comptes rendus palevol
2022 • 21 • 23

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Palaeobiology and palaeobiogeography of amphibians and reptiles — Jean-Claude Rage —

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art. 21 (23) — Published on 6 July 2022
www.cr-palevol.fr

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ISSN (imprimé / *print*): 1631-0683/ ISSN (électronique / *electronic*): 1777-571X

The scratch-digging lifestyle of the Permian “microsaur” *Batropetes* Carroll & Gaskill, 1971 as a model for the exaptative origin of jumping locomotion in frogs

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Submitted on 1 March 2019 | Accepted on 12 February 2021 | Published on 6 July 2022

urn:lsid:zoobank.org:pub:4F811DDB-A7B1-4EB0-B04C-E6DAA26A4D2C

Jansen M. & Marjanović D. 2022. — The scratch-digging lifestyle of the Permian “microsaur” *Batropetes* Carroll & Gaskill, 1971 as a model for the exaptative origin of jumping locomotion in frogs, *in* Folie A., Buffetaut E., Bardet N., Houssaye A., Gheerbrant E. & Laurin M. (eds), Palaeobiology and palaeobiogeography of amphibians and reptiles: An homage to Jean-Claude Rage. *Comptes Rendus Palevol* 21 (23): 463-488. https://doi.org/10.5852/cr-palevol2022v21a23

ABSTRACT

Recent studies have shown that the Triassic stem-frog *Triadobatrachus* Kuhn, 1962 lacked the ability to jump, but nonetheless had the forelimb strength to withstand the impact of landing from a jump. We propose a hypothesis to resolve this pseudoparadox: the strengthened forelimbs are former adaptations to forelimb-based digging that later made jumping possible by exaptation. Micro-CT data from a skeleton of *Batropetes palatinus* Glienke, 2015 reveal thin cortical bone, confirming *Batropetes* Carroll & Gaskill, 1971 as terrestrial. Combining adaptations to walking and digging, confirmed by statistical analyses, *Batropetes* is thought to have searched for food in leaf litter or topsoil. We interpret *Batropetes* as having used one forelimb at a time to shove leaf litter aside. *Batropetes* may thus represent an analog, or possibly a homolog, of the digging stage that preceded the origin of Salientia Laurenti, 1768. We discuss the possibility of homology with the digging lifestyles of other “microsaurs” and other amphibians.

KEY WORDS
Batropetes,
Triadobatrachus,
“Microsauria”,
Salientia,
Anura,
digging,
jumping.

RÉSUMÉ

Le mode de vie gratteur-fouisseur du « microsaure » permien Batropetes *Carroll & Gaskill, 1971 comme modèle pour l’origine de la saltation des anoures par exaptation.*

Selon des études récentes, le salientien-souche *Triadobatrachus* Kuhn, 1962 n’était pas capable de sauter, mais ses membres antérieurs pouvaient néanmoins résister à la force d’atterrissage. Nous proposons une hypothèse pour résoudre ce pseudoparadoxe : ce renforcement des membres antérieurs serait une ancienne adaptation permettant de creuser, qui aurait, plus tard, rendu possible le saut par exaptation. Les données de microtomographie numérique d’un squelette de *Batropetes palatinus* Glienke, 2015 révèlent un os cortical mince, confirmant que *Batropetes* Carroll & Gaskill, 1971 était terrestre. Comme *Batropetes* combine des adaptations à la marche et au fouissage, confirmées par des analyses statistiques, on pense qu’il cherchait sa nourriture dans la litière de feuilles mortes ou la terre végétale. Nous interprétons *Batropetes* comme ayant utilisé un seul membre antérieur à la fois pour écarter la litière de feuilles. *Batropetes* pourrait ainsi représenter un analogue, ou peut-être un homologue du stade gratteur-fouisseur qui aurait précédé l’origine de Salientia Laurenti, 1768. Nous discutons la possibilité d’une homologie avec des modes de vie de fouisseur chez d’autres « microsaures » et d’autres amphibiens.

MOTS CLÉS
Batropetes,
Triadobatrachus,
“Microsauria”,
Salientia,
Anura,
fouiller,
sauter.

INTRODUCTION

The origin of frogs (total group: Salientia Laurenti, 1768) is the subject of two major questions. While there is now a consensus about the phylogenetic position of Salientia as the sister-group of Urodela Duméril, 1806 (the total group of salamanders), according to molecular (Irisarri *et al.* 2017; Hime *et al.* 2020; and references therein) and morphological data alike (Pardo *et al.* 2017a; Marjanović & Laurin 2019; Daza *et al.* 2020; and references therein; contradicted by Mann *et al.* 2019a, with < 50 % bootstrap support), the phylogenetic position of Salientia + Urodela (together Batrachia Latreille, 1800), as well as that of the third extant amphibian clade (the caecilians: total or near-total group Gymnophionomorpha Marjanović & Laurin, 2008), remains an unsolved problem (Marjanović & Laurin 2019; Danto *et al.* 2019; Daza *et al.* 2020; Laurin *et al.* 2022 [Fig. 1]). For well over a century, three groups of hypotheses persisted in the literature: the "temnospondyl hypothesis" (Fig. 1C), which unites the extant amphibian clades as a clade Lissamphibia Haeckel, 1866 and nests this clade within the Paleozoic temnospondyls, most recently supported by the phylogenetic analyses of Pardo *et al.* (2017a: fig. S6; 2017b), Mann *et al.* (2019a) and Daza *et al.* (2020: fig. S13); the "lepospondyl hypothesis" (Fig. 1D) which nests Lissamphibia within or close to the Paleozoic "microsaurs" (e.g. Vallin & Laurin 2004; Pawley 2006: appendix 16; Marjanović & Laurin 2013, 2019; Daza *et al.* 2020: figs S12, S15); and the "polyphyly hypothesis" (Fig. 1E), according to which the batrachians are temnospondyls while the caecilians are "microsaurs". Unlike the other two, the polyphyly hypothesis, last proposed by Anderson *et al.* (2008), appears not to be preferred by any colleagues anymore; however, it has been replaced by a similar hypothesis (Pardo *et al.* 2017a) according to which batrachians and caecilians are nested within two different clades of temnospondyls (Fig. 1F), although a minimal update to that matrix restored Lissamphibia (Daza *et al.* 2020: fig. S14). Of these four hypotheses, the "classic" polyphyly hypothesis (Fig. 1E) is the only one that is not compatible with the molecular consensus, which strongly supports reciprocal monophyly of Lissamphibia and Amniota Haeckel, 1866 (Fig. 1A). At least the 21st century versions of all four are compatible with the current paleontological consensus (Fig. 1B). Soft anatomy not preserved in fossils has not so far been able to advance the debate either, because the soft-tissue features shared by extant amphibians could all be either tetrapod symplesiomorphies lost in amniotes or lissamphibian autapomorphies. Additionally, the discovery of the fourth group of "modern amphibians", the Middle Jurassic to Pleistocene albanerpetids with their unexpected combination of character states (Estes & Hoffstetter 1976; McGowan 2002; Maddin *et al.* 2013; Matsumoto & Evans 2018; Daza *et al.* 2020), has complicated this situation further (Marjanović & Laurin 2013, 2019; Daza *et al.* 2020).

Equally unsolved remains the evolution of the unique jumping locomotion, accompanied by diagnostic skeletal peculiarities (Sigurdsen *et al.* 2012), that has characterized crown-group frogs (usually called Anura Duméril, 1806) and their closest relatives at least since the Early Jurassic *Prosalirus* Shubin & Jenkins, 1995 (Jenkins & Shubin 1998; Roček 2013; Herrel *et al.* 2016; and references therein; see also the Late Triassic ilium described by Stocker *et al.* 2019). The Early Triassic *Triadobatrachus* Kuhn, 1962 (Rage & Roček 1989; Roček & Rage 2000; Ascarrunz *et al.* 2016), the sister-group to all other salientians (probably including the fragmentary coeval *Czatkobatrachus* Evans & Borsuk-Białynicka, 1998: see Evans & Borsuk-Białynicka 2009), was not capable of frog-like jumping (Ascarrunz *et al.* 2016; Lires *et al.* 2016; and references therein). The same inference is suggested by sacral vertebrae referred to *Czatkobatrachus* (Evans & Borsuk-Białynicka 2009: 99). This indicates that jumping evolved within the early history of Salientia – specifically during the latter half of Carroll's Gap, a period poor in fossils of lissamphibians and ecologically comparable animals (Marjanović & Laurin 2013; not noted there is the coeval scarcity of pan-squamates highlighted e.g. by Simões *et al.* 2018). Mainly due to this lack of potentially informative fossils, the question of how this novel mode of locomotion evolved has received disproportionately little attention.

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

We propose below that this preceding lifestyle was a terrestrial one that involved forelimb-based digging, but not outright burrowing – most likely a search for food in leaf litter and/or topsoil. Further, we report that several lines of evidence indicate the presence of such a lifestyle in the Early Permian "microsaur" *Batropetes palatinus* Glienke, 2015; some of them can also be applied to other "microsaurs" and suggest the same lifestyle for some of them.

Although a phylogenetic analysis is beyond the scope of this paper, we note that the "lepospondyl hypothesis" opens the possibility, discussed in the section "An evolutionary scenario" below, that the ecological niches of *Batropetes* Carroll & Gaskill, 1971 and the earliest salientians were homologous. However, should that turn out not to be the case, *Batropetes* would remain useful as an analog to the origin of frogs.

MATERIAL AND METHODS

Computed microtomography

The specimen MB.Am.1232 (Museum für Naturkunde, Berlin), referred to *Batropetes palatinus* by Glienke (2015), was scanned at the MB as a 2×3-part multiscan using computed

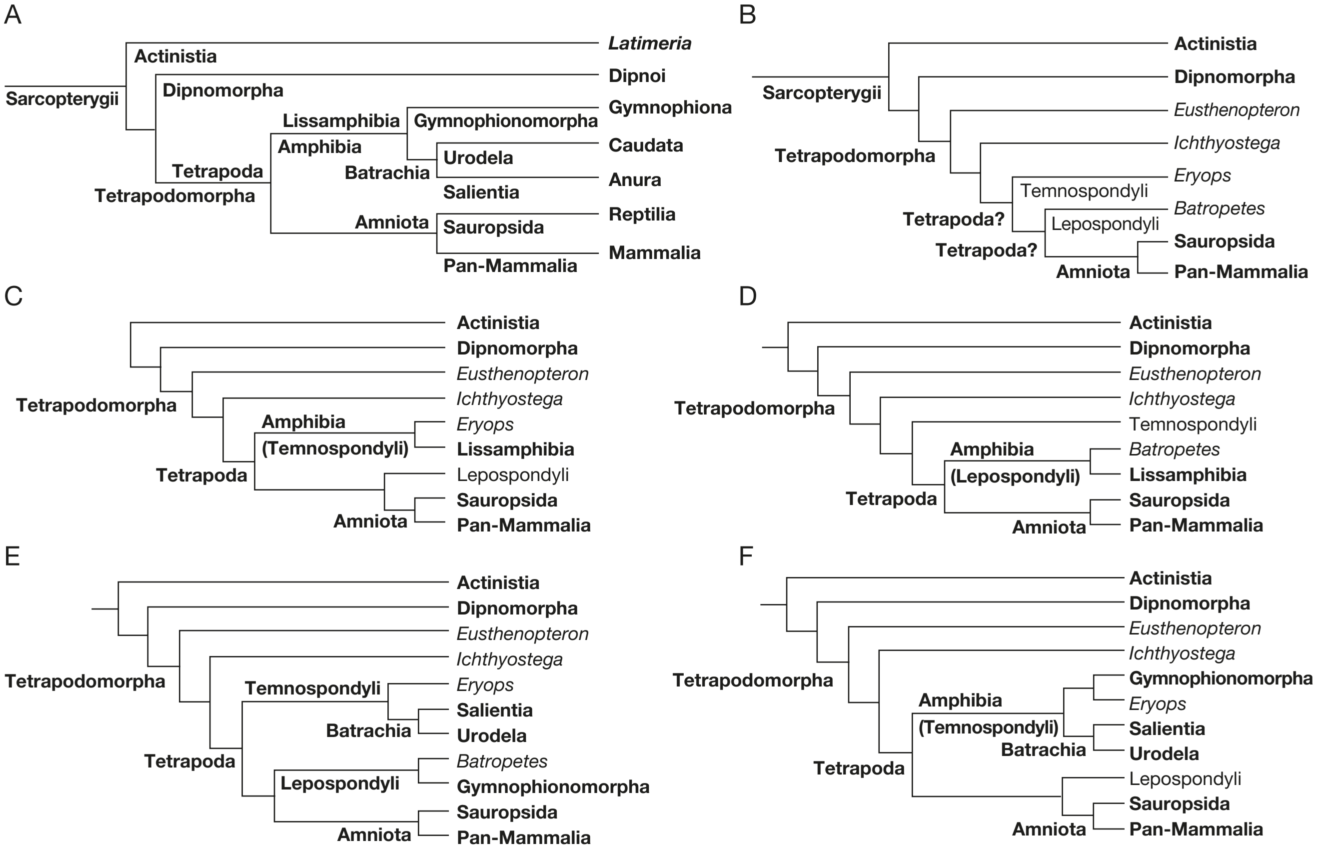

Fig. 1. — Recent hypotheses on the relationships of Salientia Laurenti, 1768: **A**, molecular consensus: Lissamphibia monophyletic with respect to Amniota (e.g. Irisarri *et al.* 2017; Hime *et al.* 2020); **B**, paleontological consensus: Lepospondyli closer to Amniota than Temnospondyli (in Pardo *et al.* [2017b], and some trees found in the update by Daza *et al.* [2020: fig. S13], at least some lepospondyls were even found within Amniota, as sauropsids); **C**, "Temnospondyl hypothesis": lissamphibians as a clade of temnospondyls (e.g. Pardo *et al.* 2017b; Mann *et al.* 2019a; Daza *et al.* 2020: fig. S13); compatible with A and B; **D**, "Lepospondyl hypothesis": lissamphibians as a clade of lepospondyls very close to *Batropetes* (e.g. Vallin & Laurin 2004; Pawley 2006: appendix 16; Marjanović & Laurin 2019; Daza *et al.* 2020: figs S12, S15); compatible with A and B; **E**, "Polyphyly hypothesis": frogs and salamanders as temnospondyls, caecilians as lepospondyls (e.g. Anderson *et al.* 2008); compatible with B but not A; **F**, hypothesis of Pardo *et al.* (2017a): extant amphibians as two separate clades of temnospondyls; compatible with A and B. **Boldface**, names of extant taxa; **parentheses**, names of junior synonyms on a given topology. Figure modified from Marjanović & Laurin (2019: fig. 2).

X-ray microtomography (phoenix|xraynanotom s) at 130 kV and 230 µA with an effective voxel size of 0.01785 mm and 1800 images/360° with a timing of 750 ms. Cone beam reconstruction was performed using datos|x-reconstruction software (GE Sensing & Inspection Technologies GmbH phoenix|x-ray). The multiscan of two parts was visualized, merged and segmented in VG Studio Max 3.0. The posterior part of the specimen was scanned separately to segment the hindlimb.

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

STATISTICAL ANALYSES OF LIMB PROPORTIONS

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

Lires *et al.* (2016) measured the lengths of the humerus, radius/ulna, femur, fibula/tibia and the proximal tarsus. Due to the rarity of sufficiently complete skeletons of our added taxa, we had to exclude the proximal tarsus from the analysis and considered only the remaining four linear measurements of the long bones. This change only had a moderate effect on the results as the different locomotor modes still separated comparably well (Table 3; Appendices 1; 2).

Apart from *Triadobatrachus*, the dataset of Lires *et al.* (2016) contains extant batrachians and squamates, which are assigned to locomotor categories: foot-propelled swimmers (Sw), jumpers (J), hoppers/walkers not using lateral undulation (HW) and swimmers as well as walkers making use of lateral undulation (LU). We divided the latter category by the presence (LUD) or absence (LU) of digging, scratching or burrowing behavior based on the data published in Oliveira *et al.* (2017a, b). Aquatic, amphibious or terrestrial animals within the LU (or the LUD) category cannot be distinguished by their limb proportions (Lires *et al.* 2016; and reference therein); LU and LUD can, however, be distinguished as described below.

TABLE 1. — Limb measurements (in mm) of extinct taxa (taken from the literature cited in Table 2, except for MB.Am.1232, which was measured on the specimen itself) used for the analyses. The specimens in **boldface** are explicitly referred to in Figure 6. For *Triadobatrachus massinoti* (Piveteau, 1936), *Batropetes appelensis* Glienke, 2015 and *B. niederkirchensis* Glienke, 2013, the measured specimens are the only known specimens. Abbreviations: **FeL**, femur length; **HuL**, humerus length; **MedGeo**, geometric mean of all measurements of the same taxon; **RUL**, radio-ulna length; **TFL**, tibio-fibula length.

Taxon	MedGeo	FeL	TFL	HuL	RUL
Triadobatrachus massinoti (Piveteau, 1936): MNHN.F.MAE126 (holotype)	12.72962887	22.08	14.37	18.43	11.23
Batropetes palatinus Glienke, 2015: MB.Am.1232 right side	4.463624692	6.1	3.3	6.8	2.9
B. palatinus: MB.Am.1232 left side	4.523522736	6.1	3.3	6.5	3.2
B. appelensis Glienke, 2015: MNHM PW 2001/308-LS (holotype)	3.282525095	4.3	2.4	4.5	2.5
B. palatinus: MNHM PW 2001/306-LS	4.9801242	6.9	3.4	6.9	3.8
B. palatinus: MNHM PW 2001/307-LS (holotype)	3.698932968	4.8	2.5	6	2.6
B. palatinus: MNHM PW 2001/309-LS	3.76810184	4.8	2.5	6	2.8
B. niederkirchensis Glienke, 2013: SMNS 55884 (holotype) left side	5.321222698	7.7	3.5	8.5	3.5
B. niederkirchensis: SMNS 55884 (holotype) right side	5.471145628	7.7	3.7	8.5	3.7
B. fritschi (Geinitz & Deichmüller, 1882): SLFG SS 13558/SS 13559 (lectotype)	3.295192812	7.7	3.5	8.5	2.8
Celtedens ibericus McGowan & Evans, 1995: LH 6020 (holotype) left side	4.361255335	6.25	4.25	4.5	3
C. ibericus: LH 030 R left side	5.614696514	8.25	5.25	5.75	3.99
Platyrhinops lyelli (Wyman, 1858): AMNH 6841 (holotype) right side	14.12396468	20.24	11.62	16.13	10.49
Doleserpeton annectens Bolt, 1969: FMNH UR 1320, 1321, 1381, 1382	7.766963956	9.11	5.06	10.64	7.43
Pantylus cordatus Cope, 1881: UT 40001-16, UT 40001-61	15.26259	19.05	10.82	21.93	12.01
Micropholis stowi Huxley, 1859: BSM 1934 VIII E	11.97421141	16.96	10.94	15.81	7.01
M. stowi: BSM 1934 VIII C	12.09437666	16.12	10.97	16.53	7.32
Tuditanus punctulatus Cope, 1875: forelimb: AMNH 6926 (holotype); hindlimb: USNM 4457	9.064425629	12.76	7.57	10.80	6.47
Diabloroter bolti Mann & Maddin, 2019: ACFGM V-1634 (holotype)	3.387741	4.38	3.01	3.66	2.74

To this dataset, we added extinct taxa without assigning them to one of the established locomotor modes: the albanerpetid near-lissamphibian (Daza *et al.* 2020) *Celtedens ibericus* McGowan & Evans, 1995 (two individuals); the "microsaurs" *Tuditanus punctulatus* Cope, 1875, *Pantylus cordatus* Cope, 1881 and *Diabloroter bolti* Mann & Maddin, 2019, as well as individuals (left and right sides measured separately in two cases) belonging to all four species (Glienke 2015) of *Batropetes*, including MB.Am.1232; and the amphibamiform (Schoch 2018) temnospondyls *Platyrhinops lyelli* (Wyman, 1858), *Micropholis stowi* Huxley, 1859 (two individuals), and *Doleserpeton annectens* Bolt, 1969 (composite of several individuals scaled to the same size). Despite its importance in recent studies on lissamphibian origins (Anderson *et al.* 2008; Marjanović & Laurin 2009, 2019; Pardo *et al.* 2017a; Mann *et al.* 2019a; and references therein), the amphibamiform *Gerobatrachus hottoni* Anderson, Reisz, Scott, Fröbisch & Sumida, 2008 had to be excluded from the linear discriminant analysis (LDA) because the preserved limbs of the only known specimen are not complete enough.

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

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

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

Both of these analyses do not take phylogeny into account. We have not performed a phylogenetic Flexible Discriminant Analysis (pFDA; Motani & Schmitz 2011) because time-calibrated phylogenies are not available for squamates or batrachians at the required phylogenetic resolution; we would need to interpolate the divergence dates for a large number of nodes. Additionally, divergence times of extinct taxa can only be dated by paleontological means. To compose a "supertimetree" including divergences dated by both paleontological and molecular means (for extant taxa without a fossil record) would be well beyond the scope of this paper.

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

ABBREVIATIONS

HW	hoppers or walkers that do not use lateral undulation;
J	jumpers;

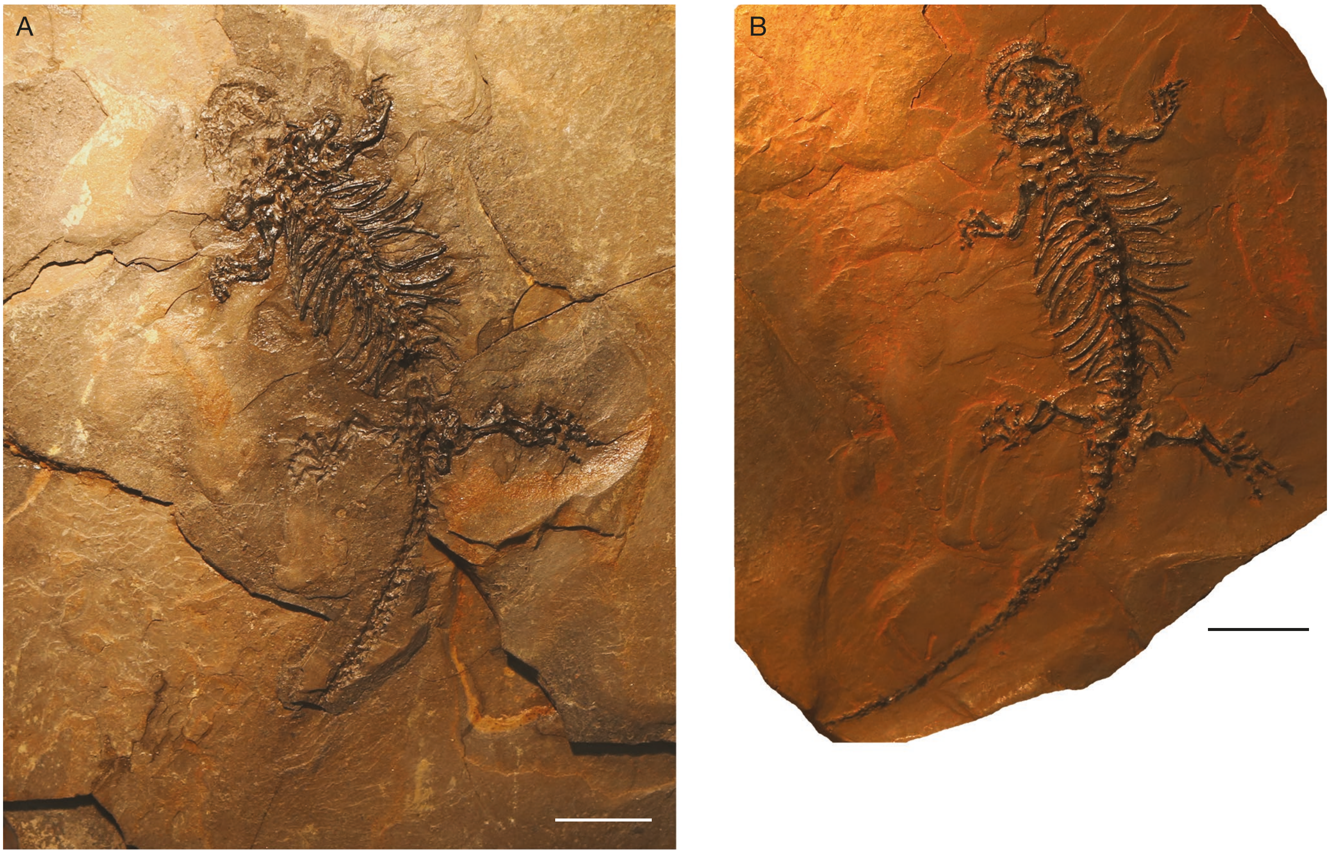

Fig. 2. — *Batropetes palatinus* Glienke, 2015 (MB.Am.1232), in dorsal view: **A**, the original fossil specimen with parts of the skeleton preserved as a natural mould; **B**, a composite cast of the specimen. Scale bars: 1 cm.

LDA	linear discriminant analysis;
LU	swimmers or walkers using lateral undulation, without a digging component to their lifestyle;
LUD	swimmers or walkers using lateral undulation, with a digging component to their lifestyle;
Sw	foot-propelled swimmers.

RESULTS

Bone microanatomy, proportions and lifestyle of *Batropetes*

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

The µCT data allow us to reconstruct the humerus of MB.Am.1232 in three dimensions (Fig. 3C-E). We find a dorsal process (accentuated by breakage) as reported in various lissamphibians, "microsaurs" and amphibamiforms, and a triangular deltopectoral crest that is not deflected medially as it is in salamanders (e.g. *Ambystoma* Tschudi, 1838: Sigurdsen *et al.* 2012: fig. 3A) or to a lesser degree in *Eocaecilia* Jenkins & Walsh, 1993 (Jenkins *et al.* 2007: fig. 42; Sigurdsen *et al.* 2012), but slightly laterally, producing a shallow concavity lateral of it (Fig. 3D), similar to the less extreme cases among salientians (Sigurdsen *et al.* 2012).

Comparative limb proportions and lifestyles

The morphometric variability of the limbs of the sampled taxa, both extant and extinct, reflects different locomotor functions, which we categorize for the extant species following Lires *et al.* (2016), Oliveira *et al.* (2017a, b), and references therein. In our LDA (Figs 4-6; Table 3; Appendices 2-4), the fossil individuals mostly plot with caudates and squamates (which retain much of the ancestral tetrapod body shape) in a wider cluster including the LU cluster of extant species and the separately categorized cluster of extant individuals known to routinely engage in digging behavior (LUD).

Table 2. — Sources of the measurements in Table 1. The specimens in **boldface** are explicitly referred to in Figure 6.

Taxon	Source	Comment
Triadobatrachus massinoti (Piveteau, 1936): MNHN.F.MAE126 (holotype)	Lires *et al.* (2016)	–
Batropetes palatinus Glienke, 2015: MB.Am.1232	This work; Glienke (2015)	Measured on the specimen and validated with measurements in the literature
B. appelensis Glienke, 2015: MNHM PW 2001/308-LS (holotype)	Glienke (2015)	–
B. palatinus: MNHM PW 2001/306-LS	Glienke (2015)	–
B. palatinus: MNHM PW 2001/307-LS (holotype)	Glienke (2015)	–
B. palatinus: MNHM PW 2001/309-LS	Glienke (2015)	–
B. niederkirchensis Glienke, 2013: SMNS 55884 (holotype)	Glienke (2013)	–
B. fritschi (Geinitz & Deichmüller, 1882): SLFG SS 13558/SS 13559 (lectotype)	Glienke (2013)	–
Celtedens ibericus McGowan & Evans, 1995: LH 6020 (holotype) left side	McGowan (2002)	–
C. ibericus: LH 030 R left side	McGowan (2002)	–
Platyrhinops lyelli (Wyman, 1858): AMNH 6841 (holotype) right side	Clack & Milner (2009)	Measured on specimen photo
Doleserpeton annectens Bolt, 1969: FMNH UR 1320, 1321, 1381, 1382	Sigurdsen & Bolt (2010)	Reconstruction as well as separate specimens scaled to same size
Pantylus cordatus Cope, 1881: UT 40001-1, UT 40001-6	Carroll (1968)	Illustrated specimens
Micropholis stowi Huxley, 1859: BSM 1934 VIII E	Schoch & Rubidge (2005)	Illustrated limb bones (Fig. 6)
M. stowi: BSM 1934 VIII C	Schoch & Rubidge (2005)	Illustration of specimen BSM 1934 VIII A–E (Fig. 5)
Tuditanus punctulatus Cope, 1875: forelimb: AMNH 6926 (holotype); hindlimb: USNM 4457	Carroll & Baird (1968)	Measured on specimen photos
Diabloroter bolti Mann & Maddin, 2019: ACFGM V-1634 (holotype)	Mann & Maddin (2019)	–

In the LDA, the LU and LUD clusters do not separate well in most comparisons (Figs 4-6; Appendices 2-4). Indeed, the right side of MB.Am.1232 is classified as LU, the left side as LUD (Table 3). Only the comparison of canonical variant 1 to canonical variant 4 (Fig. 5; Appendix 2) shifts the digging individuals further away from all other locomotor categories, but they still retain a large overlap. This is in part due to the wide definition of "digging" in the analysis, and in part to the facts that LU is the plesiomorphic state and that LUD is directly derived from it (while e.g. Sw is evolutionarily derived from J, not directly from LU). Nonetheless, MANOVA finds all five locomotor categories to be clearly distinct (F = 50.037, df = 16 and *p*-value = 9.28×10^{-109}, well below the detection threshold of 2.2×10^{-16}).

The LDA prediction of the added extinct taxa using Bayesian posterior probability (Table 3) recovers most of them as digging and plots them outside the overlap area of LU and LUD (Fig. 5; compare Fig. 4), but classifies one of the *Batropetes* specimens (the only one included of *B. fritschi* (Geinitz & Deichmüller, 1882)) as a toad-like HW. The other *Batropetes* specimens are classified as LUD, except for the right side of MB.Am.1232 as mentioned.

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

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

Doleserpeton Bolt, 1969 is the only taxon that does not cluster with any of the defined groups representing locomotor categories in Figures 4 and 5. It plots as a distant outlier in the LDA (Figs 4-6), because once the measurements are divided by the geometric mean, the femur length appears to be smaller than in all other specimens used in this analysis, while the radius-ulna length appears to be greater. Because sufficiently articulated or associated skeletons are not known (Bolt 1969; Sigurdsen & Bolt 2010; Gee *et al.* 2020), the measurements were taken from different specimens, corrected for size, as well as from the skeletal reconstruction by Sigurdsen & Bolt (2010), and both linear measurements (from the figured bones as well as from the reconstruction) show the same relation once they are divided by the geometric mean. However, we cannot exclude a measurement error in the literature at this point. Nor can we exclude the possibility that some of the measured material comes from other amphibamiform taxa, of which two are known from skulls found at the same site (Fröbisch & Reisz 2008; Anderson & Bolt 2013; Atkins *et al.* 2020), as discussed in detail by Gee *et al.* (2020).

Of the other two amphibamiform temnospondyls that we were able to sample, *Platyrhinops* Steen, 1931 is classified as a lateral undulator as expected, with absence of digging behavior (LU) weakly favored (BPP = 59 %) over its presence (LUD; BPP = 41 %), while *Micropholis* Huxley, 1859, with its particularly short trunk and long limbs (Schoch & Rubidge 2005), emerges unambiguously as a hopper/walker (90 % and 95 % for the two specimens) – more froglike in this respect than *Triadobatrachus* (BPP = 71 % for LU, < 0.1 % for HW). The LDA reveals that *Micropholis* is particularly close to *Bufo bufo* (Linnaeus, 1758) in linear discriminants 1 and 2, though widely separated by linear discriminant 4 (Figs 4; 5; Appendix 2).

The three "microsaurs" other than *Batropetes* are classified as lateral undulators, in agreement with their interpretations as terrestrial in the literature. For *Tuditanus* Cope, 1871, with its particularly lizardlike proportions (very similar to those of contemporary early amniotes of the same size), LU is favored

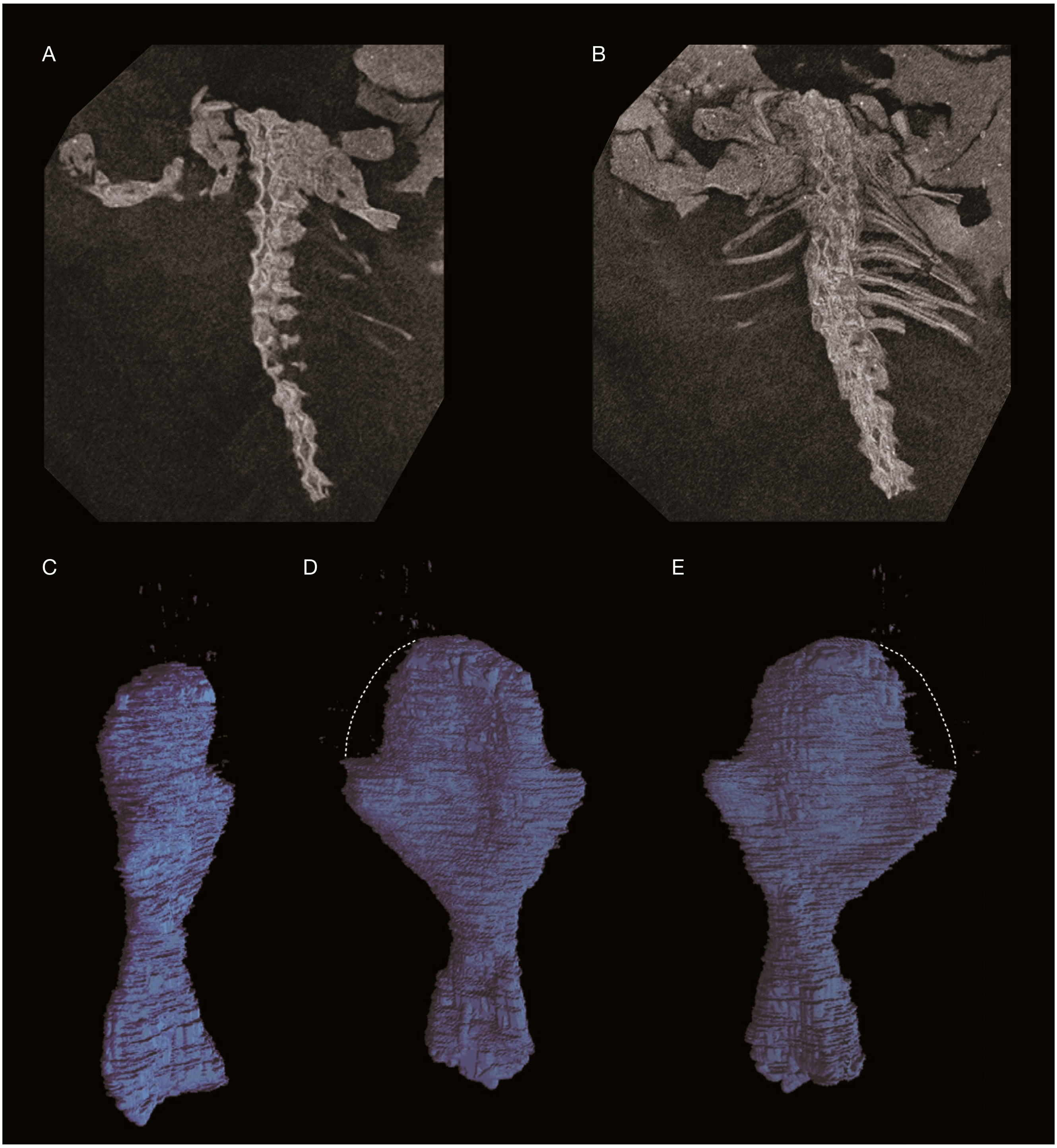

Fig. 3. — **A**, **B**, CT images showing thin cortex in the craniodorsal part of the vertebral column and the humerus of *Batropetes palatinus* Glienke, 2015 (MB. Am.1232); **C**-**E**, right humerus in anterior (**C**), dorsal (**D**) and ventral views (**E**); the stippled line indicates a broken portion of the dorsal process (not shown in **C**) opposite the deltopectoral process.

(64%) over LUD (36%), while the opposite is the case for the early brachystelechid *Diabloroter* Mann & Maddin, 2019 (34% vs 66%), and for the particularly stocky *Pantylus* Cope, 1881 (20% vs 80%).

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

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

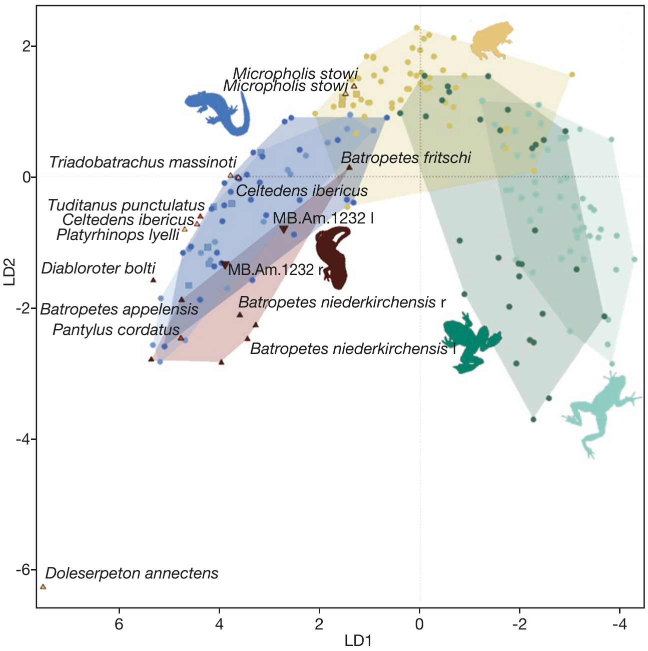

FIG. 4. — First two canonical axes of the discriminant function analysis (LDA) of corrected morphometric variables and the five defined locomotor categories. Locomotor categories: ●, HW; ●, J; ●, LU; ●, LUD; ●, Sw. Symbols: ▲, Brachystelechids (always *Batropetes palatinus* Glienke, 2015 if unlabeled) – the two larger triangles that point downward mark the left and the right side of MB.Am.1232 –; ▲, other "microsaurs"; △, amphibamiform temnospondyls; △, lissamphibians; **squares** indicate *Ambystoma tigrinum* (Green, 1825) (■, LUD) and *Bufo bufo* (Linnaeus, 1758) (■, HW); for a version with every extant taxon labeled, see Appendix 3. All extinct taxa plot within or closest to the LU/LUD cluster. Extant taxa from Lires *et al.* (2016), distinction of LU and LUD from Oliveira *et al.* (2017a, b). Abbreviations: **HW**, hopping and walking; **J**, jumping; **l**, left side; **LD**, linear discriminants; **LU**, laterally undulating, not digging; **LUD**, laterally undulating, digging to some degree; **r**, right side; **Sw**, swimming.

DISCUSSION

THE LOCOMOTION AND FORAGING MODE OF *BATROPETES* AND OTHER BRACHYSTELECHIDS

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

The same is suggested by the general proportions of all species of *Batropetes* (Fig. 3). As noted in previous works (Carroll 1991; Glienke 2013, 2015), *Batropetes* has an unusually short vertebral column for a "microsaur": depending on the species (Glienke 2015), there are only 17 to 19 vertebrae in the presacral region. Carroll (1998) stated that this number is the smallest known in any "microsaur", a statement that is – apart from the 17 presacral vertebrae of its fellow brachystelechid *Diabloroter* (Mann & Maddin 2019) – still valid by a considerable margin (the next smallest number is 24, for *Pantylus*: Carroll 1998) but has to be considered carefully. For many of the known "microsaurs", particularly the other described brachystelechids, only fragmentary postcrania (*Carrolla* Langston & Olson, 1986) or none (*Quasicaecilia* Carroll, 1990) are known, though there is evidence that *Carrolla* had *Batropetes*-like proportions (Mann *et al.* 2019b). (*Brachystelechus* Carroll & Gaskill, 1978 is a junior synonym of *Batropetes* [see Carroll 1991]. Further brachystelechids have not been described.) Similar numbers of presacral vertebrae are found in the very stoutest amphibamiform temnospondyls (*Gerobatrachus* Anderson, Reisz, Scott, Fröbisch & Sumida, 2008 has 17, various "branchiosaurids" have 19 or more, *Micropholis* has 20 to 21 [Broili & Schröder 1937; Boy 1985; Schoch & Rubidge 2005: fig. 5]) and in early crown-group salamanders.

Within this general locomotor mode, the unusually large forelimbs and the very large, thoroughly ossified shoulder girdle of *Batropetes* indicate large muscle attachment sites, as Glienke (2013, 2015) also inferred from the expanded ends of the limb bones; the robust first metacarpals and first manual digits further suggest some kind of digging behavior. The claw-like terminal phalanges may specifically fit scratch-digging, as does the fact that the hands are not broadened into shovels, but are instead quite narrow: of the four metacarpals, the fourth is the shortest and narrowest, and bears only a single phalanx, which has, however, the same clawlike shape and almost the same size as the other terminal phalanges. However, the large and robust humerus is not further reinforced by a thickened cortex as often occurs in limb-based diggers.

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

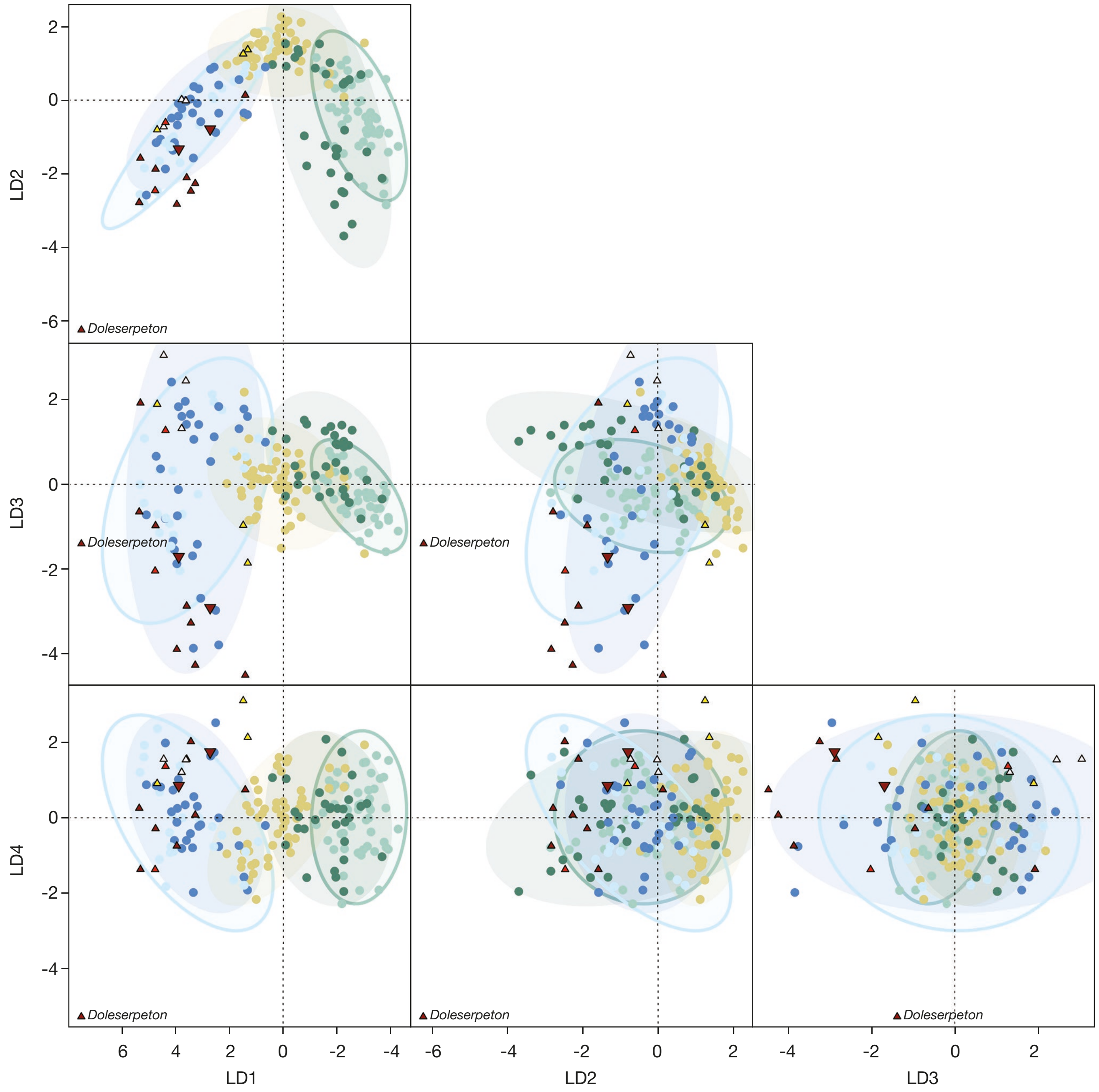

FIG. 5. — Comparisons of all linear discriminants, with 95% confidence intervals for all tested locomotor groups. Locomotor categories: ●, HW; ●, J; ●, LU; ●, LUD; ●, Sw. Symbols: ▲, fossil specimens, the two that point downwards are the left and the right side of MB.Am.1232; ▲, other “microsaurs”; △, amphibamiform temnospondyls; △, lissamphibians. The comparison (top left) of linear discriminant (LD) 1 and LD2 is identical to Figure 4 and Appendix 3, the comparison of LD1 and LD4 (bottom left) is identical to Appendices 2 and 4. Abbreviations: **HW**, hopping/walking; **J**, jumping; **l**, left side; **LD**, linear discriminants; **LU**, laterally undulating, not digging; **LUD**, laterally undulating, digging to some degree; **r**, right side; **Sw**, swimming.

apparently *Quasicaecilia* (Pardo *et al.* 2015), and seemingly only weakly in *Diabloroter* (Mann & Maddin 2019).

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

AN EXTANT MODEL?

The extant species of *Ambystoma*, or at least their terrestrial forms, are called mole salamanders because they are often found under logs, in leaf litter, or in crevices in the ground. Many occupy burrows dug by other animals. Although they often enlarge existing hollows, most species neither use a systematic method to do so, nor do most of them initiate burrows; of the five species that Semlitsch (1983) observed in an experimental setting, three (*A. opacum* (Gravenhorst, 1807), *A. annulatum* Cope, 1886, *A. maculatum* (Shaw, 1802)) did not dig into a moist sandy soil even when their life was threatened by desiccation, and one (*A. talpoideum* Holbrook, 1838) only did in half of the cases.

> "Its snout appeared to 'plow' a hole into the soil with little use of its forelimbs to dig. *Ambystoma talpoideum* were never found more than 10 cm inside the entrance of a burrow." (Semlitsch 1983: 617)

Ambystoma tigrinum (Green, 1825), however, routinely dug burrows in the experiment, "sometimes initially making a slight depression with its snout and then alternately using both forelimbs to dig", and ending up "10–70 cm from the burrow entrance" (Semlitsch 1983: 617).

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

Ambystoma maculatum, *A. mexicanum* (Shaw & Nodder, 1798) (the neotenic axolotl) and *A. tigrinum* are included in our LDA. In Figure 4, which compares the first two linear discriminants, *A. tigrinum* (as well as the other *Ambystoma* species included) fills the space between the extinct taxa classified as LUD by the MANOVA (brachystelechids and *Pantylus* [Table 3]) and those classified as LU; in Appendix 2, which compares the first and the fourth linear discriminant, it overlaps entirely with the former cluster.

The postmetamorphic teeth of *Ambystoma* are small, numerous, pedicellate and linguolabially bicuspid, as usual for salamanders or indeed lissamphibians generally and not particularly like the condition seen in *Batropetes* or *Carrolla*. Indeed, *Ambystoma* spp. are rather generalist predators not limited to tiny prey (AmphibiaWeb 2022). However, *Ambystoma* dentitions often show adaptations that prevent the teeth from penetrating prey so deeply that the prey would get stuck. These may include mesiodistally expanded, blade-shaped cusps, inflated cusps with corrugated surfaces, dense arrangements of teeth in up to five rows on one bone, or the third cusp on the dentary teeth of *A. mabeei* Bishop, 1928 (Beneski & Larsen 1989: fig. 7H). The small-sized *A. mabeei* is known to eat earthworms (AmphibiaWeb 2022). Possibly, then, the mesiodistally tricuspid teeth of *Batropetes* and *Carrolla* and the linguolabially tricuspid dentary teeth of *A. mabeei* (Fig. 7) are adaptations to relatively large rather than relatively small prey. However, these possibilities need not be mutually exclusive. Indeed, at the same time as drawing attention to the number of cusps of *Batropetes*, Glienke (2015) pointed out that only the cusps bear enamel, while the stalk of each tooth crown consists of dentine only; this may have rendered the teeth somewhat flexible and avoided damage in attacks on much larger, struggling prey, not unlike the weakly mineralized or unmineralized hinge zone of the pedicellate teeth widely found in lissamphibians.

Linguolabially tricuspid teeth (with blade-shaped cusps in all cases) have also been reported in five extant anuran species (the alytid *Alytes obstetricans* (Laurenti, 1768), the rhacophorid *Polypedates maculatus* (Gray, 1830), the hyperoliid *Heterixalus madagascariensis* (Duméril & Bibron, 1841) and the hylids *Agalychnis callidryas* (Cope, 1862) and *Phyllomedusa bicolor* (Boddaert, 1772): Greven & Ritz 2009). Unfortunately, the function of such teeth, in anurans as well as in *Ambystoma mabeei*, remains very poorly understood; diets of anurans are generally understudied and insufficiently documented. However, *Al. obstetricans* – coincidentally a forelimb-based burrower (Nomura *et al.* 2009) – preys on large arthropods, earthworms and slugs, as well as ants (Glandt 2018: 161); and *P. maculatus* is known to have an unusually wide prey size range that includes insect larvae as well as large arthropods and small vertebrates (Das & Coe 1994). Tricuspid teeth therefore seem to be compatible with both small and very large prey relative to the predator's own size.

The three similarly tall, mesiodistally arranged cusps of the teeth of *Batropetes* have invited comparison (Mann & Maddin 2019) to those of the extant marine iguanas (*Amblyrhynchus* Bell, 1825), which scrape algae off rocks in the sea, and to the mesial teeth of the Early Triassic amphibamiform temnospondyl *Tungussogyrinus* Efremov, 1939, all known individuals of which seem to have been aquatic (larval or possibly neotenic). A lifestyle as aquatic or amphibious herbivores, however, is contradicted not only by the lack of unambiguous adaptations for swimming or diving – notably osteosclerosis – in *Batropetes*, but also by the shapes of the teeth themselves: the apical part of the crown, measured across all three cusps, is much wider mesiodistally in

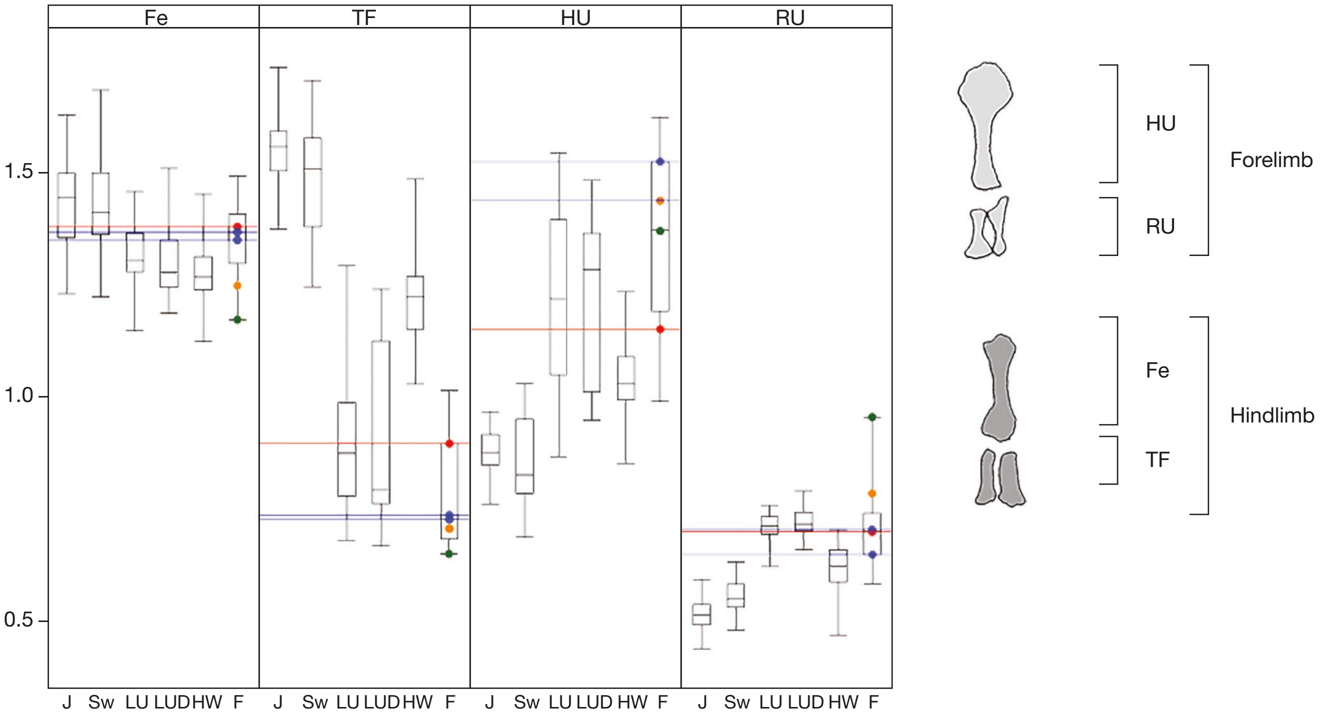

Fig. 6. — The different locomotor categories and selected fossil specimens (**F**, not assigned to a locomotor category) are plotted against the linear measurements of the long bones (in mm) of all included taxa. Box plots show the variation in length. Locomotor categories: **HW**, hopping/walking; **J**, jumping; **LU**, laterally undulating, not digging; **LUD**, laterally undulating, digging to some degree; **Sw**, swimming. Colours: **red dots and lines**, *Triadobatrachus* Kuhn, 1962; **blue**, left and right sides of MB.Am.1232 (*Batropetes palatinus* Glienke, 2015); **orange**, *Pantylus* Cope, 1881; **green**, *Doleserpeton* Bolt, 1969. The drawings at the right show the holotype of *Batropetes palatinus* (after Glienke 2015: fig. 1A). Abbreviations: **Fe**, femur; **HU**, humerus; **RU**, radius and ulna; **TF**, tibia and fibula.

Amblyrhynchus than the basal stalk part, and the apical parts of successive teeth more or less touch or overlap, forming a largely continuous cutting surface (e.g. Miralles *et al.* 2017: figs 9D; 10A), while there is scarcely any, and on average no, such apical widening in *Batropetes*, where the noticeable gaps between the teeth extend for the entire height of the teeth (Glienke 2013: fig. 3A, B; 2015: fig. 10K-O; *contra* Carroll 1991). We prefer to compare the teeth of *Amblyrhynchus* to the quite similar teeth of its terrestrial sister-group, the herbivorous Galápagos land iguanas (*Conolophus* spp.), which are identical except for more prominent central cusps and, in the more distal teeth, an additional mesial fourth cusp (Melstrom 2017: fig. 1D). This shape seems to be a special case of the leaf-shaped, coarsely denticulated tooth crowns of other herbivorous and omnivorous squamates (e.g. Melstrom 2017: figs 10A, B; 11D) and indeed most herbivores among toothed non-mammalian amniotes – not to mention certain Permian aquatic seymouriamorphs (Bulanov 2003) among non-amniotes. The combination of three cusps with a lack of apical widening of the crown in *Batropetes* and *Carrolla* (Fig. 7) is instead shared with many insectivorous squamates (e.g. Melstrom 2017: figs 1B; 3; 9B, D). Apart from the size of the cusps, this shape is also found in the albanerpetid near-lissamphibians. The teeth of *Batropetes palatinus* and the albanerpetids *Albanerpeton* Estes & Hoffstetter, 1976 and *Anoualerpeton* Gardner, Evans & Sigogneau-Russell, 2003, and the mesial teeth of *Tungussogyrinus*, are compared in Werneburg (2009: fig. 10).

Digging in brachystelechids in phylogenetic context

Recently, four phylogenetic analyses based on two very different large datasets (Pardo *et al.* 2017b: ext. data fig. 7; Marjanović & Laurin 2019; Mann & Maddin 2019; Mann *et al.* 2019a) found Brachystelechidae Carroll & Gaskill, 1978 and Lysorophia Romer, 1930 as sister-groups. In some ways, this is an odd pair. The lysorophians, in all four analyses represented by *Brachydectes* Cope, 1868 (Pardo & Anderson 2016), and in the fourth also by *Infernovenator* Mann, Pardo & Maddin, 2019 (Mann *et al.* 2019a), are very long-bodied animals (with up to 97 presacral vertebrae) whose limbs are correspondingly small (though the digits are not reduced in number). Their skulls show some adaptations to head-first digging (Pardo & Anderson 2016). Daza *et al.* (2020: fig. S15) updated the scores of Albanerpetidae Fox & Naylor, 1982 in Marjanović & Laurin (2019), applied implied weighting, and found Brachystelechidae and Lysorophia as successively closer relatives of Albanerpetidae + Lissamphibia.

The further relationships of this grouping remain unclear. The two very different datasets of Vallin & Laurin (2004) and Marjanović & Laurin (2019: fig. 14) found *Rhynchonkos* Schultze & Foreman, 1981 to be closely related; it seems to have been a head-first burrower (only the skull is known). However, this position of *Rhynchonkos* appears to depend on the lissamphibians: when some or all lissamphibians are constrained to be temnospondyls, *Rhynchonkos* groups next to a clade formed by the head-first burrowing Gymnarthridae

Case, 1910 and Ostodolepididae Romer, 1945 in Marjanović & Laurin (2019: figs 15; 17). Such a clade was also found by Daza *et al.* (2020: fig. S15) despite the lack of a constraint. Postcranial material is known from *Aletrimyti* Szostakiwskyj, Pardo & Anderson, 2015, a taxon found as a close relative of *Rhynchonkos* by Pardo *et al.* (2017b), Mann & Maddin (2019) and Mann *et al.* (2019a), and indeed included in *Rhynchonkos* until the taxonomic revision by Szostakiwskyj *et al.* (2015). (Marjanović & Laurin [2019] preferred not to include it in their phylogenetic analysis to avoid straining the character sample.) *Aletrimyti* is moderately elongate and has limbs similar to those of *Brachydectes*. Rhynchonkidae Zanon, 1988, Gymnarthridae and Ostodolepididae also formed a clade in Pardo *et al.* (2017b), where, however, very few other "microsaurs" were included in the sample, as well as in the unconstrained exploratory Bayesian analysis of Marjanović & Laurin (2019: fig. 20). Adding "microsaurs" to the matrix of Pardo *et al.* (2017b), Mann & Maddin (2019) found a clade of gymnarthrids and rhynchonkids but not necessarily ostodolepidids; Mann *et al.* (2019a) found a clade of gymnarthrids, rhynchonkids and brachystelechids + lysorophians as the sister-group of Ostodolepididae. Gymnarthridae and Ostodolepididae did not approach Brachystelechidae + *Brachydectes* in any analyses of Marjanović & Laurin (2019).

The hapsidopareiid "microsaurs" may be similarly close to Brachystelechidae + Lysorophia (Marjanović & Laurin 2019: fig. 14; Gee *et al.* 2019; Daza *et al.* 2020: fig. S15). One of them, *Llistrofus* Carroll & Gaskill, 1978, was recently redescribed as having cranial adaptations for digging, though not as strongly developed as in the brachystelechid *Carrolla* (Gee *et al.* 2019); this was interpreted as indicating that *Llistrofus* lived in leaf litter, in crevices or in burrows dug by other animals, and was compared to the abovementioned *Ambystoma*.

In the unconstrained parsimony analysis of the full dataset of Marjanović & Laurin (2019: fig. 14), and similarly in Daza *et al.* (2020: fig. S15), Lissamphibia is even closer to Brachystelechidae + *Brachydectes* than *Rhynchonkos* or Hapsidopareiidae Daly, 1973. It is likely that some amount of digging behavior is plesiomorphic for Lissamphibia: except for the extant, highly nested typhlonectids, all known total-group caecilians (Gymnophionomorpha) are fossorial (Jenkins *et al.* 2007), and a lesser degree of head-based digging is inferred (Wiechmann 2000; Gardner 2001; and references therein) for Albanerpetidae, a clade extinct since the early Pleistocene that appears to be the sister-group of Lissamphibia (Daza *et al.* 2020). Daza *et al.* (2020), followed by Skutschas *et al.* (2021), briefly argued for an arboreal lifestyle in at least some albanerpetids, based mostly on the ballistic tongue and the curved terminal phalanges. The smallest chameleons live in leaf litter, however, and plethodontid salamanders with ballistic tongues span about the same range of lifestyles. Clawlike terminal phalanges are shared, as it happens, with *Batropetes*.

There is no evidence of digging behavior in early urodeles or salientians. However, almost all early (i.e., Jurassic) urodeles known to date are only known from skeletally immature individuals, prompting Skutschas (2018) to suggest that neoteny is plesiomorphic for urodeles and that metamorphic life-history strategies are derived within the clade; in that case, some of the morphology of postmetamorphic urodeles may not be homologous with that of other animals, and their lifestyles evidently would not be (see, however, Jia *et al.* 2022).

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

THE ORIGIN OF JUMPING AND LANDING IN SALIENTIANS

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

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

Gans & Parsons (1965) reviewed the then current hypotheses on the origin of jumping as a basic locomotor mode in salientians. In that time, no Jurassic salientians (or other modern amphibians) were yet known, both the anatomy of *Triadobatrachus* (cited under its preoccupied name *Protobatrachus* Piveteau, 1936) and its relevance to early salientian evolution were poorly understood, other Triassic salientians were unknown, and even the behavior of the extant amphicoelan frogs (*Ascaphus* Stejneger, 1899 and *Leiopelma* Fitzinger, 1861) that has figured so prominently in the most recent works on this topic (Essner *et al.* 2010; Sigurdsen *et al.* 2012; Herrel *et al.* 2016) had yet to be observed in detail. Under these limitations, Gans & Parsons (1965) made two important postulates: 1) "Pre-frogs" were, at first, fundamentally aquatic animals that climbed the shore to search for food, but escaped predators by fleeing into the water. Jumping was an escape mechanism from land into water before it also became a mode of locomotion on land; as jumping abilities gradually improved, the pre-frogs were gradually able to increase their radius of activity on land without losing the ability to escape into the water. Thus, the ability to land was trivial, because it was the ability of small animals to land in water after a brief fall. Only the ability to land on dry land would have had to evolve after the ability to jump; and 2) the very origin of jumping was to be found in sit-and-wait predation, as pre-frogs would keep their heads well above the ground by propping themselves up with their forelimbs, then, when prey approached, pivot over their hands by extending one hindlimb or two; the simultaneous use of both hindlimbs emerged as the better solution and was favored by natural selection. We think both of these hypotheses are now testable.

In support of hypothesis 1, Essner *et al.* (2010) and Herrel *et al.* (2016) pointed out that the extant amphicoelans, the sister-group to the rest of the anuran crown-group, generally do not use their forelimbs to decelerate when they land from a jump; amphicoelans are small, do not jump often, and mostly jump into water. Both Essner *et al.* (2010) and Herrel *et al.* (2016) followed Gans & Parsons (1965) in suggesting that this lifestyle was ancestral for the anuran crown-group and beyond, so that the use of the forelimbs as shock absorbers would only have evolved in the sister-group of Amphicoela Scudder, 1882. This hypothesis does not, however, seem to explain how the forelimbs became adapted to providing this function in the latter half of the crown-group. Furthermore, Sigurdsen *et al.* (2012) pointed out two interesting facts: *Leiopelma* pronates the forearms before landing, despite not usually landing on its hands; and both *Ascaphus* and *Leiopelma* have features that are considered related to this use of the forelimbs, such as the fusion of radius and ulna, which is not only present throughout the crown-group without exception, but also found outside the crown-group in the Jurassic stem-salientians *Notobatrachus* Reig in Stipanicic & Reig, 1955, *Vieraella* Reig, 1961 and *Prosalirus* (Báez & Basso 1996; Jenkins & Shubin 1998; Báez & Nicoli 2004; Sigurdsen *et al.* 2012). We therefore follow Sigurdsen *et al.* (2012) in regarding the lifestyle and locomotion of Amphicoela in general and *Ascaphus* in particular as autapomorphic, and conversely the use of the forelimbs to absorb the impact of landing as plesiomorphic for the anuran crown-group.

This interpretation is further bolstered by the shoulder girdle. The contact between the left and the right shoulder girdle is formed by soft tissue (mostly cartilage) that is elastic to compression in extant anurans, amphicoelans included, and thus functions as a shock absorber (Emerson 1984; Havelková & Roček 2006). Only the ossified parts are known in extinct taxa, but their shape suggests that this additional shock absorber was in place not only in the Cretaceous *Liaobatrachus* Ji & Ji, 1998 (Dong *et al.* 2013: fig. 7), which may belong just inside or just outside the crown-group, but even in the Jurassic stem-salientian *Notobatrachus* (Báez & Nicoli 2004), though probably not in *Triadobatrachus* (Ascarrunz *et al.* 2016).

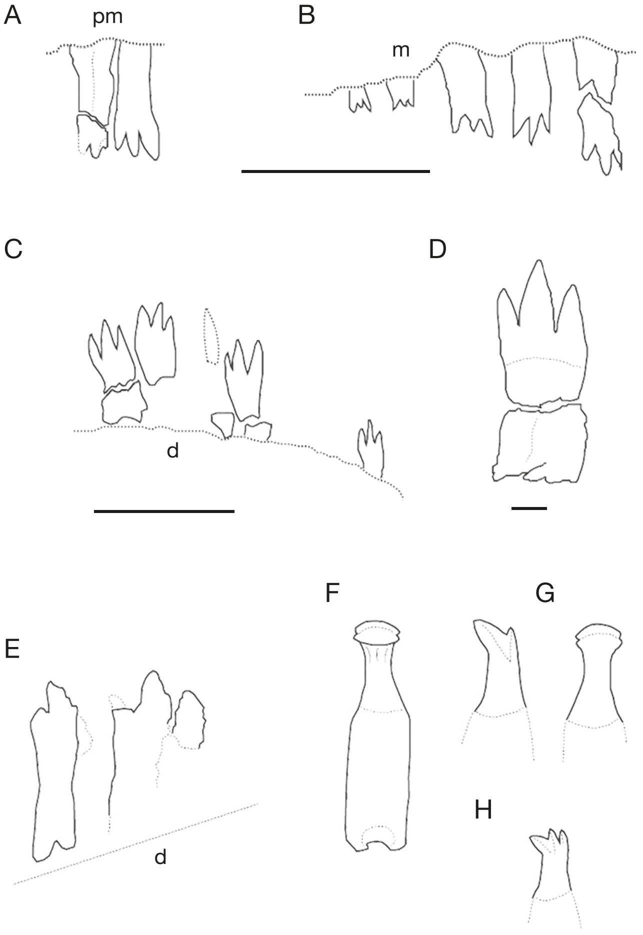

Fig. 7. — Illustration of teeth of several “microsaurs” and salamanders: **A**, *Batropetes palatinus* Glienke, 2015, MNHM PW 2001/309, left premaxilla; **B**, *B. palatinus*, MNHM PW 2001/307, right maxilla; **C**, *B. palatinus*, MNHM PW 2001/307, right dentary; **D**, *B. palatinus*, MNHM PW 2001/307, isolated dentary tooth; **E**, *Carrolla craddocki* Langston & Olson, 1986, TMM 40031-54, left dentary (left side), not to scale, **F**, **G**, general organisation of adult caudate tooth in lingual and mesial or distal views, similar to tooth morphology of *Ambystoma* Tschudi, 1838; **H**, shows a tricuspid tooth as found in *A. mabeei* Bishop, 1928. Sources: A-D, after Glienke (2015); E, based on Mann *et al.* (2019b), F-H, summarized from Beneski & Larsen (1989). Abbreviations: d, dentary; m, maxilla; pm, premaxilla. Scale bars: A-C, 1 mm; D, 0.1 mm.

Thus, we postulate that jumping evolved instead among mostly or entirely terrestrial walkers that escaped predators by hiding or perhaps running on land rather than by jumping into water. Terrestrial walking has a long history among the potential relatives of jumping salientians. Lires *et al.* (2016) found, and we confirm (Figs 4-6; Table 3), that *Triadobatrachus* locomoted by lateral undulation, agreeing with its latest redescription (Ascarrunz *et al.* 2016) as not a habitual or good jumper; although lateral undulation is equally compatible with walking and swimming, the highly reduced tail in combination with the short trunk argues strongly against the latter option. The numerous isolated bones described as *Czatkobatrachus* (Evans & Borsuk-Białynicka 2009), among them long, gracile, but very well ossified limb bones, are at the very least compatible with an ecologically *Triadobatrachus*-like animal. Outside Salientia, the presence of very short trunks in all Triassic (Schoch *et al.* 2020) to Early Cretaceous urodeles argues at least for a terrestrial walking ancestry of these animals (most of which are only known from individuals that had not undergone metamorphosis and were therefore aquatic); there is no evidence for a water-bound adult lifestyle in early gymnophionomorphs or albanerpetids. Beyond the modern amphibians, we have to turn both to the amphibamiform temnospondyls (Fig. 1C-F) and to the brachystelechid “microsaurs” (Fig. 1D, E) to cover the phylogenetic possibilities. Bone microanatomy suggests a terrestrial lifestyle both in the amphibamiform *Doleserpeton* (more or less: Laurin *et al.* 2004; see also Gee *et al.* 2020) and, as we report here, the brachystelechid *Batropetes palatinus*; the amphibamiform *Micropholis* has also been qualitatively described as terrestrial (McHugh 2015), though the very thick cortex reported there

TABLE 3. — Locomotion mode predictions of the LDA of the extinct taxa in our dataset. The numbers are the Bayesian posterior probabilities for each locomotion mode. *Doleserpeton* Bolt, 1969, is an extreme outlier (Figs 4-6). Abbreviations: **HW**, hopping/walking; **J**, jumping; **LU**, laterally undulating, not digging; **LUD**, laterally undulating, digging to some degree; **Sw**, swimming.

Specimens	Locomotion mode	J	Sw	LU	LUD	HW
Triadobatrachus massinoti (Piveteau, 1936): MNHN.F.MAE126 (holotype)	LU	3.01E-10	3.67E-07	0.710651	0.288364	0.000985
Batropetes palatinus Glienke, 2015: MB.Am.1232 left side	LUD	2.48E-10	3.86E-08	0.46604	0.533916	4.48E-05
B. palatinus: MB.Am.1232 right side	LU	4.83E-07	6.90E-06	0.60321	0.392094	0.004689
B. appelensis Glienke, 2015: MNHM PW 2001/308-LS (holotype)	LUD	8.29E-13	6.96E-10	0.320407	0.679592	9.92E-07
B. palatinus: MNHM PW 2001/306-LS	LUD	1.46E-14	3.59E-11	0.259963	0.740037	2.40E-08
B. palatinus: MNHM PW 2001/307-LS (holotype)	LUD	1.42E-08	1.74E-07	0.295067	0.704894	3.95E-05
B. palatinus: MNHM PW 2001/309-LS	LUD	1.46E-10	5.84E-09	0.195283	0.804715	1.33E-06
B. niederkirchensis Glienke, 2013: SMNS 55884 (holotype) left side	LUD	4.59E-09	1.34E-07	0.416793	0.583189	1.82E-05
B. niederkirchensis: SMNS 55884 (holotype) right side	LUD	1.71E-09	1.45E-07	0.422295	0.577682	2.31E-05
B. fritschi (Geinitz & Deichmüller, 1882): SLFG SS 13558/SS 13559 (lectotype)	HW	0.000973	0.000795	0.25385	0.137076	0.607305
Celtedens ibericus McGowan & Evans, 1995: LH 6020 (holotype) left side	LU	1.40E-09	2.97E-06	0.780707	0.216535	0.002755
C. ibericus: LH 030 R left side	LU	1.91E-09	5.82E-06	0.805259	0.192301	0.002434
Platyrhinops lyelli (Wyman, 1858): AMNH 6841 (holotype) right side	LU	8.84E-13	5.48E-09	0.592132	0.407855	1.26E-05
Doleserpeton annectens Bolt, 1969: FMNH UR 1320, 1321, 1381, 1382	LUD	3.32E-21	1.07E-16	0.012122	0.987878	7.63E-15
Pantylus cordatus Cope, 1881: UT 40001-1, UT 40001-6	LUD	7.06E-13	2.93E-10	0.197864	0.802135	2.41E-07
Micropholis stowi Huxley, 1859: BSM 1934 VIII E	HW	6.23E-05	0.000715	0.088317	0.01057	0.900335
M. stowi: BSM 1934 VIII C	HW	0.000112	0.000531	0.040551	0.00654	0.952266
Tuditanus punctulatus Cope, 1875: forelimb: AMNH 6926 (holotype); hindlimb: USNM 4457	LU	7.01E-12	1.79E-08	0.63513	0.364823	4.61E-05
Diabloroter bolti Mann & Maddin, 2019: ACFGM V-1634 (holotype)	LUD	0.00	0.00	0.3412	0.6588	0.00

suggests the possibility that *Micropholis* was actually amphibious. Interestingly, our analyses of limb proportions find (Figs 4-6; Table 3) that both *Micropholis* and *Batropetes fritschi* cluster with toads and other hopping or walking anurans that are not habitual long-distance jumpers, but do not make use of lateral undulation either. In sum, no matter whether salientians are temnospondyls or "microsaurs", they are nested in a group with a mostly terrestrial history that reaches back to the Early Permian (if not earlier), and jumping most likely evolved in a terrestrial context together with one of three independent reductions of lateral undulation.

Having cast great doubt on hypothesis 1, we need to predict animals that were able to land safely on dry land but not to jump. We think that Sigurdsen *et al.* (2012) found one, and that we can offer another.

Sigurdsen *et al.* (2012) reviewed the anatomical adaptations to the use of the forelimbs as shock absorbers in landing. One of them, the apomorphic lateral deflection of the deltopectoral crest (or at least a shallow concavity lateral to the crest), was to varying degrees found in all investigated extant anurans (including *Leiopelma*), except for the more or less straight ventral orientation of the crest (without a simple concavity) in *Ascaphus*. Lateral deflection was likewise found in the Jurassic stem-salientians *Notobatrachus* and *Vieraella* as well as, if it is not due to crushing in this case, *Prosalirus*. Surprisingly, it was also found in the Early Triassic stem-salientian *Triadobatrachus*. We here report it in *Batropetes palatinus* as well. The presence of this anatomical feature suggests that *Triadobatrachus* and *Batropetes* could have landed safely if they could have jumped – which they could not, at least not as a routine mode of locomotion (*Triadobatrachus*: Ascarrunz *et al.* 2016; Lires *et al.* 2016; Table 3; *contra* Sigurdsen *et al.* 2012, who assumed the ability to jump based only on the ability to land; *Batropetes*: Table 3). The plesiomorphic medial deflection, in contrast, was found in all caudates considered by Sigurdsen *et al.* (2012), as well as in *Eocaecilia* and the amphibamiform *Doleserpeton*. The humeri referred to the Early Triassic stem-salientian *Czatkobatrachus* were found to have an intermediate condition – a just barely medially deflected crest with a large lateral attachment site for the deltoideus clavicularis muscle.

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

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

All this leads us to the following scenario. Although its details are rather speculative at present, they are testable by future discoveries of further fossils. More of its stages can be identified with known parts of the tree under the lepospondyl hypothesis than under the temnospondyl hypothesis of

Fig. 8. — Life reconstruction of *Batropetes palatinus* Glienke, 2015, as an animal that used its forelimbs to scratch in leaf litter or topsoil. Credits: original artwork by M. Jansen.

lissamphibian origins, so we illustrate the scenario on the former hypothesis first – but none of the hypotheses in Figure 1 contradict the scenario given our current knowledge of the fossil record, and all require convergence between amphibamiform temnospondyls and brachystelechids in any case.

AN EVOLUTIONARY SCENARIO

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

The long-bodied, limb-reduced lysorophian *Brachydectes* is often found in burrow casts, and Pardo & Anderson (2016) have shown that its skull was more robust and consolidated than previously thought, as well as that the orbits proper only made up a small part of the large orbitotemporal embayment (which also housed jaw muscles and was ventrally open); even so, they reconstructed a terminal mouth and terminal nostrils, which may argue against routine burrowing in hard or heavy soils. The forelimbs, however, can hardly have played a role in the locomotion or foraging of these elongate animals. The humerus is tiny; the generally incompletely ossified deltopectoral crest shows the plesiomorphic medial deflection, though a shallow lateral concavity is arguably present (Wellstead 1991: fig. 21). Finally, although Pardo & Anderson (2016) argued against the traditional interpretation of *Brachydectes* as aquatic (and burrowing only to estivate), the very plesiomorphic, heavily ossified hyobranchial apparatus (Wellstead 1991; Witzmann 2013) is hard to explain if it did not support external gills or at least open gill slits, and the extremely broad cultriform process of the parasphenoid recalls neotenic salamanders (and, to a lesser degree, highly immature temnospondyls: e.g. Werneburg 2012). The long retention in ontogeny of sutures between the neural arches and the centra, and even between the left and right neural arches (Wellstead 1991; Pardo & Anderson 2016), also argues against weight support and for a decelerated ontogeny (e.g. Marjanović & Laurin 2008). In short, the lysorophian lifestyle may be derived from the one apparently seen in *Batropetes* by body size increase, body elongation and possibly neoteny (or paedomorphosis more broadly). Unfortunately, however, the early life history of brachystelechids, or indeed any "microsaurs", remains completely unknown.

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

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

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

Digging would have been abandoned wholesale in urodeles and salientians, most likely separately, though possibly in their last common ancestor (the first batrachian) if the enlarged size of the limbs was secondarily abandoned in urodeles (perhaps through neoteny: Skutschas 2018; but see Jia *et al.* 2022) as the lateral deflection of the deltopectoral crest would have been in this scenario. The trunk was shortened further (15 presacral vertebrae in *Triadobatrachus*, 16 in the Triassic stem-urodele *Triassurus* Ivachnenko, 1978, 13 in the Jurassic metamorphic stem-urodele *Karaurus* Ivachnenko, 1978), and the limbs elongated further on the salientian side (including *Czatkobatrachus*: Evans & Borsuk-Białynicka 2009) for more efficient walking – as also, independently (regardless of lissamphibian relationships), in the contemporary amphibamiform *Micropholis* – until jumping became possible and drove further elongation of the limbs and further shortening of the trunk. The head remains restricted to dorsoventral movements in batrachians, as in caecilians.

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

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

The amphibamiform *Doleserpeton*, which has played an outsized role in in most hypotheses on lissamphibian origins, plots as an outlier from the laterally undulating cluster (Figs 4; 5). Its proportions with long zeugopods are reminiscent of – much larger – cursorial amniotes and could indicate a unique lifestyle that should be researched further; but we cannot exclude the possibility that the measured bones represent a mixture of the cooccurring amphibamiforms *Doleserpeton*, *Pasawioops* Fröbisch & Reisz, 2008, and ?*Tersomius dolesensis* Anderson & Bolt, 2013 as discussed by Gee *et al.* (2020).

CONCLUSIONS

New data from computed microtomography (µCT) of MB.Am.1232, a skeleton of the Early Permian "microsaur" *Batropetes palatinus* (Fig. 2), allowed us to study the microanatomy of the limb bones and axial skeleton, and thus to infer a terrestrial lifestyle for the taxon that involved digging but not outright burrowing – most likely "rummaging through leaf litter" (Glienke 2013: 90).

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

A mixture of adaptations to walking and digging has led to the hypothesis that the Early Permian "microsaur" *Batropetes* searched for food in leaf litter and perhaps topsoil. Our µCT data confirm that at least *Batropetes palatinus* was terrestrial and not strongly adapted to limb-based burrowing; two statistical analyses of limb proportions, however, indicate that some kind of digging behavior was part of the lifestyle of at least *B. palatinus*, *B. niederkirchensis* and *B. appelensis*. Comparing it further to the extant mole salamander *Ambystoma tigrinum*, we interpret *Batropetes* as a terrestrial scratch-digger that may have used one forelimb to shove leaf litter aside while standing on the other.

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

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

Acknowledgements
Jean-Claude Rage, one of the greatest contributors to the current understanding of *Triadobatrachus* and many other taxa, was one of the giants on whose shoulders we stand. It is tragic that he cannot grow any further. We thank Andrés Lires for access to additional data used in Lires *et al.* (2016), Michael Buchwitz for commenting on a part of a draft of the manuscript, Johan Renaudie for technical support, Florian Witzmann for access to literature, and Raúl Gómez, two anonymous reviewers and the editor Michel Laurin for their reviews which helped strengthen the manuscript. Finally, we would like to commemorate the fact that the number of known extant amphibian species as counted by AmphibiaWeb (2022) surpassed 8 000 on 28 March 2019, 8 100 on 12 December 2019, 8 200 on 22 July 2020, 8 300 on 9 March 2021 and 8400 on 3 November 2021. 48 species published in 2022 bring the count to 8 483 in early July. May this count continue to increase.

Funding

This research did not receive any funding, including any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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Submitted on 1 March 2019;
accepted on 12 February 2021;
published on 6 July 2022.

APPENDICES

Appendix 1. — Measurements (in mm) by Lires *et al.* (2016) and of our added extinct taxa. Abbreviations: **A**, aquatic; **A/T**, aquatic and terrestric at the same time or at different postmetamorphic ontogenetic stages; **F**, fossil (habitat and locomotor mode treated as unknown); **FeL**, femur length; **HuL**, humerus length; **HW**, hopping or walking; **J**, jumping; **LU**, laterally undulating; **LUB**, laterally undulating and digging; **RUL**, radio-ulna length; **Sw**, foot-propelled swimmer; **SwB**, swimming (foot-propelled) and digging; **T**, terrestrial; **TFL**, tibio-fibula length; **WHB**, walking, hopping and digging.

	Taxon	MedGeo	FeL	TFL	HuL	RUL	Family	Locomode	Specimen no.
A/T	*Astylosternus diadematus*	12.065	17.40	20.36	11.47	7.05	Arthroleptidae	J	A 136850 MCZ
A/T	*Astylosternus diadematus*	14.479	21.42	24.21	13.75	8.83	Arthroleptidae	J	A 23249 MCZ
A/T	*Astylosternus diadematus*	10.534	15.47	17.87	9.79	6.17	Arthroleptidae	J	A 136804 MCZ
A/T	*Ascaphus truei*	10.891	14.42	17.55	9.25	6.64	Ascaphidae	J	A 57970 AMNH
A/T	*Ascaphus truei*	13.189	17.39	20.63	12.20	7.89	Ascaphidae	J	A 176858 AMNH
A/T	*Ascaphus truei*	10.261	12.88	16.09	9.69	5.97	Ascaphidae	J	A 57969 AMNH
A/T	*Conraua goliath*	39.948	70.08	71.70	35.29	19.38	Conrauidae	J	A 177110 AMNH
A/T	*Conraua goliath*	62.921	108.88	108.56	60.30	32.80	Conrauidae	J	A 94325 AMNH
A/T	*Cycloramphus asper*	10.560	16.84	17.20	9.05	5.97	Cycloramphidae	J	R 25709 MCZ
A/T	*Cycloramphus asper*	10.921	17.41	18.40	9.59	5.85	Cycloramphidae	J	A 15828 MCZ
A/T	*Cycloramphus asper*	10.794	17.55	18.04	10.21	5.42	Cycloramphidae	J	A 85973 MCZ
A/T	*Thoropa miliaris*	16.992	25.54	29.25	15.10	9.48	Cycloramphidae	J	A 20256 AMNH
A/T	*Thoropa miliaris*	17.321	26.66	29.31	15.61	9.34	Cycloramphidae	J	No. 595 FCEN
A/T	*Hoplobatrachus tigerinus*	17.705	29.13	29.89	17.29	8.29	Dicroglossidae	J	A 57875 AMNH
A/T	*Hoplobatrachus tigerinus*	25.218	39.19	42.25	22.83	13.17	Dicroglossidae	J	A 58077 AMNH
A/T	*Hoplobatrachus tigerinus*	21.040	33.93	34.23	20.48	10.04	Dicroglossidae	J	A 57967 AMNH
A/T	*Mantidactylus majori*	12.969	21.01	22.17	12.43	6.87	Hylidae	J	A 120176 MCZ
A/T	*Mantidactylus majori*	12.841	21.36	22.38	12.59	6.53	Hylidae	J	A 120177 MCZ
A/T	*Mantidactylus majori*	11.558	18.46	18.84	11.01	6.43	Hylidae	J	A 120180 MCZ
A/T	*Pseudacris regilla*	10.431	15.40	16.65	9.18	5.76	Hylidae	J	A 176972 AMNH
T	*Hyla cinerea*	10.099	15.37	16.56	8.32	5.67	Hylidae	J	A 58314 AMNH
T	*Hyla cinerea*	11.226	17.33	19.64	8.67	5.59	Hylidae	J	A 176950 AMNH
T	*Hyla cinerea*	15.009	22.86	25.96	12.10	7.56	Hylidae	J	A 176956 AMNH
T	*Hyla gratiosa*	14.385	22.44	22.16	13.13	7.68	Hylidae	J	A 57968 AMNH
T	*Hyla gratiosa*	17.347	26.64	26.38	15.75	9.54	Hylidae	J	A 128244 AMNH
T	*Hyla gratiosa*	17.253	25.80	26.09	16.35	9.48	Hylidae	J	A 57640 AMNH
A/T	*Leptodactylus latrans*	17.891	27.06	31.13	15.91	8.78	Leptodactylidae	J	No.1931 FCEN
A/T	*Leptodactylus latrans*	21.143	30.81	34.74	21.67	10.82	Leptodactylidae	J	No. 283 FCEN
A/T	*Leptodactylus latrans*	27.514	41.79	45.78	25.79	14.50	Leptodactylidae	J	No. 571 FCEN
A/T	*Leptodactylus pentadactylus*	36.457	55.10	59.82	37.55	20.31	Leptodactylidae	J	A 69729 AMNH
A/T	*Leptodactylus pentadactylus*	41.761	61.66	67.29	41.94	23.20	Leptodactylidae	J	A 42888 AMNH
A/T	*Leptodactylus pentadactylus*	34.024	48.54	54.57	34.25	18.38	Leptodactylidae	J	A 40435 AMNH
A/T	*Mantella baroni*	6.653	9.11	10.13	6.60	3.88	Mantellidae	J	A 119917 MCZ
A/T	*Mantella baroni*	6.410	9.00	9.69	6.50	3.58	Mantellidae	J	A 119922 MCZ
A/T	*Mantella baroni*	6.536	9.07	9.56	6.68	4.04	Mantellidae	J	A 119921 MCZ
T	*Anodonthyla boulengerii*	4.484	6.81	6.87	4.06	2.48	Microhylidae	J	A 120757 MCZ
T	*Anodonthyla boulengerii*	5.274	7.45	7.77	5.12	3.10	Microhylidae	J	A 119980 MCZ
T	*Anodonthyla boulengerii*	4.740	6.74	7.47	4.52	2.66	Microhylidae	J	A 119979 MCZ
T	*Platypelis pollicaris*	5.941	8.37	9.02	5.81	3.27	Microhylidae	J	A 120100 MCZ
T	*Platypelis pollicaris*	6.699	9.30	10.19	6.30	4.02	Microhylidae	J	A 120099 MCZ
T	*Platypelis pollicaris*	6.658	9.00	10.13	6.40	3.99	Microhylidae	J	A 120098 MCZ
A/T	*Lithobates catesbeianus*	37.767	57.74	60.81	35.89	20.08	Ranidae	J	S/N FCEN
A/T	*Lithobates catesbeianus*	35.593	57.86	58.28	34.46	17.92	Ranidae	J	A 177098 AMNH
A/T	*Lithobates catesbeianus*	29.915	47.55	50.22	27.52	15.06	Ranidae	J	A 177099 AMNH
A/T	*Lithobates pipiens*	19.685	29.52	34.55	17.01	10.24	Ranidae	J	A 177117 AMNH
A/T	*Lithobates pipiens*	30.283	48.14	51.46	28.10	15.90	Ranidae	J	A 177118 AMNH
A/T	*Lithobates pipiens*	20.284	32.23	35.97	16.45	11.30	Ranidae	J	A 177119 AMNH
A/T	*Hylarana erythraea*	22.161	33.43	37.40	18.95	11.66	Ranidae	J	A 87262 AMNH
A/T	*Hylarana erythraea*	17.742	25.38	29.82	15.99	9.63	Ranidae	J	A 177109 AMNH
A/T	*Hylarana erythraea*	20.087	27.97	34.82	17.45	11.30	Ranidae	J	A 177108 AMNH
T	*Anaxyrus americanus*	17.358	22.92	22.28	20.35	13.20	Bufonidae	HW	A 67672 AMNH
T	*Anaxyrus americanus*	15.163	21.96	22.10	16.08	10.04	Bufonidae	HW	A 67673 AMNH
T	*Anaxyrus americanus*	17.106	22.17	22.12	18.61	12.70	Bufonidae	HW	A 55671 AMNH
T	*Anaxyrus woodhousii*	15.915	23.62	23.36	16.73	10.24	Bufonidae	HW	No. 487 FCEN
T	*Anaxyrus woodhousii*	23.972	34.34	34.51	26.43	15.31	Bufonidae	HW	A 176922 AMNH
T	*Anaxyrus woodhousii*	20.978	31.00	30.50	22.92	13.52	Bufonidae	HW	A 176924 AMNH
T	*Rhaebo blombergi*	53.569	73.55	73.49	58.41	38.11	Bufonidae	HW	A 55321 AMNH
T	*Rhaebo blombergi*	47.176	65.49	64.67	50.68	31.45	Bufonidae	HW	A 176865 AMNH
A/T	*Rhinella marina*	34.559	46.67	47.11	37.47	25.04	Bufonidae	HW	A 55670 AMNH
A/T	*Rhinella marina*	40.618	56.24	55.77	44.72	27.68	Bufonidae	HW	A 56009 AMNH
A/T	*Rhinella marina*	40.321	55.03	54.29	46.27	28.22	Bufonidae	HW	A 69089 AMNH
A/T	*Rhinella arenarum*	27.576	36.47	37.72	30.40	18.25	Bufonidae	HW	No. 2 FCEN
A/T	*Rhinella arenarum*	28.410	38.18	39.37	30.73	19.33	Bufonidae	HW	No. 5 FCEN

APPENDIX 1. — Continuation.

	Taxon	MedGeo	FeL	TFL	HuL	RUL	Family	Locomode	Specimen no.
A/T	*Rhinella arenarum*	26.558	35.18	35.81	28.80	17.68	Bufonidae	HW	No. 12 FCEN
A/T	*Bufo bufo*	15.949	20.40	19.21	18.84	12.09	Bufonidae	HW	No. 1543 FCEN
A/T	*Bufo bufo*	17.163	21.94	20.38	20.57	12.89	Bufonidae	HW	No. 1541 FCEN
A/T	*Bufo bufo*	15.555	19.18	18.63	19.06	11.77	Bufonidae	HW	A 176870 AMNH
A/T	*Megophrys nasuta*	27.578	38.33	36.67	29.12	20.49	Megophryidae	HW	A 177047 AMNH
A/T	*Megophrys nasuta*	14.699	21.86	20.73	13.82	10.96	Megophryidae	HW	A 177048 AMNH
A/T	*Pseudophryne corroboree*	5.230	6.60	6.87	6.06	3.54	Myobatrachidae	HW	A 64512 AMNH
A/T	*Pseudophryne corroboree*	5.651	6.57	6.79	6.37	4.11	Myobatrachidae	HW	A 64510 AMNH
A/T	*Pseudophryne corroboree*	5.499	7.28	7.03	5.83	3.52	Myobatrachidae	HW	A 84048 AMNH
A/T	*Proceratophrys boiei*	13.256	17.84	18.22	14.84	9.84	Odontophrynidae	HW	No. 699 FCEN
A/T	*Proceratophrys boiei*	12.638	17.21	16.90	14.77	9.72	Odontophrynidae	HW	A 64634 MCZ
A/T	*Breviceps adspersus*	9.593	13.38	10.83	12.78	6.61	Brevicipitidae	WHB	A 137778 MCZ
A/T	*Breviceps adspersus*	8.399	11.42	9.73	11.13	5.34	Brevicipitidae	WHB	A 137790 MCZ
T	*Epidalea calamita*	12.254	16.45	15.78	15.42	8.36	Bufonidae	WHB	S/N FCEN
T	*Epidalea calamita*	19.139	26.31	25.74	21.36	12.84	Bufonidae	WHB	A 56011 AMNH
T	*Epidalea calamita*	11.226	14.78	12.97	13.72	8.69	Bufonidae	WHB	A 176871 AMNH
T	*Ceratophrys ornata*	25.789	35.74	34.22	30.73	16.23	Ceratophryidae	WHB	No. 1051 (2) FCEN
T	*Ceratophrys ornata*	21.268	28.91	27.15	24.85	13.89	Ceratophryidae	WHB	A 56320 AMNH
A/T	*Smilisca fodiens*	11.196	16.98	16.98	11.00	5.91	Hylidae	WHB	A 62585 AMNH
A/T	*Smilisca fodiens*	12.026	17.96	18.11	11.52	6.79	Hylidae	WHB	A 177005 AMNH
A/T	*Smilisca fodiens*	12.084	18.33	18.80	11.39	6.55	Hylidae	WHB	A 177004 AMNH
A/T	*Dermatonotus muelleri*	13.334	18.45	16.01	17.06	9.43	Microhylidae	WHB	A 30131 MCZ
A/T	*Dermatonotus muelleri*	13.673	19.37	16.66	16.73	9.94	Microhylidae	WHB	A 30128 MCZ
A/T	*Dermatonotus muelleri*	13.302	18.89	16.07	17.11	9.36	Microhylidae	WHB	A 30130 MCZ
A/T	*Hypopachus variolosus*	8.418	12.69	12.54	9.78	4.25	Microhylidae	WHB	A 21312 MCZ
A/T	*Hypopachus variolosus*	7.879	11.50	11.43	7.85	4.99	Microhylidae	WHB	A 26532 MCZ
A/T	*Hypopachus variolosus*	7.813	11.87	11.61	7.82	4.34	Microhylidae	WHB	A 26533 MCZ
T	*Kaloula pulchra*	10.849	15.17	14.12	12.62	7.31	Microhylidae	WHB	A 177033 AMNH
T	*Kaloula pulchra*	14.996	20.89	18.38	18.04	10.80	Microhylidae	WHB	A 177032 AMNH
A/T	*Odontophrynus americanus*	8.644	12.10	11.30	10.05	6.60	Odontophrynidae	WHB	No. 781 (13) FCEN
A/T	*Odontophrynus americanus*	13.018	18.17	16.56	15.53	9.36	Odontophrynidae	WHB	No. 852 FCEN
A/T	*Odontophrynus americanus*	10.587	14.99	13.79	12.23	7.51	Odontophrynidae	WHB	No. 781 FCEN
T	*Rhinophrynus dorsalis*	11.492	17.70	15.44	15.31	7.71	Rhinophrynidae	WHB	No. 42617 MACN
T	*Rhinophrynus dorsalis*	11.476	17.40	14.94	14.45	7.59	Rhinophrynidae	WHB	S/N FCEN
A/T	*Scaphiopus couchii*	13.571	19.73	17.47	16.49	10.67	Scaphiopodidae	WHB	S/N FCEN
A/T	*Scaphiopus couchii*	14.833	21.32	19.46	18.02	10.66	Scaphiopodidae	WHB	A 177055 AMNH
A/T	*Scaphiopus couchii*	14.050	21.09	19.99	16.15	10.00	Scaphiopodidae	WHB	A 56294 AMNH
A/T	*Spea hammondi*	12.661	19.47	17.46	13.97	8.04	Scaphiopodidae	WHB	A 177061 AMNH
A/T	*Spea hammondi*	11.808	18.02	15.93	13.08	7.67	Scaphiopodidae	WHB	A 177062 AMNH
A/T	*Spea hammondi*	11.767	17.01	16.44	12.88	7.88	Scaphiopodidae	WHB	A 177063 AMNH
A	*Calyptocephalella gayi*	30.729	43.40	43.06	31.71	19.64	Calyptocephalellidae	Sw	No. 1433 FCEN
A	*Calyptocephalella gayi*	27.448	37.24	38.16	28.90	17.71	Calyptocephalellidae	Sw	S/N FCEN
A	*Calyptocephalella gayi*	27.263	38.75	39.02	29.07	17.75	Calyptocephalellidae	Sw	A 51510 AMNH
A/T	*Litoria dahli*	14.873	23.49	24.96	12.85	7.65	Hylidae	SwB	S/N FCEN
A	*Pseudis minuta*	12.300	21.96	20.59	10.43	6.37	Hylidae	Sw	S/N FCEN
A	*Pseudis platensis*	15.288	27.37	26.55	12.26	7.85	Hylidae	Sw	No. 727 FCEN
A	*Pipa arrabali*	10.654	17.14	17.32	8.58	5.96	Pipidae	SwB	A 51175 AMNH
A	*Pipa carvalhoi*	14.313	22.41	22.58	12.00	8.12	Pipidae	SwB	No. 42608 MACN
A	*Pipa pipa*	25.493	38.84	35.89	26.40	16.27	Pipidae	SwB	No.1434
A	*Pipa pipa*	7.501	11.88	11.01	7.70	4.08	Pipidae	SwB	QCAZ 8333
A	*Pipa pipa*	16.297	24.61	22.06	17.02	10.64	Pipidae	SwB	QCAZ 11919
A/T	*Silurana tropicalis*	10.080	14.64	15.91	7.89	6.39	Pipidae	Sw	A 11871 MCZ
A/T	*Silurana tropicalis*	10.459	15.83	18.35	8.47	5.47	Pipidae	Sw	A 115390 MCZ
A/T	*Silurana tropicalis*	10.239	15.51	17.49	7.12	5.88	Pipidae	Sw	A 11865 MCZ
A/T	*Xenopus fraseri*	8.863	13.38	14.71	6.49	5.14	Pipidae	Sw	A 21630 MCZ
A/T	*Xenopus fraseri*	11.041	16.79	18.49	8.36	6.25	Pipidae	Sw	A 46474 MCZ
A/T	*Xenopus fraseri*	9.556	13.63	15.58	7.78	5.73	Pipidae	Sw	A 46478 MCZ
A/T	*Xenopus laevis*	18.658	28.61	29.12	15.97	11.67	Pipidae	Sw	S/N FCEN
A/T	*Xenopus laevis*	15.374	24.13	24.88	12.94	8.55	Pipidae	Sw	A 177085 AMNH
A/T	*Xenopus laevis*	17.203	27.82	28.41	13.95	9.06	Pipidae	Sw	A 177086 AMNH
A/T	*Xenopus muelleri*	13.179	20.58	21.64	10.94	7.53	Pipidae	Sw	No. 42631 MACN
A/T	*Xenopus wittei*	8.185	11.95	13.20	6.98	4.64	Pipidae	Sw	No. 42624 MACN
A	*Telmatobius culeus*	17.644	25.40	25.53	19.16	10.62	Telmatobiidae	Sw	A 1080 MCZ
A	*Telmatobius culeus*	33.351	47.95	49.96	33.56	20.75	Telmatobiidae	Sw	A 1078 MCZ
A	*Telmatobius hauthali*	10.533	15.37	16.76	10.61	5.74	Telmatobiidae	Sw	No. 320 FCEN
A	*Telmatobius hauthali*	13.645	19.60	21.39	13.27	7.67	Telmatobiidae	Sw	S/N FCEN
A	*Telmatobius macrostomus*	34.422	46.70	47.80	39.32	24.17	Telmatobiidae	Sw	No. 1208-1 (1) FCEN
A	*Telmatobius schreiteri*	14.153	20.26	21.26	14.35	8.33	Telmatobiidae	Sw	No. 00541 FML
A	*Telmatobius scrocchii*	14.368	21.32	22.71	14.03	8.22	Telmatobiidae	Sw	No. 1515 (355)FCEN
A	*Telmatobius scrocchii*	14.682	21.58	23.56	14.49	8.59	Telmatobiidae	Sw	No. 1515 (356) FML

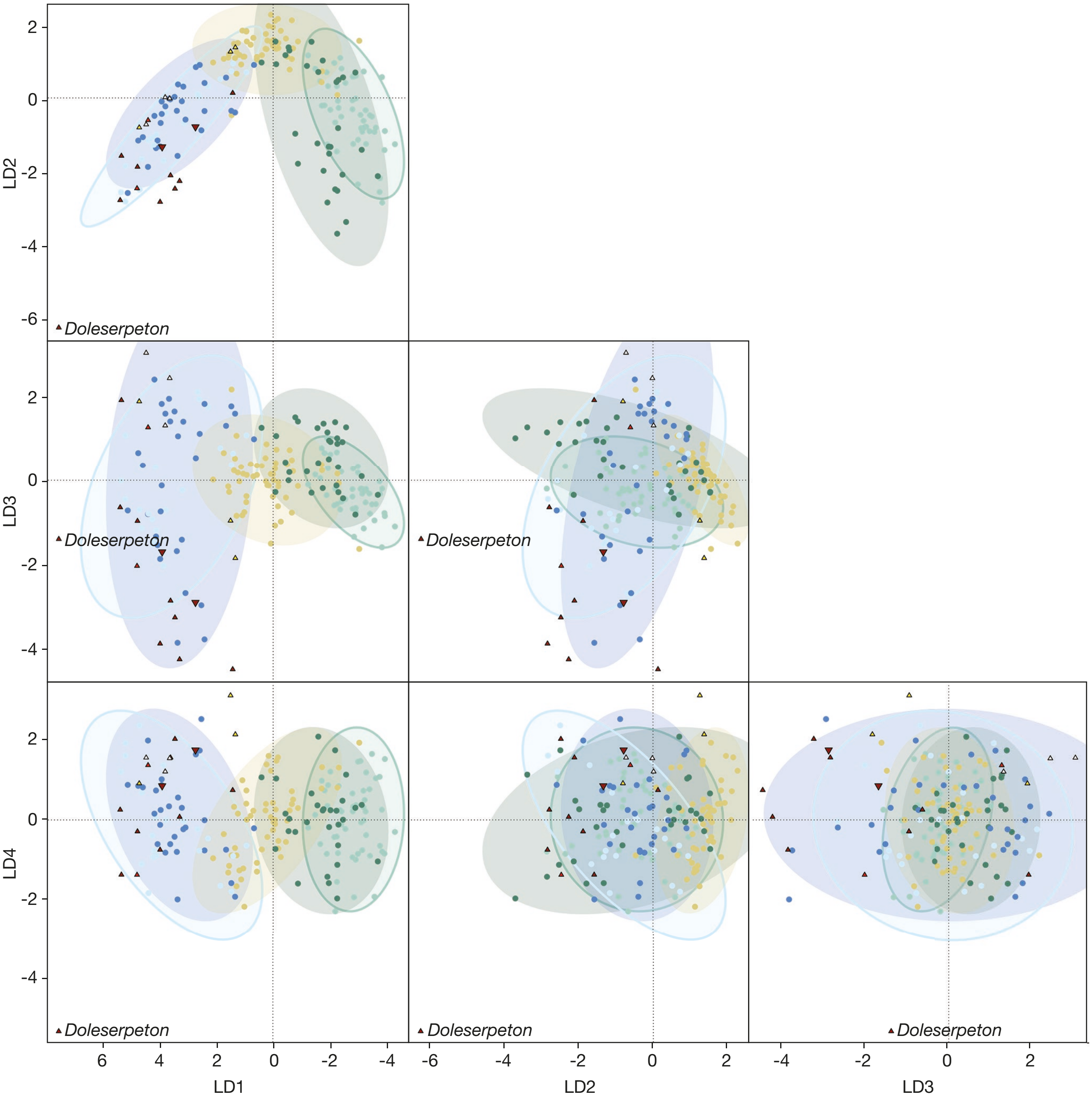
Appendix 1. — Continuation.

	Taxon	MedGeo	FeL	TFL	HuL	RUL	Family	Locomode	Specimen no.
A/T	*Ambystoma maculatum*	4.548	7.59	5.41	7.41	4.29	Ambystomidae	LUB / A	A 87252 AMNH
A/T	*Ambystoma maculatum*	4.312	6.83	4.23	7.58	4.2	Ambystomidae	LUB / A	A 87255 AMNH
A/T	*Ambystoma maculatum*	4.650	7.71	4.95	7.89	4.4	Ambystomidae	LUB / A	A 87254 AMNH
A/T	*Ambystoma mexicanum*	7.674	12.83	8.25	13.92	7.89	Ambystomidae	LUB / A	A 56010 AMNH
A/T	*Ambystoma tigrinum*	5.613	10.1	6.15	10.95	6.3	Ambystomidae	LUB / A	A 177133 AMNH
A/T	*Ambystoma tigrinum*	8.280	13.59	8.82	12.8	7.71	Ambystomidae	LUB / A	A 79931 AMNH
A/T	*Ambystoma tigrinum*	7.187	12.11	7.42	12.72	7.14	Ambystomidae	LUB / A	A 58448 AMNH
A/T	*Dicamptodon ensatus*	9.136	16.19	10.44	17.28	8.97	Ambystomidae	LU / A	A 177136 AMNH
A	*Andrias japonicus*	23.985	42.46	25.68	40.7	22.5	Cryptobranchidae	LU / A	A 57991 AMNH
A	*Cryptobranchus alleganiensis*	11.990	22.02	12.66	20.5	11.88	Cryptobranchidae	LUB / A	A 55996 AMNH
A	*Cryptobranchus alleganiensis*	17.402	35.8	17.07	33.47	18.27	Cryptobranchidae	LUB / A	A 88985 AMNH
A	*Cryptobranchus alleganiensis*	12.342	26.39	13.15	22.5	12.78	Cryptobranchidae	LUB / A	A 69080 AMNH
A	*Necturus maculosus*	5.921	12.59	5.63	11.9	5.75	Proteidae	LUB / A	A 55994 AMNH
A	*Necturus maculosus*	6.245	12.26	5.55	11.63	6	Proteidae	LUB / A	A 55997 AMNH
A/T	*Rhyacotriton olympicus*	2.573	4.91	2.79	4.44	2.61	Rhyacotritonidae	LU / A	A 177159 AMNH
A/T	*Notophthalmus viridescens*	2.910	5.7	3.26	5.28	3.04	Salamandridae	LU / A	A 67412 AMNH
A	*Pachytriton brevipes*	3.759	7.14	3.44	7.06	3.73	Salamandridae	LU / A	A 22346 MCZ
A	*Pachytriton brevipes*	4.420	8.19	3.95	7.93	3.89	Salamandridae	LU / A	A 101047 MCZ
A	*Pachytriton brevipes*	3.220	6.11	3.15	6.64	2.68	Salamandridae	LU / A	A 7986 MCZ
A	*Pleurodeles waltl*	5.956	9.6	5.9	11.23	5.43	Salamandridae	LUB / A	S/N FCEN
A	*Pleurodeles waltl*	4.061	7.51	3.79	8	3.73	Salamandridae	LUB / A	A 117166 AMNH
A/T	*Taricha granulosa*	6.103	9.24	6.25	11.84	5.53	Salamandridae	LU / A	A 58444 AMNH
A/T	*Taricha granulosa*	6.428	10.2	6.69	13.52	6.76	Salamandridae	LU / A	A 85377 AMNH
A/T	*Taricha rivularis*	6.933	12.54	6.83	13.1	6.67	Salamandridae	LU / A	A 56006 AMNH
A/T	*Taricha rivularis*	6.094	9.78	6.68	10.96	5.96	Salamandridae	LU / A	A 56214 AMNH
A/T	*Taricha torosa*	6.017	9.79	6.01	10.79	5.86	Salamandridae	LU / A	A 177167 AMNH
A/T	*Taricha torosa*	5.106	8.95	5.19	9.93	5.12	Salamandridae	LU / A	A 53765 AMNH
A/T	*Triturus cristatus*	4.255	6.98	4.26	7.12	3.9	Salamandridae	LU / A	A 68241 AMNH
A/T	*Mertensiella caucasica*	4.382	7.11	4.47	8.36	4.08	Salamandridae	LU / A	A 56317 AMNH
A/T	*Salamandra salamandra*	6.804	11.23	7.76	12.08	7.45	Salamandridae	LUB / A	A 177160 AMNH
A/T	*Salamandra salamandra*	7.796	12.27	7.55	13.5	7.45	Salamandridae	LUB / A	A 177161 AMNH
T	*Aspidoscelis tigris*	9.387	17.5	15.23	12.79	9.59	Teiidae	LUB	R 155237 AMNH
T	*Aspidoscelis tigris*	8.972	16.74	14.04	12	8.81	Teiidae	LUB	R 155239 AMNH
T	*Aspidoscelis tigris*	10.259	18.75	16.34	13.84	10	Teiidae	LUB	R 155242 AMNH
T	*Cordylus niger*	7.262	14.63	9.78	11.62	7.5	Cordylidae	LU	R 154708 AMNH
T	*Gambelia wislizenii*	13.431	26.6	27.01	18.16	14.63	Crotaphytidae	LU	R 154785 AMNH
T	*Gambelia wislizenii*	13.118	24.88	24.57	16.77	13.39	Crotaphytidae	LU	R 154787 AMNH
T	*Gambelia wislizenii*	13.905	26.95	25.71	19.81	13.24	Crotaphytidae	LU	R 154788 AMNH
T	*Leiolepis belliana*	6.478	11.68	11.26	8.62	5.99	Agamidae	LUB	R 154817 AMNH
T	*Petrosaurus thalassinus*	11.670	22.97	17.88	18.47	12.97	Phrynosomatidae	LU	R 154860 AMNH
T	*Petrosaurus thalassinus*	12.376	25.15	18.32	19.58	13.41	Phrynosomatidae	LU	R 154861 AMNH
T	*Petrosaurus thalassinus*	17.300	34.69	24.69	26.05	18.77	Phrynosomatidae	LU	R 154862 AMNH
T	*Uma notata notata*	11.250	21.95	21.07	18.11	12.96	Phrynosomatidae	LUB	R 154830 AMNH
T	*Uma notata notata*	7.742	13.47	13.37	11.48	8.01	Phrynosomatidae	LUB	R 154831 AMNH
T	*Uma notata notata*	7.337	13.81	13.04	11.31	7.62	Phrynosomatidae	LUB	R 154832 AMNH
T	*Sauromalus ater*	17.198	34.15	24.39	29.15	18.17	Iguanidae	LU	R 155153 AMNH
T	*Sauromalus ater*	16.336	33.37	22.89	29.04	16.14	Iguanidae	LU	R 155158 AMNH
T	*Sauromalus ater*	15.505	31.68	22.48	25.74	14.95	Iguanidae	LU	R 155161 AMNH
T	*Stenocercus caducus*	9.824	19.54	18.09	14.73	10.46	Tropiduridae	LU	R 154827 AMNH
T	*Stenocercus caducus*	8.539	16.41	13.75	12.11	8.52	Tropiduridae	LU	R 162751 AMNH
T	*Tropidurus malenopleurus*	8.685	17.38	13.45	14.28	10.21	Tropiduridae	LU	R 154981 AMNH
T	*Tropidurus malenopleurus*	8.077	15.5	12.17	12.67	8.61	Tropiduridae	LU	R 154982 AMNH
T	*Tropidurus malenopleurus*	8.715	17.56	13.52	14.66	10.17	Tropiduridae	LU	R 154984 AMNH
–	*Triadobatrachus massinoti*	12.730	22.08	14.37	18.43	11.23	–	F	MNHN.F.MAE126
–	*Batropetes palatinus*	4.464	6.1	3.3	6.8	2.9	–	F	MB.Am.1232 (right)
–	*Batropetes palatinus*	4.524	6.1	3.3	6.5	3.2	–	F	MB.Am.1232 (left)
–	*Batopetes appelensis*	3.283	4.3	2.4	4.5	2.5	–	F	MNHM PW 2001/308-LS
–	*Batropetes palatinus*	4.980	6.9	3.4	6.9	3.8	–	F	MNHM PW 2001/306-LS
–	*Batropetes palatinus*	3.699	4.8	2.5	6	2.6	–	F	MNHM PW 2001/307-LS
–	*Batropetes palatinus*	3.768	4.8	2.5	6	2.8	–	F	MNHM PW 2001/309-LS
–	*Batropetes niederkirchensis*	5.471	7.7	3.7	8.5	3.7	–		SMNS 55884 (right)
–	*Batropetes niederkirchensis*	5.321	7.7	3.5	8.5	3.5	–	F	SMNS 55884 (left)
–	*Batropetes fritschi*	3.295	4.1	2.63	5.2	2.1	–	F	SLFG SS 13558 / SS 13559
–	*Celtedens ibericus*	4.361	6.25	4.25	4.54	3.00	–	F	LH 6020 (left)
–	*Celtedens ibericus*	5.615	8.25	5.25	5.75	3.99	–	F	LH 030 R (left)
–	*Platyrhinops lyelli*	13.645	19.11	11.73	15.43	10.02	–	F	AMNH 6841 (right)
–	*Doleserpeton annectens*	7.767	9.11	5.06	10.64	7.43	–	F	FMNH UR 1320, 1321, 1381, 1382
–	*Pantylus cordatus*	15.263	19.05	10.82	21.93	12.01	–	F	UT 40001-1, 40001-6

APPENDIX 1. — Continuation.

	Taxon	MedGeo	FeL	TFL	HuL	RUL	Family	Locomode	Specimen no.
–	*Micropholis stowi*	11.974	16.96	10.94	15.81	7.01	–	F	BSM 1934 VIII E
–	*Micropholis stowi*	12.094	16.12	10.97	16.53	7.32	–	F	BSM 1934 VIII C
–	*Tuditanus punctulatus*	9.064	12.76	7.57	10.80	6.47	–	F	AMNH 6926 (forelimb), USNM 4457 (hindlimb)
–	*Diabloroter bolti*	3.388	4.38	3.00	3.66	2.74	–	F	ACFGM V-1634

Appendix 2. — First and fourth canonical axes of the discriminant function analysis (LDA) of corrected morphometric variables and the five defined locomotor categories. Locomotor categories: •, HW; •, J; •, LU; •, LUD; •, SW. Symbols: ▲, Brachystelechids (always *Batropetes palatinus* Glienke, 2015 if unlabeled) – the two larger triangles that point downward mark the left and the right side of MB.Am.1232 –; ▲, other “microsaurs”; △, amphibamiform temnospondyls; △, lissamphibians; **squares** indicate *Ambystoma tigrinum* (Green, 1825) (■, LUD) and *Bufo bufo* (Linnaeus, 1758) (■, HW). All extinct taxa plot within or closest to the LU/LUD cluster. Extant taxa from Lires *et al.* (2016), distinction of LU and LUD from Oliveira *et al.* (2017a, b). Abbreviations: **HW**, hopping/walking; **J**, jumping; **l**, left side; **LD**, linear discriminants; **LU**, laterally undulating, not digging; **LUD**, laterally undulating, digging to some degree; **r**, right side; **Sw**, swimming. For a version with every extant taxon labeled, see Appendix 4.



Appendix 3. — Figure 4 with all specimens labeled: https://doi.org/10.5852/cr-palevol2022v21a23_s1

Appendix 4. — Appendix 2 with all specimens labeled: https://doi.org/10.5852/cr-palevol2022v21a23_s2