The scratch-digging lifestyle of the Permian “microsaur” *Batropetes* as a model for the exaptive origin of jumping locomotion in frogs

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Abstract

Recent studies have shown that the Triassic stem-frog *Triadobatrachus* lacked the ability to jump off, 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* reveal thin cortical bone, confirming *Batropetes* 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.

We discuss the possibility of homology with the digging lifestyles of other “microsaurs” and other amphibians.

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

1. Introduction

The origin of frogs (total group: Salientia) 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 (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; Marjanovi &

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), as well as that of the third extant amphibian clade (the caecilians: total or near-total group Gymnophionomorpha Marjanovi & Laurin, 2008), remains an unsolved problem (Marjanovi & Laurin, 2019; Danto et al., 2019; Laurin et al., 2019; Daza et al., 2020; 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 and nests this clade within the Paleozoic temnospondyls, most recently supported by the phylogenetic analyses of Pardo et al. (2017a: fig. S6; 2017b), and 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; Marjanovi & Laurin, 2013, 2019; Daza et al., 2020: fig. 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 (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 (Marjanovi & Laurin, 2013, 2019; Daza et al., 2020).

Equally unsolved remains the evolution of the unique jumping locomotion, accompanied by diagnostic skeletal peculiarities (Sigurdson et al., 2012), that has characterized crown-group frogs (usually called Anura) and their closest relatives at least since the Early Jurassic *Prosalirus* (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

Fig. 1. Modified from Marjanovič & Laurin (2019: fig. 2). Names of extant taxa in boldface, names of junior synonyms on a given topology in parentheses. **(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; Marjanovič & Laurin, 2019; Daza et al., 2020: fig. 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.

Early Triassic *Triadobatrachus* (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, 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 (Marjanovič & 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 (Sigurdson et al., 2012; Ascarrunz et al., 2016). This suggests an exaptation: the forelimbs were reinforced, and their posture modified (Jenkins & Shubin, 1998; Sigurdson 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*; 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 section 4.5, that the ecological niches of *Batropetes* 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.

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

2. Material and Methods

2.1 Computed microtomography

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

2.2 Statistical analyses of limb proportions

We have 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 Table S1, 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 (Tables 3, S1; Fig. S1).

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.

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) *Celtdens ibericus* (two individuals); the “microsaurs” *Tuditanus punctulatus*, *Pantylus cordatus* and *Diabloroter bolti*, 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 “2019”) temnospondyls *Platyrhinops lyelli*, *Micropholis stowi* (two individuals), and *Doleserpeton annectens* (composite of several individuals scaled to the same size). Despite its importance in recent studies on lissamphibian origins (Anderson et al., 2008; Marjanovi & Laurin, 2009, 2019; Pardo et al., 2017a; Mann et al., 2019a, and references therein), the amphibamiform *Gerobatrachus hottoni* 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 (Mostellar & 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 and 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 “supertimetre” 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).

3. Results

3.1 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. de Buffrénil & Rage, 1993; Laurin et al., 2004, 2011; Cubo et al., 2005; Germain & Laurin, 2005; Krilloff et al., 2008; Canoville & Laurin, 2009, 2010; de Buffrénil et al., 2010; Cooper et al., 2011 “2012”; Dumont et al., 2013; Quémeneur et al., 2013) previous interpretations of *Batropetes* as terrestrial (Gliénke, 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 μ CT 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*: Sigurdson et al., 2012: fig. 3A) or to a lesser degree in *Eocaecilia* (Jenkins et al., 2007: fig. 42; Sigurdson et

Fig. 3. (A, B) CT images showing thin cortex in the craniodorsal part of the vertebral column and the humerus of *Batropetes palatinus* (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.

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

Fig. 4. First two canonical axes of the discriminant function analysis (LDA) of corrected morphometric variables and the five defined locomotor categories. The different locomotor categories are plotted in different colors. Brachystelechids are shown as dark red triangles (always *Batropetes palatinus* if unlabeled); the two larger ones that point downward mark the left and the right side of MB.Am.1232. Bright red triangles: other “microsaurs”; yellowish triangles: amphibamiform temnospondyls; pale red triangles: lissamphibians. Squares indicate *Ambystoma tigrinum* (in light blue for LUD) and *Bufo bufo* (in yellow-green for HW); for a version with every extant taxon labeled, see Fig. S2. 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; LU =

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

3.2 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 (Fig. 4–6, S1–S3; Table 3), the fossil individuals mostly plot with caudates and squamates (which retain much of the ancestral tetrapod body shape) in a wider cluster including the lateral undulator (LU) cluster of extant species and the separately categorized cluster of extant individuals known to routinely engage in digging behavior (LUD).

In the LDA, the LU and LUD clusters do not separate well in most comparisons (Fig. 4–6, S1–S3). 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, S1) 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 $p\text{-value} = 9.28 \times 10^{-109}$, 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*) as a toad-like hopper/walker (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 elongated 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 is the only taxon that does not cluster with any of the defined groups representing locomotor categories in Fig. 4 and 5. It plots as a distant outlier in the LDA (Fig.

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

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; Sigurdson et al., 2010; Gee et al., 2020), the measurements were taken from different specimens, corrected for size, as well as from the skeletal reconstruction by Sigurdson et al. (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* 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*, 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* in linear discriminants 1 and 2, though widely separated by linear discriminant 4 (Fig. 4, 5, S1).

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

The two specimens of the albanerpetid near-lissamphibian *Celtdens 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 et al., 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.

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

4. Discussion

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

Its 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 for presacral vertebrae 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 (*Carrollia*) or none (*Quasicaecilia*) are known, though there is evidence that *Carrollia* had *Batropetes*-like proportions (Mann et al., 2019b). (*Brachystelechus* 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* 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 clawlike terminal phalanges may specifically fit scratch-digging, as does the fact that the hands are not broadened into shovels, but 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 – unlike 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 elongated 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: fig. 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 apparently *Quasicaecilia* (Pardo et al., 2015), and seemingly only weakly in *Diabloroter* (Mann & Maddin, 2019).

Fig. 7. Illustration of teeth of several “microsaurs” and salamanders. (A) *Batropetes palatinus*, 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*, TMM 40031-54, left dentary (left side), not to scale. (F, G, H) models: general organisation of adult caudate tooth in lingual and mesial or distal views, similar to *Ambystoma* tooth morphology; (H) shows a tricuspid tooth as found in *A. mabeei*. (A–D) after Glienke (2015), (E) based on Mann et al. (2019b), (F–H) summarized from Beneski & Larsen (1989).

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. 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.

4.2 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*, *A. annulatum*, *A. maculatum*) did not dig into a moist sandy soil even when their life was threatened by desiccation, and one (*A. talpoideum*) 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) *A. tigrinum*, 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 (Fig. 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, rostr dorsally facing nares and very large, lateroventrally open orbitotemporal fenestrae (DigiMorph Staff, 2008b).

Ambystoma maculatum, *A. mexicanum* (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 Figure S1, 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, 2021). 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* (Beneski & Larsen, 1989; Fig. 7H). The small-sized *A. mabeei* is known to eat earthworms (AmphibiaWeb, 2021). Possibly, then, the mesiodistally tricuspid teeth of *Batropetes* and *Carrolla* and the linguolabially tricuspid dentary teeth of *A. mabeei* 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 cusps of *Batropetes*, Gliénke (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*, the rhacophorid *Polypedates maculatus*, the hyperoliid *Heterixalus madagascariensis* and the hylids *Agalychnis callidryas* and *Phyllomedusa bicolor*: 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 *Po. 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*), which scrape algae off rocks in the sea, and to the mesial teeth of the Early Triassic amphibamiform temnospondyl *Tungussogyrinus*, 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 *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: fig. 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 (Gliénke, 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: fig. 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 *Carrollia* is instead shared with many insectivorous squamates (e.g. Melstrom, 2017: fig. 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* and *Anoualerpeton*, and the mesial teeth of *Tungussogyrinus*, are compared in Werneburg (2009: fig. 10).

4.3 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 and Lysorophia as sister-groups. In some ways, this is an odd pair. The lysorophians, in all four analyses represented by *Brachydectes* (Pardo & Anderson,

2016) and in the fourth also by *Infernovenator* (Mann et al., 2019a), are very elongate 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 in Marjanovič & Laurin (2019), applied implied weighting, and found Brachystelechidae and Lysorophina 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 Marjanovič & Laurin (2019: fig. 14) found *Rhynchonkos* to be closely related, which 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 and Ostodolepididae in Marjanovič & Laurin (2019: fig. 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*, 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). (Marjanovič & 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, 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 Marjanovič & 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 Marjanovič & Laurin (2019).

The hapsidopareiid “microsaurs” may be similarly close to Brachystelechidae + Lysorophina (Marjanovič & Laurin, 2019: fig. 14; Gee et al., 2019; Daza et al., 2020: fig. S15). One of them, *Llistrofus*, 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 Marjanovič & Laurin (2019: fig. 14), and similarly in Daza et al. (2020: fig. S15), Lissamphibia is even closer to Brachystelechidae + *Brachydectes* than *Rhynchonkos* or Hapsidopareiidae. 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 et al., 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. Triassic or 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.

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.

4.4 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; Sigurdson 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*) 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* and *Leiopelma*) that has figured so prominently in the most recent works on this topic (Essner et al., 2010; Sigurdson 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. 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. This hypothesis does not, however, seem to explain how the forelimbs became adapted to providing this function in the other half of the crown-group. Furthermore, Sigurdson 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*, *Vieraella* and *Prosalirus* (Báez & Basso, 1996; Jenkins & Shubin, 1998; Báez & Nicoli, 2004; Sigurdson et al., 2012). We therefore follow Sigurdson 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 jumping 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* (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).

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 (Fig. 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 suggests the possibility that *Micropholis* was actually amphibious. Interestingly, our analyses of limb proportions find (Fig. 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 Sigurdson et al. (2012) found one, and that we can offer another. Sigurdson 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 Sigurdson 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 Sigurdson 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.

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

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 assuming 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 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.

4.5 An evolutionary scenario

If brachystelechids and lissamphibians are as closely related as found by Marjanović & Laurin (2019) or 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 elongate, 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* (Gliénke, 2013, 2015; see above), but also in *Dolesempetron*, 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 (Marjanovič & 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 *Celtdens ibericus* and probably the mid-Cretaceous *Yaksha*: McGowan, 2002; Daza et al., 2020: S2.3; otherwise unknown). Already in the original description of *Albanerpeton inexpectatum* (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 Sigurdson 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*, 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) 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*, 13 in the Jurassic metamorphic stem-urodele *Karaurus*), 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 (Fig. 1C, F; Pardo et al., 2017a, b, and references therein), 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.

Marjanovič & Laurin (2013, 2019) have 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 (Fig. 4–6), plotting them in the same part of morphospace as extant limbed squamates as well as the “microsaurs” *Pantylus* and *Tuditanus* (Fig. 4, 5).

The amphibamiform *Doleserpeton*, which has played an outsized role in most hypotheses on lissamphibian origins, plots as an outlier from the laterally undulating cluster (Fig. 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* and *?Tersomius dolesensis* as discussed by Gee et al. (2020).

5. Conclusions

New data from computed microtomography (μCT) of MB.Am.1232, a skeleton of the Early Permian “microsaur” *Batropetes palatinus* (Fig. 2), have 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” (Gliénke, 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 Sigurdson 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

μ CT 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 *Platyrrhinops* 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.

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Finally, we would like to commemorate the fact that the number of known extant amphibian species as counted by AmphibiaWeb (2021) surpassed 8,000 on 28 March 2019,

8,100 on 12 December 2019, 8,200 on 22 July 2020 and 8,300 on 9 March 2021. It stands at 8,381 in mid-September 2021. May this count continue to increase.

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- 1138

1139 **Table 1**

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

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

1140

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

1146 **Table 2**

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

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

1147

1148 Sources of the measurements in Table 1.

1149 **Table 3**

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

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

1150

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

Supplementary information

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

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

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

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