



General palaeontology, systematics and evolution (Vertebrate palaeontology)

A new dissorophid (Temnospondyli, Dissorophoidea) from the Early Permian of New Mexico (United States)



Un nouveau dissorophidé (Temnospondyli, Dissorophoidea) du Permien inférieur du Nouveau-Mexique (États-Unis)

Robert Holmes^{a,*}, David S. Berman^b, Jason S. Anderson^c

^a Department of Biological Sciences, University of Alberta, Alberta T6E 1A2, Canada

^b Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, USA

^c Faculty of Veterinary Medicine, University of Calgary, 3330 Hospital Drive, Calgary, Alberta T2N 4N1, Canada

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ABSTRACT

An amphibian skull and partial skeleton found from the El Cobre Canyon Formation of New Mexico, USA, is identified as a new species of the dissorophoid temnospondyl genus *Broiliellus*. Significant anatomical features include: a relatively long, narrow preorbital region, with both nasals and vomers no more than half as wide anteriorly than posteriorly; extended ventral projection of the postorbital; a unilaterally retained lateral exposure of the ectopterygoid (in addition to the normally present lateral exposure of the palatine); supratemporal lacking a semilunar flange; highly vaulted vomers forming a median internasal septum; and an angular with a swollen posteroventral keel. Phylogenetic analysis strongly supports a sister group relationship with *Broiliellus brevis* and clearly distinguishes it from another dissorophoid, 'B.' *novomexicanus* from New Mexico. The medially restricted supraneural osteoderms are more similar to those seen in *Cacops* than *Broiliellus*, which reinforces the importance of avoiding using single 'key features' to discriminate taxa.

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R É S U M É

Un crâne et un squelette partiel d'amphibien de la formation El Cobre Canyon au Nouveau-Mexique (États-Unis) ont été identifiés comme appartenant au genre *Broiliellus*, temnospondyle dissorophoïdé. Les traits significatifs sont les suivants : une région pré-orbitale relativement longue et étroite, avec à la fois des nasaux et des vomers moitié moins larges antérieurement que postérieurement ; une projection ventrale étendue du post-orbital ; une exposition latérale unilatéralement retenue de l'ectoptérygoïde (en plus d'une exposition latérale normalement présente du palatin) : un supratemporal ne présentant pas de bord en demi-lune ; des vomers très arqués formant un septum médian internasal et un angulaire avec une « carène » postéroventrale gonflée. L'analyse phylogénétique va nettement dans le sens d'une relation de type groupe frère de *Broiliellus brevis* et le distingue d'un autre dissorophoïdé, *B. novomexicanus* du Nouveau-Mexique. Les ostéoderms supra-neuraux médialement réduits sont davantage semblables à ceux observés chez *Cacops* que chez *Broiliellus*, ce qui renforce l'importance d'éviter d'utiliser les seules caractéristiques clés pour discriminer les taxa.

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* Corresponding author.

E-mail addresses: holmes1@ualberta.ca (R. Holmes), bermand@carnegiemnh.org (D.S. Berman), janders@ucalgary.ca (J.S. Anderson).

1. Introduction

The Temnospondyli is a large and diverse clade of archaic terrestrial anamniotes (amphibians) that persisted for approximately 200 Ma, from the Visean to the Early Cretaceous (Holmes, 2000). One temnospondyl clade in particular, the Dissorophoidea, has received much attention in recent years as a result of its hypothesized involvement in the origins of crown amphibians (frogs, salamanders, and caecilians, collectively known as Lissamphibia – Anderson, 2008; Schoch and Milner, 2004). Dissorophoids are terrestrial amphibians that comprised an important component of Paleozoic terrestrial communities (Eberth et al., 2000). These animals are conspicuously represented in the tetrapod assemblage collected from the karst fill of Richard's Spur, Oklahoma, which preferentially preserved terrestrial vertebrates from the Early Permian (Sullivan et al., 2000; Woodhead et al., 2010). Dissorophoidea comprises three clades of small- to medium-sized animals. The smallest are the members of the Amphibamidae, within which recent hypotheses include the aquatic and/or neotenic Branchiosauridae (Fröbisch and Schoch, 2009a, 2009b; Sanchez et al., 2010; Schoch and Milner, 2008). This group, which has been studied extensively (Anderson and Bolt, 2013; Anderson et al., 2008a, 2008b; Bolt, 1979; Bourget and Anderson, 2011; Clack and Milner, 1993, 2010 [for 2009]; Fröbisch and Reisz, 2008; Huttenlocker et al., 2007; Schoch and Rubidge, 2005), is thought to have given rise to Lissamphibia by most authors (Bolt, 1977, 1991; Maddin and Anderson, 2012; Maddin et al., 2012; Milner, 1988, 1993; Ruta and Coates, 2007; Ruta et al., 2003; Sigurdson and Bolt, 2010; Sigurdson and Green, 2011; Trueb and Cloutier, 1991; but see also Carroll, 2007; Marjanović and Laurin, 2008, 2009; Vallin and Laurin, 2004 for alternate views and Steyer, 2012, for a review of the debate). Within amphibamids are seen several morphological trends that build, in step-wise fashion, numerous character transformation series in a lissamphibian-like direction. These include overall reduction in the degree of ossification of the skull, especially in the postorbital skull table, reduction in body size, enlargement of the orbits and otic notch, modification of the elbow, reduction in number of vertebrae, and reduction in size and increase in number of teeth (Anderson, 2008; Maddin and Anderson, 2012; Sigurdson, 2008; Sigurdson and Bolt, 2009). Unambiguous synapomorphies with lissamphibians that are acquired within the amphibamid clade include pedicellate teeth and the fusion of distal tarsals one and two into a basale commune (Anderson et al., 2008a; Bolt, 1969, 1977). As in other dissorophids (e.g., Branchiosauridae, Sanchez et al., 2010), amphibamids are also known to exhibit life history plasticity, which they appear to have exploited evolutionarily in the form of neoteny comparable to that exhibited by extant salamanders (Fröbisch and Schoch, 2009a, 2009b; Schoch, 2009, 2010; Schoch and Carroll, 2003; Schoch and Fröbisch, 2006; Schoch and Milner, 2008).

Less attention has been devoted to the other groups of dissorophoids, the Trematopidae and Dissorophidae, although this is rapidly changing. The Trematopidae is characterized by a posterior emargination of the external

nares (Berman et al., 2009, 2011; Bolt, 1974a; Dilkes, 1990, 1993; Olson, 1941), and most of the Dissorophidae by dorsal osteoderms associated with the neural spines of the trunk vertebrae (the 'armoured dissorophids' of Schoch, 2012). Some phylogenetic hypotheses unite these two families into the Olsoniformes (Anderson et al., 2008b). Recent studies have introduced new species and have increased resolution of the anatomy of both groups. Among dissorophids in particular, *Cacops* has been studied intensively for the first time since it was described over 90 years ago, and details of cranial sutures have been published (Anderson, 2006; Dilkes, 2009; Dilkes and Brown, 2007; Fröbisch and Reisz, 2012; Reisz et al., 2009). This has facilitated the inclusion of this genus into phylogenetic analyses which are based primarily upon cranial anatomy.

The Dissorophidae comprises the basal *Platyhystrix* (Berman et al., 1981), *Aspidosaurus* (Berman and Lucas, 2003; Carroll, 1964; DeMar, 1966a), *Conjunctio* (Carroll, 1964), and *Brevidorsum* (Carroll, 1964), and two derived clades: (1) *Cacopinae* (Schoch, 2012) that includes *Cacops*, *Kamacops*, *Anakamacops* (Li and Cheng, 1999), *Alegeinosaurus* (Case, 1911), *Zygosaurs*, and possibly *Fayella* (Olson, 1972), and (2) *Dissorophinae* (Schoch, 2012) that includes *Dissorophus* and *Broiliellus*. *Longiscitula* (DeMar, 1966b) has been synonymized more recently with *Dissorophus* (Milner, 2003). These derived taxa are characterized by specific patterns of dermal ornamentation, large promontories and depressions on the surface of the skull, and in the pattern of overlap of their dorsal dermal osteoderms. However, most of these taxa have not been reconsidered in light of the newly described anatomy of *Cacops*, current hypotheses of overall dissorophoid relationships, or discussion of the evolutionary mechanisms thought to have been responsible for the emergence of modern amphibians. A number of workers around the world are now engaged in this research, and a better understanding of dissorophoid phylogeny and evolution is imminent (Schoch, 2012).

The genus *Broiliellus* was first established based on material collected in Baylor County, Texas, near Mitchell and Timber Creeks northeast of the town of Maybelle (Romer, 1928). This material was described as *Broiliellus texensis* (Williston, 1914). *Broiliellus arroyoensis*, collected at the nearby Coffee Creek locality appears to be distinct from *B. texensis* in the possession of a distinctly triangular skull (DeMar, 1967). Both localities are now considered to be within the Waggoner Ranch Formation (Hentz, 1989), which is essentially equivalent to the Clyde Formation of the traditional literature (Romer, 1935). *Broiliellus brevis* was collected from the Archer City Bonebed in Archer County, Texas (Carroll, 1964). This bonebed is located in the significantly older Archer City Formation (Hentz, 1989), which is equivalent to the Putnam Formation of the traditional literature. This species can be distinguished by a relatively short skull table and shallow otic notch (Carroll, 1964). *Broiliellus olsoni* was recovered from the Thaxton Ranch Locality, Clay County, Texas, from sediments of the Nocona Formation (J.C. Sagebiel, pers. comm. May, 2013), which is equivalent in age to the Admiral Formation of the traditional literature (Hentz, 1989). This species is characterized by a ventrally convex maxillary margin, a short

postorbital portion of the skull, deep lateral skull profile, and large, circular nares and orbits (DeMar, 1967). The status of *Broiliellus hekotos* (Berman and Berman, 1975) is contentious. May et al. (2011) suggest that it may be more closely related to the more basal amphibamid dissorophoids; however, we choose to include it provisionally within the Dissorophidae.

In 1979, a joint field party from the Carnegie Museum of Natural History and the University of Toronto, Mississauga, recovered the remains of a partial, articulated postcranial skeleton of the basal pelycosaur-grade synapsid *Sphenacodon ferox* (CM 38039) from the lower Permian El Cobre Canyon Formation, Cutler Group, Rio Arriba County, New Mexico (Lucas et al., 2005a, 2005b). The specimen was collected from the uppermost part of the formation on the outskirts of the village of Arroyo del Agua from sediments equivalent in age to the Archer City Formation of North-central Texas (Berman et al., 2013, fig. 5). During preparation of this specimen, the skull and partial skeleton of a dissorophid (CM 41705) were discovered beneath its rib cage. The latter specimen was tentatively identified as *Broiliellus*, but remained undescribed.

Dissorophoid material from New Mexico is rare. Other than CM 41705, only a few poorly preserved, incomplete specimens attributable to *Broiliellus* have been described from the state. All are considerably older than the better known *Broiliellus texensis*, and almost certainly represent a distinct species – referred to as ‘*Broiliellus*’ *novomexicanus* by Langston (1953), and currently being studied by R. Schoch (Stuttgart). Although this taxon shares some features, and is probably coeval, with the specimen described here, it also exhibits some distinct differences. As such, we posit that the new specimen represents a second, previously unrecognized New Mexican dissorophid species.

In this paper, we describe this new species, compare it with other dissorophoids, include these new data in a recently published cladistics analysis of the dissorophoids by Schoch (2012) to test the placement of this new species as well as establish its impact on the phylogenetic relationships of Dissorophoidea.

1.1. Anatomical abbreviations

a cor, anterior coronoid; **ang**, angular; **art**, articular; **at**, atlas; **ax**, axis; **bo**, basioccipital; **b pr**, basal process; **b tub**, basal tuber; **ch**, choana; **cl**, clavicle; **cle**, cleithrum; **cor**, coracoid; **cor pr**, coronoid process; **d**, dentary; **ect**, ectopterygoid; **eo**, exoccipital; **e oss**, external ossicle; **f**, frontal; **hum**, humerus; **ic**, intercentrum; **icl**, interclavicle; **in sept**, internarial septum; **i oss**, internal ossicle; **l**, lacrimal; **lee**, lateral exposure of the ectopterygoid; **lep**, lateral exposure of the palatine; **mx**, maxilla; **op**, opisthotic; **m cor**, middle coronoid; **n**, nasal; **na**, neural arch; **nar**, external naris; **p**, parietal; **pal**, palatine; **palp**, palpebral; **para**, parasphenoid; **part**, prearticular; **pc**, pleurocentrum; **pcor**, posterior coronoid; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**, prefrontal; **pro**, prootic; **psp**, postsplenial; **pt**, pterygoid; **ptf**, posttemporal fossa; **q**, quadrate; **qj**, quadratojugal; **r**, rib; **sa**, surangular; **sc**, scapula; **sp**, splenial; **sph**, sphenethmoid; **sq**,

squamosal; **st**, supratemporal; **stap**, stapes; **sym**, symphysis of dentary; **t**, tabular; **v**, vomer.

2. Systematic palaeontology

Temnospondyli Zittel 1887–1890

Dissorophoidea Bolt, 1969

Dissorophidae Boulenger, 1902

Broiliellus Williston, 1914

Type species: *Broiliellus texensis* Williston, 1914.

Holotype: UC (University of Chicago) 684.

Paratype: UC 685.

Diagnosis (modified from Schoch, 2012): Medium-sized dissorophids bearing dorsal osteoderms of variable width; skull triangular in dorsal outline, snout bluntly pointed (not broadly rounded or rectangular); preorbital region sub-equal or shorter than postorbital region; interorbital region broad, equivalent in width to 0.27 or more of the midline length of the skull; tabular horn elongate, forming most of the body of the tabular; skull with elevated eminences on frontals, parietals, postfrontals and postparietals; parasphenoid plate with prominent laterally projecting wings and posteriorly facing pockets for attachment of axial musculature (these last two characters shared with *Dissorophus*); interpterygoid vacuities greatly expanded laterally at mid-length (shared with *Dissorophus*)

Broiliellus reiszi, sp. nov.

(Figs. 1–10)

Etymology: *reiszi*, in honour of Robert R. Reisz, whose contributions to vertebrate paleontology, in particular Permian carboniferous tetrapod faunas, are many and highly regarded.

Holotype: CM 41705, skull and partial postcranial skeleton.

Diagnosis: Autapomorphies: nasals and vomers that are half as wide anteriorly than posteriorly; posterior third of choana narrowed by an anterior projection of the palatine; maxilla with alveolar shelf projecting medially into choana; parasphenoid plate greatly flared posteriorly to a width almost twice that measured at the level of the basal articulation; supratemporal does not form any part of the supratympanic flange; basioccipital and exoccipitals co-ossified, exoccipitals meet above the foramen magnum (although this may simply indicate that this specimen is a relatively old individual); basioccipital large, forming ventral portion of the horizontally oval–kidney bean-shaped occipital condyle (distinct from the bi-lobed condyle of other dissorophids); vomers deflected dorsally at the midline to form an internarial septum (however, the distribution of this character within dissorophoids is incompletely known); angular abbreviated anteriorly, and bears a laterally compressed, distally swollen keel at its posteroventral corner; dorsal osteoderms small, no wider than the distance across transverse processes of trunk vertebrae, bearing ornamentation similar to that on dermal skull bones; two sets of osteoderms; an internal set

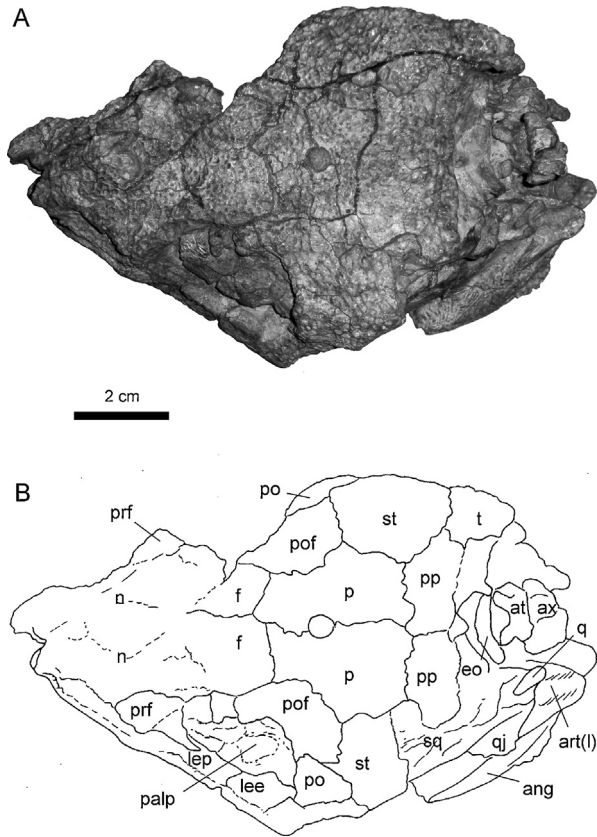


Fig. 1. *Broiliellus reiszii*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, dorsal view of skull.

Fig. 1. *Broiliellus reiszii*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, vue dorsale du crâne.

closely associated with (if not fused to) the neural spines, and an external set alternating between the internal series and partly overlapping them dorsally.

Features shared with *B. olsoni*: skull with triangular profile in dorsal view; skull tall with nearly vertical cheeks; nearly vertical anterior margin of otic embayment; dorsally arched snout; ventrally convex maxillary margin; large postorbital that extends far ventrally; tooth count in upper jaw (including premaxilla) 47 or 48.

Features shared with *B. olsoni*, '*B. novomexicanus*, and *B. brevis*: large, circular nares and orbits; preorbital region of the skull relatively long (approximately the same length as the postorbital portion).

3. Description and comparisons

3.1. Skull, general

The skull, including mandible, is essentially complete. The relationships among the elements are little disturbed, and the topographical features (sulci, ridges, and eminences) as well as most of the sutures are clear. The skull table (Fig. 1), left circumorbital region, and left side of the snout (Fig. 2) exhibit minor distortion. The left postorbital region has been folded toward the midline and is slightly

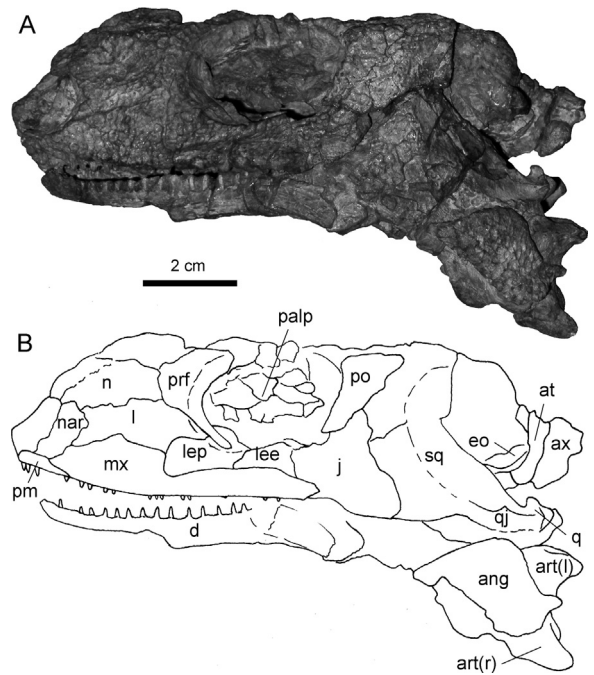


Fig. 2. *Broiliellus reiszii*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, left lateral view of skull.

Fig. 2. *Broiliellus reiszii*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, vue latérale gauche du crâne.

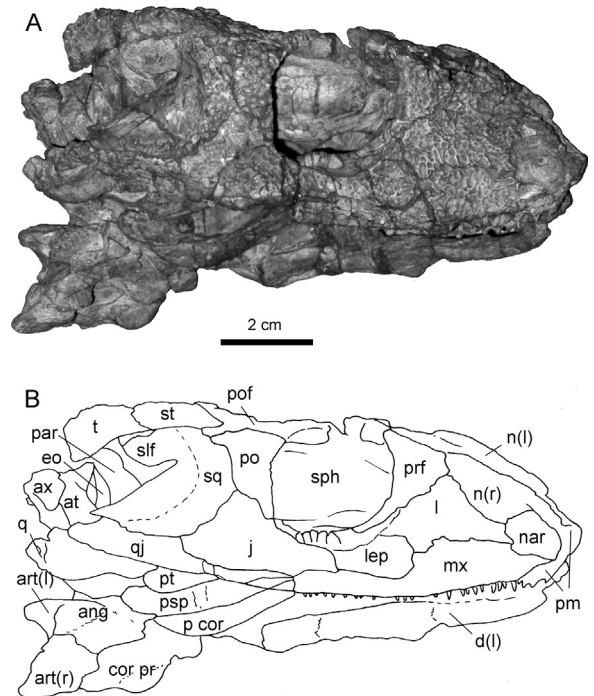


Fig. 3. *Broiliellus reiszii*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, right lateral view of skull.

Fig. 3. *Broiliellus breiszi*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, vue latérale droite du crâne.

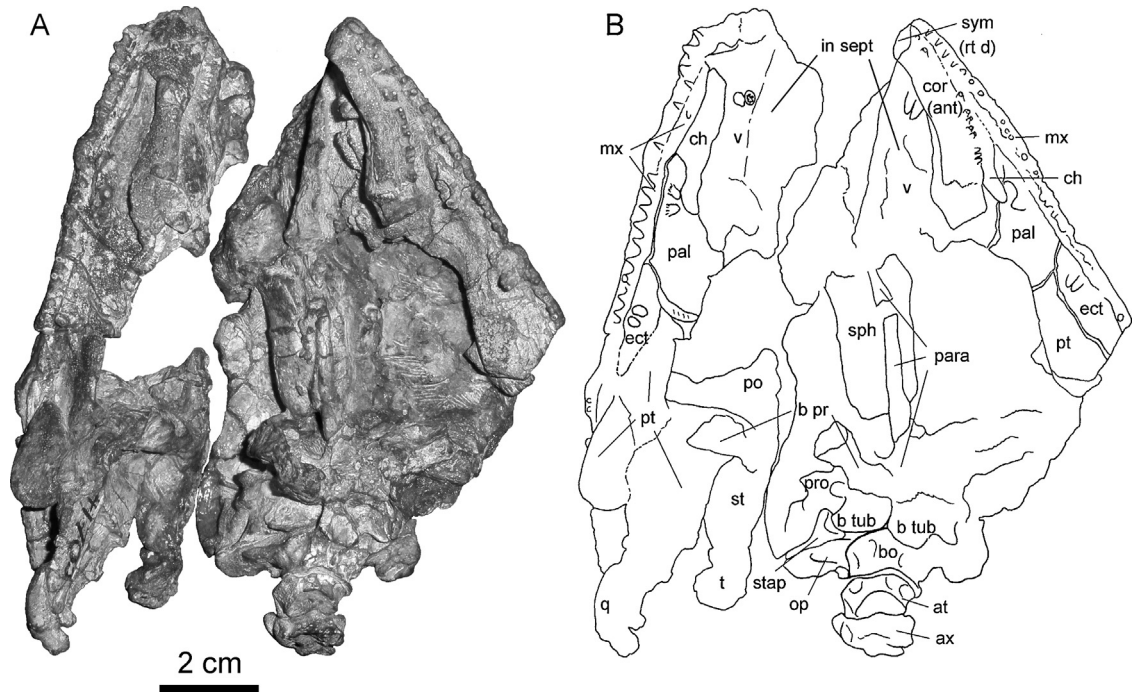


Fig. 4. *Broiliellus reiszi*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, ventral view of skull.
Fig. 4. *Broiliellus reiszi*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, vue ventrale du crâne.

disarticulated, but can be interpreted with the help of the less distorted right cheek (Fig. 3). A preservation break has allowed the right cheek and right lateral portion of the snout to be removed, permitting preparation of the ventral aspect of the braincase, palate, and medial surface of the cheek (Fig. 4). Although the left lower jaw is preserved in place (Fig. 2), most of the posterior portion

of the surangular is missing and the angular and articular are slightly displaced. The lateral and ventral aspects of the ramus are well exposed, but most of the medial aspect is obscured. The right ramus has been displaced to the left and rotated 180 degrees about its long axis, and rests upside down against the medial surface of the left ramus, exposing much of its medial surface (Fig. 3).

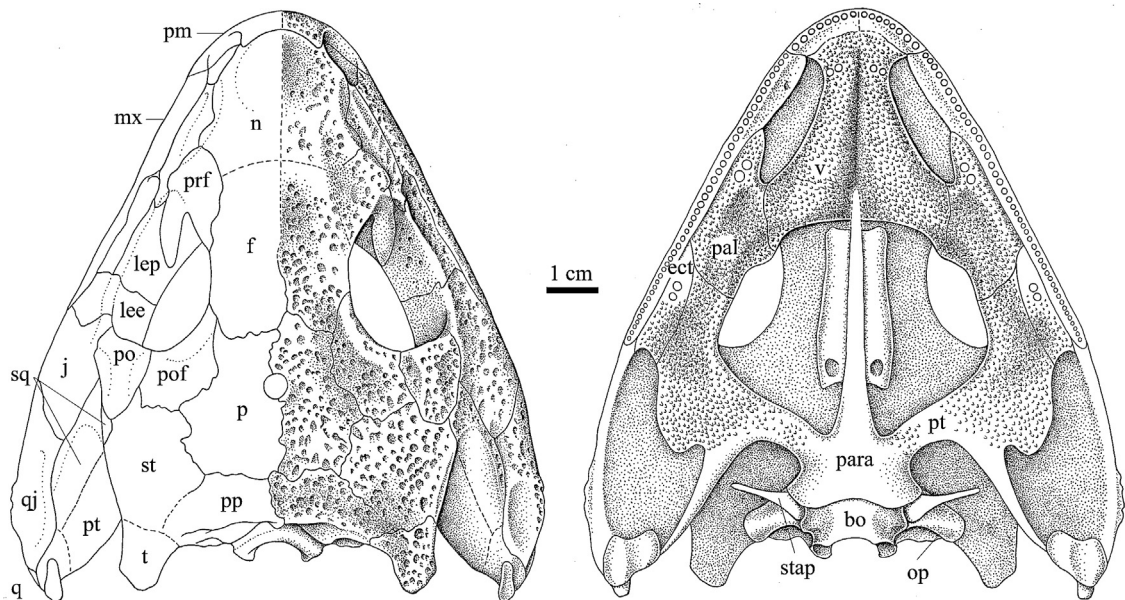


Fig. 5. *Broiliellus reiszi*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, reconstruction of skull in A, dorsal, and B, ventral views.
Fig. 5. *Broiliellus reiszi*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, reconstitution du crâne en vues dorsale (A) et ventrale (B).

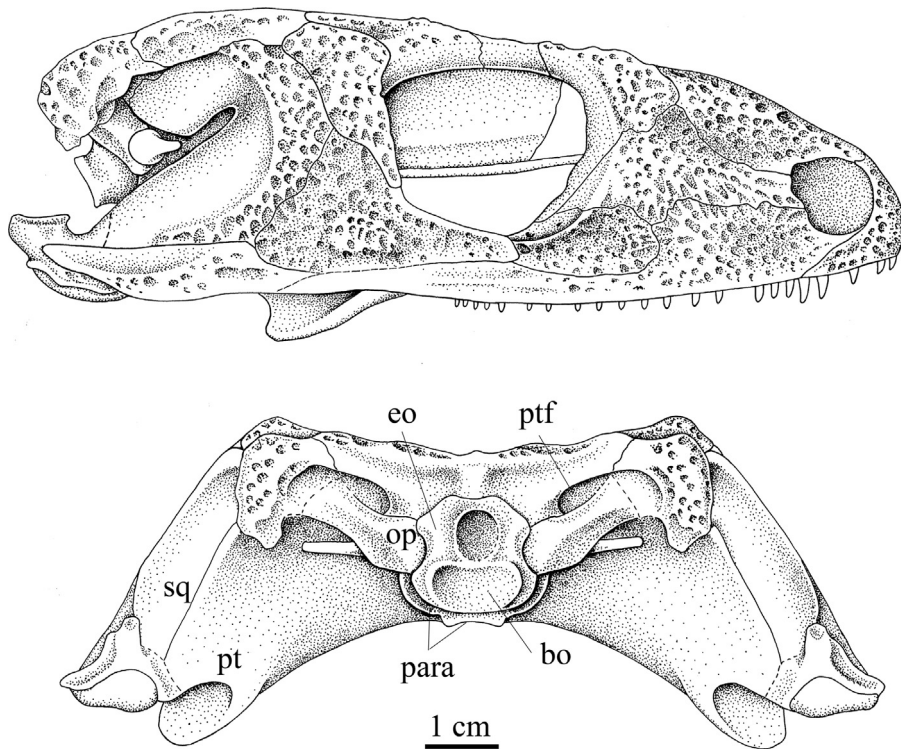


Fig. 6. *Broiliellus reiszii*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, reconstruction of skull in A, right lateral, and B, occipital views.

Fig. 6. *Broiliellus reiszii*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype 41705, reconstitution du crâne en vues latérale droite (A) et occipitale (B).

3.2. Skull, proportions

As most of the skull has sustained only minor deformation, the shape and contours of the skull can be reconstructed with confidence (Figs. 5 and 6). Measured along the midline, the preorbital region is slightly

longer than the postorbital region (Fig. 5), giving the skull distinctly different proportions compared to those of *B. texensis* (Williston, 1914, fig. 1; Table 1), but is more closely comparable to those of *B. brevis* (Carroll, 1964), *B. olsoni* (DeMar, 1967; Schoch, 2012, figs. 1D, 4D), and '*B.*' *novomexicanus* (Langston, 1953, fig. 12; Schoch, 2012, fig. 1B). The snout is narrow anteriorly, conferring a sub-triangular outline to the skull in dorsal view. This is distinct from the parabolic outline typical of *B. texensis* and *B. brevis*, but resembles more closely that of *B. olsoni* (Schoch, 2012). Even allowing for diagenetic distortion, the skull is much taller than that of *B. texensis* (Fig. 6; Table 1) or *Dissorophus* (Schoch, 2012, fig. 4C), with nearly vertical cheeks and snout sides. In lateral profile, the snout rises rapidly over the external nares, and at a point midway between the nares and the anterior margin of the orbit, the skull is nearly as tall as it is over the occiput. Therefore, with the exception of a small central bowl-shaped depression between the external nares, the snout is strongly arched dorsally. This is distinctly unlike the gradually sloping, wedge-shaped profile exhibited by most dissorophoids (Schoch, 2012, fig. 4) or the dorsally concave lateral profile of the snout seen in *Cacops* (Fröbisch and Reisz, 2012; Reisz et al., 2009), but is much more comparable to that of *B. olsoni* (Schoch, 2012, fig. 4D). The orbits and external nares are relatively larger than those described for *Dissorophus* or *B. texensis*, but more comparable in size to those in *B. olsoni*, '*B.*' *novomexicanus*, and *B. brevis* (Schoch, 2012, fig. 1). The jaw articulation is slightly posterior to the occipital plate.

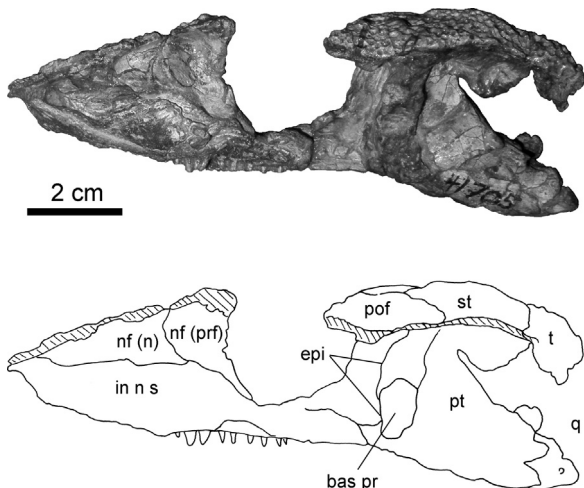


Fig. 7. *Broiliellus reiszii*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, medial (internal) view of right cheek and snout.

Fig. 7. *Broiliellus reiszii*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, vue médiale (interne) de la joue droite et du museau.

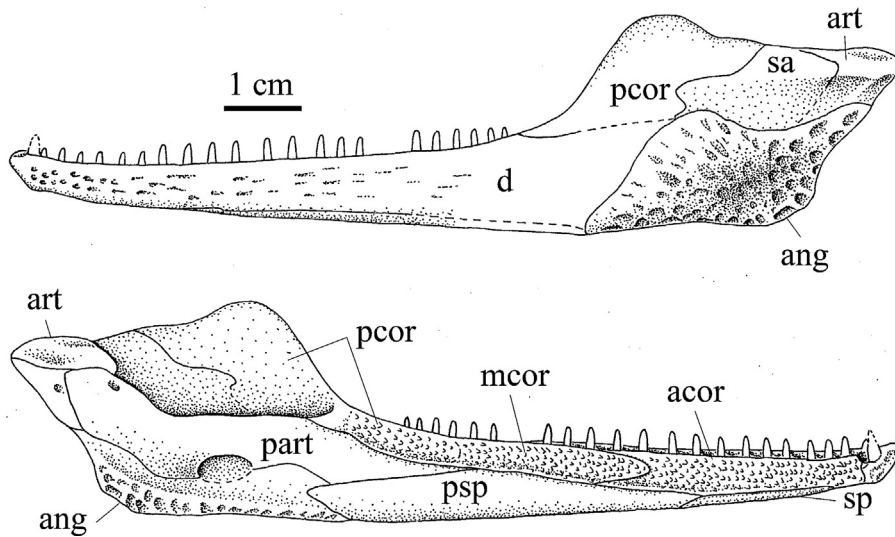


Fig. 8. *Broiliellus reisi*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, lower jaw in A, lateral, and B, medial views.

Fig. 8. *Broiliellus reisi*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, mâchoire inférieure en vues latérale (A) et médiale (B).

3.3. Skull, ornamentation

As in *Broiliellus* and *Cacops*, the skull roof bears a bilaterally symmetrical series of low coarsely ornamented ridge-like swellings. The most conspicuous of these are borne by the prefrontal, lateral edge of the frontal, postorbital, lateral edges of the supratemporal and tabular, the central portion of the parietal and along the posterior edge of the postparietal. The frontals and nasals may also have borne similar ridges, but this portion of the skull has been too disturbed to confirm this. The ventral edge of the quadratojugal bears a rugose, laterally projecting shelf. Immediately above the shelf, the external surface of the quadratojugal is devoid of sculpturing. Low, rounded swellings also project from the anteroventral portion of the jugal and dorsal lamina of the maxilla. As in *Broiliellus*, *Cacops*, and *Dissorophus*, these ridges are accentuated by adjacent shallow depressions on the bone surface. Median dorsal depressions are located between the external nares, between the orbits near their anterior margins, and on the skull table between the parietal foramen and occipital

plate. A bilateral series comprises, on each side, a large depression on the dorsolateral surface of the snout that occupies most of the surface between the orbit and naris, a smaller, horizontally elongate depression immediately below the previous, a circumorbital series including a deeply dished depression on the lateral exposure of the palatine, on the prefrontal anteromedial to the prefrontal depression, on the frontal and parietal medial to the frontal depression, on the postfrontal/postorbital medial to the postorbital protuberance and the postorbital/jugal ventral to the postorbital depression.

3.4. Skull roof

The premaxilla forms the anterior margin of the large external naris. The posterodorsally directed alary process is modestly developed. The dorsal surface of the snout between the nares is slightly compressed toward the midline and distorted, but there is no trace of an inter-premaxillary fontanelle. Although considerable matrix was

Table 1

Selected skull measurements (in mm) of UC 684 and 685 (*Broiliellus texensis*), and CM 41705 (*Broiliellus reisi*).

Tableau 1

Sélection de mesures crâniennes (en mm) d'UC 684 et 685 (*Broiliellus texensis*), et de CM 41705 (*Broiliellus reisi*).

	CM 41705	UC 684	UC 685
Total skull length (horizontal)	96	84.5	73
Pineal–posterior edge of postparietal	27	27.5	24.5
Postorbital midline length (horizontal)	32	38	32
Preorbital midline length (horizontal)	36	24	20
Snout width at posterior rim of naris	29 (est.)	37	32
Anteroposterior diameter of naris	– L/17 R	11 L/11.5 R	7 L/9 R
Dorsoventral diameter of naris	– L/10.5 R	6 L/7 R	4.5 L/4.5 R
Height of snout at posterior rim of naris	19	11	10
Width across postorbitals	65	70	63
Maximum cheek height	40 L/37 R	23 L/27 R	21 L/27 R
Minimum interorbital width	27.5	26	25
Anteroposterior width of orbit	34 L/30 R	26 L/24 R	26 L/24
Dorsoventral height of orbit	28 L/25 R	21 L/24 R	16.5 L/20 R

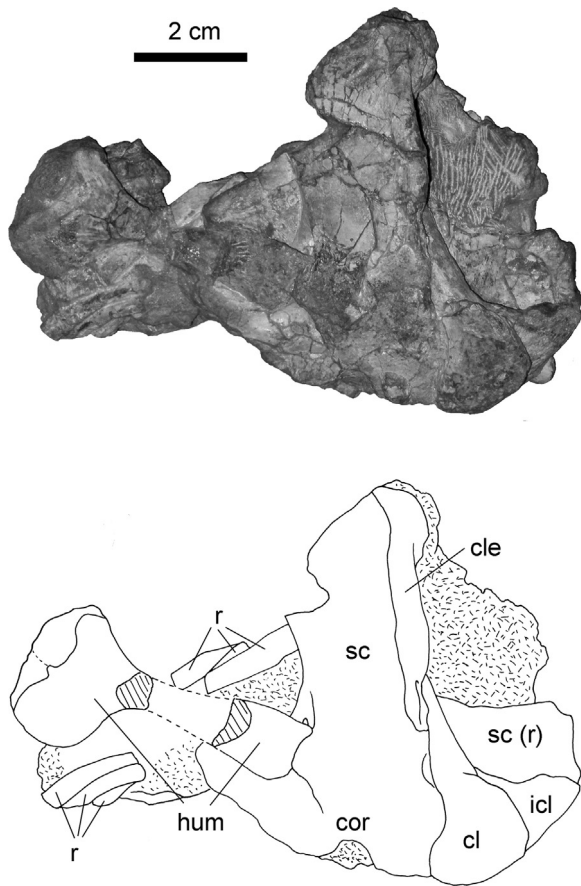


Fig. 9. *Broiliellus reisi*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, postcranial material.

Fig. 9. *Broiliellus reisi*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, matériel post-crânial.

removed from the external naris, a septomaxilla could not be found.

The dorsal surface of the snout is disrupted, making it impossible to trace some of the sutures. The nasal in CM 41705 is unlike that in most dissorophoids in not being rectangular (Bourget and Anderson, 2011), or widest at their mid-length (Fröbisch and Reisz, 2008; Schoch and Rubidge, 2005), but rather is much narrower anteriorly, at most half as wide at its suture with the premaxilla than posteriorly at its suture with the frontal. This is correlated with the distinctly narrow anterior portion of the snout.

The prefrontal forms the anterodorsal margin of the orbit. It does not contact the postfrontal, permitting the frontal to contribute to the dorsal orbital rim. A slender, ventral process of the prefrontal extends ventrally along the anterior orbital wall medial to the lacrimal to contact the dorsal surface of the palatine.

The parietals are narrowest anteriorly and widest at mid-length, where each wedges between the postfrontal and supratemporal. The maximum length of each parietal does not exceed twice its maximum width. Their common median suture is interrupted by a large, circular parietal foramen. The supratemporals are large and

pentagonal in outline. Laterally, each forms the anterior part of the supratympanic shelf and dorsal rim of the otic embayment (Fig. 6). The dorsoventrally thickened tabular forms the posterior portion of the supratympanic shelf and posterodorsal part of the otic embayment, whereas ventrally it forms a small portion of the supratympanic flange. Posteriorly, the tabular is drawn out into a large, blunt 'horn' that curves ventrally a short distance toward the dorsal process of the quadrate. At its posteroventral apex, it bears a short ventrally directed process that is clearly too short to have reached the dorsal process of the quadrate, leaving the notch open posteriorly. The postparietals have considerable dorsal exposure on the skull table. The anteroposterior length of each postparietal is approximately half its transverse width. The more or less transverse parietal-postparietal suture is clearly visible, but the precise relationships of the postparietal with the supratemporal and tabular are more difficult to determine. The postparietals bear the raised, rugose posterior rim of the skull table. Pits cover the posterior slope of this rim, but sculpturing does not extend onto their occipital flanges (discussed below under 'Occiput').

The maxilla forms the ventral and posteroventral portions of the external naris, and the slightly convex ventral margin of the upper jaw (Fig. 6). Its dorsal lamina is well developed anteriorly, whereas posteriorly it is abruptly narrowed by a large, lateral exposure of the palatine (lep) and suborbital process of the jugal. Together, the latter two bones form a narrow suborbital bar. Neither maxilla is complete posteriorly, and the skull is poorly preserved in this region (Figs. 2 and 3); as a result, the mutual relationships of the quadratojugal, jugal, and maxilla are unclear. However, as in other dissorophoids (Schoch, 2012), the maxilla probably contacted the quadratojugal posteriorly, preventing the jugal from forming any part of the ventral margin of the skull (Fig. 6). The lacrimal contributes a short, ventrally directed, wedge-shaped process to the anterior orbital wall lateral to the ventral palatine process of the prefrontal. A lacrimal duct could not be recognized on the anterior wall of either orbit. Anterior to the orbit, the lacrimal expands dorsally and ventrally to its maximum height at about one-third the distance to the external naris. Anterior to this level, it is constricted strongly by a convex ventral lamina of the nasal and dorsal lamina of the maxilla, and ends as a small contribution to the posterior margin of the external naris.

The large lep extends from the midpoint of the orbit to well anterior to the anterior border of the orbit. On the left side, a lateral exposure of the ectopterygoid (lee) is clearly visible (Fig. 2), whereas on the right side (Fig. 3), it has fused indistinguishably with the anterior end of the jugal. A separate lee has been described in some trematopids (Dilkes, 1990) and in juvenile *Cacops* (Reisz et al., 2009), but its occurrence in the latter suggests that it might be an ontogenetic feature (Reisz et al., 2009). The large postorbital tapers to a narrow triangular process as it extends far ventrally along the posterior orbital wall to its posteroventral corner. A very similar configuration is seen in *B. olsoni* (Bolt, 1974b, fig. 4) and in at least some specimens of *Cacops* (Reisz et al., 2009), but is otherwise unreported in other dissorophoids. The broadly rounded posterior

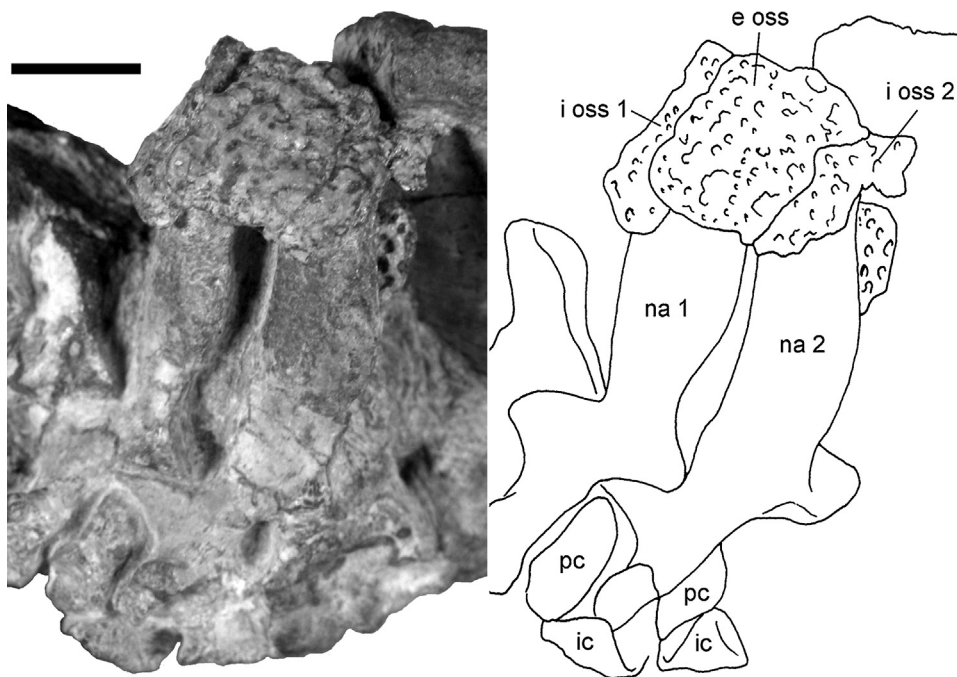


Fig. 10. *Broiliellus reiszii*, nov. sp. from the early Permian of New Mexico, holotype CM 41705, two articulated vertebrae with associated osteoderms.
Fig. 10. *Broiliellus reiszii*, nov. sp. du Permien inférieur du Nouveau-Mexique, holotype CM 41705, deux vertèbres articulées avec ostéodermes associés.

portion of the postorbital narrows as it inserts between the postfrontal and squamosal to contact the supratemporal. The lateral edge of its modest contribution to the anterolateral corner of the skull table bears a ridge-like eminence that separates a distinct dorsally facing depression and a more poorly developed lateral depression. A similar morphology is seen in *Cacops* (Williston, 1910), although the ridge and depressions are better developed and occupy a slightly different position. The jugal and postorbital form most of the cheek. The superficial portion of the squamosal (i.e., that bearing dermal sculpturing) is restricted to a narrow crescent that forms the anterior margin of the otic embayment. The extensive, inset surface of the embayment is formed almost exclusively by a non-sculptured portion of the squamosal. Dorsal exposure of the squamosal on the lateral margin of the skull table is limited to a small triangular area at the postorbital-supratemporal suture (Fig. 5). The quadratojugal exhibits a low profile in lateral view, with its anterior portion beneath the jugal narrowing to a process-like extension that narrowly contacts the posterior end of the maxilla (Fig. 3).

Both quadrates are preserved, but the left is more complete. Each bears a short, stout dorsal process that flares slightly at its dorsal end. It terminates in a facet of unfinished bone (Fig. 2), suggesting that it had not finished growing, or perhaps supported a ligament that extended up to the tabular.

3.5. Otic region

The otic embayment is large and nearly circular in outline (Fig. 6) rather than horizontally oval as in *B. texensis* and *B. brevis*. The shape of the embayment in the latter

taxa is a consequence of the low profile of their skulls, but may have been exaggerated by postmortem compression. The squamosal includes extensive, non-sculptured, slightly inset ventral portion that borders the otic embayment. Anterodorsally, the embayment becomes increasingly depressed below the superficial, sculptured surface of the squamosal. Together, the supratemporal and tabular form an extremely narrow, laterally projecting supratympanic shelf that borders the dorsal margin of the embayment. Its lateral edge bears a continuation of the dermal ornamentation of the skull roof, whereas its ventral surface is smooth. A large supratympanic flange forms the inset dorsal surface of the otic embayment. It is unusual in that, unlike other dissorophids, the supratemporal does not appear to contribute a semilunar flange (Bolt, 1974a); rather, the supratympanic flange appears to be almost completely formed by the squamosal. Elongate, horizontal striations on the external surface of the flange suggest rapid posterior growth of the squamosal rather than ventral-ward growth from the ventral surface of the supratemporal. The tabular contribution to the flange is restricted to a small portion of its posterodorsal corner (Fig. 6). The otic notch is small, especially anteriorly, where it is restricted to a narrow, anterodorsally oriented slot, much as in *B. olsoni* (Bolt, 1974a, fig. 4) and *B. brevis* (Carroll, 1964, fig. 9B), as well as in some trematopids.

3.6. Orbit

The orbits of CM 41705 (Figs. 2 and 3; Table 1) are relatively much larger than in *Dissorophus* and *B. texensis* (Schoch, 2012, fig. 1C, E), but are comparable to those of '*B.*' *novomexicanus*, *B. olsoni*, and *B. brevis* (Schoch, 2012,

fig. 1B, D, F). The orbital margins of most of the circum-orbital bones are deflected inward, producing a distinctly thickened orbital wall, especially anteriorly. Between the orbit and naris, the medial surfaces of the prefrontal, nasal, and possibly the lacrimal contribute to a sheet of bone that projects ventromedially from their ventral surfaces to form the dorsal wall of the bony nasal capsule (Fig. 7). This appears to be homologous to the narial flange described by Bolt (1974b) and Dilkes (1993). Several small rectangular plates of bone are visible along the ventral edge of the right orbit (Fig. 3). They appear to be associated with the medial margins of the palatine. Similar ossifications have been described in *Cacops* (Reisz et al., 2009, fig. 3) and may represent ossifications of soft palate that spans the interpterygoid vacuity.

3.7. Palate

The vomers, palatines, ectopterygoids, and pterygoids all bear a shagreen of small, closely spaced denticles, but conspicuous longitudinal denticle-bearing ridges are absent. In addition, small bony plates bearing denticles overlie, but do not attach to, the ventral surface of the vomers. Similar ossicles have been reported in amphibamids, dissorophids, and trematopids (Fröbisch and Reisz, 2008; Schoch and Rubidge, 2005). The vomers narrow rapidly anteriorly to about half their maximum posterior width as they extend between the internal nares. In contrast to the vomers in *Broiliellus* and *Dissorophus*, in which they form a broad, flat plate, the vomers of CM 41705 are narrowly separated at the midline along nearly their entire length. Here they turn sharply dorsally as vertical laminae to form a median structure referred to as the internasal septum by Bolt (1974c), each forming the medial wall of a bony nasal capsule (Figs. 4 and 7). Together, they define a deep, narrow, median internarial furrow (Fig. 5B), the external surface of which is covered by denticles almost to its dorsal margin (Fig. 7). Dorsally, the laminae converge, each approaching, and possibly articulating with, the ventromedially projecting narial flange formed by the prefrontal and nasal (Fig. 7; see 'Orbit' above). A similar morphology has been described in trematopids (Dilkes, 1990, 1993; Polley and Reisz, 2011), and possibly in *B. brevis* (Schoch, 2012, fig. 2F), although Carroll (1964) does not mention this feature in his description of the latter species. Each vomer bears a fang and companion replacement pit that flank the anterior end of the internarial furrow. Preservation is too poor to establish whether an intervomerine fontanelle was present. Laterally, each vomer forms the long, dorsally inflected medial margin of a choana.

The palatine forms the anterolateral margin of an interpterygoid vacuity, widely separating the vomer and pterygoid. The palatine extends anteriorly as a long, triangular process along the medial surface of the maxilla, partially constricting the lateral posterior third of the choana (Figs. 4 and 5B). A pair of stout fangs occupies the posterior base of the process. The lateral margin of the choana is formed by a medially projecting alveolar shelf of the maxilla. Posteriorly, the palatine articulates with the pterygoid medially, and the small ectopterygoid laterally. A pair of small ectopterygoid fangs are located

a short distance posterior to the palatine-ectopterygoid suture. The anterior palatal process of the pterygoid is short and borders the posterior half of the interpterygoid vacuity. A modest transverse flange projects into the ventral opening of the adductor chamber. The basal process of the pterygoid is stout and dorsoventrally expanded distally (Figs. 4 and 7). Its articulation with the basiptyergoid process of the basisphenoid cannot be identified on either side, suggesting that the basicranial joint had co-ossified, but the bone is broken in this area, and preservation is too poor to be sure.

3.8. Occipital/braincase

Because the elements of the occiput are slightly disarticulated, and the atlas-axis complex remains in articulation with the occipital condyle (Figs. 1 and 4), some details of this portion of the braincase are obscured. Nevertheless, it is clear that the postparietals have extensive, smooth occipital flanges (Fig. 6B). Although their common median suture cannot be traced, their sutures with the much smaller occipital flanges of the tabulars are clearly visible. The paroccipital processes of the opisthotics are poorly preserved, and in neither case is the sutural contact with the prominent, ventromedial occipital flange of the tabular that forms the ventral border of the posttemporal fossa in other temnospondyls evident. Nevertheless, a deep sulcus on the dorsal portion of the posterior surface of the right opisthotic just ventral to its suture with the lateral edge of the postparietal probably represents a small posttemporal fossa. However, dorsoventral compression has forced the opisthotic and postparietal together, making it impossible to determine whether the fossa leads to a fenestra opening anteriorly into the adductor chamber. The right stapes is preserved in approximately its correct position. It comprises a modestly expanded footplate and a straight, distally narrowing shaft. A stapedia foramen is not evident. The slightly displaced right prootic is preserved immediately anterior to the stapedia footplate. The exoccipital and basioccipital appear to form a strongly co-ossified complex, with the exoccipitals being fused indistinguishably above the foramen magnum, which may simply indicate advanced maturity (Maddin et al., 2010). The exoccipital-basioccipital complex is slightly separated from the skull table, and the ventral edges of the occipital flanges of the postparietals with which it articulated are consequently broken into displaced fragments. The atlas is firmly articulated with the concave occipital cotyle (= 'condyle'), but it is clear that the cotyle is not 'figure-8' shaped, as it is in most dissorophoids. Rather, the basioccipital forms the greater portion of the cotyle, giving it a dorsoventrally compressed oval or 'kidney bean'-shaped outline with a gently convex ventral margin.

The parasphenoid comprises a broad, posteriorly widening basal plate approximately twice as wide (measured across the basal tubers), as long (measured at the midline), and an anteriorly projecting cultriform process. The latter is narrow in ventral view, and approximately circular in cross-section. It is broken and poorly preserved anteriorly. Foramina for the carotid arteries could not be identified. The basal plate lacks denticles, but small,

scattered plates bearing denticles are preserved in this area. Several small plates lacking denticles and similar to those preserved associated with the right palatine (see ‘Orbit’ above) are preserved in close proximity to the cultriform process. In *Dissorophus* and other species of *Broiliellus*, the basal plate bears deep pockets for attachment of axial musculature (Schoch, 2012, character 65). The presence of this character cannot be established in CM 41705 as a result of postmortem disruption of the bone surface and presence of the overlying bony plates.

The sphenethmoid (Figs. 4 and 5) is large and quasi-barrel-shaped. It appears to be co-ossified with the ventral surface of the skull roof. The posterior portion of the cultriform process of the parasphenoid remains attached to its midventral surface. The sphenethmoid is separated from the otic region by a large gap, presumably for passage of branches of the fifth, sixth and seventh cranial nerves. A pair of foramina at the posterior end of the sphenethmoid probably allowed anterior passage for the optic nerves.

3.9. Mandible

The mandible (Figs. 2 and 3) is not completely exposed or preserved, but most of its anatomy can be reconstructed (Fig. 8) by referring to both rami. The left dentary, better exposed (Fig. 2), reveals a broken parasymphysial tusk and companion replacement alveolus adjacent to the symphysis. As in most other dissorophoids, there is no evidence for a separate adsymphyseal ossification, but preservation is poor in this area. The anterolateral surface of the dentary bears the typical temnospondyl ‘pit and ridge’ ornamentation. Posteriorly, this ornamentation rapidly transitions into elongated horizontal grooves that become progressively shallower. The posterior end of the dentary is incomplete, making its relationship with the surangular unclear. The ventral edge of the ramus is not well preserved, but lateral exposure of the splenial and postsplenial appears to have been extremely marginal. The lateral surface of the angular is strongly ornamented, and at its posteroventral corner is drawn out into a distinct, distally swollen keel. Its anterior tip, which appears to be complete, does not extend as far forward as it does in most temnospondyls.

The medial surface is better preserved on the right ramus. All three coronoids are completely covered with small denticles, but there is no evidence for coronoid fangs. The large anterior coronoid forms nearly the entire anterior half of the coronoid series, restricting the exposures of the dentary and splenial to the symphysis and ventral edge of the ramus, respectively. This morphology is confirmed on the left ramus, which also shows that the splenial extends almost to the symphysis. The left ramus preserves the sutural contact between the anterior and middle coronoids. Most of the posterior coronoid is preserved, but its suture with the middle coronoid could not be identified. The medial exposure of the postsplenial extends anteriorly as a narrow triangular wedge beneath the middle coronoid and posterior end of the anterior coronoid, ending in a very narrow contact with the posterior end of the anterior splenial. Posteriorly, the contact between the postsplenial and angular is preserved. The dorsal and posterior

rim of a modest-sized Meckelian fenestra is preserved. The posterior portion of the left ramus is disrupted, but essentially complete. The dorsal rim of the posterior coronoid forms a prominent, rounded crest. Coarse dermal sculpturing extends onto the ventromedial surface of the angular. The prearticular has been broken into several pieces, and displaced posteriorly to expose a portion of the articular. It exhibits no evidence of a medial inflection along the rim of the adductor chamber, as seen in trematopids (Dilkes, 1990).

3.10. Dentition

The marginal dentition is not well preserved, and about half of the teeth being missing. The preserved teeth are small, and most have lost the tips of their crowns, but the most complete form simple, blunt, conical pegs. They show little recurvature, and there is no evidence of accessory cusps, pedicellate structure, or labyrinthine infolding. Neither premaxilla is complete ventrally, but it probably supported seven or eight teeth. A few of the more posterior premaxillary teeth are relatively well preserved, and appear to be the largest of the upper tooth row. The anterior-most two or three maxillary teeth are slightly larger than the others, but there is no significant development of caniniform dentition. Each maxilla would have had spaces for approximately 40 tooth positions. DeMar (1967, p. 126) estimated 47 or 48 teeth in the “upper jaw” of *B. olsoni*, but did not specify whether this includes the premaxillary dentition. ‘*B. novomexicanus*’ has “at least 56” (Langston, 1953, p. 381). Eighteen small, straight-sided conical teeth, most alternating with replacement pits, are preserved in the left dentary; the total count is estimated at 45 tooth positions. Tooth size increases gradually toward the posterior end of the dentary, although in the last several teeth of the series, this trend is reversed.

3.11. Palpebral ossifications

The left orbit is almost completely filled with large, irregular-shaped palpebral ossifications that bear muted dermal ornamentation on their external surfaces similar to that on the skull roof (Fig. 2).

3.12. Postcranial material

The right scapulocoracoid, cleithrum and clavicle are preserved in articulation (Fig. 9). The cleithrum expands slightly at its dorsal termination, but does not extend posteriorly over the dorsal edge of the scapula. The interclavicle is partly covered by the ventral, horizontal plate of the clavicle. Too little of the former is exposed to estimate the shape of the bone, but it does not appear to be very large. The right humerus is preserved in articulation with the glenoid of the scapula. Most of the proximal head and surrounding margin of the glenoid are badly eroded. The central portion of the shaft was lost at some point after collection, but its impression is preserved in the surrounding matrix. The distal head and enough of the distal portion of the shaft are preserved to confirm that neither a supinator process nor entepicondylar foramen was present.

Posterior to the scapular blade and dorsal to the humerus are three short, curved, blade-like ribs (Fig. 9).

Ten rhachitinous presacral vertebrae are preserved in articulation. Four successive vertebrae in the middle of this series lack the dorsal portions of their neural spines that appear to have been lost during collection. The other vertebrae (Fig. 10) retain their neural spines and associated dorsal osteoderms, although some of the latter are slightly displaced. The osteoderms are organized into an internal and an external series. Each osteoderm of the internal series is closely associated with, if not fused to, the dorsal edge of a neural spine. There is no evidence of ventrally projecting flanges inserting between successive neural spines as described in *Dissorophus* or *Broiliellus* (DeMar, 1966a). Each osteoderm of the external series is intersegmental in position, apparently contacting dorsally facing facets on the anterior and posterior margins of successive internal osteoderms. A sculpturing of sub-circular pits, resembling that on the skull roof, covers the external surfaces of all osteoderms. This pattern is quite distinct from that exhibited by the osteoderms of the type of *B. texensis* (Williston, 1914, fig. 3), which comprises mediolaterally elongate grooves. None of the osteoderms extend far laterally, being at most half as wide as those in the type of *B. texensis* (Williston, 1914, fig. 3) despite the fact that the skull of CM 41705 is approximately 10% larger (Table 1). They also appear to be much smaller than the osteoderms described in '*B. novomexicanus*' (Williston, 1911, plate XXXVIII). Of all known dissorophoids, the osteoderms of CM 41705 most closely resemble those of *Cacops* (DeMar, 1966a; Dilkes and Brown, 2007) in relative size, shape, number per segment, arrangement, and relationship to the neural spines.

4. Phylogenetic analysis

We conducted a phylogenetic analysis to test the relationships of CM 41705 with other dissorophoids. We started with the matrix recently assembled by Schoch (2012), but made a number of changes to individual cell codings and character descriptions:

Character 1 of Schoch (2012), which pertains to the modality of the lateral exposure of the palatine (lep), is problematic as originally defined because it did not allow for the establishment of homology between the two morphological variants of the lep (Brazeau, 2011). This character was here reduced to the absence or presence of the lep. The morphological variant of the lep in which it is present but excluded from the orbital margin by a lacrimal-jugal contact (original state 3) is an autapomorphy of *Acheloma* and thus not phylogenetically informative for parsimony analysis, and so it was removed from this version of the matrix. The alternate state, as originally coded (state 2), represents a unique interruption of the normal articulation between the jugal and lacrimal by the maxilla. However, it bears no obvious relationship to the lep, so it was added here as a new character (new character 2).

Characters 17 and 30 of Schoch (2012), as defined, do not appear to vary independently. Postparietals reduced to a "narrow, poorly ornamented strut" (character state 17 (1) of Schoch, 2012, p. 123) are much wider than antero-posteriorly long by definition. This overlaps with character

30—"postparietals less (0) or more than (1) four times wider than long" (Schoch, 2012, p. 125). There also appears to be a qualitative difference between the state observable in amphibamids and in, for example, *Cacops*, in which the postparietals exhibit exactly the same degree of ornamentation as do all other skull roof bones, and extends a broad lamina onto the occipital surface (i.e., is not strut-like, as in amphibamids). We opted to restrict the description of state '1' in character 17 to differentiate the clearly reduced postparietal in amphibamids, and allow character 30 to capture the additional variation in the relative shape of the postparietal seen in other dissorophoids. Character 30 of Schoch (character 31 in the present matrix) was recoded for all taxa, leading to the change of state '1' to '0' in all taxa but the amphibamids, *Doleserpeton*, and *Platyrhinops*, making it overlap with character 17. Variation occurs in the relative proportion of the postparietals between the taxa recoded, which would be recaptured were the criterion set to 'over three times wider than long' rather than "four times wider than long" (character 30 of Schoch, 2012, p. 125). Furthermore, many of the taxa coded as having a reduced postparietal appeared to be so because a large amount of the surface exposure of the postparietal in these taxa has become reoriented to assume an occipital, rather than dorsal, position. We measured the entire extent of the dorsal exposure of the postparietal, including any visible occipital exposure, rather than restricting measurement to the skull roof only for our coding of character 30, which might be the source of difference with the original codings.

Some taxon-specific recodings were also made. The coding for character 23 of Schoch (2012), presence of a palpebral ossification, was changed to '1' for the 'Rio Arriba Taxon' ('*B. novomexicanus*') because such ossifications were originally described as present by Langston (1953).

Schoch (2012) coded '*B. novomexicanus*' as lacking the long tabular horn (character 45, "tabular process", p. 125) shared by all other *Broiliellus* species including CM 41705; however, it appears to us to be present in the figure of Langston (1953, fig. 12) and we have coded it as such in our analysis.

The coding of character 51 of Schoch (2012) was changed to '2' for *B. texensis*, and in character 63, the coding for the 'Rio Arriba Taxon' ('*B. novomexicanus*') was changed to '1'. However, because the specimen is under study, additional preparation may have been done (although we were unable to confirm this with the investigator). Because of this, we ran an additional analysis with Schoch's (2012) original codings for this taxon (found in the preceding three paragraphs).

This matrix (Appendix A) was subject to maximum parsimony analysis in PAUP* 4.0b10 (Swofford, 1999) using an heuristic search, TBR swapping with 1000 replicates. The analysis produced 25,025 most parsimonious trees with 140 steps (consistency index = 0.550, retention index = 0.766). The strict consensus and majority rule trees are given in Fig. 11. Our analysis recovers broadly the topology of Schoch (2012), although it is much less strongly supported, as demonstrated by the lower resolution seen in the strict consensus tree (Schoch only presented the majority rule consensus topology with no indication of nodal frequency of occurrence; pers. com. to J.S.A. 2013). *B. reiszii*

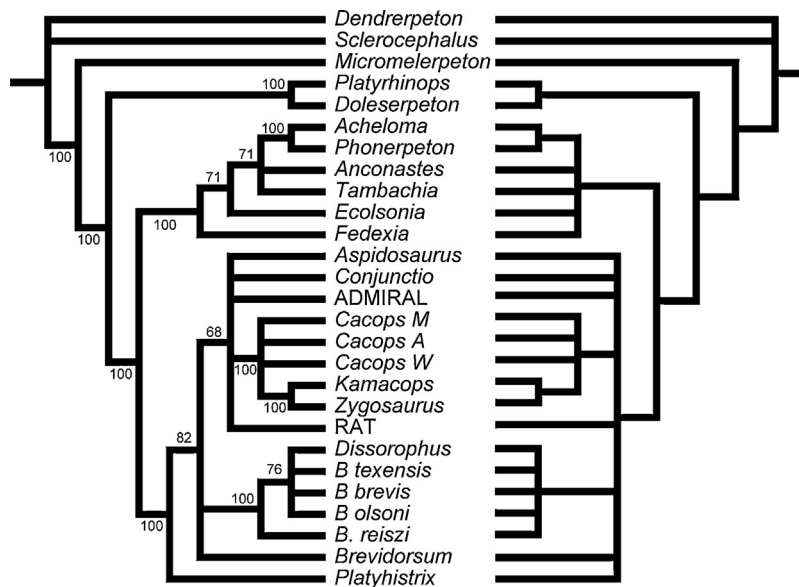


Fig. 11. Results of phylogenetic analysis using a modified version of the data matrix of [Schoch \(2012\)](#). Tree on the left, 50% majority rule consensus, tree on right, strict consensus. Numbers on nodes represent percent occurrence of that node in the most parsimonious trees. **Admiral**, ‘Admiral Taxon’—see [Schoch, 2012](#); **RAT**, ‘Rio Arriba Taxon’—see [Schoch, 2012](#). See text for details.

Fig. 11. Résultats de l’analyse phylogénétique utilisant une version modifiée de la matrice de données de [Schoch \(2012\)](#). À gauche, arbre de consensus majoritaire à 50 %; à droite, arbre de strict consensus. Les nombres sur les nœuds représentent le pourcentage d’occurrence dudit nœud dans les arbres les plus parcimonieux. **Admiral**, « Admiral taxon »—voir [Schoch \(2012\)](#); **RAT**, « Rio Arriba Taxon »—voir [Schoch \(2012\)](#). Voir le texte pour davantage de détails.

is placed as outgroup to all other species of *Broiliellus*. Oddly, *Dissorophus* was placed within the *Broiliellus* group.

The additional analysis with the codings of [Schoch \(2012\)](#) for ‘*B. novomexicanus* unmodified produced 5560 MPTs of 137 steps (CI=0.562, RI=0.774), the strict and majority rule consensus of which are given in [Fig. 12](#).

Overall resolution of the majority rule consensus was improved, although the strict consensus shows little change. In the majority rule tree *Dissorophus* was placed as sister group to *Broiliellus*, and *B. reisi* was found to be sister taxon to *B. brevis*. In neither analysis was the Rio Arriba Taxon (‘*B. novomexicanus*’) placed close to *Broiliellus*; rather

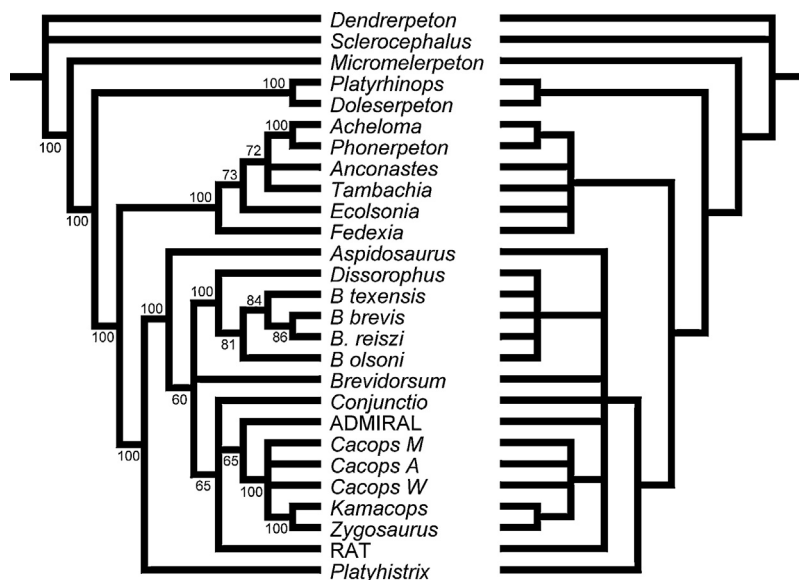


Fig. 12. Results of alternate phylogenetic analysis, with original codings of [Schoch \(2012\)](#) for RAT (see text for details). Tree on the left, 50% majority rule consensus, tree on right, strict consensus. Numbers on nodes represent percent occurrence of that node in the most parsimonious trees.

Fig. 12. Résultats de l’analyse phylogénétique alternée, avec les codages originaux de [Schoch \(2012\)](#) pour RAT (voir texte pour davantage de détails). À gauche, arbre de consensus majoritaire à 50 %; à droite, arbre de strict consensus. Les nombres sur les nœuds représentent le pourcentage d’occurrence sur ledit nœud dans les arbres les plus parcimonieux.

it shares a more recent common ancestry with *Cacops*, as found by Schoch (2012).

5. Discussion

5.1. *Broiliellus reisi*

Our phylogenetic analysis nests CM 41705 securely within the genus *Broiliellus*. However, it exhibits a number of autapomorphies that clearly establish it as a distinct species, *B. reisi*. The nasals, rather than being anteroposteriorly elongate rectangles, are very narrow anteriorly, no more than half as wide anteriorly as they are posteriorly. Similarly, the vomers are half as wide anteriorly as posteriorly. The vomers in other dissorophoids are only slightly narrower anteriorly. These unusual proportions are the consequence of the triangular, anteriorly narrowing snout. The width of the posterior third of the choana is somewhat narrowed as the result of an anterior projection of the palatine. The parasphenoid basal plate is greatly flared posteriorly to a width nearly twice that measured at the level of the basal articulation; only the amphibamid *Doleserpeton* shares this feature.

The suture pattern on the supratympanic flange is unusual. Typically in dissorophoids, the supratemporal, tabular, and squamosal intersect in a roughly 'Y'-shaped pattern, on or just posterior to the semilunar flange of the supratympanic flange (Bolt, 1974a, fig. 2). In dissorophoids, the supratemporal typically forms a portion of the flange, but a ventral contact between the squamosal and tabular precludes the supratemporal from forming any part of its ventral margin. In *B. reisi*, the supratemporal does not seem to form any part of the flange, the latter being formed almost entirely by the squamosal, with only a small contribution from the tabular.

The basioccipital is large and contributes significantly to the ventral portion of the occipital condyle. As a result, the condyle is horizontally oval or kidney-shaped in posterior outline rather than the 'figure-8'-shape typical for other dissorophoids. The medial edges of the vomers are deflected dorsally, forming an 'internarial septum' (character 44 of Schoch, 2012). However, this feature might have a wider distributed than is currently appreciated. It has been reported in trematopids (Dilkes, 1990, 1993; Polley and Reisz, 2011) and possibly in *B. brevis* (Schoch, 2012, fig. 2F). CT scans have revealed its presence in *Doleserpeton* and numerous other taxa (J.S.A., per. obs.) to be described elsewhere. As such, the phylogenetic significance of this feature is unclear. Finally, the angular has a prominent swollen keel on its posteroventral corner. More typical for dissorophoids is the presence of a sharp keel, as seen in *Cacops* (Reisz et al., 2009; Williston, 1910).

5.2. *B. reisi* and other species of *Broiliellus*

Our majority rule consensus tree hypothesizes a sister group relationship between *B. reisi* and all other species of *Broiliellus* + *Dissorophus* (Fig. 11) despite the numerous differences seen in cranial and osteoderm morphology amongst these taxa. Of all *Broiliellus* species, *B. reisi* bears the least resemblance, in terms of its 'Gestalt', to *B. texensis*.

In the latter, the preorbital region is distinctly shorter than the postorbital region. Its snout is more broadly parabolic in dorsal aspect, and lacks any trace of a facial constriction. The skull is low and wedge-shaped in lateral profile, with the dorsal surface rising gradually from above the external nares to the skull table. The cheeks are not as tall, resulting in an anterodorsally oriented oval otic embayment that is distinct from the circular embayment in *B. reisi*. The nares and orbits are distinctly smaller. The vomerine plate is essentially flat, with no vaulting or other indication that it possessed an internarial septum.

These many differences, in particular between *B. reisi* and *B. texensis* despite the close relationships hypothesized in our analysis, highlights the importance of avoiding establishing 'key features' to define taxa, because the test of congruence of all features can lead to contradictory topologies. For example, the arrangement and structure of osteoderms is most similar to the more distantly related *Cacops*. However, as Schoch (2012) noted, the monophyly of Dissorophoidea does not rest on the presence, composition and structure of osteoderms (many other non-related characters supports this). In any case, there is considerable variation in osteoderm morphology within at least some dissorophid taxa, as well as overlap in morphology between taxa (Berman and Lucas, 2003), indicating that the various patterns may have evolved convergently from the simple osteoderms of a basal dissorophid such as *Aspidosaurus*. If so, osteoderm morphology is of doubtful utility in dissorophid systematics.

On the other hand, *B. reisi* shares a number of obvious similarities with *B. olsoni* despite the more remote relationship hypothesized by our majority rule consensus tree. As in *B. olsoni*, the skull is triangular in dorsal profile (DeMar, 1967, fig. 1; Schoch, 2012, fig. 1). This form is distinct from the more parabolic shape seen in most dissorophids, including other *Broiliellus* species (but not *Dissorophus*, interestingly; Schoch, 2012, fig. 1C). Most dissorophids except *B. olsoni* and *B. reisi* have a straight ventral maxillary and premaxillary margin. With the exception of *B. olsoni* and '*B.*' *novomexicanus* ('Rio Arriba Taxon' of Schoch, 2012), the external nares and orbits are relatively large compared with other *Broiliellus* species and dissorophids in general except juvenile individuals. The nares are also circular, unlike the ventrally compressed ellipses present in other *Broiliellus* species.

B. reisi has a high skull, with nearly vertical cheeks, a dorsal profile that quickly rises posteriorly over the external nares, and by the midpoint between the naris and the anterior margin of the orbit, is nearly as high as it is over the occiput. This profile is very similar to that in *B. olsoni*, but distinct from that seen in other *Broiliellus* species, which is distinctly wedge-shaped in lateral view. This high-sided skull results in a nearly vertical anterior margin of the otic embayment, much as described for *B. olsoni* by DeMar (1967). The slit-like extension of the anterior portion of the otic notch is very similar to that of *B. olsoni* (Bolt, 1974a, fig. 4). *B. reisi* also shares with *B. olsoni* the unusually large postorbital that extends far ventrally (Bolt, 1974a, fig. 4). Among dissorophoids, this feature has been otherwise described only in *Cacops* (Reisz et al., 2009). Finally, the tooth count is similar between these two taxa (47 or 48

teeth in the upper jaw in *B. olsoni* compared with an estimated 40 maxillary teeth and seven or eight premaxillary teeth in *B. reiszii*).

5.3. *B. reiszii* and 'B.' *novomexicanus*

One other species of *Broiliellus* has been described from New Mexico. Originally named '*Aspidosaurus*' *novomexicanus* (Williston, 1911) on the basis of an incomplete skull and partial postcranial skeleton, probably from El Cobre Canyon, Langston (1953) reassigned the material to *Broiliellus* based on a slightly better skull from the Arroyo de Agua region (about 15 miles west of El Cobre Canyon). Schoch (2012), referring to it simply as the 'Rio Arriba Taxon', provided a reconstruction of the skull and included it in a phylogenetic analysis. In his analysis, it was placed as the sister taxon to the cacopines (*Cacops* + (*Kamacops* + *Zygosaurus*)). It retains this position in our majority rule consensus (Fig. 11), although now forms an unresolved polytomy with cacopines, *Conjunctio*, *Aspidosaurus*, and the 'Admiral Taxon' of Schoch (2012). This specimen is currently under study by R. Schoch, and we look forward to a resolution of this taxon's relationship to *Broiliellus*.

Although the general proportions of 'B.' *novomexicanus* are similar to those of *B. reiszii* (relative length of snout, large orbits and nares, etc.), the snout is blunter, and the quadrate is placed further rostrally—distinctly anterior to the occiput (Schoch, 2012). In *B. reiszii*, the quadrate is slightly posterior to the occiput. Other features that distinguish 'B.' *novomexicanus* from *B. reiszii* include: the presence of an interpremaxillary fontanelle, much narrower skull table, relatively narrow interorbital distance (Schoch, 2012), a higher maxillary tooth count (56 compared with approximately 40, Langston, 1953), an unusually large postfrontal that inserts posteriorly between the postorbital and supratemporal, preventing the latter two bones from making contact (character 55 of Schoch, 2012), and considerably larger dorsal osteoderms (Williston, 1911, plate XXXVIII).

5.4. *B. reiszii* and *Cacops*

B. reiszii is similar to *Cacops* in a number of features. Other than the long ventral extension of the postorbital and the lateral extent of the osteoderms, it shares with *Cacops* the general distribution of cranial eminences and ridges on the skull. Additionally, this new species preserves a lee on the left (but not on the right) side of the skull. Some juvenile specimens of *Cacops* also exhibit a separate lee, suggesting the possibility that the lee is more widespread among dissorophoids but has gone unnoticed because of its fusion with the jugal relatively early in development. However, the holotype of *B. reiszii* appears to pertain to a relatively mature individual. Both dermal and endochondral skull elements are well ossified, co-ossification of sutures are generally well advanced, dermal sculpturing is coarse, vertebral elements are well ossified, and limb bones bear well-formed articular surfaces. As such, it is unclear whether the retention of an open suture between the jugal and lee in *B. reiszii* represents individual variation,

or a heterochronic shift. Further study of dissorophoids using CT could dissect this area and more clearly delineate any connection between the jugal and ectopterygoid in other taxa.

5.5. Morphological disparity in *Broiliellus*

The morphological disparity exhibited by the species of *Broiliellus* is striking. The variation in much of the morphology (e.g., the proportions of the snout, the very low and wedge-shaped skull in *B. texensis* but tall and convex in *B. reiszii* and *B. olsoni*) is more conspicuous than expected in closely related taxa. Species within a genus, or genera within a family tend to conform more closely to a standard morphology. Furthermore, some species within the genus *Broiliellus* share features with 'B.' *novomexicanus* and *Cacops* despite their apparently more remote relationships (Fig. 11). Whether this is a consequence of historical taxonomic practice, a failure of the current character by taxon matrix to capture existing variation, poor taxonomic sampling, or a real biological phenomenon, remains to be discovered.

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Appendix A. Character scoring for dissorophoid amphibians, modified from Schoch (2012), and including CM 41705 (*Broiliellus reiszii*). See text for details.

We have provided a separate nexus file (Appendix B). If you opt to use it, it can be substituted for the abbreviated matrix below.

						5					10
1	1	1	1	–		15	1	0	0	1	1
0	1	1	1	0		25	1	0	1	1	0
1	1	1	1	0		35	1	0	?	1	0
1	0	1	1	1		45	0	0	0	0	0
0	0	0	1	0		55	0	0	0	1	0
0	0	1	1	0		65	1	1	0	1	?
0	?	1	1	?			1	?	1	1	1

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2013.07.002>.

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