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Reappraisal of the Early Permian amphibamid *Tersomius texensis* and some referred material



Réexpertise de l'amphibamidé du Permien inférieur *Tersomius texensis* et matériel associé

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ABSTRACT

The accuracy of the taxonomic assignment of three skulls in the collections of the Museum of Comparative Zoology (Harvard University) to the Early Permian taxon *Tersomius texensis* has been called into question. Here, we re-evaluate the holotype of *T. texensis* and the three MCZ specimens within the context of discoveries made over the last few years. The results of our phylogenetic analyses corroborate our morphological assessments, revealing that only one of the three skulls (MCZ 1912) is assignable to *T. texensis*. We identify MCZ 1415 as *Pasawioops* cf. *P. mayi*, otherwise known only from Oklahoma, and MCZ 1911 as a new genus and species of dissorophid. Study of the three MCZ skulls reveals previously unrecognized diversity of temnospondyls in the coastal fauna represented in the Archer City Formation of Texas.

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R É S U M É

La précision de l'attribution taxonomique de trois crânes dans les collections du Museum of Comparative Zoology (université de Harvard) à un taxon du Permien inférieur, *Tersomius texensis*, a posé question. Ici, nous réévaluons l'holotype de *T. texensis* et les trois spécimens MCZ dans le contexte des découvertes effectuées ces dernières années. Les résultats de nos analyses phylogénétiques corroborent nos estimations morphologiques, à savoir que seul l'un des trois crânes (MCZ 1912) est attribuable à *T. texensis*. Nous avons identifié MCZ 1415 comme étant *Pasawioops* cf. *P. mayi*, par ailleurs, déjà connu dans l'Oklahoma, et MCZ 1911 comme étant un nouveau genre et une nouvelle espèce de dissorophidé. L'étude de ces trois crânes révèle une diversité, non reconnue précédemment, des Temnospondyles dans la faune côtière de la formation Archer City au Texas.

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1. Introduction

The relevance of amphibamid dissorophoid temnospondyls to the discussion of the evolutionary origin of some or all of the modern amphibian groups (lissamphibians) has prompted a recent increase of studies focused on this group of small, mostly Permian-aged taxa. Several new species have been described in recent years (Anderson et al., 2008; Bourget and Anderson, 2011; Fröbisch and Reisz, 2008; Huttenlocker et al., 2007), greatly increasing our knowledge of amphibamid diversity and variation. Additionally, many previously known taxa have been re-evaluated in the light of these discoveries (e.g., Clack and Milner, 2009; Schoch and Rubidge, 2005; Sigurdson and Bolt, 2010) and for their potential to offer new perspectives on patterns and processes of evolution of lissamphibians (Clack and Milner, 2009; Fröbisch et al., 2007; Fröbisch and Schoch, 2009; Schoch, 2013).

Despite these advances, many questions remain, including the nature of relationships among amphibamids. There is a growing consensus that a monophyletic Amphibamidae contains two clades: the so-called “*Micropholis*” and the “*Amphibamus*” clades (Bourget and Anderson, 2011; Huttenlocker et al., 2007). In general, members of the *Micropholis* clade possess a more elongate skull shape in comparison to members of the *Amphibamus* clade (Bourget and Anderson, 2011). Overall, members of the *Amphibamus* clade share a much more lissamphibian-like cranial morphology, and as a result have been hypothesized to be more closely related to lissamphibians than members of the *Micropholis* clade (Fröbisch and Schoch, 2009). For some taxa, however, it has been difficult to establish a stable position within amphibamid phylogeny and it remains unclear as to which group, if any, certain taxa belong.

One such taxon is *Tersomius texensis*. A small skull recovered from the Permian sediments of Archer County, Texas, was described by Case (1910) and, along with a second small skull fragment, comprises the holotype of *T. texensis* (AMNH FR 4719). Following the discovery of additional material and the detailed descriptions by Carroll (1964) and Bolt (1968), Daly (1973) and Bolt (1977) recognized similarities between *T. texensis* and *Doleserpeton*, the latter of which is a member of the *Amphibamus* clade. Further assessments of the phylogenetic position of *T. texensis* yielded hypotheses of its clustering with *Doleserpeton* (Clack and Milner, 1994). More recently, however, analyses utilizing better-preserved material referred to *T. texensis* have hypothesized a close relationship between *T. texensis* and members of the *Micropholis* clade. The specimens historically assigned to *T. texensis* represent a heterogeneous assemblage of small dissorophoids, which became apparent only through the increased knowledge of the taxonomic diversity and phylogenetic relationships of dissorophoids in general and amphibamids in particular. This has led authors to question the identities and affinities of the material currently assigned to *T. texensis*, and in some cases *T. texensis* has been excluded from further phylogenetic study with authors citing these uncertainties as justification for its exclusion.

The Museum of Comparative Zoology (MCZ) specimen 1912 forms the bulk of the detailed description of

T. texensis presented by Carroll (1964), and has since been used to represent *T. texensis* in the majority of phylogenetic analyses that have included the taxon. However, Carroll (1964) mentioned the possibility that the specimens of *T. texensis* housed in the MCZ may represent a species distinct from the holotype, but a lack of evidence to support this precluded Carroll from formally differentiating the MCZ material from *T. texensis*. Two other well-preserved skulls are presently assigned to *T. texensis* in the MCZ collection (MCZ 1415 and MCZ 1911). Carroll (1964) illustrated these specimens, but since then they have received little attention in the literature (Bolt, 1974, 1977; DeMar, 1968; Schoch, 2012). As all three specimens are relatively well-preserved, they represent specimens that will add critical data points to our understanding of morphological variation and evolution of amphibamids and lissamphibians characters.

The goal of the presented contribution is to:

- re-investigate the holotype of *T. texensis* to establish a diagnosis of the taxon;
- re-evaluate the MCZ material in light of this revised diagnosis, to determine their taxonomic affinities and phylogenetic positions.

Institutional abbreviations: AMNH: American Museum of Natural History, New York; FMNH: Field Museum of Natural History, Chicago; MCZ: Museum of Comparative Zoology, Cambridge.

2. Materials

The current study focuses on the holotype of *Tersomius texensis* (AMNH FR 4719) and three skulls referred to *T. texensis* that are housed in the Museum of Comparative Zoology (MCZ 1912, 1415, and 1911).

3. Systematic paleontology

TEMNOSPONDYLI Zittel, 1888
EUSKELIA Yates and Warren, 2000
DISSOROPHOIDEA Bolt, 1969
AMPHIBAMIDAE Moodie, 1909
TERSOMIUS Case, 1910
(Figs. 1–3)

Type species: *Tersomius texensis* Case (1910).

Diagnosis: Amphibamid characterized by the following combination of characters. An almost circular outline of the skull in dorsal view achieved in part by short and wide elements of the posterior skull table, in particular the squamosals, supratemporals, and parietals, and also by the quadrate positioned at the end of a distinct medial curvature of the maxillary arcade. Other features which may be homoplastic, include a tabular much smaller than postparietal, a relatively straight occiput in dorsal view, and an elongate jugal resembling an equilateral triangle with the quadratojugal ramus subequal to suborbital ramus.

Comment: Anderson and Bolt (2013), describing a new species of *Tersomius*, identify some of the above characters (jugal shape, quadrate position) as diagnostic of the genus

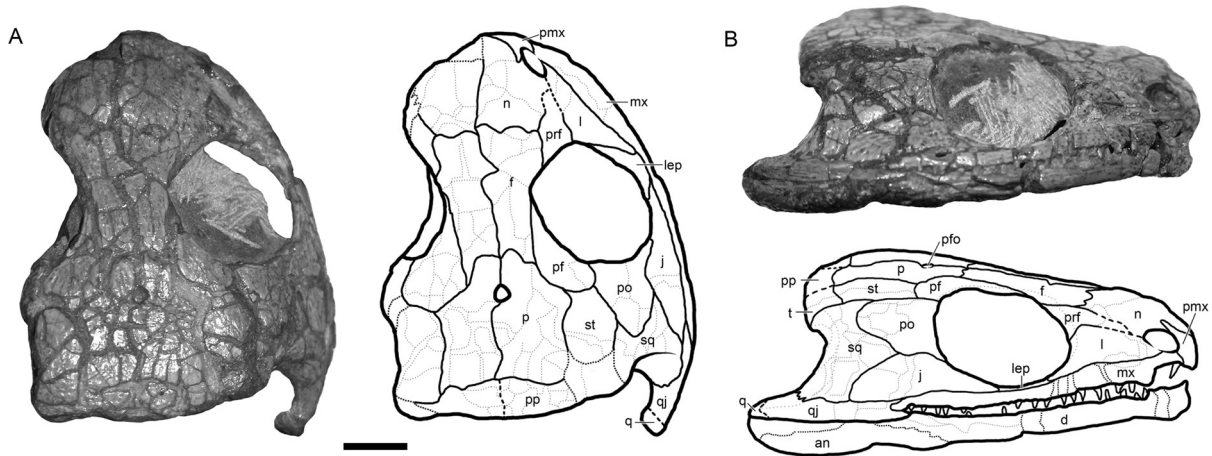


Fig. 1. Photographs and drawings of the holotype of *Tersomius texensis* (AMNH FR 4719) in dorsal (A) and right lateral views (B). Abbreviations: an, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; lep, lateral exposure of the palatine, mx, maxilla; n, nasal; p, parietal; pf, postfrontal; pfo, pineal foramen; prf, prefrontal; po, postorbital; pmx, premaxilla; pp, postparietal; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal; t, tabular. Scale bars = 5 mm. **Fig. 1.** Photographies et dessins de l'holotype de *Tersomius texensis* (AMNH FR 4719) en vues dorsale (A) et latérale droite (B). Abréviations: an, angulaire; d, dentaire; f, frontal; j, jugal; l, lacrimale; lep, exposition latérale du palatin; mx, maxillaire; n, nasal; p, pariétal; pf, postfrontal; pfo, foramen pinéal; prf, préfrontal; po, postorbital; pmx, prémaxillaire; pp, post-pariétal; q, carré; qj, quadratojugal; sq, squamosal; st, supratemporal; t, tabulaire. Barres d'échelle = 5 mm.

Tersomius. Our analysis below fails to recover *T. texensis* and this new species (*T. dolesensis*) as sister taxa, rendering the significance of these characters uncertain.

TERSOMIUS TEXENSIS Case, 1910
(Figs. 1–3)

Type specimen: AMNH FR 4719.

Referred specimens: AMNH FR 4719 (second partial skull, referred to as AMNH FR 4719-2 herein), MCZ 1912 (see below).

Locality and horizon: AMNH FR 4719, FR 4719-2: south side of the Little Wichita River, Archer County, Texas; Petrolia Formation of the Wichita Group, Lower Permian. MCZ 1912: southwest of Archer City, Archer County, Texas; Archer City Bonebed, Archer City Formation, Bowie Group, Lower Permian.

Diagnosis: *Tersomius* characterized by a high maxillary tooth count, with space for 45 to 50 small teeth (contra *T. mosesi* with space for 30 to 38 marginal teeth). Differs from *T. dolesensis* in a larger ratio of interorbital width to

skull length (0.21 in *T. texensis* vs 0.18 in *T. dolesensis*), in a distinctly larger distance between the posterior rim of the orbit and the anterior edge of the otic notch, a bluntly crescent-shaped postfrontal compared to an angular postfrontal in *T. dolesensis*.

Comment: Inspection of MCZ 1912 did not yield any features that permit us to distinguish it from the holotype specimen, except for the size. Specimen MCZ 1912 shares with AMNH FR 4719 the distinctly round skull shape. As in the holotype, this specimen has short posterior skull table elements; however, not to the same degree as in the strongly foreshortened skulls of taxa like *Georgenthalia*, *Amphibamus* and *Eoscopus*. We, therefore, support the referral of MCZ 1912 to *T. texensis*.

3.1. Description of the holotype material AMNH FR 4719

The holotype material of *T. texensis* consists of a partial skull, 31 mm in length measured from the tip of the

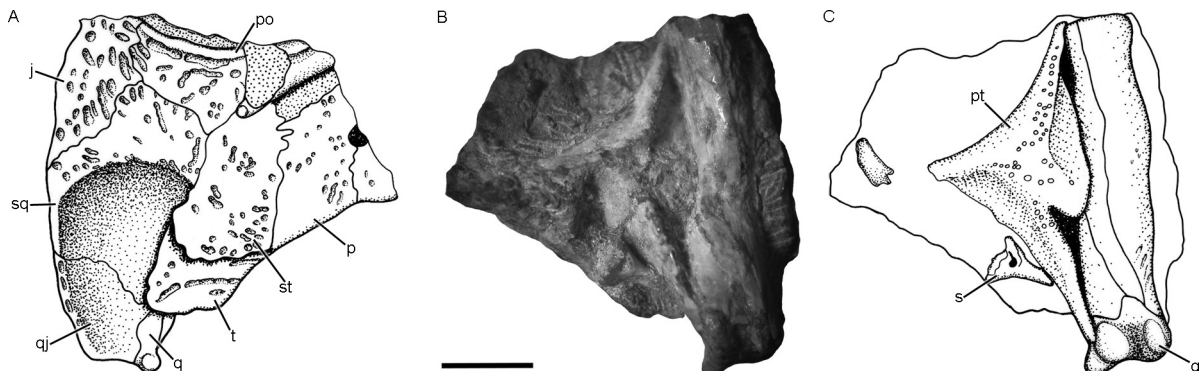


Fig. 2. Drawings and photograph of the second partial skull also assigned to the holotype of *Tersomius texensis* (AMNH FR 4719-2 herein). A, dorsal view; B, ventral view photo; and C, ventral view drawing. Abbreviations additional to the Fig. 1 caption: pt, pterygoid; s, stapes. Scale bar = 5 mm.

Fig. 2. Dessins et photographie du second crâne partiel attribué à l'holotype *Tersomius texensis* (MNH 4719-2 dans l'article). A, Vue dorsale; B, photo en vue ventrale; et C, dessin en vue ventrale. Abréviations supplémentaires par rapport à celles de la Fig. 1 : pt, ptéridoïde; s, étriers. Barre d'échelle = 5 mm.

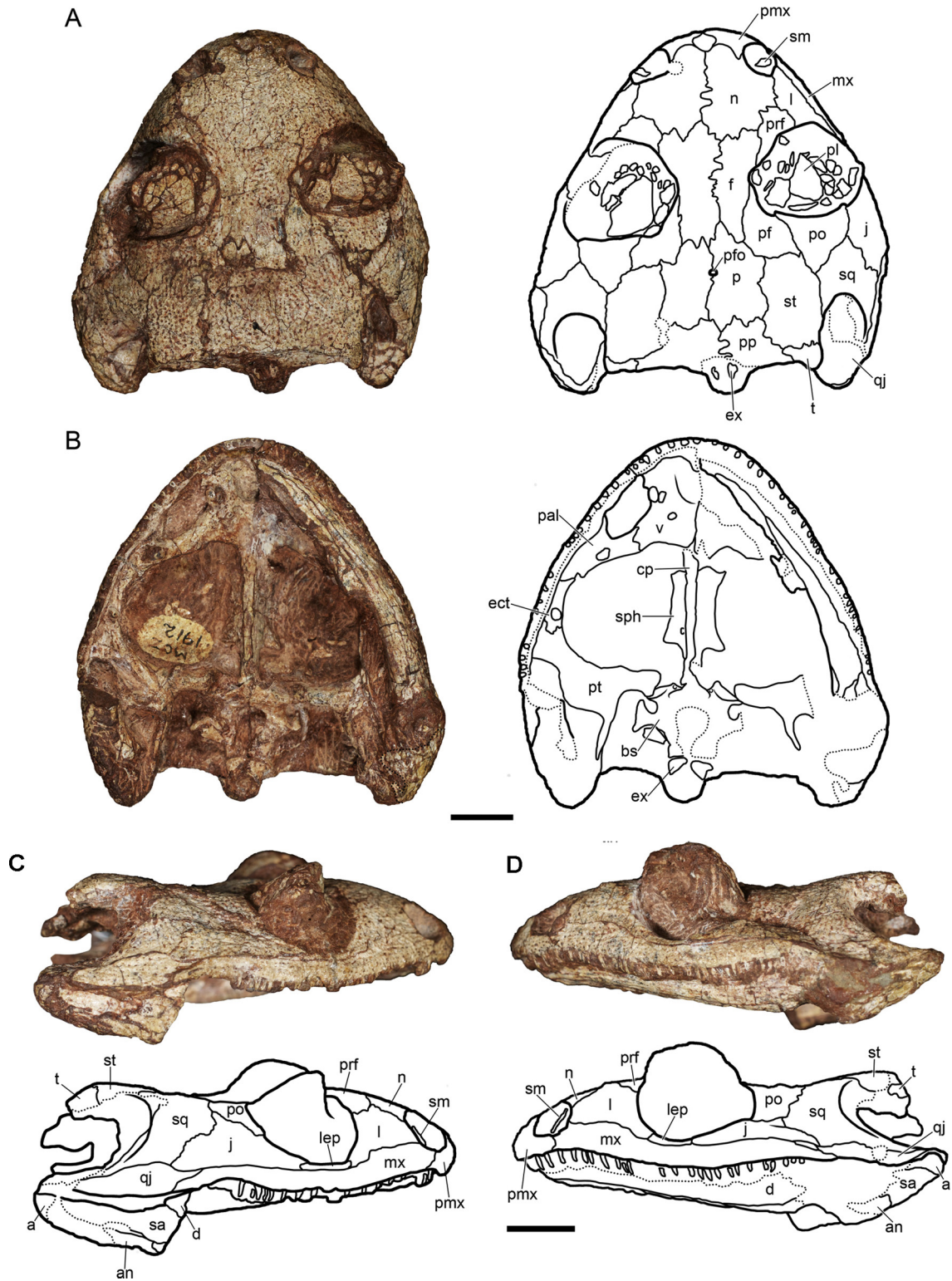


Fig. 3. Photographs and drawings of referred specimen MCZ 1912 (*Tersomius texensis*). A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Abbreviations additional to Fig. 1 caption: a, articular; bs, basisphenoid; cp, cultriform process of the parasphenoid; ect, ectopterygoid; ex, exoccipital; pal, palatine; pl, palpebral; pt, pterygoid; sa, surangular; sm, septomaxilla; sph, sphenethmoid; v, vomer. Scale bar = 1 cm.

Fig. 3. Photographies et dessins du spécimen référencé MCZ 1912 (*Tersomius texensis*). Vues dorsale (A); ventrale (B); latérale droite (C) et latérale gauche (D). Abréviations supplémentaires par rapport à celles de la Fig. 1 : a, articulaire; bs, basisphénoïde; processus cultriforme du parasphénoïde; ect, ectoptéridoïde; ex, exoccipital; pal, palatine; pl, palpébral; pt, ptéridoïde; sa, surangulaire; sm, septomaxillaire; sph, sphénothénoïde; v, vomer. Barre d'échelle = 1 cm.

snout to the posterior end of the skull table. Parts of the left side of the skull are missing posterior to the nasal region (Fig. 1). An additional specimen bearing the same collection number (referred to as AMNH FR 4719-2 herein) is also assignable to *T. texensis* and consists of a skull fragment preserving the posterior left region of the skull roof as well as the left pterygoid, left quadrate, parts of the lower jaw, and a partial stapes.

The bone surface of both specimens is heavily weathered and cracked and large gaps occur along most of the cranial sutures, which has led to earlier suggestions that the holotype is an immature specimen (Bolt, 1977; Carroll, 1964). The original dermal sculpturing is only poorly preserved, but what is left of it suggests that it was a finely pitted structure with a few more elongate grooves radiating out from a central area.

The most characteristic feature of the skull is its almost circular outline, including a rounded and blunt snout region, a short posterior skull table (though not as strongly foreshortened as in taxa like *Georgenthalia*) and a strongly curved maxillary arcade. The quadratojugal and quadrate curve medially, thereby, further contributing to the round appearance of the skull. The orbit is very large and circular in shape. The interorbital width is 6.5 mm, resulting in a ratio of interorbital width to skull length of 0.21 as compared to 0.18 in *T. dolesensis*.

The premaxilla is a transversely narrow element at the anterior end of the snout. It bears a small alary process medial to the external nares. Due to the poor preservation of the left side of the skull, it remains uncertain if the premaxillaries enclosed an internarial fontanelle. The nasal occupies a large portion of the medial snout region and is almost square in shape. It sutures with the prefrontal. A short sutural contact with the lacrimal anterolaterally and a somewhat longer sutural contact with the prefrontal posterolaterally are present. Posteriorly, the nasal connects to the frontal in a straight transverse suture. The frontals are elongate, almost twice as long as wide, which make up the medial region of the skull table. They occupy the interorbital region in its entirety precluding a sutural contact of the pre- and the postfrontal. Although the skull shape is generally very round and wide, the elements of the posterior skull table retain a comparatively rectangular shape more similar to *Micropholis* and *Pasawioops* than to *Amphibamus*. Therein, the parietals are the largest elements of the skull table and enclose a large, round pineal foramen. They narrow anteriorly with a distinct step where they contact the postfrontal laterally and the posterior ends of the frontals anteriorly.

The postparietals form the medial part of the end of the skull table and are foreshortened, rectangular elements. The occipital flanges of the postparietals, as well as the tabulars, are not preserved in the holotype.

The prefrontal forms the anterodorsal border of the orbit. From there, it extends anteriorly, contacting the frontal and nasal medially, and the lacrimal laterally. Its anterior end is not preserved and it remains unclear how far anteriorly it extended. The lacrimal is a long triangular element and extends from the anterior rim of the orbit to the posterior rim of the external nares. Laterally, it shares a long, straight suture with the maxillary and

posterolaterally, it contacts with the lateral exposure of the palatine (LEP).

The maxilla is a long and narrow element extending from the posteroventral edge of external naris posteriorly beyond the posterior rim of the orbit to the middle of the cheek region. The lateral exposure of the palatine and the anterior process of the jugal exclude it from the ventral rim of the orbit. Fifteen straight, conical and pointed teeth are preserved in the maxilla, but there was room for 45 to 50 teeth. The teeth do not appear to be pedicellate and labyrinthine infolding is visible.

The postfrontal is bluntly crescent-shaped and although it has a quite long anterior process. As mentioned above, it makes no contact with the prefrontal anteriorly. The postfrontal forms the posterodorsal border of the orbit. It contacts the parietal posteromedially, the supratemporal posteriorly, and the postorbital laterally. The posterior region seems to be somewhat more broadened on the left side of the skull than on the right side, which could represent real variation. However, the bone surface is cracked and poorly preserved in this area and it may just be a relic of preservation.

The postorbital is roughly triangular and forms the posterior border of the orbit. Anterodorsally, it contacts the postfrontal in a short suture. Dorsally, the postorbital is flanked by the supratemporal, which contacts it in a straight suture. The posterior tip of the postorbital is enfolded by the squamosal and laterally, the postorbital contacts the apical portion of the dorsal process of the jugal.

The supratemporal is roughly rectangular and contacts the parietals laterally in a long and straight suture. Laterally, it is bordered by the postorbital anteriorly and the squamosal posteriorly. The posterior suture to the tabular is obscured due to poor preservation of the bone surface in this region.

The squamosal is a prominent element of the posterior skull table. It is strongly foreshortened and consists of a dorsal sculptured part that abruptly slopes posteriorly into a smooth unsculptured surface forming the anteromedial margin of the otic notch. Anterolaterally, the squamosal is bordered by the jugal and posterolaterally by the quadratojugal. Dorsally the squamosal contacts the supratemporal and tabular, while anteriorly, it contacts the postorbital. The quadratojugal is long, slender and forms the posteroventral portion of the cheek region. Dorsally, it shares a straight suture with the jugal anteriorly and the squamosal posteriorly. The quadratojugal forms the ventral part of the otic notch, the smooth surface of which continues beyond the squamosal-quadratojugal suture. At its anteroventralmost edge, the quadratojugal makes contact with the quadrate. The dorsal process of the quadrate, typical for dissorophoids, is present in the holotypic skull.

The palatal region is very poorly preserved in the holotype. However, a pterygoid is visible in the second partial skull (AMNH FR 4719-2; Fig. 2). The pterygoid is a typical triradiate element. Its quadrate process is still in tight articulation with the quadrate posteromedially. The slender palatine process projects anteriorly, but the anterior portion of the skull, including the palatine and ectopterygoid, is not preserved. The basicranial process projects medially,

but the basisphenoid is not preserved and hence, no details of the basicranial articulation are observable.

An isolated stapes is located near the quadrate process of the pterygoid in AMNH FR 4719-2 (Fig. 2). This fairly broad footplate showing a stapedia foramen is visible, but the stapedia shaft is partially obscured by sediment and it remains unknown how long the shaft was.

3.2. Description of referred specimen MCZ 1912

This specimen formed the basis of the detailed description of *Tersomius texensis* of Carroll (1964), and was extensively illustrated therein. The specimen consists of a well-preserved skull with articulated lower jaws (Fig. 3). The anterior portion of the right lower jaw has been removed since the time of description given by Carroll (1964) and, as a result, additional features of the palate that were previously obscured can now be seen.

Specimen MCZ 1912 bears a strong, overall resemblance to the holotype of *T. texensis*, and is virtually indistinguishable from the latter, except for the former's much larger size (MCZ 1912 is 50 mm in length in contrast to 31 mm for AMNH FR 4719). Specimen MCZ 1912 shares with the holotype a nearly circular skull outline in dorsal view, large orbits and a shortened posterior skull table. The premaxillaries, with their short alary processes, reveal an internarial fontanelle that is not preserved in the holotype. Broad, square-shaped nasals, in combination with the arched maxillaries, contribute to the circular appearance of the skull. The large orbits are separated by an interorbital to skull length ratio of 0.22, similar to the value of 0.21 obtained for the holotype. The skull table elements, especially the parietals and supratemporals, are shorter and wider than those of taxa, like *Pasawioops*, *Rubeostratilia*, and *Micropholis*. However, the orbit to otic notch distance is much greater than the strongly foreshortened skull tables of taxa, like *Georgenthalia*, and *Amphibamus*. The maxillaries have room for 47 small pointed, non-pedicellate teeth.

The excellent preservation of specimen MCZ 1912 provides additional anatomical information to assist in diagnosing *T. texensis*. The anterior border of the prefrontal is poorly preserved in the holotype. In MCZ 1912, the complete sutural outline confirms that the prefrontal is a small semi-lunar shaped element bounded mostly by the nasal anteriorly. Interestingly, variation between the size of the right and left postfrontals in MCZ 1912 exists, similar to that seen in the holotype specimen. Also, the posterior portion of the postparietal is incomplete in the holotype. In MCZ 1912, the small, rectangular postparietal can be seen to bear a fairly large, smooth occipital flange. The flanges of both postparietals form the dorsal margin of the foramen magnum. The tabulars are also preserved in MCZ 1912, the right side being more complete than the left. There the tabular is a small element, with a poorly developed posteriorly directed horn. The occipital flange of the tabular is smaller than that of the postparietal.

A large portion of the palate is exposed in MCZ 1912. Anteriorly, the vomers meet at the midline and form a deep depression. A fang pair is present lateral to this, along the medial edge of the choana. An additional fang is present

posterior and slightly medial to the other fang pair. Posterolaterally, the vomer narrows as it extends to meet the palatine. The palatine is narrow and forms the posterior margin of the choana. A single fang pair is present on the palatine. Posteriorly, the palatine contacts the ectopterygoid.

The ectopterygoid is interpreted here as a much more elongate element than illustrated by Carroll (1964), and is observed to prevent the pterygoid from contacting palatine. The right pterygoid is more complete than the left. It bears the typical triradiate pattern. The anterior margin is strongly curved to accommodate a large interpterygoid vacuity. The palatine ramus extends anteriorly along the lateral margin of the palate, reaching the ectopterygoid. The basicranial process is robust. It has fallen out of articulation with the basisphenoid in MCZ 1912, and a large articular facet can be seen in the latter.

The parasphenoid is unknown in MCZ 1912. The use of MCZ 1415 to reconstruct the parasphenoid of *T. texensis* (see Carroll, 1964, Fig. 4) is problematic due to the unlikely affinity of that specimen to *T. texensis* (see below). However, the overall proportions of the remainder of the braincase of MCZ 1912 are short and wide, suggesting that the basal plate of the parasphenoid would have been similarly proportioned. The dorsal basisphenoid region appears to be present. The anterolateral margins of both sides are incised by the posterior margins of the prootic foramina. Posteriorly portions of the opisthotic may be preserved, but their damaged condition prevents detailed description. Posteriorly portions of the exoccipitals are visible. These have been somewhat displaced from their natural position.

With all else being so similar between MCZ 1912 and the holotype, the much larger size and more tightly interdigitated sutures of MCZ 1912 support the hypothesis that it represents a mature individual of *T. texensis*. This is consistent with previous suggestions that the holotype is an immature individual of *T. texensis* (Bolt, 1977; Carroll, 1964).

3.3. Description of specimen MCZ 1415

This specimen differs markedly from the holotype of *T. texensis* and co-occurring MCZ 1912 in terms of the overall shape of its skull and proportions of its features. The skull of MCZ 1415 is much more elongate and triangular in outline when viewed dorsally (Fig. 4), similar to that of *Pasawioops*, the narrow-headed morph of *Micropholis*, and *Rubeostratilia*. In comparison to the similarly sized MCZ 1912, MCZ 1415 bears a longer snout region, a slightly narrower interorbital distance (ratio equals 0.17), a narrower posterior skull table and a longer ventral margin of the otic notch, resulting in a more posteriorly placed jaw articulation.

Specimen MCZ 1415 is virtually indistinguishable from the holotype of *Pasawioops mayi*, except for the much larger size of the former. Specimen MCZ 1415 is, however, comparable in size to referred specimen OMNH 73509 (Fröbisch and Reisz, 2008), indicating that the MCZ specimen falls within a known size range for the species. Recently, referred specimen FMNH PR 3027 (Anderson and Bolt, 2013) is intermediate in size between the holotype of

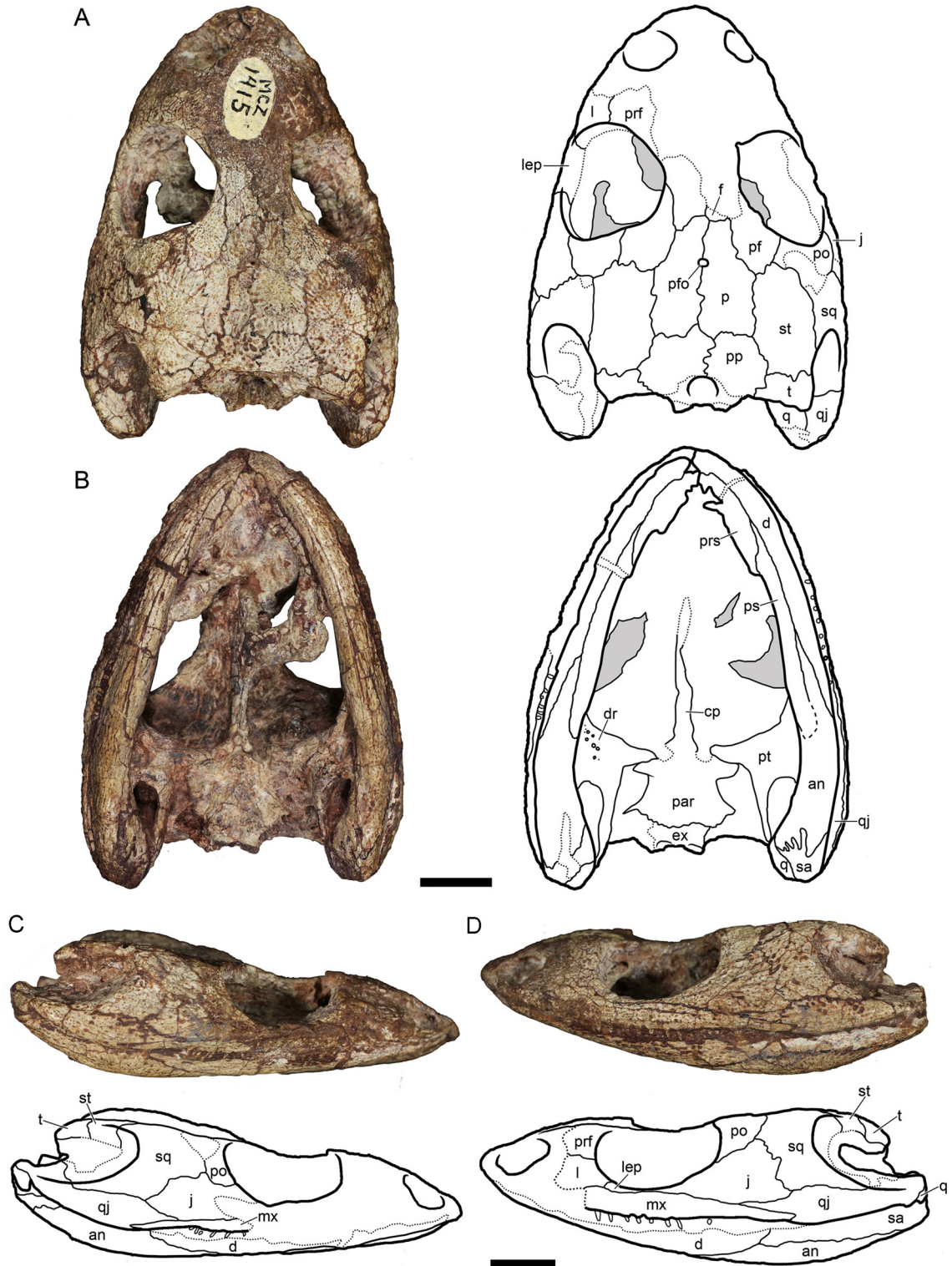


Fig. 4. Photographs and drawings of specimen MCZ 1415, referred to *Pasawioops* cf. *P. mayi*. A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Abbreviations additional to the Fig. 1 caption: cp, cultriform process of the parasphenoid; dr, dentigerous ridge of the pterygoid; ex, exoccipital; par, parasphenoid; prs, presplenial; ps, postsplenial; pt, pterygoid; sa, surangular. Scale bar = 1 cm.

Fig. 4. Photographies et dessins du spécimen MCZ 1415, attribué à *Pasawioops* et *P. mayi*. Vues dorsale (A), ventrale (B), latérale droite (C) et latérale gauche (D). Abréviations supplémentaires par rapport à la Fig. 1 : cp, processus cultriforme du parasphénoïde ; dr, crête dentigère du ptérygoïde ; ex, exoccipital ; par, parasphénoïde ; prs, présplénial ; ps, post-splénial ; pt, ptérygoïde ; sa, surangulaire. Barre d'échelle = 1 cm.

Pasawioops and the herein referred MCZ and OMNH specimens. Specimen MCZ 1415 shares with *P. mayi* an elevated dentigerous ridge on the palatine flange of the pterygoid. Unfortunately, the preservational state of MCZ 1415 does not permit the identification of additional features characteristic of *P. mayi*, such as the dentigerous ridge of bone ventral to the cultriform process. The description of *Pasawioops* (Fröbisch and Reisz, 2008) largely applies to MCZ 1415 as well and the readers are referred to Fröbisch and Reisz (2008) for details. The poorer quality of preservation of MCZ 1415 renders a detailed description somewhat unnecessary; however, the few additional insights that MCZ 1415 can provide are described below.

The right tabular appears to have an unornamented ventrolateral surface, thereby, contributing to the smooth flange within the otic notch (Fig. 4). Carroll's (1964) reconstruction of the parasphenoid of *T. texensis* was based largely on specimen MCZ 1415. Its depicted morphology, however, is uncharacteristic of amphibamids, questioning its affinity to both *T. texensis* and the amphibamid clade in general. Inspection of MCZ 1415 reveals the shape of the parasphenoid reconstructed by Carroll does not accurately represent the observed morphology. The parasphenoid of MCZ 1415 is short and broad, as depicted; however, its lateral margins are fairly concave. In this regard, the parasphenoid of MCZ 1415 resembles that of *P. mayi* and other amphibamids.

3.4. Description of specimen MCZ 1911

This specimen differs markedly from all the other referred material. Superficial inspection reveals several features suggestive of dissorophid affinity, rather than amphibamid affinity, as currently referred, thus, warranting its detailed description here. These include the broad basicranial articulations and a tooth row that ends below the orbit.

MCZ 1911 consists of a nearly complete skull and articulated lower jaw (Figs. 5A–D). The skull roof of the specimen is sheared to the right, and the right face of the specimen has been folded over onto the ventral surface. The posterior portion of the skull table is incomplete, having been broken off at a diagonal break running from the posterior margin of the right orbit to the medial edge of the left tabular.

The shape of the skull outline in dorsal view is difficult to assess given the extent of shearing and compression; however, it seems the snout was rounded and quite blunt, and the rest of the skull may have been somewhat oval-shaped in outline. The orbits are large, roughly the same diameter as the length of the antorbital region. The orbit to otic notch distance is narrow (11 mm); however, it is not as narrow as that of *Brevidorsum profundus* (9 mm), the other, much larger dissorophid from the same locality. A few fragments of ornamented bone within the orbit likely represent remnants of the palpebral ossifications. The margin of the left external naris appears to be intact, revealing that it is a fairly large opening. The bone surface is only gently ornamented, in contrast to the heavily ornamented condition common among most adult dissorophids. Additionally, the sutures are very tightly articulated, suggesting

that this animal was or was close to maturity at the time of death, despite its relatively small size for a dissorophid.

The small premaxilla forms the anteriormost tip of the snout and bounds the anterior margin of the large external naris. A small alary process on the premaxilla, similar to that seen in *Cacops*, is visible; however, due to the crushing of the specimen, it is uncertain whether the premaxillaries enclosed an internarial fontanelle at their midline. The premaxilla contacts the nasal posteriorly.

In MCZ 1911, the nasal is longer than wide, as in many dissorophids, and in contrast to the square-like condition seen in many amphibamids. The nasal contacts the lacrimal and prefrontal laterally, and the frontal posteriorly. The frontal is also rectangular, comparable in width to the nasal. Anteriorly, the frontal forms a longitudinally oriented suture with the prefrontal and posteriorly with postfrontal. The midpoint of the lateral edge of the frontal contributes to the orbital margin, as in all dissorophids, thereby, preventing contact between the pre- and post-frontal.

The parietal contacts the frontal at a nearly transverse suture. Posterior to its contact with the postorbital the parietal expands in width; however, the full shape of the parietal's outline is unknown due to its incomplete posterior portion. Posteriorly the lateral margin of the parietal contacts the supratemporal. A large parietal foramen is enclosed between the parietals at roughly the midpoint of the length of the preserved portion. Postparietals are not preserved in MCZ 1911.

The left supratemporal is preserved and occupies a large portion of the posterior skull table. It is nearly square-shaped in outline like in many dissorophids, in contrast to the more rectangular shape seen in many amphibamids, like *Pasawioops* and *Micropholis*. The supratemporal contacts the squamosal ventrally; however, the latter is a short element in MCZ 1911 and so this suture is relatively short also. The supratemporal possesses a smoothed ventral flange (supratympanic flange) that contributes to the surface lining the otic notch. Posteriorly, the supratemporal contacts the small fragment of the tabular that is preserved on the left side.

The prefrontal is somewhat elongate, in contrast to the more crescent-shaped prefrontal seen in many amphibamids and some dissorophids. Its ventral margin contacts the long, narrow lacrimal, and a ventral process that prevents contact between the lacrimal and palatine in some taxa appears to be absent. Anteriorly the lacrimal contributes to the external naris and posteriorly, it is separated from the jugal by the lateral exposure of the palatine (LEP).

The maxilla is long and narrow with a small dorsal expansion located between the external naris and orbit. The maxilla extends to the level just posterior to the jugal and has space for at least 30 small teeth, 28 of which (monocuspid and non-pedicellate) are preserved on the right side. Despite this high tooth count, the dentigerous portion of the maxilla does not extend posterior to the orbit, and this is a feature shared in common with dissorophids.

The postfrontal is fairly large and contacts the parietal along its posteromedial margin and the supratemporal

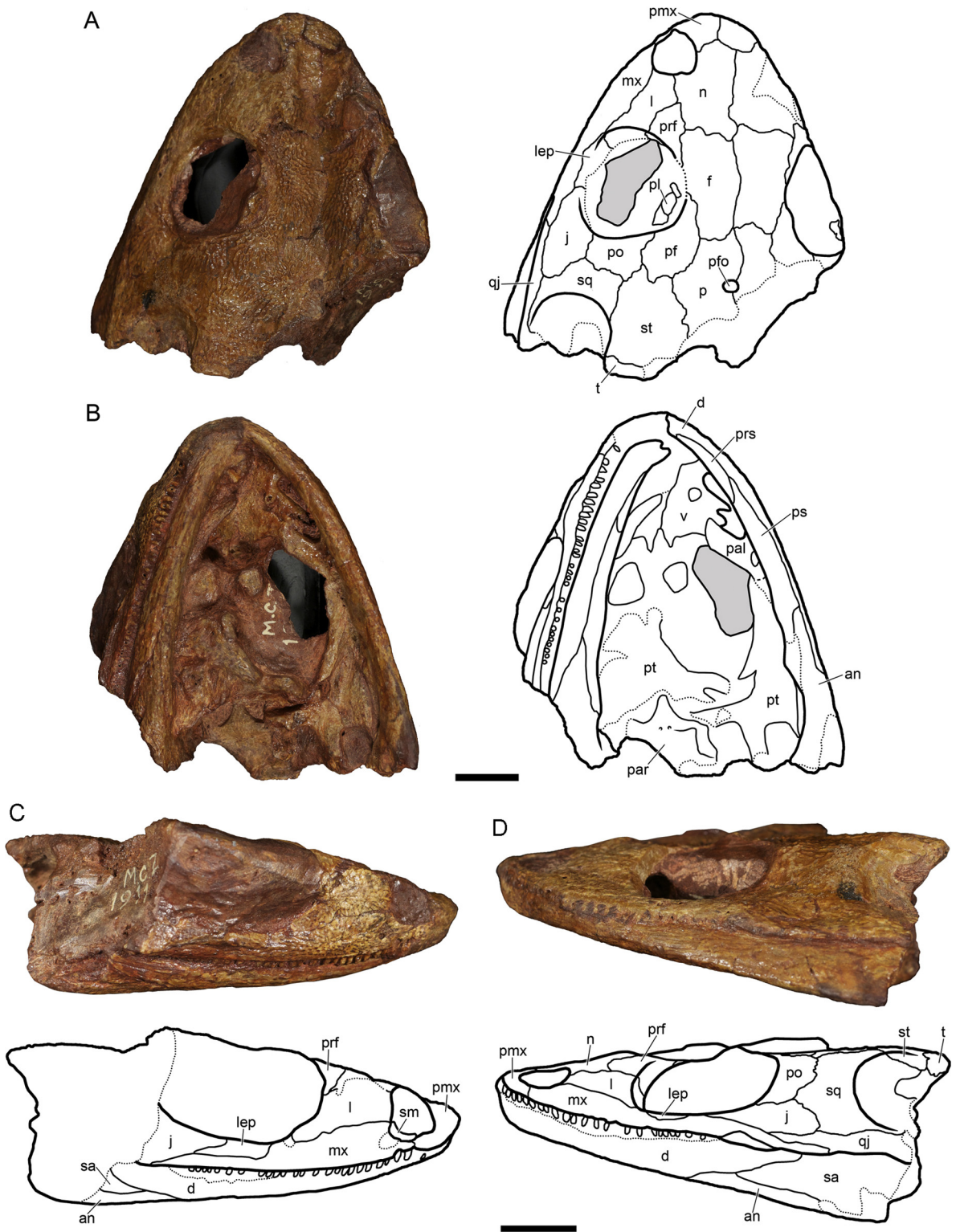


Fig. 5. Photographs and drawings of the holotype specimen of *Reiszperpeton renascentis*, gen. et. sp. nov. (MCZ 1911). A, dorsal; B, ventral; C, right lateral; and D, left lateral views. Abbreviations additional to the Fig. 1 caption: pal, palatine; par, parasphenoid; pl, palpebrals; prs, presplenial; ps, postsplenial; pt, pterygoid; sa, surangular; sm, septomaxilla; v, vomer. Scale bar = 1 cm.

Fig. 5. Photographies et dessins du spécimen holotype de *Reiszperpeton renascentis*, gen. et sp. nov. (MCZ 1911). Vues dorsale (A), ventrale (B), latérale droite (C) et latérale gauche (D). Abréviations supplémentaires par rapport à la Fig. 1 : pal, palatin ; par, parasphénoïde ; pl, éléments palpébraux ; prs, presplénial ; ps, postsplénial ; pt, ptérygoïde ; sa, surangulaire ; sm, septomaxillaire ; v, vomer. Barre d'échelle = 1 cm.

along its posterolateral margin. The postfrontal, along with the similarly sized postorbital, completes the posterodorsal margin of the orbit. The postorbital contacts the supratemporal along a short sutural surface; however, the majority of the posterior margin of the postorbital contacts the squamosal.

The squamosal forms the posterior half of the cheek wall in MCZ 1911. It is shorter than the squamosal of many amphibamids and this results in a short orbit to otic notch distance, though this is not as short as it is in taxa like *Cacops*. A smooth flange of the squamosal (semi-lunar flange) lines the anterior portion of the otic notch. It is separated from the tabular by the supratympanic flange of the supratemporal. A deep notch incises the posterior margin of the semi-lunar flange, similar to the condition seen in most dissorophids. The squamosal contacts the jugal anteroventrally and the quadratojugal posterovertrally. The jugal, with its long anterior ramus, forms the posteroventral margin of the orbit. There, it contacts the maxilla ventrally, but posteriorly it is otherwise separated from the maxilla by the wedge-shaped quadratojugal. The quadratojugal is an elongate and narrow element forming the posteroventral portion of the cheek region and underplates the squamosal within the otic notch.

The palate consists of the paired vomers, palatines, ectopterygoids, and pterygoids and by the median parasphenoid. Much of the left vomer is visible in MCZ 1911, where it can be seen to be a broad element spanning the anteriormost region of the palate. Where the vomers meet, a depression is present. Laterally, the vomer forms the medial margin of the choana and along this margin is a single fang. The posterior margin of the vomer forms the anterior margin of the interpterygoid vacuity. A posteriorly directed process is present on the medial region of the posterior margin of the vomer, similar to that seen in many dissorophids.

A portion of the left palatine is present; however, its posterior portion is damaged. A fairly broad process extends anteromedially to contact the vomer, and in the process forms the posterior margin of the choana. Posterior to the choana, a single fang is present on the palatine. An ectopterygoid cannot be confidently identified and is possibly obscured by a piece of the pterygoid. The palatine and pterygoid are very close to one another in proximity, suggesting that the two elements made contact in life.

The pterygoid is a large element of the palate. The palatine ramus of the pterygoid is damaged but its general form can be discerned. Its medial margin is gently curved, contributing to the margin of the interpterygoid vacuity. The palatine ramus bears a nearly square-shaped posterolateral margin due to a broad transverse flange. The basipterygoid articulation is damaged; however, the process is seen to be a robust structure. The quadrate ramus is not preserved in MCZ 1911.

The posterior portion of the parasphenoid is interpreted as being present; however, it has been flipped 180° such that the dorsal surface is visible when viewing the ventral surface of the specimen. The parasphenoid appears to have been wide and possibly quite short, although its posterior margin is incomplete. A pair of foramina is present at what is interpreted as the base of the cultriform process.

Fragments of unidentifiable bone and matrix obscure the remainder of the palate.

The lower jaw is incomplete posteriorly on both sides. The dentary appears to have been a long element, reaching a level posterior to the orbit. The dentary narrows along a posterodorsally oriented suture with the angular and surangular. The angular appears to be a larger element forming much of the posterolateral surface of the lower jaw on the left side. The surangular has only a narrow lateral exposure along the ventralmost margin of the posterior lower jaw. No teeth of the dentary can be observed due to the tight articulation of the lower jaw to the skull roof.

The lingual surface of the lower jaw appears to include a small anteriorly located presplenial and more elongate postsplenial posteriorly. The presplenial does not contribute to the symphysis.

3.5. Phylogenetic analysis

Comparative anatomy of the three MCZ skulls referred to *Tersomius texensis* reveals diverse morphologies suggesting the necessity to test their affinities separately in a phylogenetic analysis. The presence of definitive amphibamid characters (e.g., reduction of palatine and ectopterygoid to narrow rods and resulting large interpterygoid vacuities, pterygoid with short palatine ramus) in MCZ 1912 and 1415 suggests that it is most appropriate to investigate their phylogenetic affinities in the context of an amphibamid matrix. Specimen MCZ 1911 possesses two synapomorphies of Dissorophidae: marginal dentition that terminates under the orbit and a wide, firmly sutured basipterygoid articulation (Schoch, 2012). It was therefore most appropriate to test the phylogenetic affinities of MCZ 1911 within a matrix of olsoniform taxa (i.e., dissorophid and trematopid taxa).

To investigate the affinities of MCZ 1912 and 1415, the character list and matrix were taken from Fröbisch and Schoch (2009). This character list (Supplementary data online information) represents the amalgamation of Fröbisch and Reisz (2008) amphibamid character list [characters 1–61; character 31 deleted by Fröbisch and Schoch (2009)] and Schoch and Milner (2008) branchiosaurid character list [characters 62–80; modified by Fröbisch and Schoch (2009)]. Character state 1 of character 11 was rephrased to account for taxa in which the pterygoid does not contact the palatine either. Character 17 was rephrased, as per Anderson et al. (2008), to eliminate reference to labyrinthodonty, which is unrelated to the occurrence of pedicely. Character state 2 of character 51 [character 45 of Huttenlocker et al. (2007)] was deleted as no taxa receive this score. Character 52 was redefined by combining states 0 and 1, thereby, eliminating state 2. Character 70 was deleted as it is redundant with character 49.

Codings in the matrix of Fröbisch and Schoch (2009) were modified in the following ways. Character 5 was recoded to incorporate the not applicable (–) state of this character for Dissorophinae and Cacopinae, following Anderson et al. (2008). *Georgenthalia* was recoded as having state 1 instead of 0 and 1 for character 30, since only a single specimen is available and can therefore not be scored as polymorphic. *Micropholis* was also rescored for character

30 (1 changed to 0), as it does not express the truly broad size of the other taxa scored for this state. *Platyrhinops* was changed from score 0 to 1 for character 30, as it shares the much broader morphology. We changed the score for character 47 for *Rubeostratilia* from 1 to 0 based on the observations from the specimen drawing (Bourget and Anderson, 2011). *Gerobatrachus* was recoded as state 1 for character 48, as state 2 does not exist in the character description. *Cacopinae* was also changed to state 1 for character 48 since the orbit to otic notch distance is short. *Micropholis* was rescored for character 50 (0 and 1 to 0) because even the wide-headed morph does not appear as wide as other taxa sharing this score. *Pasawioops*, *Rubeostratilia* and *Micropholis* were all rescored as state 0 for character 54. These taxa bear a much more elongate posterior skull table than the other taxa coded for state 1. *Gerobatrachus* was rescored as uncertain (?) for character 57, as the ontogeny of the taxon is not known. *Gerobatrachus* was also rescored as state 0 for character 62 as its interorbital width to skull length ratio was measured as less than 0.26. *Cacopinae* was scored as state 1 for character 75, as the parasphenoid plate is now known in *Cacops morrissi* (Reisz et al., 2009).

In addition, several taxa were added to the matrix. Two recently described taxa, *Rubeostratilia texensis* (scores added from Bourget and Anderson, 2011) and *T. dolesensis* (Anderson and Bolt, 2013), as well as the two MCZ specimens of amphibamid affinity previously assigned to *T. texensis* (MCZ 1912 and 1415) were added and scored in the matrix individually. In the matrix of Fröbisch and Schoch (2009), the codings for *T. texensis* were based on MCZ 1912. The holotype specimen, AMNH FR 4719, is now coded in its place, separately from MCZ 1912 and any other referred material.

The recent olsoniform matrix of Schoch (2012) was used to investigate the phylogenetic affinities of MCZ 1911. Specimen MCZ 1911 was scored for 46% of the characters listed, and no further changes to the characters or codings are proposed.

The final matrices, consisting of 36 taxa and 80 characters (amphibamid matrix) and 26 taxa and 70 characters (olsoniform matrix), were analyzed using parsimony. The analyses were run using PAUP* v.4.0b10 (Swofford, 2002) on the OSX platform. *Dendrerpeton*, *Sclerocephalus*, *Balanerpeton* and Eryopidae were designated outgroups in the amphibamid analysis and *Dendrerpeton* and *Sclerocephalus* were designated outgroups in the olsoniform analysis. The heuristic search option was used with the tree bisection and reconnection (TBR) option selected, with the multiple trees (MulTrees) option in effect. Multistate taxa were treated as polymorphic and all characters were unordered and equally weighted. Bootstrap support was determined using the full heuristic search option for 500 replicates. Indices of goodness of fit of the character data to the topology (e.g., consistency index [CI], retention index [RI], rescaled consistency index [RC], and homoplasy index [HI]) were calculated in PAUP.

4. Results

The analysis of the amphibamid matrix results in the generation of 70 most parsimonious trees, each

278 steps in length (CI=0.49, HI=0.51, RI=0.77, and RC=0.38). Both the strict consensus tree (Fig. 6A) and the 50% majority-rule consensus tree (Fig. 6B) retrieve the dichotomy of Amphibamidae into discrete “*Amphibamus*” and “*Micropholis*” clades, similar to the results of Huttenlocker et al. (2007), Fröbisch and Reisz (2008), and Fröbisch and Schoch (2009), in contrast to the results of Bourget and Anderson (2011) and Sigurdson and Bolt (2010). In the current analysis, specimen MCZ 1912 clusters with the holotype of *T. texensis* with relatively high support (bootstrap support 75%). *Rubeostratilia* is resolved as the sister taxon to *Tersomius texensis*. Specimen MCZ 1415 is resolved as the sister taxon to the clade composed of *Pasawioops* and *Micropholis*. As described above, MCZ 1415 is indistinguishable from *Pasawioops*. Despite this, the character data is both incomplete and apparently insufficient to drive the clustering of MCZ 1415 with *Pasawioops* to the exclusion of *Micropholis*. Together, this clade is recovered as the sister taxon to the *T. texensis* plus *Rubeostratilia* clade. *T. dolesensis* fails to cluster with its congeners. Here, it is recovered as the sister taxon to the clade composed of the above two sister clades (*Pasawioops* plus *Micropholis* and *T. texensis* plus *Rubeostratilia*).

Incorporation of MCZ 1911 to the olsoniform matrix of Schoch (2012) results in the generation of 570 most parsimonious trees, each 140 steps in length (CI=0.54, HI=0.45, RI=0.74, RC=0.41). The strict consensus tree is poorly resolved (Fig. 6C); however, the topology of the 50% majority-rule consensus tree (Fig. 6D) is identical to the results of the analysis of Schoch (2012) except that in our tree *Conjunctio* sp. is resolved on the stem of the clade composed of *Dissorophus* and *Broiliellus*, albeit with low support (less than 50% bootstrap support; Fig. 6D). Specimen MCZ 1911 is resolved as nested within the greater cacopine clade, also with low support (less than 50% bootstrap support; Fig. 6). More specifically, MCZ 1911 is recovered on the stem of *Cacopinae*.

The clustering of MCZ 1911 with *Cacopinae* is driven by a single unique synapomorphy: the position of the foramina for the carotid arteries at the base of the cultriform process (character 62, state 1). Schoch (2012) noted in the description of this character that although it seems that only cacopines may share this character state, its occurrence in other taxa of the greater cacopine clade is unknown. Therefore, this character state may actually unite a larger clade, and the position of MCZ 1911 could change.

5. Discussion

The above analyses of morphology and the results of the phylogenetic analyses support the revision of the current taxonomic assignments of specimens MCZ 1415 and 1911.

5.1. Revised systematic paleontology of MCZ 1415

TEMNOSPONDYLI Zittel, 1888

DISSOROPHOIDEA Bolt, 1969

AMPHIBAMIDAE Moodie, 1909

PASAWIOOPS cf. *P. MAYI* Fröbisch and Reisz, 2008

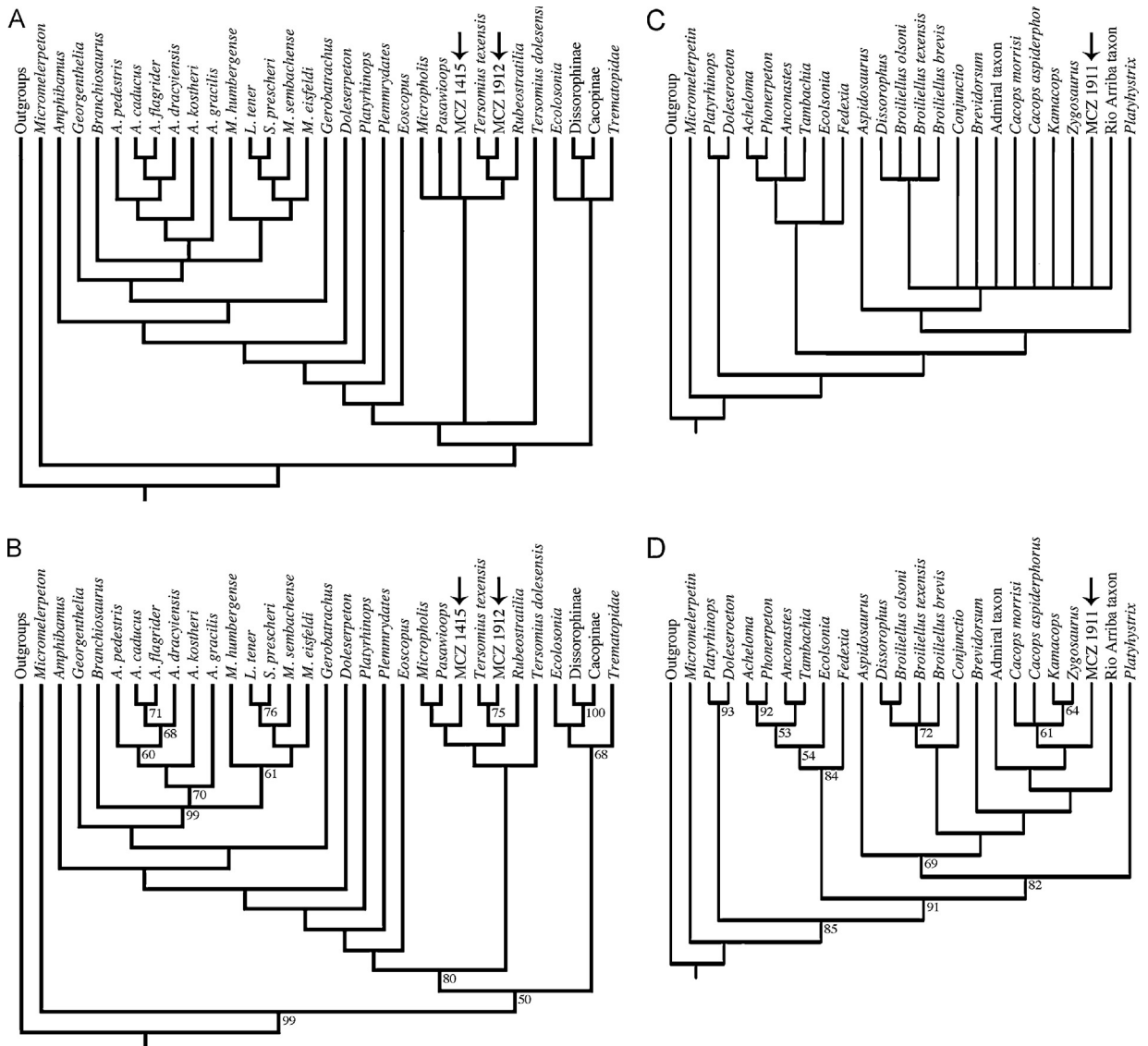


Fig. 6. Results of the phylogenetic analyses. Strict consensus (A) and 50% majority-rule consensus tree (B) from the analysis of the amphibamid matrix, including the holotype of *Tersomius texensis*, MCZ 1912, and MCZ 1415. The holotype specimen of *T. texensis* clusters with referred specimen MCZ 1912. Previously referred specimen MCZ 1415 clusters with *Pasawioops* and *Micropholis*. *Tersomius dolesensis* fails to cluster with *T. texensis*. Strict consensus (C) and 50% majority-rule consensus tree (D) from the analysis of the olsoniiform matrix, including MCZ 1911. Specimen MCZ 1911 is recovered on the stem of Cacopinae. Arrows indicate location of MCZ “*Tersomius*” material.

Fig. 6. Résultats des analyses phylogénétiques. Strict consensus (A) et arbre de consensus à règle de majorité simple d’après l’analyse de la matrice amphibamidé, incluant l’holotype de *Tersomius texensis*, MCZ 1912 et MCZ 1415. Le spécimen précédemment référencé MCZ 1415 se groupe avec *Pasawioops* et *Micropholis*. *Tersomius dolesensis* ne parvient pas à se grouper avec *T. texensis*. Strict consensus (C) et arbre de consensus à majorité simple (D), d’après l’analyse de la matrice olsoniiforme incluant MCZ 1911. Le spécimen MCZ 1911 est récupéré sur la branche des Cacopinae. Les flèches indiquent la localisation du matériel MCZ « *Tersomius* ».

Diagnosis: As for the type specimen, OMNH 73019.

Referred specimen: MCZ 1415 consisting of a skull and articulated lower jaws. The snout region is poorly preserved, with inadequate bone surface to evaluate the nature of the anterior elements.

Locality and horizon: Gully #80, southwest of Archer City, Texas; Archer City Bonebed, Archer City Formation, Bowie Group, Lower Permian.

Comment: Specimen MCZ 1415 is morphologically indistinguishable from the holotype of *Pasawioops mayi*,

OMNH 73019, and is comparable in size to referred specimen OMNH 73509 of *P. mayi*. Specimen MCZ 1415 shares with *P. mayi* the presence of a dentigerous ridge on the palatine process of the pterygoid. Bones of the anterior snout region are not preserved in MCZ 1415, precluding an assessment of the length of the alary processes of MCZ 1415. A single foramen that served to transmit the carotid artery to the brain cavity is possibly present in MCZ 1415. However, this apparent foramen could be due to damage, and so the nature of this character state remains as

uncertain (?) in the coding presented here. Interestingly, the palatal region contains numerous small fragments of bone, possibly representing dentigerous plates that are found in *P. mayi*.

5.2. Revised systematic paleontology of MCZ 1911

TEMNOSPONDYLI Zittel, 1888
DISSOROPHOIDEA Bolt, 1969
DISSOROPHIDAE Boulenger, 1902
REISZERPETON, gen. nov.

Etymology: *Reiszerpeton* in honour of Robert R. Reisz, and his contributions to our knowledge of Early Permian vertebrates.

Diagnosis: As for species.

REISZERPETON RENASCENTIS, sp. nov.

(Fig. 5)

Etymology: *R. renascentis* in recognition of the diverse contributions of Robert R. Reisz, the “Renaissance Paleontologist”, to the field of vertebrate paleontology.

Holotype: MCZ 1911. Nearly complete skull with articulated lower jaw. Right side of the skull compressed to the ventral surface, and the postorbital region of the right side and posteriormost skull table missing.

Locality and horizon: Section 1834, Texan Emigration and Land Co., Texas, north of West Fork-Trinity River, Archer Co., Texas; base of Archer City Formation, Bowie Group, Lower Permian.

Diagnosis: A small dissorophid temnospondyl characterized by a high marginal tooth count, consisting of very small pointed teeth. Differs from *Cacops* in its overall smaller size at maturity, much smaller and more numerous maxillary teeth (34), much smoother cranial ornamentation at maturity, and greater orbit to otic notch distance. Differs from the co-occurring *Brevidorsum profundum* in a longer orbit to otic notch distance. Shares with members of Dissorophidae marginal dentition that terminates the anterior to the posterior margin of the orbit and the wide firmly sutured basiptyergoid articulation. Shares with Dissorophoidea the presence of a lateral exposure of the palatine (LEP).

5.3. Other *Tersomius* material and implications for amphibamid diversity

As well as the above-described Texas material, two assemblages of small amphibamid temnospondyls from the Garber and Hennessey Formations of Oklahoma have been referred to *Tersomius*. Having redefined *T. texensis* on a more restricted set of specimens, it is appropriate to give some provisional consideration to this referred material, to confirm that it is still appropriate to associate with *Tersomius*. Both assemblages, examined by one of us (ARM), represent small amphibamids in which:

- the frontal enters the orbit margin;
- a medial internarial fontanelle is present;
- the skull table is not as elongate as in *Pasawioops* or as abbreviated as in *Amphibamus* and;
- two sets of vomerine fangs are usually present.

None of these features is unambiguously generically diagnostic but, together with origin in the Lower Permian of central USA, has led to them being considered as *Tersomius*.

Material from the Hennessey Formation from near Norman, Cleveland County, Oklahoma was first described as *T. mosesi* by Olson (1970) from at least 75 specimens. This locality appears to be equivalent to mid-late Clear Fork age and so significantly younger in age than the Texas material (Simpson, 1979). Olson's (1970: fig. 9) reconstruction was rather schematic, but his description was supplemented by comments from Daly (1973), Bolt (1977) and a more detailed account by Daly (1994) including a more precise figure of a skull (op.cit. fig. 27). This skull is smaller than the holotype of *T. texensis* with a midline length of about 20 mm and the orbits are correspondingly larger. Of the diagnostic characters used in this work, Daly figured an elongate jugal with equally elongate suborbital and quadratojugal rami, together with the generally circular skull shape with medial curvature of the posterior maxillary arcade, therefore we can assign this set to *Tersomius*. Interestingly, and as noted by Olson (1970), the dentition is distinct from that of *T. texensis*: in AMNH FR 4719, the jaw rami had space for 45 to 50 teeth (including spaces for replacement teeth) (ARM personal observation) and MCZ 1912 shows space for 47 teeth (Carroll, 1964; and ARM pers.obs.). In *T. mosesi*, 30 to 35 marginal teeth plus spaces are counted (Olson, 1970; and ARM pers. obs. of FMNH UR1217, 1221 and 1222). It appears, therefore, that this set was a late population sample of *Tersomius* that had evolved a modified dentition of fewer larger marginal teeth.

The other large assemblage is from the Garber Formation at South Grandfield, Tillman County, Oklahoma. The productive horizon is equivalent to the Waggoner Ranch (previously Clyde) Formation of Texas (Simpson, 1979) and so intermediate in age between the type of *T. texensis* and the *T. mosesi* material. This material was first described by Daly (1973) as *Tersomius* cf. *T. texensis*, but later Bolt (1977) simply referred to it as *T. texensis*, while Daly (1994) used both designations. The 80 specimens are mostly partial skulls in cuboidal fragments of matrix and represent individuals with small 20 to 30 mm skulls. The fragments combine to suggest an animal with a skull very like that of *T. texensis*, with the characteristic circular shape. The jugal of one specimen (FMNH UR2368) is however very blunt and foreshortened posteriorly (ARM pers. obs.). The premaxilla has space for up to 12 teeth (FMNH UR2362) and the maxilla has space for up to 40 teeth (FMNH UR2277) (both ARM pers.obs.) giving a total of slightly over 50, comparable to the earlier Texas specimens. However this material is disconcertingly diverse in some features on multiple specimens. Firstly, as noted by Bolt (1977), there are specimens with bicuspid teeth and others with monocuspid teeth. Secondly, there are specimens where the lacrimal duct has anything from one (FMNH UR2277) to four (FMNH UR2369) openings in the orbit margin (ARM pers. obs.). Thirdly, the configuration of the vomerine pit and fang-pairs varies with one specimen (FMNH UR2362) showing a vomerine pit divided into anterior and posterior pits by two posterolateral ridges bearing the second fang-pairs, while another (FMNH UR2370) has a large

undivided pit with no second fang-pairs but a curious pair of flanges at the posterior margin (ARM pers. obs.).

This structural diversity might be due to natural variation, as it has been suggested for *Micropholis* by Boy (1985) and Schoch and Rubidge (2005). Alternatively, it might be due to ontogenetic change within the South Grandfield population, as proposed by Bolt (1977). However, recent discoveries and publications suggest a third possibility, namely that there may be more than one species of amphibamid at this locality (Fröbisch and Reisz, 2008; Anderson and Bolt, 2013). Recent work on specimens from the Fort Sill assemblage has expanded the number of amphibamids present from one to three (*Doleserpeton*, *Pasawioops* and “*Tersomius*”; Fröbisch and Reisz, 2008; Anderson and Bolt, 2013). Our work has expanded the number of amphibamids in the Archer City Bone Bed from one to two (*Tersomius* and *Pasawioops*). It is therefore possible that the diversity in tooth-crown cuspidity, lacrimal duct numbers, vomer structure and dentition may be due to the presence of two taxa in the South Grandfield assemblage. The fragmentary nature of the South Grandfield material means that a careful reevaluation of its taxonomic content is in order. Some specimens certainly seem consistent with attribution to *T. texensis* while others do not, and pending restudy, this assemblage should not be treated as a simple population of *T. texensis*.

In addition, our reassessment of the genotype and this phylogenetic analysis question the recent assignment of the new taxon *T. dolesensis* to this genus. Our analysis reveals significant morphological differences between the two, which suggests that *T. dolesensis* is more distantly related to *T. texensis* than is *Rubeostratilia* and members of the *Micropholis-Pasawioops* clade taxa. Further comparative work, as suggested above, including other material currently assigned to *Tersomius* is needed to confirm the relationships of *T. dolesensis*, and we therefore prefer refraining from erecting a new generic name for this taxon at this stage.

Comparative study of material from the Bowie Group, Texas, previously referred to *T. texensis* has revealed more diversity than previously recognized. The recognition of *P. mayi* in the coastal lowlands of Texas expands the geographic range of this taxon, and demonstrates that it occurred in a range of paleoenvironmental settings. As with *Varanops brevirostris*, the occurrence of *P. mayi* in both the Richard Spur upland locality of Oklahoma and the more coastal Bowie Group of Texas supports previous biostratigraphic assessments of general contemporaneity of these localities (Maddin et al., 2006). Reassessing material previously referred to *T. texensis* suggests a restudy of historical collections from the Permian of Texas, which may reveal a greater alpha diversity and important occurrences of taxa that will further contribute to our understanding of the Early Permian ecosystems.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2013.06.007>.

References

- Anderson, J.S., Bolt, J.R., 2013. New information on amphibamids (Tetrapoda; Temnospondyli) from Richards Spur (Ft. Sill) Oklahoma. *J. Vertebr. Paleontol.* 33, 553–567.
- Anderson, J.S., Henrici, A.C., Sumida, S.S., Martens, T., Berman, D.S., 2008. *Georgenthalia clavinasica*, a new genus and species of dissorophoid temnospondyl from the Early Permian of Germany, and the relationships of the family Amphibamidae. *J. Vertebr. Paleontol.* 28, 61–75.
- Bolt, J.R., 1968. The osteology and relationships of *Doleserpeton annexens*: a new rhachitomous amphibian from the Lower Permian of Oklahoma. PhD Thesis. University of Chicago, Chicago.
- Bolt, J.R., 1969. Lissamphibian origins—possible protolissamphibian from Lower Permian of Oklahoma. *Science* 166, 888–891.
- Bolt, J.R., 1974. Armor of dissorophoids (Amphibia: *Labyrinthodontia*): an examination of its taxonomic use and report of a new occurrence. *J. Paleontol.* 48, 135–142.
- Bolt, J.R., 1977. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. *J. Paleontol.* 51, 235–249.
- Bourget, H., Anderson, J.S., 2011. A new amphibamid (Temnospondyli: Dissorophoidea) from the Early Permian of Texas. *J. Vertebr. Paleontol.* 31, 32–49.
- Boy, J.A., 1985. Über *Micropholis*, den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). *N. Jahrb. Geol. Paläontol.* 1985, 29–45.
- Carroll, R.L., 1964. Early evolution of the dissorophoid amphibians. *Bull. Mus. Comp. Zool., Harvard* 131, 161–250.
- Case, E.C., 1910. New or little known reptiles and amphibians from the Permian (?) of Texas. *Bull. Am. Mus. Nat. Hist.* 28, 163–181.
- Clack, J.A., Milner, A.R., 1994. *Platyrrhinops* from the Upper Carboniferous of Linton and Nyřany and the family Amphibamidae (Amphibia: Temnospondyli). *Pollichia-Buch* 29, 185–191.
- Clack, J.A., Milner, A.R., 2009. Morphology and systematics of the Pennsylvanian amphibian *Platyrrhinops lyelli* (Amphibia: Temnospondyli). *Trans. R. Soc. Edinb.: Earth Environ. Sci.* 100, 275–295.
- Daly, E., 1973. A Lower Permian vertebrate fauna from southern Oklahoma. *J. Paleontol.* 47, 562–589.
- Daly, E., 1994. The Amphibamidae (Amphibia: Temnospondyli) with a description of a new genus from the Upper Pennsylvanian of Kansas. *Miscellaneous Publications, University of Kansas Museum of Natural History*, pp. 1–59.
- DeMar, R.E., 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. *J. Paleontol.* 42, 1210–1242.
- Fröbisch, N.B., Carroll, R.L., Schoch, R.R., 2007. Limb ossification in the Paleozoic branchiosaurid *Apateon* (Temnospondyli) and the early evolution of preaxial dominance in tetrapod limb development. *Evol. Dev.* 9, 69–75.
- Fröbisch, N.B., Reisz, R.R., 2008. A new Lower Permian amphibamid (Dissorophoidea, Temnospondyli) from the fissure fill deposits near Richards Spur, Oklahoma. *J. Vertebr. Paleontol.* 28, 1015–1030.
- Fröbisch, N.B., Schoch, R.R., 2009. Testing the impact of miniaturization on phylogeny: Paleozoic dissorophoid amphibians. *Syst. Biol.* 58, 312–327.
- Huttenlocker, A.K., Pardo, J.A., Small, B.J., 2007. *Plemmyradytes shintoni*, gen. et sp. nov., an Early Permian amphibamid (Temnospondyli: Dissorophoidea) from the Eskridge Formation, Nebraska. *J. Vertebr. Paleontol.* 27, 316–328.

- Maddin, H.C., Evans, D.C., Reisz, R.R., 2006. An Early Permian varanodontine varanopid (Synapsida: Eupelycosauria) from the Richards Spur locality, Oklahoma. *J. Vertebr. Paleontol.* 26, 957–966.
- Moodie, R.L., 1909. Carboniferous air-breathing vertebrates of the United States National Museum. *Proc. U.S. Nat. Mus.* 37, 11–28.
- Olson, E.C., 1970. New and little-known genera and species of vertebrates from the Lower Permian of Oklahoma. *Fieldiana: Geol.* 18, 359–434.
- Reisz, R.R., Schoch, R.R., Anderson, J.S., 2009. The armoured dissorophoid *Cacops* from the Early Permian of Oklahoma and the exploitation of the terrestrial realm by amphibians. *Naturwissenschaften* 96, 789–796.
- Schoch, R.R., 2012. Character distribution and phylogeny of the dissorophid temnospondyls. *Fossil Rec.* 15, 121–137.
- Schoch, R.R., 2013. How body size and development biased the direction of evolution in early amphibians. *Hist. Biol.* 25, 155–165.
- Schoch, R.R., Rubidge, B.S., 2005. The amphibamid *Micropholis* from the Lystrosaurus assemblage zone of South Africa. *J. Vertebr. Paleontol.* 25, 502–522.
- Schoch, R.R., Milner, A.R., 2008. The intrarelationships and evolutionary history of the temnospondyl family Branchiosauridae. *J. Syst. Palaeontol.* 6, 409–431.
- Sigurdson, T., Bolt, J.R., 2010. The Lower Permian amphibamid *Dole-serpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. *J. Vertebr. Paleontol.* 30, 1360–1377.
- Simpson, L.C., 1979. Upper Gearyan and Lower Leonardian terrestrial vertebrate faunas of Oklahoma. *Oklahoma Geol. Notes* 39, 3–21.
- Swofford, D.L., 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Sunderland.
- Yates, A.M., Warren, A.A., 2000. The phylogeny of the “higher” temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zool. J. Linn. Soc.* 128, 77–121.
- Zittel, K., 1888. *Handbuch der Palaontologie Abteilung 1. In: Palaeozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Munich and Leipzig, Oldenbourg, 900 p.