crushing in this case, *Prosalirus*. Surprisingly, it was also found in  
657 the Early Triassic stem-salientian *Triadobatrachus*. We here report it in *Batropetes palatinus*  
658 as well. The presence of this anatomical feature suggests that *Triadobatrachus* and *Batropetes*  
659 could have landed safely if they could have jumped – which they could not, at least not as a  
660 routine mode of locomotion (*Triadobatrachus*: Ascarrunz et al., 2016; Lires et al., 2016;  
661 Table 3; contra Sigurdsen et al., 2012, who assumed the ability to jump based only on the  
662 ability to land; *Batropetes*: Table 3). The plesiomorphic medial deflection, in contrast, was  
663 found in all caudates considered by Sigurdsen et al. (2012), as well as in *Eocaecilia* and the  
664 amphibamiform *Doleserpeton*. The humeri referred to the Early Triassic stem-salientian  
665 *Czatkobatrachus* were found to have an intermediate condition – a just barely medially  
666 deflected crest with a large lateral attachment site for the deltoideus clavicularis muscle.  
667



669

670 **Fig. 8.** Life reconstruction of *Batropetes palatinus* as an animal that used its forelimbs to  
671 scratch in leaf litter or topsoil.

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672

673 The existence of animals that were able to land, but did not land because they were  
674 unable to jump, adds to the classic “chicken and egg” problems of evolutionary biology that  
675 can be solved by assuming exaptation. If not jumping, what was the selection pressure that  
676 favored the evolution of the ability to land?

677 Against hypothesis 2, which states that jumping originated from a form of sit-and-wait  
678 predation, we thus argue that the lateral deflection of the deltopectoral crest, which makes it  
679 easier to powerfully abduct the humerus, arose as an adaptation to an earlier lifestyle that  
680 involved using one forelimb to move leaf litter or topsoil aside while placing the hand of the  
681 other in or close to the sagittal plane to ensure symmetric weight support – the foraging mode  
682 we infer for *Batropetes* (Fig. 8).

683 All this leads us to the following scenario. Although its details are rather speculative at  
684 present, they are testable by future discoveries of further fossils. More of its stages can be  
685 identified with known parts of the tree under the lepospondyl hypothesis than under the  
686 temnospondyl hypothesis of lissamphibian origins, so we illustrate the scenario on the former  
687 hypothesis first – but none of the hypotheses in Figure 1 contradict the scenario given our  
688 current knowledge of the fossil record, and all require convergence between amphibamiform  
689 temnospondyls and brachystelechids in any case.

690

#### 691 *4.5 An evolutionary scenario*

692 If brachystelechids and lissamphibians are as closely related as found by Marjanovič & Laurin  
693 (2019) or Daza et al. (2020; see Fig. 1D), it becomes an obvious question whether the lifestyle  
694 of the former is homologous to the same lifestyle of hypothetical early salientians (or yet  
695 earlier batrachians).

696 The elongate, limb-reduced lysorophian *Brachydectes* is often found in burrow casts,  
697 and Pardo & Anderson (2016) have shown that its skull was more robust and consolidated  
698 than previously thought, as well as that the orbits proper only made up a small part of the  
699 large orbitotemporal embayment (which also housed jaw muscles and was ventrally open);  
700 even so, they reconstructed a terminal mouth and terminal nostrils, which may argue against  
701 routine burrowing in hard or heavy soils. The forelimbs, however, can hardly have played a  
702 role in the locomotion or foraging of these elongate animals. The humerus is tiny; the



703 generally incompletely ossified deltopectoral crest shows the plesiomorphic medial  
704 deflection, though a shallow lateral concavity is arguably present (Wellstead, 1991: fig. 21).  
705 Finally, although Pardo & Anderson (2016) argued against the traditional interpretation of  
706 *Brachydectes* as aquatic (and burrowing only to estivate), the very plesiomorphic, heavily  
707 ossified hyobranchial apparatus (Wellstead, 1991; Witzmann, 2013) is hard to explain if it did  
708 not support external gills or at least open gill slits, and the extremely broad cultriform process  
709 of the parasphenoid recalls neotenic salamanders (and, to a lesser degree, highly immature  
710 temnospondyls: e.g. Werneburg, 2012). The long retention in ontogeny of sutures between the  
711 neural arches and the centra, and even between the left and right neural arches (Wellstead,  
712 1991; Pardo & Anderson, 2016), also argues against weight support and for a decelerated  
713 ontogeny (e.g. Marjanovič & Laurin, 2008). In short, the lysorophian lifestyle may be derived  
714 from the one apparently seen in *Batropetes* by body size increase, body elongation and  
715 possibly neoteny (or paedomorphosis more broadly). Unfortunately, however, the early life  
716 history of brachystelechids or indeed any “microsaurs” remains completely unknown.

717 Throughout the modern amphibians (Lissamphibia and Albanerpetidae), the  
718 interclavicle – the median dermal bone of the shoulder girdle – is lost without a trace. This  
719 differentiates them from all other anamniote tetrapodomorphs except the most limb-reduced  
720 ones, and contrasts starkly with the situation not only in *Batropetes* (Gliénke, 2013, 2015; see  
721 above), but also in *Doleserpeton*, where the contacts between the interclavicle and the  
722 clavicles are likewise immobile and prevent any movement of the left and right shoulder  
723 girdles relative to each other. Loss of the interclavicle would promptly increase the reach of  
724 the forelimbs beyond their own length; that could be an adaptation to walking or running, but  
725 also to scratch-digging in leaf litter, the lifestyle we propose for *Batropetes*. There would be a  
726 tradeoff with the size of the attachment sites of the pectoralis muscles. During the evolution of  
727 jumping on the salientian stem, the shortening of the trunk would increase the need for  
728 stability and shock absorption in the shoulder girdle (Ascarrunz et al., 2016); this would have  
729 been accomplished by the appearance of an apparently neomorphic cartilage called the  
730 omosternum, which provides attachment surfaces for the pectoralis muscles and limits  
731 independent movement of the shoulder girdles just like the interclavicle that it replaces  
732 topographically, but, as cartilage, remains elastic to mediolateral pressure (Emerson, 1984;  
733 Havelková & Roček, 2006). In quadrupedally walking and running amniotes, interestingly,  
734 mobility between the shoulder girdles seems to have been enabled several times  
735 independently by the evolution of mobile sliding contacts between the interclavicle and the  
736 coracoids; the clavicles seem to be lost more often than the interclavicle, while they are still

737 present in most frogs today, where they are usually essential for bracing the shoulder girdle  
738 against too much compression (Emerson, 1984).

739 Albanerpetidae would have replaced the lateral movements of the forelimbs with  
740 lateral movements of the head and atlas, accommodated at a novel joint between the atlas and  
741 the axis (Marjanovič & Laurin, 2019, and references therein). The limbs would have been  
742 reduced to a size seen in many terrestrial salamanders (the deltopectoral crest is insufficiently  
743 known: McGowan, 2002), but the length of the trunk would have stayed almost the same (21  
744 presacral vertebrae in the Early Cretaceous *Celtdens ibericus* and probably the mid-  
745 Cretaceous *Yaksha*: McGowan, 2002; Daza et al., 2020: S2.3; otherwise unknown). Already  
746 in the original description of *Albanerpeton inexpectatum* (Estes & Hoffstetter, 1976: 320), it  
747 was suggested that the large orbitotemporal fenestrae housed large eyes adapted to the  
748 darkness in the karst fissures whose fill constitutes the type locality. The absence of sclerotic  
749 rings (McGowan, 2002; Daza et al., 2020) may indicate the same.

750 The known fossil record of Gymnophionomorpha begins with the Early Jurassic  
751 *Eocaecilia*, an elongate, limb-reduced burrower with a solid, bullet-like skull that bears rather  
752 small orbits, although the mouth is still terminal (Jenkins et al., 2007). Body size increase,  
753 body elongation and a transition to burrowing could derive this lifestyle from the one we  
754 postulate for *Batropetes*. As noted by Sigurdson et al. (2012), the deltopectoral crest on the  
755 small humerus is deflected medially (Jenkins et al., 2007: fig. 42). (The Late Triassic  
756 stereospondyl temnospondyl *Chinlestegophis*, a likely head-first burrower described and  
757 interpreted as a stem-gymnophionomorph by Pardo et al. [2017a] but not found as such by  
758 Daza et al. [2020: fig. S14], will be discussed elsewhere. Its limbs remain unknown.)

759 Digging would have been abandoned wholesale in urodeles and salientians, most  
760 likely separately, though possibly in their last common ancestor (the first batrachian) if the  
761 enlarged size of the limbs was secondarily abandoned in urodeles (perhaps through neoteny:  
762 Skutschas, 2018) as the lateral deflection of the deltopectoral crest would have been in this  
763 scenario. The trunk was shortened further (15 presacral vertebrae in *Triadobatrachus*, 16 in  
764 the Triassic stem-urodele *Triassurus*, 13 in the Jurassic metamorphic stem-urodele *Karaurus*),  
765 and the limbs elongated further on the salientian side (including *Czatkobatrachus*: Evans &  
766 Borsuk-Białyńska, 2009) for more efficient walking – as also, independently (regardless of  
767 lissamphibian relationships), in the contemporary amphibamiform *Micropholis* – until  
768 jumping became possible and drove further elongation of the limbs and further shortening of  
769 the trunk. The head remains restricted to dorsoventral movements in batrachians, as in  
770 caecilians.



771 If the extant amphibian clades are temnospondyls (Fig. 1C, F; Pardo et al., 2017a, b,  
772 and references therein), naturally, no part of the above scenario would be suggested by the  
773 phylogeny; no indications of a digging lifestyle have been reported from any amphibamiform  
774 temnospondyl. However, our inference that the origin of Salientia involved a lifestyle shared  
775 by *Batropetes* would not be invalidated; it would merely add to the convergence between  
776 lissamphibians and brachystelechids that would have to be inferred (all over the skeleton), just  
777 as convergence between lissamphibians and amphibamiforms has to be inferred otherwise.

778 Marjanovič & Laurin (2013, 2019) have pointed out that amphibamiform  
779 temnospondyls, *Batropetes* and modern amphibians share a large number of features that must  
780 have evolved at least twice, and that many of them may be explained as adaptations to  
781 terrestrial walking. Indeed, our statistical analyses infer walking with use of lateral undulation  
782 for all of these groups (Fig. 4–6), plotting them in the same part of morphospace as extant  
783 limbed squamates as well as the “microsaurs” *Pantylus* and *Tuditanus* (Fig. 4, 5).

784 The amphibamiform *Doleserpeton*, which has played an outsized role in in most  
785 hypotheses on lissamphibian origins, plots as an outlier from the laterally undulating cluster  
786 (Fig. 4, 5). Its proportions with long zeugopods are reminiscent of – much larger – cursorial  
787 amniotes and could indicate a unique lifestyle that should be researched further; but we  
788 cannot exclude the possibility that the measured bones represent a mixture of the cooccurring  
789 amphibamiforms *Doleserpeton*, *Pasawioops* and *?Tersomius dolesensis* as discussed by Gee  
790 et al. (2020).

791

## 792 **5. Conclusions**

793 New data from computed microtomography ( $\mu$ CT) of MB.Am.1232, a skeleton of the Early  
794 Permian “microsaur” *Batropetes palatinus* (Fig. 2), have allowed us to study the  
795 microanatomy of the limb bones and axial skeleton, and thus to infer a terrestrial lifestyle for  
796 the taxon that involved digging but not outright burrowing – most likely “rummaging through  
797 leaf litter” (Gliénke, 2013: 90).

798 The enlarged, powerful forelimbs of *Batropetes*, along with the laterally deflected  
799 deltopectoral crest that appears to be uniquely shared with salientians (for which see  
800 Sigurdson et al., 2012), suggest to us that the forelimbs of salientians, too, were originally  
801 adapted to a terrestrial lifestyle that involved pushing leaf litter and/or topsoil aside in search  
802 of food.

803 A mixture of adaptations to walking and digging has led to the hypothesis that the  
804 Early Permian “microsaur” *Batropetes* searched for food in leaf litter and perhaps topsoil. Our

805  $\mu$ CT data confirm that at least *Batropetes palatinus* was terrestrial and not strongly adapted to  
806 limb-based burrowing; two statistical analyses of limb proportions, however, indicate that  
807 some kind of digging behavior was part of the lifestyle of at least *B. palatinus*, *B.*  
808 *niederkirchensis* and *B. appelensis*. Comparing it further to the extant mole salamander  
809 *Ambystoma tigrinum*, we interpret *Batropetes* as a terrestrial scratch-digger that may have  
810 used one forelimb to shove leaf litter aside while standing on the other.

811 The same analyses, an LDA and a MANOVA, support digging as part of the lifestyle  
812 of another Early Permian “microsaur”, *Pantylus*, and of the Late Carboniferous *Diabloroter* (a  
813 close relative of *Batropetes*), but not of the Late Carboniferous *Tuditonus*. Of the three  
814 included amphibamiform temnospondyls, the Late Carboniferous *Platyrrhinops* emerges as a  
815 laterally undulating walker, the Early Triassic *Micropholis* as a toadlike walker which did not  
816 make use of undulation, and the Early Permian *Doleserpeton* as an extreme outlier that invites  
817 further research (one way or another – the measured material could be chimeric).

818 The latest publications on the Early Triassic stem-group frog *Triadobatrachus*  
819 concluded that early salientian evolution was not driven by specialization for efficient  
820 jumping, as *Triadobatrachus* morphologically still lacked the ability to jump off, even though  
821 it had the forelimb strength necessary to withstand the impact of landing. Confirming  
822 *Triadobatrachus* as a terrestrial walker that made some use of lateral undulation (unlike  
823 *Micropholis* or any crown-group frogs) and shows no indications of digging, we postulate that  
824 these forelimb features, in particular the lateral deflection of the deltopectoral crest, are  
825 exaptations from forelimb-based scratch-digging, for which *Batropetes* may represent an  
826 analog or possibly a homolog.

827

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838 amphibian species as counted by AmphibiaWeb (2021) surpassed 8,000 on 28 March 2019,

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841

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845

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1139 **Table 1**

<b>Taxon</b>	<b>MedGeo</b>	<b>FeL: Femur length</b>	<b>TFL: Tibio- Fibula length</b>	<b>HuL: Humerus length</b>	<b>RUL: Radio- Ulna length</b>
<i>Triadobatrachus massinoti</i> MNHN.F.MAE126 (holotype)	12.72962887	22.08	14.37	18.43	11.23
<i>Batropetes palatinus</i> MB.Am.1232 right side	4.463624692	6.1	3.3	6.8	2.9
<i>B. palatinus</i> MB.Am.1232 left side	4.523522736	6.1	3.3	6.5	3.2
<i>B. appelensis</i> MNHM PW 2001/308-LS (holotype)	3.282525095	4.3	2.4	4.5	2.5
<i>B. palatinus</i> MNHM PW 2001/306-LS	4.9801242	6.9	3.4	6.9	3.8
<i>B. palatinus</i> MNHM PW 2001/307-LS (holotype)	3.698932968	4.8	2.5	6	2.6
<i>B. palatinus</i> MNHM PW 2001/309-LS	3.76810184	4.8	2.5	6	2.8
<i>B. niederkirchensis</i> SMNS 55884 (holotype) left side	5.321222698	7.7	3.5	8.5	3.5
<i>B. niederkirchensis</i> SMNS 55884 (holotype) right side	5.471145628	7.7	3.7	8.5	3.7
<i>B. fritschi</i> SLFG SS 13558/SS 13559 (lectotype)	3.295192812	7.7	3.5	8.5	2.8
<i>Celtedens ibericus</i> LH 6020 (holotype) left side	4.361255335	6.25	4.25	4.5	3
<i>C. ibericus</i> LH 030 R left side	5.614696514	8.25	5.25	5.75	3.99
<i>Platyrrhinops lyelli</i> AMNH 6841 (holotype) right side	14.12396468	20.24	11.62	16.13	10.49

<b><i>Doleserpeton annectens</i></b>	7.766963956	9.11	5.06	10.64	7.43
FMNH UR 1320, 1321, 1381, 1382					
<b><i>Pantylus cordatus</i></b>	15.26259	19.05	10.82	21.93	12.01
UT 40001-16, UT 40001-61					
<i>Micropholis stowi</i>	11.97421141	16.96	10.94	15.81	7.01
BSM 1934 VIII E					
<i>M. stowi</i> BSM 1934 VIII C	12.09437666	16.12	10.97	16.53	7.32
<i>Tuditonus punctulatus</i>	9.064425629	12.76	7.57	10.80	6.47
forelimb: ANMNH 6926 (holotype); hindlimb: USNM 4457					
<i>Diabloroter bolti</i> ACFGM V- 1634 (holotype)	3.387741	4.38	3.01	3.66	2.74

1140

1141 Limb measurements (in mm) of extinct taxa (taken from the literature cited in Table 2 except  
1142 for MB.Am.1232, which was measured on the specimen itself) used for the analyses. The  
1143 specimens in boldface are explicitly referred to in Fig. 6. For *Triadobatrachus massinoti*,  
1144 *Batropetes appelensis* and *B. niederkirchensis*, the measured specimens are the only known  
1145 specimens. MedGeo: geometric mean of all measurements.

1146 **Table 2**

<b>Taxon</b>	<b>Source</b>	<b>Comment</b>
<i>Triadobatrachus massinoti</i> MNHN.F.MAE126 (holotype)	Lires et al. (2016)	
<i>Batropetes palatinus</i> MB.Am.1232	This work; Glienke (2015)	Measured on the specimen and validated with measurements in the literature
<i>B. appelensis</i> MNHM PW 2001/308-LS (holotype)	Glienke (2015)	
<i>B. palatinus</i> MNHM PW 2001/306-LS	Glienke (2015)	
<i>B. palatinus</i> MNHM PW 2001/307-LS (holotype)	Glienke (2015)	
<i>B. palatinus</i> MNHM PW 2001/309-LS	Glienke (2015)	
<i>B. niederkirchensis</i> SMNS 55884 (holotype)	Glienke (2013)	
<i>B. fritschi</i> SLFG SS 13558/SS 13559 (lectotype)	Glienke (2013)	
<i>Celtedens ibericus</i> LH 6020 (holotype) left side	McGowan (2002)	
<i>C. ibericus</i> LH 030 R left side	McGowan (2002)	
<i>Platyrrhinops lyelli</i> AMNH 6841 (holotype) right side	Clack & Milner (2010)	Measured on specimen photo
<i>Doleserpeton annectens</i> FMNH UR 1320, 1321, 1381, 1382	Sigurdson et al. (2010)	Reconstruction as well as separate specimens scaled to same size
<i>Pantylus cordatus</i> UT 40001-1, UT 40001-6	Carroll (1968)	Illustrated specimens

<i>Micropholis stowi</i> BSM 1934 VIII E	Schoch & Rubidge (2005)	Illustrated limb bones (fig. 6)
<i>M. stowi</i> BSM 1934 VIII C	Schoch & Rubidge (2005)	Illustration of specimen BSM 1934 VIII A–E (fig. 5)
<i>Tuditonus punctulatus</i> forelimb: ANMH 6926 (holotype); hindlimb: USNM 4457	Carroll & Baird (1968)	Measured on specimen photos
<i>Diabloroter bolti</i> ACFGM V-1634 (holotype)	Mann & Maddin (2019)	

1147

1148 Sources of the measurements in Table 1.



1149 **Table 3**

Specimens	Locomotion					
	mode	J	Sw	LU	LUD	HW
<i>Triadobatrachus massinoti</i> MNHN.F.MAE126 (holotype)	LU	3.01E-10	3.67E-07	0.710651	0.288364	0.000985
<i>Batropetes palatinus</i> MB.Am.1232 left side	LUD	2.48E-10	3.86E-08	0.46604	0.533916	4.48E-05
<i>B. palatinus</i> MB.Am.1232 right side	LU	4.83E-07	6.90E-06	0.60321	0.392094	0.004689
<i>B. appelensis</i> MNHM PW 2001/308-LS (holotype)	LUD	8.29E-13	6.96E-10	0.320407	0.679592	9.92E-07
<i>B. palatinus</i> MNHM PW 2001/306-LS	LUD	1.46E-14	3.59E-11	0.259963	0.740037	2.40E-08
<i>B. palatinus</i> MNHM PW 2001/307-LS (holotype)	LUD	1.42E-08	1.74E-07	0.295067	0.704894	3.95E-05
<i>B. palatinus</i> MNHM PW 2001/309-LS	LUD	1.46E-10	5.84E-09	0.195283	0.804715	1.33E-06
<i>B. niederkirchensis</i> SMNS 55884 (holotype) left side	LUD	4.59E-09	1.34E-07	0.416793	0.583189	1.82E-05
<i>B. niederkirchensis</i> SMNS 55884 (holotype) right side	LUD	1.71E-09	1.45E-07	0.422295	0.577682	2.31E-05
<i>B. fritschi</i> SLFG SS 13558/SS 13559 (lectotype)	HW	0.000973	0.000795	0.25385	0.137076	0.607305
<i>Celtedens ibericus</i> LH 6020 (holotype) left side	LU	1.40E-09	2.97E-06	0.780707	0.216535	0.002755

<i>C. ibericus</i> LH 030 R left side	LU	1.91E-09	5.82E-06	0.805259	0.192301	0.002434
<i>Platyrrhinops lyelli</i> AMNH 6841 (holotype) right side	LU	8.84E-13	5.48E-09	0.592132	0.407855	1.26E-05
<i>Doleserpeton annectens</i> FMNH UR 1320, 1321, 1381, 1382	LUD	3.32E-21	1.07E-16	0.012122	0.987878	7.63E-15
<i>Pantylus cordatus</i> UT 40001-1, UT 40001-6	LUD	7.06E-13	2.93E-10	0.197864	0.802135	2.41E-07
<i>Micropholis stowi</i> BSM 1934 VIII E	HW	6.23E-05	0.000715	0.088317	0.01057	0.900335
<i>M. stowi</i> BSM 1934 VIII C	HW	0.000112	0.000531	0.040551	0.00654	0.952266
<i>Tuditonus punctulatus</i> forelimb: ANMH 6926 (holotype); hindlimb: USNM 4457	LU	7.01E-12	1.79E-08	0.63513	0.364823	4.61E-05
<i>Diabloroter bolti</i> ACFGM V-1634 (holotype)	LUD	0.00	0.00	0.3412	0.6588	0.00

1150

1151 Locomotion mode predictions of the LDA of the extinct taxa in our dataset. The numbers are  
1152 the Bayesian posterior probabilities for each locomotion mode. *Doleserpeton* is an extreme  
1153 outlier (Fig. 4–6). Abbreviations as in Tables 1 and 2.

1154 **Supplementary information**

1155

1156 Table S1: Measurements by Lires et al. (2016) and of our added extinct taxa.

1157

1158 Fig. S1: First and fourth canonical axes of the discriminant function analysis (LDA) of  
1159 corrected morphometric variables and the five defined locomotor categories. See the legend of  
1160 Fig. 4 for more information. For a version with every extant taxon labeled, see Fig. S3.

1161

1162 Fig. S2: Fig. 4 with all specimens labeled.

1163

1164 Fig. S3: Fig. S1 with all specimens labeled.