

## Original Article

# A new amphibamiform from the Early Permian of Texas elucidates patterns of cranial diversity among terrestrial amphibamiforms

Calvin So<sup>1,\*</sup>, Jason D. Pardo<sup>2</sup> and Arjan Mann<sup>2,3</sup>

<sup>1</sup>Department of Biological Sciences, George Washington University, 800 22nd St NW, Suite 6000, Washington, DC 20052, USA

<sup>2</sup>Negaunee Integrative Research Center, Field Museum of Natural History, 1400 S Lake Shore Dr, Chicago, IL, USA

<sup>3</sup>Department of Paleobiology, National Museum of Natural History, NHB MRC 121, Washington, DC 20013, USA

\*Corresponding author. Department of Biological Sciences, George Washington University, 800 22nd St NW, Suite 6000, Washington, DC 20052, USA.  
E-mail: [calvincso@gmail.com](mailto:calvincso@gmail.com)

### ABSTRACT

Amphibamiform temnospondyls are at the forefront of discourse surrounding modern amphibian evolutionary origins. Here we present a new amphibamiform, *Kermitops gratus* gen. et sp. nov., from the Lower Clear Fork Formation of the Early Permian of Texas. *Kermitops* reveals a mosaic of features shared with other amphibamiforms and possesses unique characteristics, including an internarial fontanelle formed by the premaxillae without contribution of the nasals. It possibly possesses a basioccipital that contributes to the occipital condyle, which has significant implications for recent hypotheses of the evolution of the modern amphibian neurocranium. Parsimony analyses recover non-traditional amphibamiform relationships but place *Kermitops* within Amphibamiformes. Bayesian inference analysis captures a more traditional hypothesis of amphibamiform relationships; however, the time-calibrated analysis under the fossilized birth–death model recovers a topology that mirrors the parsimony topologies. The low robusticity of topologies across different permutations employing traditional and modern methods suggest a need for improvement of current morphological datasets of lissamphibian origins. A morphometric analysis of the crania of terrestrial amphibamiforms reveals the evolution of disparate cranial morphologies among coeval taxa from the Early Permian of Texas.

**Keywords:** Permian; Lissamphibia; Temnospondyli; Amphibamiformes; morphometrics; phylogenetic analysis

### INTRODUCTION

Modern amphibian origins among temnospondyls has been the primary focus of temnospondyl research over the past two decades, with the small, lightly-built, terrestrial amphibamiforms at the centre of these discussions (Schoch and Milner 2004, Anderson *et al.* 2008; Sigurdson and Bolt 2010, Maddin *et al.* 2012, Schoch 2013, 2014, 2020, Pardo *et al.* 2017, Pérez-Ben *et al.* 2018, Atkins *et al.* 2019, Schoch *et al.* 2020, Kligman *et al.* 2023). Amphibamiforms are considered to be the immediate outgroups to lissamphibians or within Lissamphibia, placing a premium on advancement in understanding amphibamiform diversity. The close relationship between amphibamiforms and lissamphibians has largely hinged on the presence of bicuspid, pedicellate teeth in some adult amphibamiforms (Parsons and Williams 1963). These features are one of the few skeletal characteristics uniting the three modern lissamphibian orders (Bolt

1969, Milner 1988) and, therefore, have been used to identify amphibamiforms as the progenitors of modern amphibians (Bolt 1969, Anderson *et al.* 2008, Sigurdson and Bolt 2010). Further emphasis is placed on the significance of general skull shape and cranial dermal bones as plesiomorphies of lissamphibians and amphibamiforms (Anderson *et al.* 2008b, Maddin *et al.* 2012, Schoch 2019, Mann and Gee 2019). The changes in timing and rate of developmental processes have also been proposed as significant contributors to the reduction and simplification of elements in the origin of lissamphibians (Schoch 2013, 2014, Pérez-Ben *et al.* 2018, Atkins *et al.* 2019). However, changes in morphology achieved primarily through shifts in timing and rate of development can produce convergent anatomy due to physical and developmental constraints (Hanken and Wake 1993, Yeh 2002). This may obscure anatomy differentiating lissamphibian synapomorphies from amphibamiform symplesiomorphies.

Received 24 August 2023; revised 30 October 2023; accepted 10 January 2024

[Version of Record, first published online 21 March 2024, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN; <http://zoobank.org/urn:lsid:zoobank.org:pub:2F57C323-B87B-44AB-8080-0BAC554B2EC7>]

© The Author(s) 2024. Published by Oxford University Press on behalf of The Linnean Society of London. All rights reserved. For permissions, please e-mail: [journals.permissions@oup.com](mailto:journals.permissions@oup.com)

Further anatomical and ecomorphological investigations of amphibamiform temnospondyls could identify new anatomical character complexes and inform current hypotheses on the evolutionary relationships of temnospondyls and lissamphibian origins.

Here we describe a previously unreported amphibamiform from the lower Clear Fork Formation ('Arroyo Formation' beds) of Texas, USA. *Kermitops gratus* gen. et sp. nov. exhibits a divergent morphology among amphibamiforms, with an elongate antorbital region and a greatly abbreviated postorbital region. This increases known amphibamiform diversity in the Early Permian, as well as improves our understanding of morphological diversity within the group. We tested the phylogenetic relationships of *Kermitops* with the recent matrix of Schoch and Werneburg (2023) and Werneburg et al. (2023) using maximum parsimony, Bayesian inference, and time-calibration under the fossilized birth–death (FBD) model, revealing discordant topologies. Furthermore, given the unique skull morphology of *Kermitops*, we were prompted to investigate the morphological diversity of the amphibamiform cranium to glean information on the ecomorphotypes of coeval terrestrial amphibamiform taxa spanning the Carboniferous to Triassic.

## MATERIALS AND METHODS

### Imagery and comparative methods

All specimens were photographed with a Canon EOS 80D camera using a Canon EF 100 mm f/2.8L IS USM macro lens. Digital photographs were processed using ADOBE PHOTOSHOP 2023, and figures were assembled using ADOBE ILLUSTRATOR 2023. Relevant amphibamiform comparative material was observed at the Field Museum of Natural History, Chicago (FMNH), Smithsonian National Museum of Natural History, Washington, DC (USNM), and Yale Peabody Museum, New Haven (YPM). See Phylogenetic analysis section for phylogenetic methodology.

### Morphometric methods

Seven morphometric measurements of the skull roof were collected from 37 amphibamiform skulls across 16 taxa. The measurements of the skull roof were as follows: (i) skull length; (ii) antorbital length; (iii) postorbital length; (iv) postorbital bar length; (v) orbital–nasal distance; (vi) interorbital distance; and (vii) width of the skull at the posteriormost termination of the maxilla (Supporting Information, S1). We excluded the obligate aquatic Branchiosauridae from our sampling to restrict our analysis to primarily terrestrial amphibamiforms similar to *Kermitops*. We conducted a principal components analysis to reduce the dimensionality of the data and to collect eigenvalues that were used to determine the axes of greatest variation. We transformed the original data into lower dimensions and projected them onto the first three principal components. We then observed patterns in the projected data.

### Anatomical abbreviations

a, angular; bo, basioccipital; d, dentary; dt, denticles; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; o, opisthotic; p, parietal; prf, prefrontal; po, postorbital; pof,

postfrontal; psp, postplenial; pp, postparietal; ps, parasphenoid; pt, pterygoid; pm, premaxilla; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer; vt, vomerine tooth.

## RESULTS

Systematic palaeontology

Tetrapoda Jaekel 1909

Temnospondyli Zittel 1888

Dissorophoidea Bolt 1969

Amphibamiformes Schoch 2019

*Kermitops* So et al. gen. nov.

*Diagnosis:* As for type and only species (see below).

*Zoobank* LSID: urn:lsid:zoobank.org:act:E22A475F-A2C2-4060-BC9E-CD32D90E394C.

*Kermitops gratus* SO et al. sp. nov.

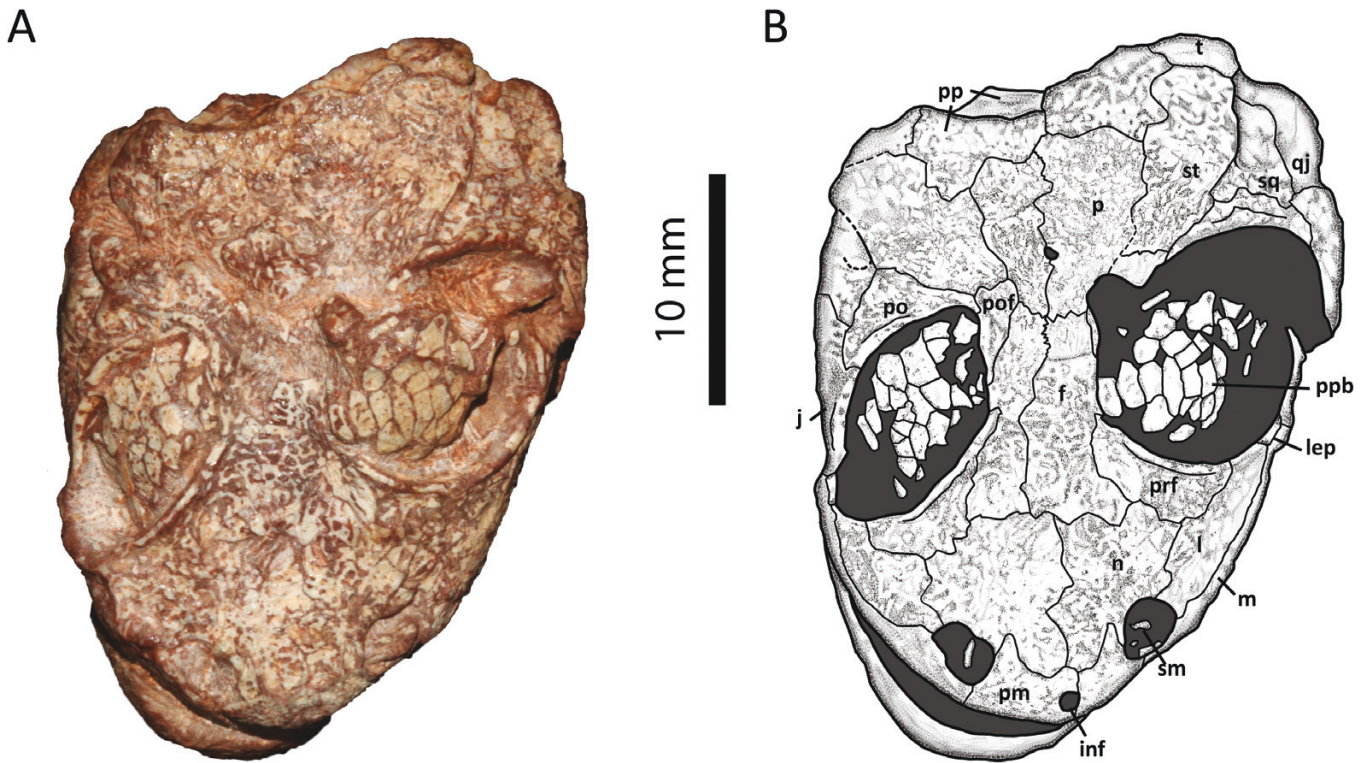
*Zoobank* LSID: urn:lsid:zoobank.org:act:039A8C39-E226-4C54-9357-CB2161A07551.

*Holotype:* USNM 407585 (Figs 1–3), a near complete skull roof, occiput with partial braincase, and mandibles preserved. Aside from partially preserved right vomerine teeth, the anterior palatal elements are not preserved. Marginal teeth are not well-preserved or exposed.

*Etymology:* Generic epithet is derived from a combination of 'Kermit' the famous lissamphibian and beloved Muppets' character created and originally performed by Jim Henson, and the Greek suffix '-ops', meaning face. Specific epithet 'gratus' meaning 'gratitude' in Latin for the contributions of specimen collector and former USNM vertebrate palaeontology curator Nicholas Hotton III, and other members of the USNM field party that were involved in the collection effort.

*Locality and Horizon:* East Coffee Creek, Lake Kemp (NE Quad), Wilbarger County, Lower Clear Fork Formation, Leonardian, Early Permian. USNM PAL 407585 was collected by Nicholas Hotton III and the USNM field party on 6 April 1984 (field number 84-).

*Differential Diagnosis:* An amphibamiform differentiated from all other amphibamiforms by the following autapomorphies: a small internarial fontanelle contained solely between the premaxillae and a double-pronged anterolateral process of the postparietal that incises the supratemporal. Further differentiated from *Plemmyradytes*, *Micropholis*, *Pasawioops*, *Rubeostratilia*, and *Tersomius* by anteroposteriorly shortened postorbital, resulting in a proportionally shorter postorbital bar. Differentiated from *Platyrhinops*, *Amphibamus*, *Georgenthalia*, *Gerobatrachus*, and branchiosaurids by a narrower skull width. Further differentiated from *Platyrhinops*, *Amphibamus*, and branchiosaurids by the participation of the frontal in the orbital margin. Shares with *Platyrhinops*, *Amphibamus*, *Nanobamus*, *Tersomius*, *Pasawioops*,



**Figure 1.** Photograph (A) and interpretive illustration (B) of *Kermitops gratus*, gen. et sp. nov. (USNM PAL 407585) in dorsal view.

*Rubeostritalia*, *Georgenthalia*, and *Gerobatrachus*, but differs from *Doleserpeton*, *Micropholis*, and branchiosaurids by the presence of an anterior flaring of the frontal. Differs from at least *Georgenthalia* and *Nanobamus* in the absence of a keyhole-shaped external narial opening, where the lacrimal is emarginated.

## DESCRIPTION

### General morphology and preservation

The skull is approximately 3 cm long along the midline and 2 cm wide at the level of the occiput (Figs 1–3). There is some taphonomic distortion on both sides, making the orbits appear slightly more ovoid than they would have in life, and the left orbit is partially disarticulated. The anterior palate and braincase are lost but the remainder of the skull is well-preserved, even showing a full arrangement of palpebral ossicles in place and showcasing fine dermal ornamentation on the dorsal skull. The margins of the orbit are slightly raised, resulting in a differentiation of the orbital margin from the rest of the skull roof surface. The snout is long and parabolic in shape, consistent with the morphology seen in micropholids (Fig. 1; e.g. Fröbisch and Reisz 2008). However, the postorbital region of the skull is markedly shorter than that of all micropholids, including a foreshortened postorbital bar and a short postorbital skull table that is shared with *Doleserpeton*, *Amphibamus*, *Platyrrhinops*, *Gerobatrachus*, and *Georgenthalia* (Bolt 1979, Anderson et al 2008a, b, Clack et al 2009, Sigurdson and Bolt 2010). The combination of a long parabolic snout and short post-orbital skull table appears to be unique to this taxon (Fig. 1).

### Premaxillae

The premaxillae are the anteriormost elements of the skull and are gently curved (Figs 1A, B, 3A, C). Laterally, the premaxillae

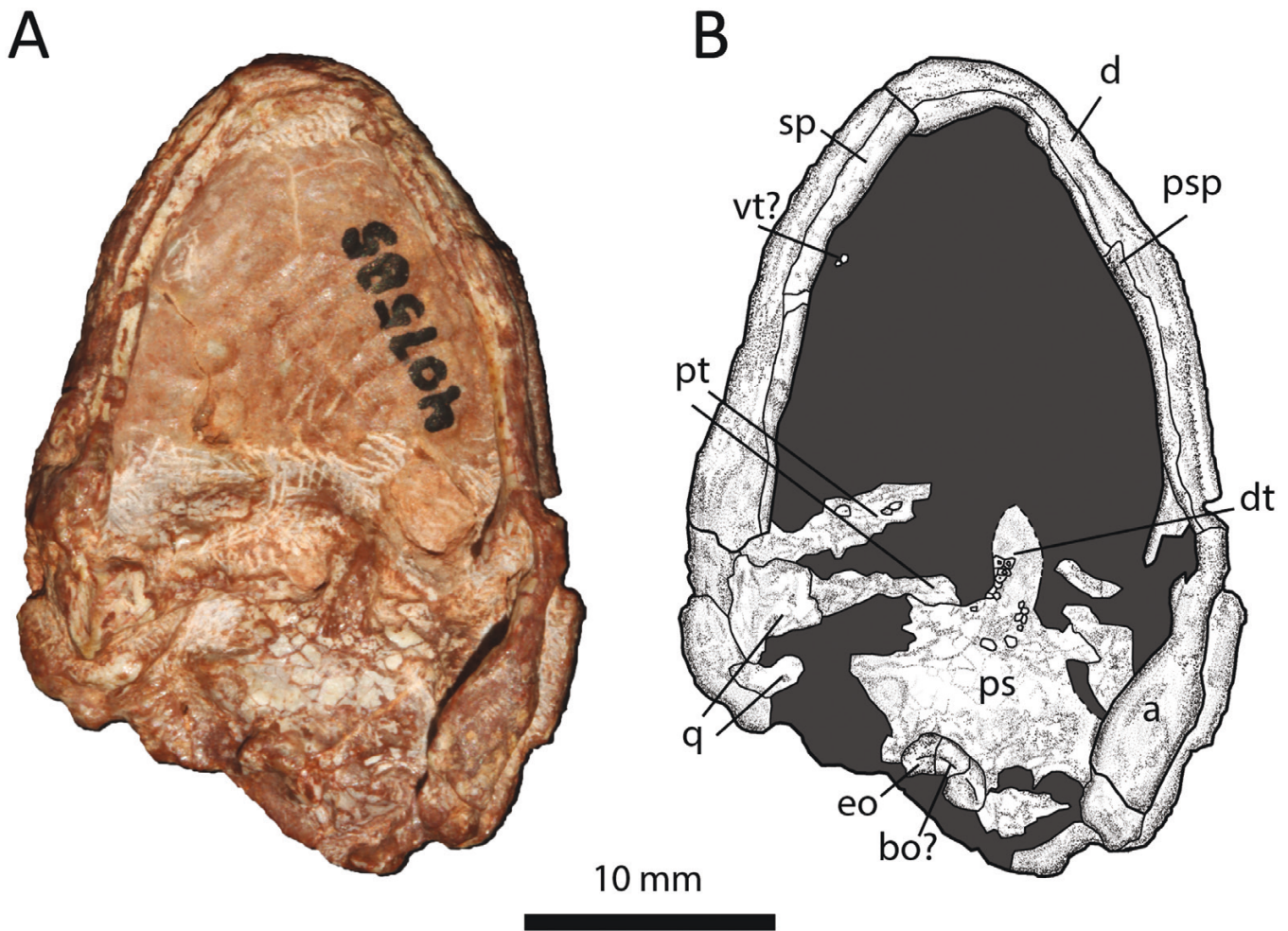
contribute to the anteromedial wall of the narial opening. The dorsal processes terminate with long posteriorly projecting alary processes similar to *Pasawioops* (Fröbisch and Reisz 2008). There is a small internarial fontanelle between both premaxillae (Fig. 1). Internarial fontanelles are present among the amphibamiforms *Pasawioops*, *Georgenthalia*, *Tersomius*, and *Doleserpeton*, but their internarial fontanelles are larger and partially formed by a contribution of the nasal, which is not present here. Fine pitting adorns the premaxillae, though the ornamentation is not as distinct as in the dorsal skull roof. No teeth are preserved on the premaxillae.

### Nasals

Both nasals are preserved, roughly quadrangular in shape and are broad, occupying an expansive region of the snout similar to other amphibamiforms (Fig. 1). The nasals are ornamented with anastomosing ridges and pits. Anteriorly, the nasals are incised by the invading alary processes of the premaxillae similar to the condition seen in *Pasawioops* (Fröbisch and Reisz 2008). The midline nasal suture is slightly interdigitated as are the surrounding sutures with the frontal, prefrontal, and lacrimal. The nasals form the majority of the dorsomedial margin of the external nares.

### Maxillae

The maxillae are preserved on either side of the skull as thin, elongated elements that reach from the anteriormost tip of the nares to the posteriormost portion of the postorbital bar (Figs 1 and 3B, D). Anteriorly, the maxillae bear a small but pronounced facial lamina that extends dorsally and forms the ventral margin of the external nares (Fig. 3B, D). The facial lamina is slightly more pronounced than micropholids, such



**Figure 2.** Photograph (A) and interpretive illustration (B) of *Kermitops gratus*, gen. et sp. nov. (USNM PAL 407585) in ventral view.

as *Pasawioops* and *Tersomius texensis* (Fröbisch and Reisz 2008, Maddin et al. 2013). While there isn't much ornament visible on the lateral surface of the maxillae, this is most likely due to poor preservation or over-preparation, and there are hints of rugose ornamentation present, similar to the rest of the skull. As the maxillae elongate towards the posterior, it underplates the lateral exposure of the palatine (LEP), and the jugal (Fig. 3B, D). The maxillae terminates at the contact with the jugal, where it appears to taper to a point. No teeth are preserved on the maxillae.

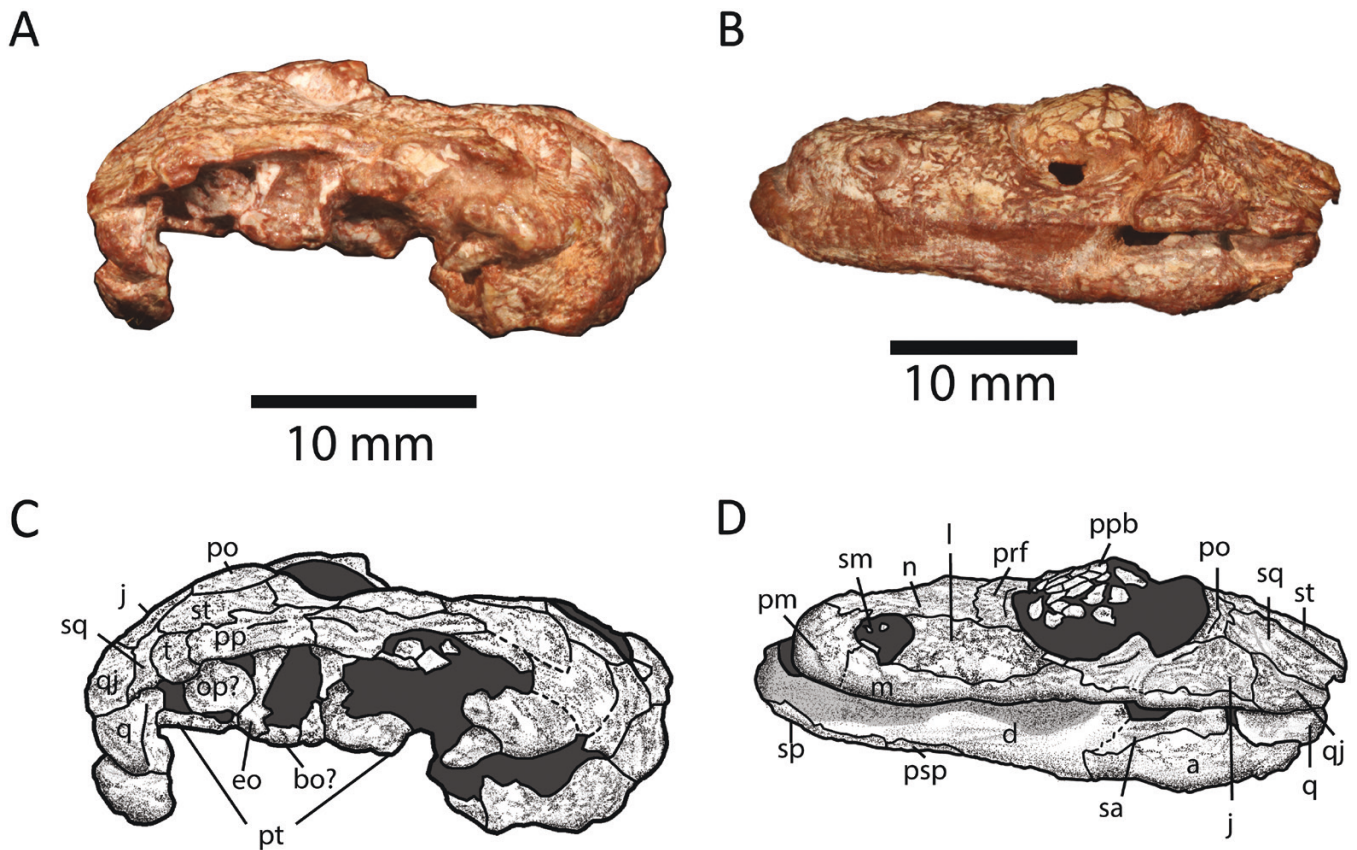
#### Lacrimals

The lacrimals can be located on both sides of the skull as an elongate element that gently curves laterally on its anterior–posterior axis, leading to its contribution to both the dorsal and lateral skull roof similar to most micropholids. The elements reach from the posterior external nares to the antorbital margin (Fig. 1). The lacrimals are ornamented, though ventrally the ornamentation is subdued compared to more dorsal areas of the element (Fig. 3A, C). They form the posterolateral margin of the external nares and the anterolateral margin of the orbit. The lacrimals emarginate the anterior and ventral margins of the orbit. The posterior process of the lacrimal ventral to the orbit narrows to the point and sutures to the LEP. The dorsal margin of

the lacrimal bears a process that invades the suture between the nasal and the prefrontal resembling the condition in *Pasawioops* (Fröbisch and Reisz 2008). On the left lacrimal, the step is less pronounced. Laterally, the sutural contact between the lacrimal and the maxilla is straight.

#### Prefrontals

The prefrontals are falciform elements that comprise the majority of the anterodorsal margin of the orbit similar to most amphibamiforms (Figs 1, 3B, D). The posterodorsal process of the right prefrontal narrows to a point between the frontal and the orbit and contacts the anterior half of the frontal. The posterodorsal process of the left prefrontal is more robust compared to the same process of the right prefrontals. The ventral process of the prefrontals is blunt and form a simple suture with the lacrimals, but invades into the lacrimal as a consequence of the medial lacrimal process (Fig. 1) This condition is unlike the less prominent ventral prefrontal process in *Pasawioops* and *Tersomius* (Fröbisch and Reisz 2008, Maddin et al. 2013) but similar to *Rubeostratilia* (Bourget and Anderson 2011). The anterior suture of the prefrontals with the nasals are interdigitating, with the right prefrontal having more pronounced interdigitation (Fig. 1). The ornamentation of the prefrontals is well-defined with pits and ridges.



**Figure 3.** Photograph of *Kermitops gratus*, gen. et sp. nov. (USNM PAL 407585) in occipital (A) and lateral (B) view, and the interpretation in occipital (C) and lateral (D) view.

#### Frontals

The paired frontals are quadrangular elements in the interorbital skull roof. They are asymmetric, with the right frontal narrower than the left (Fig. 1). The midline is a simple wavering suture until the posterior quarter, where the suture becomes a significantly interdigitating suture. Anteriorly, the frontals widen; the anterior of the left frontal is twice as wide as its posterior, while the anterior of the right frontal is only marginally wider than its posterior. Anterior flaring of the frontals can be seen in *Rubeostratilia*, *Tersomius*, *Nanobamus*, *Gerobatrachus*, and *Georgenthalia* (Anderson et al. 2008a, b, Gee and Reisz 2020). A small process of the frontals contacts a very small portion of the medial orbital margin, restricted by the supraorbital processes of the prefrontal and postfrontal (Fig. 1). The posterior contact with the parietals forms an interdigitating suture. Some of the most well-defined ornamentation can be observed on the anterior half of the frontals.

#### Palpebral ossifications

Palpebral ossifications are commonly found in Amphibamiformes, and a well-preserved series of these mosaic plates line the orbit adjacent to the frontals in *Kermitops*. These plates vary in size and are mostly unornamented, but bear a very slight pitting on some of the largest plates (Fig. 1). Amphibamiforms that preserve similar palpebral ossifications include *Tersomius texensis* (Maddin et al. 2013), *Rubeostratilia texensis* (Bourget and Anderson 2011), and the likely amphibamiform ‘*Broiliellus hektotopos*’ (Berman and Berman 1975).

#### Postfrontals

Based on the right postfrontal, the postfrontals are the smallest elements of the interorbital region and contribute to a small posteromedial segment of the orbital margin, most similar to *Plemmyradytes* (Huttenlocker et al. 2007), *Pasawioops* (Fröbisch and Reisz 2008), and *Rubeostratilia* (Bourget and Anderson 2011), but vastly different than the expansive postfrontals of *Nanobamus* (Gee and Reisz 2020). They are subtriangular in shape, with the anterior terminus of the supraorbital process narrowing to a point between the frontal and the orbit (Fig. 1). The contacts with the surrounding elements—the frontal, parietal, supratemporal, and postorbital—are straight.

#### Postorbitals

The postorbitals are falciform elements that form a significant portion of the postorbital margin and are most similar to *Plemmyradytes* (Huttenlocker et al. 2007) and *Georgenthalia* (Anderson 2008). Anterodorsally, the dorsal process of the postorbitals narrows to a point between the postfrontal medially and the orbit laterally (Figs 1, 3B, D). The ventral process of the postorbitals tapers to a point anterior of the jugal, forming the posterior margin of the orbit. The postorbitals form simple and straight sutures with the postfrontal, supratemporal, and jugal, and form an undulating suture with the squamosal that is not preserved on the right.

#### Jugals

The jugals are subtriangular in shape in lateral view and most similar in shape to other micropholids, such as *Micropholis* and

*Rubeostratilia* (Bourget and Anderson 2011) (Fig. 3B, D). They contribute to the posteroventral margin of the orbit. The anterior process of the jugals narrows to a point in between the orbit dorsally and the maxilla ventrally. The posterior termination marks the posterior extent of the postorbital bar. Well-defined pit and ridge ornamentation is present on the left jugal, whereas on the right it is either eroded or over-prepared and partially obscured by matrix.

### Parietals

The parietals are both preserved; however, the left side is much less distorted (Fig. 1). The parietals are quadrangular and narrow anteriorly, as in most amphibamiforms (e.g. *Pasawioops* Fröbisch and Reisz 2008 and *Doleserpeton* Sigurdson and Bolt 2010; but unlike *Micropholis* Schoch and Rubidge 2005). The interparietal suture is highly interdigitated and a small pineal foramen is located on the anterior third of its length. The parietals meet the frontals anteriorly at a narrow contact and form an interdigitated suture. Laterally, the parietals contact the postfrontals and supratemporals at a broad amplitude and shallow suture. Posteriorly, the parietals are at their widest and contact the postparietals at a wavy but not interdigitated suture. The parietals share the same dermal ornamentation as the rest of the skull but do not appear to have as deep grooves as the frontals and some of the snout region.

### Postparietals

The postparietals are both preserved at the occiput as the posteriormost bones of the skull roof alongside the tabulars (Figs 1, 3A, C). The postparietals are anteroposteriorly extended, unlike the narrower postparietals in *Georgenthalia* and *Eoscopus*. The postparietals have double-pronged processes that protrude anterolaterally and intrude into the supratemporal. They form complex, undulating sutures with their surrounding elements, particularly the supratemporal. The occipital margin of the right postparietal is complete but fragmented. Similar to the rest of the posterior skull table, dermal ornamentation is present on the postparietals.

### Tabulars

The tabulars are small, quadrangular elements contributing to the margin of the otic notch and to the occiput of the skull roof, as in most amphibamiforms (Figs 1, 3A, B). They are much more anteroposteriorly foreshortened compared to the postparietals, similar to *Pasawioops* (Fröbisch and Reisz 2008) and *Tersomius texensis* (Maddin et al. 2013). The ornamentation on the tabulars is very fine and not as well-defined as in other elements. A short posterolateral rim of the tabulars contributes to the margin of the otic notch. The occiput is dorsoventrally compressed and the right tabular especially so, making it difficult to discern any more of the otic notch participation by the tabulars. A paroccipital process of the left tabular is partially preserved and sutures to a possible opisthotic (Fig. 3A, B).

### Squamosals

The squamosals are elements that frame the majority of the anterior and ventral otic notch, found on either side of the cranium (Figs 1, 3). The exact shape of the squamosals is uncertain, due to dorsoventral deformation of the posterior skull roof. They

form continuous sutures with the quadratojugals ventrally and postorbitals anteriorly. There is a short suture anterolaterally with the jugals. There is poorly defined pitting on the squamosals. Due to the deformation, it is difficult to discern their sutures with the supratemporals dorsally, but the dorsal processes of the squamosals appear to underplate the supratemporals. The transition between the skull roof surface and the otic notch surface of the squamosals is poorly defined due to dorsoventral compression. However, the squamosals exhibit a lack of ornamentation similar to other amphibamiforms that allows us to infer how the otic notch may have been constructed in life.

### Supratemporals

The supratemporals are preserved on either side of the cranium and are large, subrectangular-shaped elements that contact the parietals and postparietals medially, the postfrontal anteriorly, the squamosal and postorbital ventrally, and the tabular posteriorly (Fig. 1). On either side, the medial sutures with the parietals and postparietals are noticeably wavering and slightly interdigitated. The supratemporals are highly ornamented with anastomosing ridges and pits similar to the other dorsal skull elements. In general, the morphology of the supratemporals resembles the condition found in Micropholidae, more so than the condition in Amphibamidae.

### Quadratojugals

The quadratojugals frame the otic notch ventrally. The better preserved left quadratojugal is laterally triangular and dorsally quadrangular (Figs 1, 3). The quadratojugals overplate the respective quadrates. The quadratojugals are ornamented with light pitting on both of the exposed lateral surfaces.

### Quadrates

The quadrates are found underplating the quadratojugals (Fig. 3). They are identified on the basis of their contact with the quadrate process of the pterygoid. This position is potentially a result of the element's craniomandibular articulation being shoved anterior relative to their original position. The left quadrate is not well-preserved enough to further discern additional features of the element. The right quadrate appears to be fractured into two fragments and is similarly difficult to discern further features of its anatomy.

### Septomaxillae

The septomaxillae are small bony elements found in the ventrolateral margin of the nares (Figs 1, 3B, D). They are small and fragmented; few features of the elements can be noted besides their positions.

### Vomer

Although the vomer is mostly obscured, what appears to be cross-sections of the vomerine fangs may be visible on the area of the palate where the right vomer would lie (Fig. 2).

### Parasphenoid

The base of the parasphenoid is partially crushed, distorting its original shape (Fig. 2). However, a general shape can be described; the posterior margin of the parasphenoid laterally flares out, and narrows towards the basiptyergoid processes, which

jut out laterally, forming a steep incision on the lateral margins of the parasphenoid. Only the base of the cultriform process is preserved; it is parallel-sided, narrow, and keel-shaped. A field of denticles is preserved at the interface between the cultriform process and the base of the parasphenoid, as well as further anterior on what remains of the cultriform process, differing from the condition in *Pasawioops* (Fröbisch and Reisz 2008) and *Micropholis* (Schoch and Rubidge 2005) but similar to most other amphibamiforms. The base of the parasphenoid bears shallow depressions for the attachment of muscles (Fig. 2).

### Pterygoids

The pterygoids are poorly preserved but, based on the components preserved, the pterygoids are triradiate elements composed of at least three rami: the palatal ramus, the quadrate ramus, and the basicranial process (Fig. 2). The connection between both basicranial processes of the pterygoids and the basiptyergoid processes of the parasphenoid seems to form a suturalbasicranial articulation. Both quadrate rami of the pterygoids are distorted, but the sutures between the rami and the quadrates are well-preserved and tight. Both palatal rami of the pterygoids are poorly preserved. Only a disarticulated proximate segment is preserved in the left pterygoid. In the right pterygoid, the process is broken at the base where it extends from the pterygoid and is rotated posteriorly. On the process itself, there appears to be a preserved shagreen of denticles similar to those seen in *Pasawioops* (Fig. 2; Fröbisch and Reisz 2008).

### Exoccipitals

The exoccipitals are paired elements of the occiput. Both exoccipitals preserve the ascending columns and the occipital condyles (Figs 3A, C). They are strongly sutured to the posterior margin of parasphenoid ventrally (Fig. 2). The dorsal processes of the exoccipitals extend dorsally towards the postparietals. They meet the descending ventral process of the postparietal, but it is unclear where the suture lies, if it exists, making it hard to delimit the ventral process of the postparietals. Laterally, a facet for the opisthotic is present on both exoccipitals similar to *Pasawioops* (Fröbisch and Reisz 2008); the right opisthotic is sutured (Figs 3A, C).

The shape of the foramen magnum is roughly subrectangular and slightly taller than wide. It is framed laterally by the dorsal processes of the exoccipitals, ventrally by a separate ossification from the exoccipitals, and dorsally by the postparietals (Figs 3A, C). This additional ventral, unpaired ossification is separated from the lateral exoccipitals by fine sutures, and tightly sutures to anteriorly located parasphenoid. We tentatively identify this ossification as the basioccipital.

### Mandible

The skull roof is accompanied by paired mandibular rami. While most of the elements of the mandibles are obscured by matrix, the elements that are observable indicate that the hemimandibles possess the usual amphibamiform complement of the dentary, splenial, post-splenial, coronoids, angular, surangular, pre-articular, and articular (Fig. 2). The dentaries are the longest and largest element of the mandibles (Fig. 2). Although the teeth are not visible, they are probably the sole tooth-bearing element of the mandibles. The surface of the

dentary that is exposed is worn, but it does not seem to preserve prominent ornamentation. Sutured ventrally to the dentaries are the splenials and post-splenials (Fig. 2). These elements are narrow, parallel-to-subparallel rectangles that follow the curvature of the mandibles; they form a trough shape as the element cups the ventral hemimandibles. Predominantly elements of the lingual surface, narrow slivers of the splenials and post-splenials are visible on the labial surfaces. The dentaries and the splenials both meet and contribute to a well-defined mandibular symphysis, similar to *Pasawioops* (Fröbisch and Reisz 2008). The post-splenials terminate at the same level at which the dentaries terminate posteriorly. Posterior to the post-splenials are the angulars. The angulars are significant components of the posterior labial surface of the hemimandibles; they wrap around the ventral aspect of the ramus and contribute to the lingual surface of the hemimandibles as well (Fig. 2). Dorsally, on the labial surface, the angulars form a simple suture to the surangulars (Figs 3B, D). The surangulars occupy a thin strip at the posterior mandible. Lingually, the coronoids and a pre-articular are visible in the left hemimandible, but the exact boundaries and shapes of these elements cannot be delimited. The splenials suture to the coronoids and the pre-articular dorsally.

### Phylogenetic analysis

We explored the phylogenetic relationships of *Kermitops gratus* among Dissorophoidea using a modified version of the character–taxon matrix recently published by Schoch and Werneburg (2023) and Werneburg *et al.* (2023). We added four additional taxa: *Plemmyradytes shintoni* (Huttenlocker *et al.* 2007), *Rubeostratilia texensis* (Bourget and Anderson 2011), *Milnererpeton huberi* (Hunt *et al.* 1996, Werneburg *et al.* 2021), and *Nanobamus* (Gee and Reisz 2020). Several inconsistencies were present in the original matrix and corrected before the analysis was performed (see Supporting Information, S2 and S3 for details). We made the addition of six characters concerning the variation found in the circumorbital elements of the prefrontal, postorbital, postfrontal, jugal, lacrimal, and, when applicable, the LEP:

113. Shape of the prefrontal at its circumorbital contribution: (0) wide body of the element; or (1) some or all of the element is reduced, becoming narrower and near splint-like at the anterior or dorsal orbital margin.

114. Shape of the postfrontal at its circumorbital contribution: (0) wide body of the element; or (1) some or all of the element is reduced, becoming narrower and near splint-like as it wraps around the dorsal or medial orbital margin.

115. Shape of the postorbital at its circumorbital contribution: (0) wide body of the element; or (1) some or all of the element is reduced, becoming narrower and near splint-like at the posterior orbital margin.

116. Shape of the lacrimal at its circumorbital contribution: (0) wide body of the element; or (1) some or all of the element is reduced, becoming narrower and splint-like at the ventral or anterolateral orbital margin.

117. Shape of the jugal at its circumorbital contribution: (0) wide body of the element; or (1) some or all of the element is reduced, becoming narrower and near splint-like at the ventral or posterolateral orbital margin.

118. Depth of the LEP, if present: (0) LEP tall, at least half as tall as maxilla in orbital margin; or (1) facial exposure of palatine a narrow sliver.

The final character–taxon matrix, consisting of 46 taxa and 118 characters (Supporting Information, S4) was analysed using TNT 1.5 (<https://cladistics.org/tnt>), utilizing the same conditions as reported in Schoch and Werneburg (2023). All characters were equally weighted and unordered. We used the New Technology Search option with 1000 replicates under Ratchet. Due to the possible presence of a basioccipital, we ran two different analyses—one with the basioccipital interpreted as absent and another with the basioccipital interpreted as present. Strict consensus trees were calculated from the most-parsimonious trees from each analysis (Fig. 4). Bootstrap analyses were also run, producing 1000 replicates for each condition and generating a strict consensus tree from each bootstrap analysis (Supporting Information, S5, S6).

Bayesian inference was conducted using MrBayes 3.2.7 (Huelsenbeck and Ronquist 2001, Ronquist et al. 2012) under the Mkv model (Lewis 2001), independent gamma branch rates, and equal rate of change between character states for two analyses with alternate codings of the presence of the basioccipital. The analysis was parameterized to initiate four runs with six Markov chain Monte Carlo chains and run for 10 million generations with sampling every 1000 generations and a relative burn-in of 25%. A consensus tree with posterior probabilities mapped on to the nodes was generated (Fig. 5; Supporting Information, S7, S8).

The parsimony analysis assuming the presence of a basioccipital produced five equally parsimonious trees of 360 steps each (Fig. 4A). The recovered trees had a consistency index of 0.367 and a retention index of 0.694. The strict

consensus of the most-parsimonious trees recovered monophyletic Amphibamiformes; however, the majority of relationships among them form a polytomy, with the exception of strong support for monophyletic branchiosaurids and lissamphibians. *Micropholis* was found to be the sister-taxon of *Pasawioops*, and *Kermitops* was part of the amphibamiform polytomy (Fig. 4A). The parsimony analysis assuming absence of a basioccipital produced four equally parsimonious trees of 359 steps each (Fig. 4B). The recovered trees had a consistency index of 0.368 and a retention index of 0.696. The strict consensus produced several relationships that departed from previously recognized topologies. *Nanobamus* and *Milnererpeton* were recovered as sister-taxa, which in turn are sister to the *Georgenthalia*, *Gerobatrachus*, and Lissamphibia clade. This relationship replaces amphibamids as the previously recovered closest relatives to the latter clade (Schoch 2019, Schoch and Werneburg 2023). A polytomy consisting of micropholids, *Kermitops*, *Plemmyradytes*, and *Eoscopus* was recovered with the clade of *Nanobamus*, *Milnererpeton*, *Georgenthalia*, *Gerobatrachus*, and Lissamphibia (Fig. 4B). Amphibamids and branchiosaurids are sister to each other and in turn are sister to the previous clade.

The Bayesian inference permutation considering the presence of a basioccipital in *Kermitops* produced a topology that differs starkly from the results of both of the maximum parsimony analyses (Fig. 5A). *Kermitops* and *Plemmyradytes* once again form a clade; however, in this permutation this clade is the sister-taxon of all other amphibamiforms. *Rubeostratilia* forms a clade with Micropholidae, which is the sister-taxon of the clade formed by branchiosaurs, *Nanobamus*, *Milnererpeton*, *Georgenthalia*, *Gerobatrachus*,

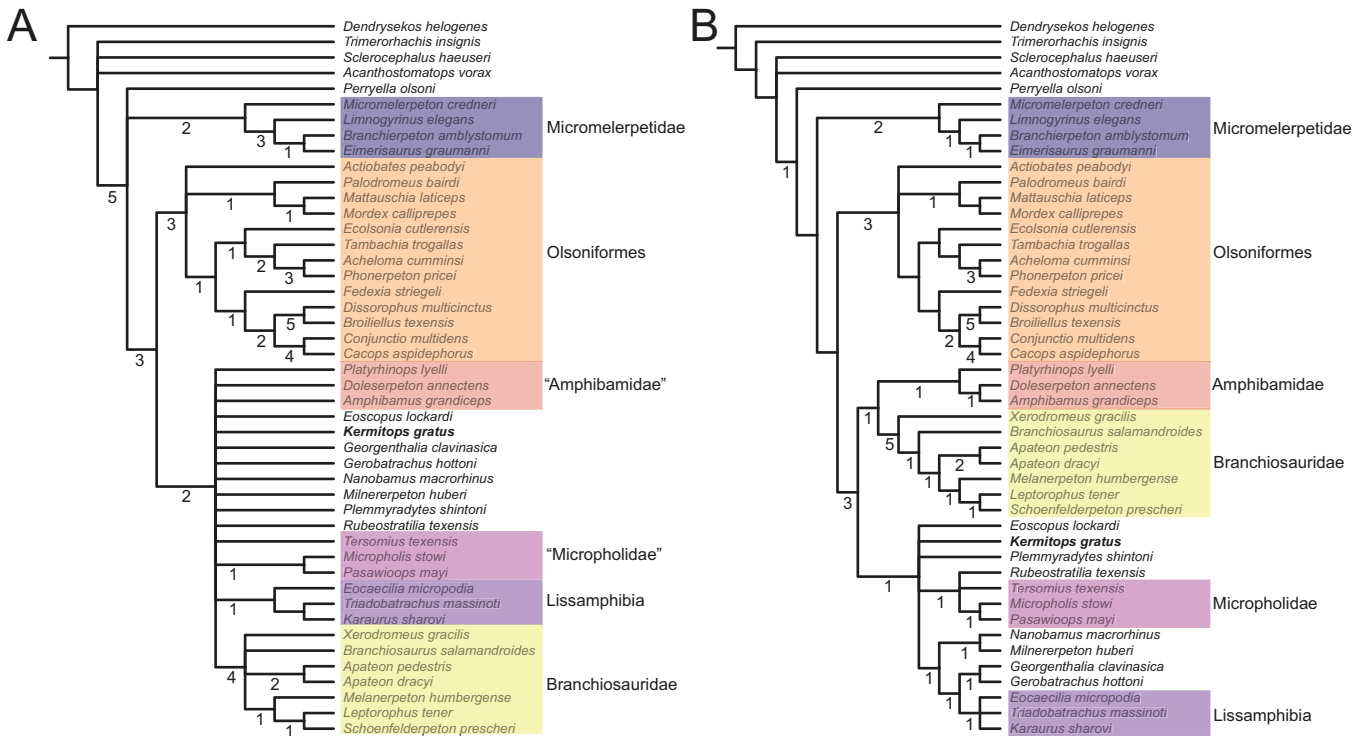
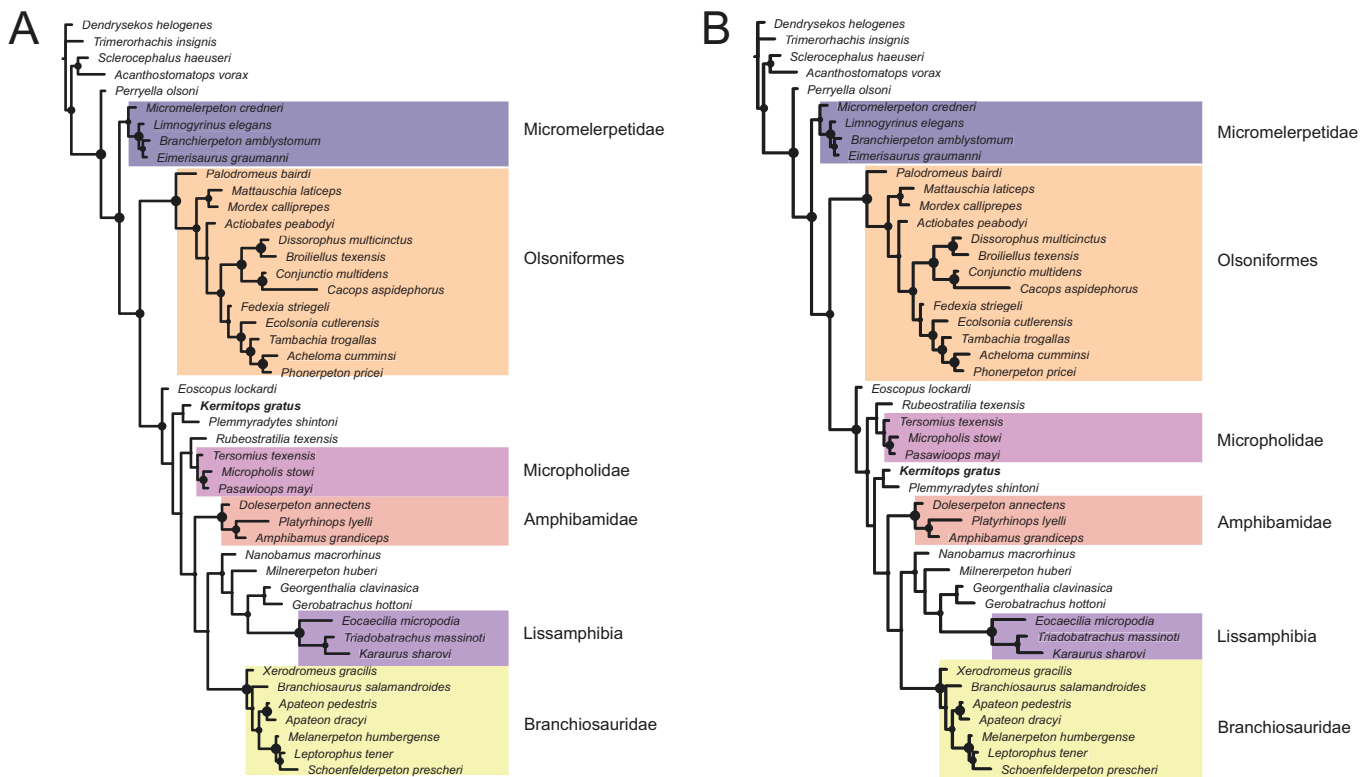


Figure 4. Strict consensus results of the maximum parsimony trees with the basioccipital coded present (A) or absent (B) and the position of *Kermitops gratus* found in the analyses. Bremer support values mapped to the left of the respective node.





**Figure 5.** Bayesian inference results with alternative codings of the basioccipital as present (A) or absent (B). Circles on the node represent posterior probability values; larger circles denote values closer to 1. See Supplementary Information (S6 and S7) for the posterior probability values.

and Lissamphibia. *Georgenthalia* formed a clade with *Gerobatrachus*; they are recovered as the sister-group to Lissamphibia to the exclusion of *Milnererpeton* and to the further exclusion of *Nanobamus*. This clade was recovered as a sister to Branchiosauridae. Further this topology recovered *Platyrhinops* forming a clade with *Amphibamus* to the exclusion of *Doleserpeton* as sister-taxon to the clade of *Nanobamus*, *Milnererpeton*, *Georgenthalia*, *Gerobatrachus*, and Lissamphibia, plus the branchiosaurid clade. *Eoscopus* was found as the sister-taxon to the *Kermitops* and *Plemmyradytes* clade, plus all other amphibamiforms. The posterior probability of Amphibamiformes clades is low (posterior probability = 0.1904) and the posterior probability of the node that unites *Kermitops* and *Plemmyradytes* with amphibamiforms is similarly low (posterior probability = 0.2492) (Fig. 5A; Supporting Information, S7).

In the Bayesian inference permutation considering the absence of the basioccipital, *Kermitops* is nested within amphibamiforms as sister-taxon to *Plemmyradytes* (Fig. 5B). They are sister to a monophyletic group consisting of branchiosaurs, *Nanobamus*, *Milnererpeton*, *Georgenthalia*, *Gerobatrachus*, and Lissamphibia (posterior probability = 0.1401) (Supporting Information, S8). Micropholids were recovered as the sister-group to *Kermitops* and *Plemmyradytes*, plus the branchiosaurs, *Nanobamus*, *Milnererpeton*, *Georgenthalia*, *Gerobatrachus*, and Lissamphibia. *Eoscopus* is once again found as the earliest divergent amphibamiform (Fig. 5B).

An additional Bayesian inference permutation was conducted for the absent state of the basioccipital under a

FBD (Heath *et al.* 2014) and a uniform distribution tree age prior between 312 and 330 Mya following a previous time-calibrated analysis (Jones *et al.* 2022). Three extant lissamphibians were added to the dataset for this analysis (*Epicrionops bicolor*, *Cryptobranchus alleganiensis*, and *Leiopelma hamiltoni*). The fossil ages for tip-calibration were obtained from the Paleobiology Database (paleobiodb.org) and supplemented with the age of the reported stage of occurrence from the publications of a taxon when needed (Supporting Information, S9). The resultant topology also recovered micropholids and micropholid-like amphibamiforms as more closely related to lissamphibians than previously expected (Fig. 6). *Kermitops* was found as the sister-taxon to *Plemmyradytes*. The *Kermitops*–*Plemmyradytes* clade was found as the sister-taxon to the clade including *Rubeostratilia* and Micropholidae, to the exclusion of *Eoscopus*. Sister to this clade, another clade of amphibamiforms was recovered containing Lissamphibia, *Gerobatrachus*, *Georgenthalia*, and *Nanobamus* with *Milnererpeton* at the base. Within Lissamphibia, the three extant lissamphibians were recovered as a monophyletic group sister to *Karaurus* (Fig. 6). This position is probably recovered due to the minimal coverage of lissamphibian morphology and to focus on amphibamiform characters. Branchiosaurs were found as the sister-taxon to amphibamids. The amphibamid–branchiosaur clade was recovered as the sister-taxon to the clade formed by micropholids, micropholid-like amphibamiforms (e.g. *Kermitops*, *Plemmyradytes*), and *Milnererpeton*, *Nanobamus*, *Georgenthalia*, *Gerobatrachus*, and lissamphibians (Fig. 6).

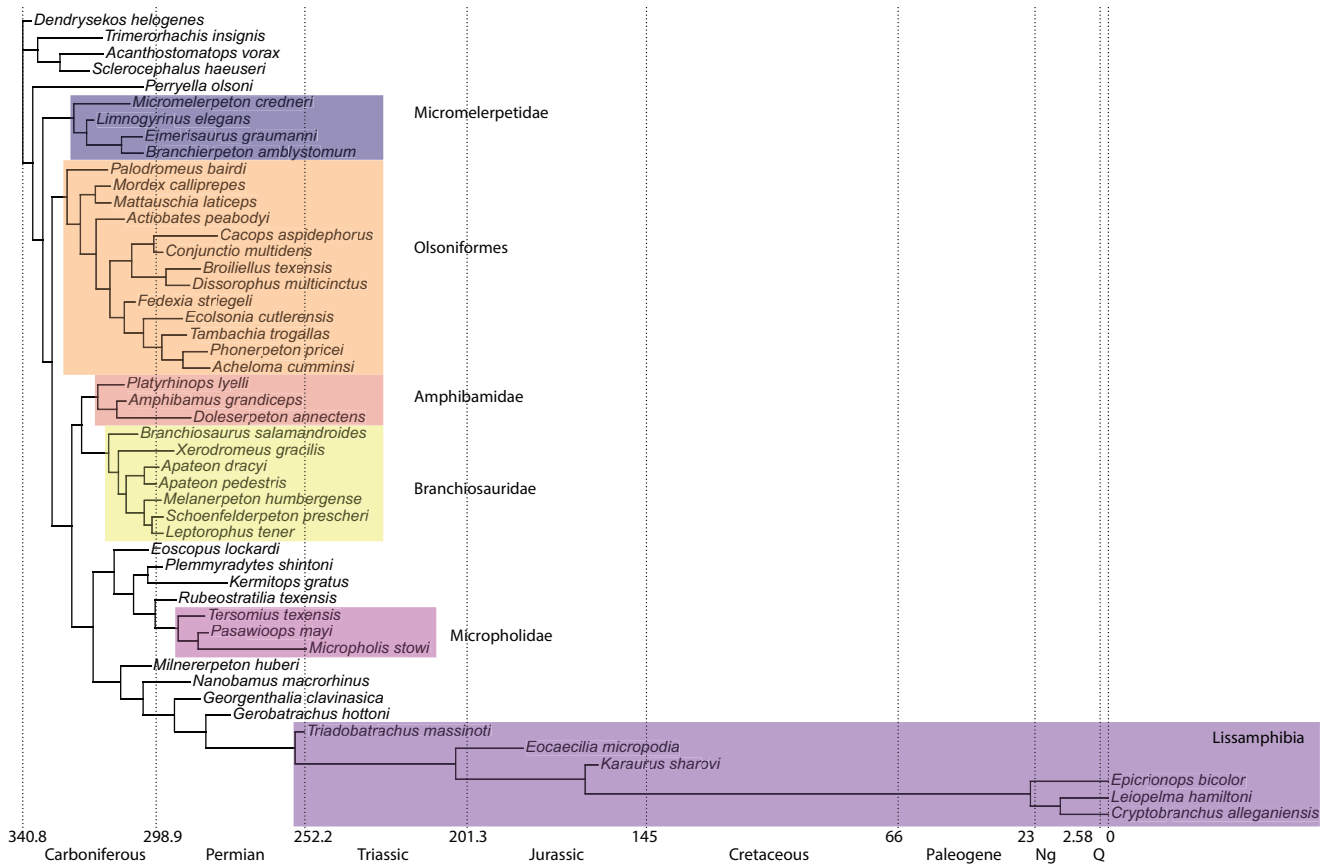


Figure 6. Fossilized birth-death tree with the coding of basioccipital as absent.

## DISCUSSION

### Phylogenetic position of *Kermitops* and interrelationships of Amphibamiformes revisited

We provide here an updated and carefully vetted character matrix for amphibamiforms, with the addition of several new taxa and characters. We present several parallel analyses of these data, including analyses using parsimony, traditional posterior probability, and FBD models implementing the tip-dating approach. These analyses consistently failed to recover traditional topologies within amphibamiforms and, in fact, reduced resolution within the clade more generally. In some cases, we recovered dubious non-traditional topologies in dissorophoids more generally, including an origin of dissorophids within trematopids and an early divergence between traditional amphibamids (*Doleserpeton*, *Amphibamus*, and *Platyrhinops*) and all other amphibamiforms, including branchiosaurs and lissamphibians. The lack of resolution and of consistent topology between maximum parsimony, Bayesian inference, and time-calibrated 'FBD' Bayesian inference phylogenetic analyses of the amphibamiform tree suggest that we have not achieved a consensus hypothesis on the evolutionary history of modern amphibians. Because our analyses presented here are standard and apply previously reported parameters, we conclude that the instability of the key nodes in the tree lies within the underlying anatomical data itself, and reinforces a community-level need to critically re-evaluate the morphological characters used to reconstruct lissamphibian evolutionary history (e.g. Schoch and Milner 2004, Anderson et

al. 2008, Marjanović and Laurin 2007, Pardo et al. 2017, Atkins et al. 2019, Schoch 2019, Schoch et al. 2020, Kligman et al. 2023, etc.).

Recent workers have suggested that time-calibrated phylogenetic inference methods (e.g. tip-dating) have the potential to improve topological estimates where current characterization of morphology is insufficient to resolve phylogenetic relationships (Hugall et al. 2007, Inoue et al. 2010, Lee and Yates 2018, King and Beck 2020, King 2021). Our results reported here show that this is not currently the case in amphibamiforms and probably not the case in the vertebrate record more generally; we caution against the use of time-calibrated analyses to 'fix' topologies where conflict exists in the interpretation of morphology and its role in supporting divergent phylogenetic hypotheses. These methods, while useful for the estimation of branch lengths as groundwork for further biogeographic and comparative method analyses, are not robust to non-random anatomical representation in characters within datasets used for phylogenetic inference.

Most interestingly, we recover a lack of clear association between lissamphibians and amphibamiform taxa with pedicellate bicuspid teeth. Previous workers have long maintained that a lissamphibian-style pedicellate tooth, where the junction between crown and orthodontine pedicel is incompletely mineralized, is the primary fossilizable anatomy uniting modern lissamphibians and, therefore, the presence of pedicellate teeth in some amphibamiforms is strong evidence of stepwise acquisition

of lissamphibian body plan(s) within amphibamiforms (Parsons and Williams 1963, Bolt 1969, Milner 1988). Our topologies suggest that bicuspid and pedicellate teeth would necessarily have either evolved numerous times in parallel or would have been plesiomorphic for amphibamiforms and lost repeatedly within the clade. Repeated evolution of this tooth morphology has previously been remarked upon by workers proposing heterodox hypotheses of lissamphibian origins (Marjanović and Laurin 2007, Anderson *et al.* 2008, Pardo *et al.* 2017, Marjanović and Laurin 2019) but our finding here of a similar pattern testing an conventional single origin within amphibamiforms suggests that our understanding of the distribution and biological basis for this morphology remains poorly understood. In fact, this is probably a broader feature of recent amphibamiform phylogenies (e.g. Schoch *et al.* 2020), although our results reported here are particularly stark. Although this character complex is probably still important in understanding the origin or origins of lissamphibians, it is misleading to present this as an unambiguous synapomorphy uniting lissamphibians and some amphibamiforms at this time.

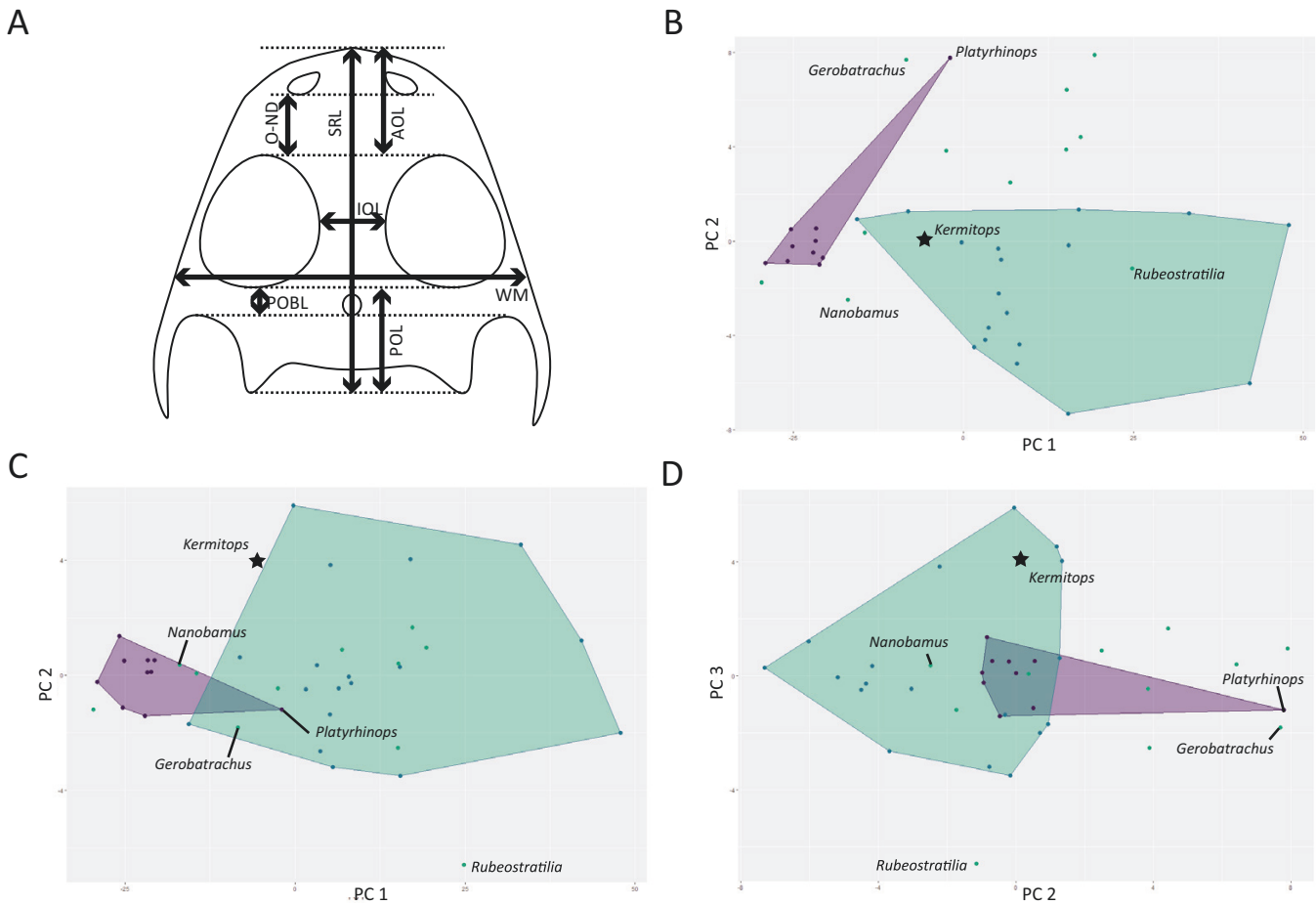
As with the character of bicuspid, pedicellate teeth, a single origin of other proposed key lissamphibian features is not unambiguously supported by the current state-of-the-art methods, and further review of anatomy across amphibamiforms is warranted. Our identification of a possible basioccipital in *Kermitops* (Fig. 2) would disrupt a recent hypothesis of stepwise reduction of the occipital arch in amphibamiforms to produce the lissamphibian condition (Atkins *et al.* 2019). Previous workers hypothesize that amphibian origins are marked by progressive reduction and loss of independent elements of the occipital arch (supraoccipital, exoccipitals, and basioccipital) associated with the reduction of the number of rhombomeres (cranial somites) integrated into the back of the developing amphibian head (Atkins *et al.* 2019, Maddin *et al.* 2010). If the ventral ossification we observe here between the exoccipitals of *Kermitops* is indeed a distinct basioccipital, then the simplification of the braincase cannot have happened at this point in lissamphibian evolution, shifting the timing of the loss of these posterior braincase elements later in the tree. This raises several questions: (i) has absence of the basioccipital been consistently investigated across amphibamiforms; and (ii) to what extent are amphibamiforms with an absent basioccipital mature adults? Absence of the basioccipital may be more difficult to determine in amphibamiforms given the large posteriorly-expanded basal plate of the parasphenoid, which floors much of the occipital arch, so studies that do not segment the occipital arch from  $\mu$ CT scans (e.g. Atkins *et al.* 2020) may miss this bone, if present. Further, the basioccipital is a relatively late-ossifying element that rapidly co-ossifies with the exoccipitals in other dissorophoids (Maddin *et al.* 2010) and, therefore, its absence in many smaller amphibamiforms may be indicative of failure to capture this critical developmental window in the available fossils of most amphibamiforms. Either or both of these explanations could confound hypotheses proposing a clear stepwise pattern of the reduction of the occipital arch, and the presence of a possible basioccipital in *Kermitops* suggests that additional work is necessary before the condition of the occipital arch is fully accepted as a resolved problem in lissamphibian origins.

The complex phylogenetic distribution of these features presents a serious challenge for current usage of these characters as a feature uniting lissamphibians with putative Paleozoic and Carboniferous relatives (Bolt 1969, Anderson 2008b, Sigurdson and Bolt 2010) and hypothesized stepwise acquisition of the lissamphibian body plan within amphibamiforms. Based on our present analyses of this dataset, characters describing the structure of adult teeth and characters capturing features of general skull shape, as currently implemented in phylogenetic analyses of the group, do not provide the information necessary to capture consistent resolution in relationships of amphibamiforms with each other and with lissamphibians. There are two possible explanations for this: (i) additional phylogenetically informative anatomical variation exists within amphibamiforms and other temnospondyls but has not been described by phylogenetic characters; and/or (ii) current samples of morphological characters over-atomize broad variation in skull shape into a large number of biologically or structurally non-independent characters that overpower real but weak phylogenetic signal in other characters. We have attempted to expand the former with our character additions reported here, but we expect additional characters can, and should, be added to describe variation in amphibamiform (and temnospondyl) morphology. Further, we note that numerous phylogenetic characters in this matrix essentially describe the two major shape axes recovered by our morphometric analyses reported here (Fig. 7), and it is, therefore, likely that characters describing orbit size and cheek length are oversampled. We strongly recommend measured consideration of the biological systems underlying variation in some of these character complexes, as well as the biological bases for some recent hypotheses of homology that have undergirded rescoring of large parts of the amphibamiform character–taxon matrices (e.g. Marjanović and Laurin 2019, Kligman *et al.* 2023, Marjanovic *et al.* 2023). This is especially the case for homology interpretations that are fundamentally circular and not founded on external aetiologies (e.g. embryology, cell lineage tracing, or gene expression characterization or quantification in modern amphibians).

#### Cranial diversity of terrestrial members of Amphibamiformes

In order to rigorously quantify skull shape in *Kermitops*, we collected seven linear measurements for the majority of amphibamiform taxa (Supporting Information, S1) and conducted an ordination analysis to reduce the dimensionality of these measurements into a few axes of covariance. Morphometric analyses of amphibamiforms have been previously conducted, particularly by Bourget and Anderson (2011), who found broad evidence for a clade characterized by small orbits and a long postorbital region ('*Micropholis* clade') and a clade characterized by large orbits and a short postorbital region ('*Amphibamus* clade'), with little overlap in shape between these two clades. They interpret this clustering to mirror the evolution of miniaturized or paedomorphic features in amphibamids shared with branchiosaurids (Fröbisch and Schoch 2009).

Our morphometric analysis does not fully replicate their findings, although we do still find an important role for orbit size (largely corresponding to our PC2) and proportions of the antorbital and postorbital skull (largely corresponding to our PC3) (Fig. 7). We do not recover distinct separation of



**Figure 7.** A, skull of a generalized amphibamiform based on *Amphibamus grandiceps*, FMNH PR 4202, with the measurements used in the morphometric analysis. B–D, morphometric space showing the variation of skull morphology in amphibamiforms. Each point represents an amphibamiform specimen; multiple specimens of the same taxon were used.

clusters, revealing that evidence for clade-specific morphospace within amphibamiforms is weak when more specimens are included. Further, we find that a generalized amphibamid allometry accounts for the majority (94%) of variation in all collected measurements, and accounting for this allometry is classic *Amphibamus*-like taxa (*Amphibamus grandiceps* and *Doleserpeton annectens*) that are closest to the mean amphibamiform skull shape. This is generally unexpected based on both the hypothesis that these forms are relatively advanced and uniquely lissamphibian-like, as well as previous morphometric analyses finding clear separation between ‘amphibamid’ and ‘micropholid’ forms. Further, we see taxa previously interpreted as ‘micropholid’ (e.g. *Tersomius texensis*, *T. mosesi*, and *Eoscopus lockardi*) clearly overlapping large portions of ‘amphibamid’ morphospace. There are several possible explanations. The first is that an *Amphibamus*-like skull shape might represent the plesiomorphic morphology for amphibamiforms. Under previous topologies, this might suggest that reduction in size alone may be the primary trend in amphibamiforms along the lissamphibian stem and was sufficient to transform a *Tersomius*-like ancestral amphibamiform into a derived *Doleserpeton*-like form. However, under our maximum parsimony and FBD topologies, this may indicate an *Amphibamus*-like cranial morphology in the ancestral amphibamiform, with micropholid

morphology secondarily acquired, possibly as an adaptation to water or heat stress (e.g. as in frogs: [Jared et al. 2019](#), [Mari et al. 2022](#)), particularly in the earliest Triassic. Another possibility is that ‘micropholids’ and ‘amphibamids’ represent ecomorphotypes rather than distinct clades, and variation in gross skull form reflects convergence within an adaptive radiation rather than an important shift in morphology associated with a stage of lissamphibian evolution. A final possibility is that the strong separation of classes in the analyses of [Bourget and Anderson \(2011\)](#) is a methodological artefact, either as a consequence of their use of cranial reconstructions or their use of a classifying function (canonical variance analysis) based on inferred clade composition instead of an unconstrained ordination method (e.g. our PCA) to quantify shape space. Future efforts to resolve amphibamiform phylogeny and to characterize amphibamiform morphospace should help distinguish between these alternatives.

We also note that more completely sampled amphibamiform species, particularly *Micropholis stowi* and *Eoscopus lockardi*, occupy rather large portions of morphospace ([Fig. 7](#)). It is unclear to us whether this is due to high intraspecific variation across amphibamiforms that is not appreciably captured in other taxa, high variation in taphonomic deformation of skulls that were less morphologically dissimilar in life, or indication of multiple

real species present within these two taxa. As the last of these hypotheses has long been suggested by workers familiar with the material (Daly 1994; A. Milner, personal communication, J. Anderson, personal communication), we strongly recommend critical revision of these two taxa.

Extreme skull shapes are distributed throughout the tree, including *Pasawioops mayi* (extremely low PC2), *Rubeostratilia texensis* (extremely low PC3), *Gerobatrachus hottoni* (extremely high PC2), *Platyrhinops lyelli* (extremely high PC2), and *Kermitops gratus* (extremely high PC3) (Fig. 7). Previously, Bourget and Anderson (2011) similarly found *Rubeostratilia texensis* as an outlier in some of their morphometric analyses, but did not comment beyond that. With the inclusion of *Rubeostratilia* in our more broadly sampled dataset, we interpret this as evidence that amphibamiforms were actively exploring novel areas of morphospace during early phases of their evolution. We cannot say whether this corresponds with novel ecologies, which may be influenced by numerous factors. The skull of modern anurans (which is relatively comparable with amphibamiforms) shows little correspondence with diet except in the case of social insect specialists (Vidal Garcia *et al.* 2017), although there are some general trends in skull shape that seemingly correspond with prey size and speed, notably longer jaws corresponding with faster prey and wider skull, and longer post-orbital skull corresponding with larger prey (Emerson 1985). By analogy, it is possible then that ‘micropholid’ morphologies (extremely low PC2, extremely low PC3; Fig. 7D) may reflect adaptations for feeding on vertebrate prey, whereas ‘amphibamid’ morphologies (extremely high PC2) may reflect adaptations for feeding on smaller invertebrate, presumably insect, prey. If so, the unique cranial morphology of *Kermitops* might indicate adaptation to feeding on faster-moving, small prey such as the abundant small holometabolous insects found in Clear-Fork-aged deposits in Oklahoma (Beckemeyer and Hall 2007). We find notable differences in skull shape between *Kermitops* and other amphibamiforms from the Early Permian Clear Fork Formation (*Gerobatrachus hottoni*, *Nanobamus macrorhinus*, and *Rubeostratilia texensis*), particularly once the allometric axis (PC1) is excluded (Fig. 7D; Supporting Information, S10). This may be evidence of ecological character displacement among the small and apparently hyperdiverse amphibamiforms, but this remains to be thoroughly tested.

## CONCLUSION

*Kermitops gratus*, a previously unreported amphibamiform, is presented here as a member of a morphologically disparate Early Permian amphibamiform diversification, adding to our knowledge of small-bodied tetrapods in the Lower Clear Fork Formation. Our study of the phylogenetic relationships of *Kermitops* complicates narratives of amphibamiform morphological evolution, and discordance of topologies between different phylogenetic inference methods, despite the same underlying dataset, lowers our confidence in the ability to investigate amphibamiform relationships. In particular, we find significant character conflict with hypotheses of stepwise acquisition of lissamphibian morphology within amphibamiforms. We find historically proposed ‘lissamphibian’ features, such as bicuspid and pedicellate teeth, to be more widely distributed and broadly

convergent within amphibamiforms than previously recognized (Bolt 1969, Milner 1988) and hypothesized timelines of progressive simplification of the occiput to be overly simplistic (Atkins *et al.* 2019). Resolving these problems requires crucial re-evaluation of amphibamiform (and temnospondyl) anatomical variation and addition of carefully constructed characters to capture that variation in order to improve phylogenetic hypotheses of relationships within these groups.

## SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

## ACKNOWLEDGEMENTS

We sincerely thank Bill Simpson, Adrienne Stroup, and Ken Angielczyk for access to collections at the Field Museum of Natural History, Chicago. We further thank Hans-Dieter Sues, Robert W. Hook, and Amanda Millhouse for access to specimens and information on Nicholas Hotton III’s Texas Permian Faunal collections at the Smithsonian National Museum of Natural History. We thank James M. Clark, Catherine Forster, and R. Alexander Pyron for their supervisory guidance and support. Finally, we are indebted to the late Nicholas Hotton III and his field crew for their tireless collections efforts in the Permian of Texas, without which this study would not be possible.

## CONFLICT OF INTEREST

C.S., J.D.P., and A.M. declare no conflict-of-interest.

## DATA AVAILABILITY

The holotype of *K. gratus* is catalogued and available for study to qualified research at the Smithsonian National Museum of Natural History. Code for TNT and MrBayes scripts used in the phylogenetic analyses conducted herein are available in Supplementary data, section 4; the matrix is available for download under project 5095 on Morphobank.org (<http://morphobank.org/permalink/?P5095>).

## REFERENCES

- Anderson JS, Bolt JR. New information on amphibamids (Tetrapoda, Temnospondyli) from Richards Spur (Fort Sill), Oklahoma. *Journal of Vertebrate Paleontology* 2008;33:553–67.
- Anderson JS, Henrici AC, Sumida SS *et al.* *Georgenthalia clavinasica*, a new genus and species of dissorophoid temnospondyl from the Early Permian of Germany, and the relationships of the family Amphibamidae. *Journal of Vertebrate Paleontology* 2008a;28:61–75. [https://doi.org/10.1671/0272-4634\(2008\)28\[61:gcanga\]2.0.co;2](https://doi.org/10.1671/0272-4634(2008)28[61:gcanga]2.0.co;2)
- Anderson JS, Reisz RR, Scott D *et al.* A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* 2008b;453:515–8. <https://doi.org/10.1038/nature06865>
- Atkins JB, Reisz RR, Maddin HC. Braincase simplification and the origin of lissamphibians. *PLoS One* 2019;14:e0213694. <https://doi.org/10.1371/journal.pone.0213694>
- Atkins JB, Sorges P, Fröbisch NB *et al.* Late ontogeny in the small Early Permian amphibamiform dissorophoid *Pasawioops mayi*. *Journal of Vertebrate Paleontology* 2020;40:e1772800.
- Beckemeyer RJ, Hall JD. The entomofauna of the Lower Permian fossil insect beds of Kansas and Oklahoma, USA. *African Invertebrates* 2007;48:23–39.

- Berman DS, Berman SL. *Broiliellus hektotopos* sp. nov. (Temnospondyli: Amphibia), Washington formation, Dunkard group. In: Barlow JA, Burkhammer S (eds.), *Proceedings of the First IC White Memorial Symposium, the Age of the Dunkard*. Morgantown: West Virginia Geological and Economic Survey, 1975, 69–78.
- Bolt JR. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science* 1969;166:888–91. <https://doi.org/10.1126/science.166.3907.888>
- Bolt JR. *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications. In: Nitecki M (ed.), *Mazon Creek Fossils*. New York: Academic Press, 1979, 529–563.
- Bourget H, Anderson JS. A new amphibamid (Temnospondyli: Dissorophoidea) from the Early Permian of Texas. *Journal of Vertebrate Paleontology* 2011;31:32–49.
- Clack JA, Milner AR. Morphology and systematics of the Pennsylvanian amphibian *Platyrhinops lyelli* (Amphibia: Temnospondyli). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 2009;100:275–95. <https://doi.org/10.1017/s1755691010009023>
- Daly E. *The Amphibamidae (Amphibia: Temnospondyli), with a Description of a new Genus from the Upper Pennsylvanian of Kansas*. Lawrence, Kan: Museum of Natural History, University of Kansas, 1994.
- Emerson SB. Skull shape in frogs: correlations with diet. *Herpetologica* 1985;41:177–88.
- Fröbisch NB, Reisz RR. A new Lower Permian amphibamid (Dissorophoidea, Temnospondyli) from the fissure fill deposits near Richards Spur, Oklahoma. *Journal of Vertebrate Paleontology* 2008;28:1015–30. <https://doi.org/10.1671/0272-4634-28.4.1015>
- Fröbisch NB, Schoch RR. Testing the impact of miniaturization on phylogeny: Palaeozoic dissorophoid amphibians. *Systematic Biology* 2009;58:312–27. <https://doi.org/10.1093/sysbio/syp029>
- Gee BM, Reisz RR. The amphibamiform *Nanobamus macrorhinus* from the early Permian of Texas. *Journal of Paleontology* 2020;94:366–77.
- Hanken J, Wake DB. Miniaturization of body size: organismal consequences and evolutionary significance. *Annual Review of Ecology and Systematics* 1993;24:501–19. <https://doi.org/10.1146/annurev.es.24.110193.002441>
- Heath TA, Huelsenbeck JP, Stadler T. The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences* 2014;111:E2957–66.
- Huelsenbeck, JP, Ronquist, F. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 2001;17:754–755.
- Hugall AF, Foster R, Lee MSY. Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG-1. *Systematic Biology* 2007;56:543–63. <https://doi.org/10.1080/10635150701477825>
- Hunt AP, Lucas SG, Berman DS. A new amphibamid (Amphibia: Temnospondyli) from the Late Pennsylvanian (Middle Stephanian) of central New Mexico, USA. *Paläontologische Zeitschrift* 1996;70:555–65. <https://doi.org/10.1007/bf02988092>
- Huttenlocker AK, Pardo JD, Small BJ. *Plemmyradytes shintoni*, gen. et sp. nov., an Early Permian amphibamid (Temnospondyli: Dissorophoidea) from the Eskridge Formation, Nebraska. *Journal of Vertebrate Paleontology* 2007;27:316–28. [https://doi.org/10.1671/0272-4634\(2007\)27\[316:psgesn\]2.0.co;2](https://doi.org/10.1671/0272-4634(2007)27[316:psgesn]2.0.co;2)
- Inoue J, Donoghue PCJ, Yang Z. The impact of the representation of fossil calibrations on Bayesian estimation of species divergence times. *Systematic Biology* 2010;59:74–89. <https://doi.org/10.1093/sysbio/syp078>
- Jared C, Mailho-Fontana PL, Mendelson J et al. Life history of frogs of the Brazilian semi-arid (Caatinga), with emphasis in aestivation. *Acta Zoologica* 2019;101:302–10. <https://doi.org/10.1111/azo.12295>
- Jones MEH, Benson RBJ, Skutschas P et al. Middle Jurassic fossils document an early stage in salamander evolution. *Proceedings of the National Academy of Sciences of the United States of America* 2022;119:e2114100119. <https://doi.org/10.1073/pnas.2114100119>
- King B. Bayesian tip-dated phylogenetics in paleontology: topological effects and stratigraphic fit. *Systematic Biology* 2021;70:283–94. <https://doi.org/10.1093/sysbio/syaa057>
- King B, Beck RM. Tip dating supports novel resolutions of controversial relationships among early mammals. *Proceedings of the Royal Society B* 2020;287:20200943.
- Kligman BT, Gee BM, Marsh AD et al. Triassic stem caecilian supports dissorophoid origin of living amphibians. *Nature* 2023;614:102–7. <https://doi.org/10.1038/s41586-022-05646-5>
- Lee MSY, Yates AM. Tip-dating and homoplasy: reconciling the shallow molecular divergences of modern gharials with their long fossil record. *Proceedings Biological Sciences* 2018;285:20181071. <https://doi.org/10.1098/rspb.2018.1071>
- Lewis PO. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 2001;50:913–25. <https://doi.org/10.1080/106351501753462876>
- Maddin HC, Fröbisch NB, Evans DC et al. Reappraisal of the Early Permian amphibamid *Tersomius texensis* and some referred material. *Comptes Rendus Palevol* 2013;12:447–61. <https://doi.org/10.1016/j.crvp.2013.06.007>
- Maddin HC, Jenkins FA Jr, Anderson JS. The braincase of *Eocaecilia micropodia* (Lissamphibia, Gymnophiona) and the origin of baecilians. *Plos One* 2012;7:e50743.
- Maddin, HC, Reisz, RR, Anderson, JS. Evolutionary development of the neurocranium in Dissorophoidea (Tetrapoda: Temnospondyli), an integrative approach. *Evolution & Development* 2010;12:393–403.
- Mann A, Gee BM. Lissamphibian-like toepads in an exceptionally preserved amphibamiform from Mazon Creek. *Journal of Vertebrate Paleontology* 2019;39:e1727490.
- Mari, RDB, Mori, GM, Vannucchi, FS, Ribeiro, LF, et al. Relationships of mineralized dermal layer of mountain endemic miniature frogs with climate. *Journal of Zoology* 2022;318:34–46.
- Marjanović D, Laurin M. Fossils, molecules, divergence times, and the origin of lissamphibians. *Systematic Biology* 2007;56:369–88. <https://doi.org/10.1080/10635150701397635>
- Marjanović D, Laurin M. Phylogeny of Paleozoic limbed vertebrates reassessed through revision and expansion of the largest published relevant data matrix. *PeerJ* 2019;6:e5565. <https://doi.org/10.7717/peerj.5565>
- Milner AR. The relationships and origin of living amphibians. In: Benton MJ (ed.), *The Phylogeny and Classification of the Tetrapod*, Vol. 1. Oxford: Clarendon Press, 1988.
- Pardo JD, Small BJ, Huttenlocker AK. Stem caecilian from the Triassic of Colorado sheds light on the origins of Lissamphibia. *Proceedings of the National Academy of Sciences* 2017;114. <https://doi.org/10.1073/pnas.1706752114>
- Parsons TS, Williams EE. The relationships of the modern Amphibia: a re-examination. *The Quarterly Review of Biology* 1963;38:26–53. <https://doi.org/10.1086/403748>
- Pérez-Ben CM, Schoch RR, Báez AM. Miniaturization and morphological evolution in Paleozoic relatives of living amphibians: a quantitative approach. *Paleobiology* 2018;44:58–75. <https://doi.org/10.1017/pab.2017.22>
- Ronquist F, Teslenko M, van der Mark P et al. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 2012;61:539–42. <https://doi.org/10.1093/sysbio/sys029>
- Schoch RR. How body size and development biased the direction of evolution in early amphibians. *Historical Biology* 2013;25:155–65. <https://doi.org/10.1080/08912963.2012.724796>
- Schoch RR. Amphibian skull evolution: the developmental and functional context of simplification, bone loss and heterotopy. *Journal of Experimental Zoology. Part B. Molecular and Developmental Evolution* 2014;322:619–30. <https://doi.org/10.1002/jez.b.22599>
- Schoch RR. The putative lissamphibian stem-group: phylogeny and evolution of the dissorophoid temnospondyls. *Journal of Paleontology* 2019;93:137–56. <https://doi.org/10.1017/jpa.2018.67>
- Schoch R, Milner A. Structure and implications of theories on the origin of lissamphibians. In: Arratia G, Wilson VH, Cloutier R (eds.), *Recent advances in the Origin and Early Radiation of Vertebrates*. München: Verlag Dr. Friedrich Pfeil, 2004.

- Schoch RR, Werneburg R. Adult branchiosaurid temnospondyls: the life cycle of *Xerodromeus gracilis*. *Papers in Palaeontology* 2023;**9**:e1513.
- Schoch RR, Werneburg R, Voigt S. A Triassic stem-salamander from Kyrgyzstan and the origin of salamanders. *Proceedings of the National Academy of Sciences of the United States of America* 2020;**117**:11584–8. <https://doi.org/10.1073/pnas.2001424117>
- Sigurdson T, Bolt JR. The Lower Permian amphibamid *Doleserpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. *Journal of Vertebrate Paleontology* 2010;**30**:1360–77. <https://doi.org/10.1080/02724634.2010.501445>
- Vidal-García M, Scott Keogh J. Phylogenetic conservatism in skulls and evolutionary lability in limbs—morphological evolution across an ancient frog radiation is shaped by diet, locomotion and burrowing. *BMC Evolutionary Biology* 2017;**17**:1–15.
- Werneburg R, Schneider J, Lucas SG. The ‘amphibamid’ and ‘branchiosaurid’ morphotype in the dissorophoid *Milnererpeton huberi* (Temnospondyli), from the Late Pennsylvanian Kinney Brick Quarry in New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 2021;**84**:425–32.
- Werneburg R, Schneider JW, Štamberg S *et al.* A new amphibamiform (Temnospondyli: Branchiosauridae) from the lower Permian of the Czech Boskovice Basin. *Journal of Vertebrate Paleontology* 2023;**0**:e2231994.
- Yeh J. The effect of miniaturized body size on skeletal morphology in frogs. *Evolution* 2002;**56**:628–41. <https://doi.org/10.1111/j.0014-3820.2002.tb01372.x>