RESEARCH ARTICLE



Revision of 'Aspidosaurus' novomexicanus, a Permo-Carboniferous dissorophid from New Mexico

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'Aspidosaurus' novomexicanus is a poorly-known dissorophid represented only by the holotype (YPM VP 810), a badly preserved partial skeleton from Permo-Carboniferous deposits of New Mexico. Compared to Paleozoic dissorophid records in other parts of North America, like Texas and Oklahoma, the New Mexican record remains relatively sparse and low in taxic diversity. Additionally, 'A.' novomexicanus is likely one of the earliest known records of dissorophids in North America. However, due to poor preservation of the holotype and a convoluted history of species-and genus-level referral of specimens to this taxon and to other dissorophids, the concept of 'A.' novomexicanus and whether the holotype is sufficiently diagnostic to merit continued designation as a valid taxon remain unclear. Recent revision of Aspidosaurus demonstrates that this species does not belong in the genus, providing an impetus for a reassessment. Here I redescribe YPM VP 810 and situate it within the contemporary framework of dissorophid anatomy and taxonomy. Based on this reanalysis, I conclude that the holotype is not diagnostic, leading 'Aspidosaurus novomexicanus' to be designated as a nomen dubium, although it is possible that it may be conspecific with 'Broiliellus' reiszi.

Dissorophoidea | Temnospondyli | Paleozoic | Olsoniformes | taxonomy | phylogeny

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Introduction

The 21st century has seen tremendous advancements in dissorophid taxonomy and phylogeny through revision of historic material (e.g., Milner, 2003; Maddin et al., 2013; Schoch and Sues, 2013, 2022; Gee, 2018; Gee et al., 2018; Dilkes, 2020), description of novel taxa from novel material (e.g., Berman and Lucas, 2003; Reisz et al., 2009; Fröbisch and Reisz, 2012; Holmes et al., 2013; Werneburg et al., 2025), augmented osteology of uncontroversial taxa (e.g., Anderson, 2005; Fröbisch et al., 2015; Gee and Reisz, 2018a; Liu, 2018; Anderson et al., 2020; Gee et al., 2025b), and reports of novel occurrences (e.g., Witzmann, 2005a; May et al., 2011; Gee and Reisz, 2018b; Gee et al., 2019, 2021). Few temnospondyl clades have received as much attention as this iconic Paleozoic group, yet there remain a number of outstanding issues to resolve in our understanding of dissorophids (Gee, 2021). A full appreciation of the rich dissorophid record requires data from not only the best-preserved specimens and the most completely known taxa but also from the less well-preserved and more taxonomically ambiguous material.

One of the areas in need of redress is the matter of wastebasket taxa – a number of genera, most notably *Aspidosaurus* Broili, 1904, and *Broiliellus* Williston, 1914, have long been populated with a relatively high number of species, some of which have a lengthy history of disagreement over their placement in one or both genera. Gee *et al.* (2025b) laid the foundation for revision of *Aspidosaurus* based on the designation of a neotype for the type species, *Aspidosaurus chiton* Broili, 1904, and restricted the genus diagnosis in a fashion that omits all other previously referred taxa. This study builds on that work and addresses one such taxon, '*Aspidosaurus*' *novomexicanus* Williston, 1911, represented by a partial skeleton (YPM VP 810) from the Permo-Carboniferous transition at Cañon del Cobre, New Mexico.

The taxon was cursorily described by Williston (1911) based on the holotype. Williston did not provide any explicit rationale for

referring the species to Aspidosaurus, which was only represented by the type species at the time (though he named a third species, 'Aspidosaurus peltatus Williston, 1911,' which is based on a single osteoderm pertaining to a dissorophine, in the same publication). Aspidosaurus was mentioned only twice in Williston's description, and one instance referred to the placement of putative juvenile specimens of Eryops Cope, 1878, from other localities that he suspected belonged to Aspidosaurus. The cranium of YPM VP 810 is incomplete anteriorly, is badly preserved, and exhibits no obvious autapomorphies. The size when complete and morphology remain unclear. Williston's generic assignment appears to have been on the basis of postcranial differentiation from Cacops Williston, 1910a, and Dissorophus Cope, 1895, the only two North American dissorophids that were known at the time (Parioxys Cope, 1878, was named but not recognized as a dissorophid until relatively recently; Moustafa, 1955; Schoch and Milner, 2014; Schoch and Sues, 2022). Specifically, 'Aspidosaurus' novomexicanus was differentiated via features such as a single median set of osteoderms that was shared with Aspidosaurus chiton but dissimilar to Cacops aspidephorus Williston, 1910a, and *Dissorophus multicinctus* Cope, 1895, both of which had been (re)described by Williston the preceding year (1910a, 1910b).

The osteology of 'Aspidosaurus' novomexicanus was expanded shortly thereafter by Case and Williston (1913), who described a largely complete cranium and associated postcranium, FMNH UC 673, from the Abo Formation of El Rito, New Mexico. As admitted by the authors (p. 7 therein), "[...] the identification of the present

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Table 1. Taxonomy of specimens previously attributed to 'Aspidosaurus' novomexicanus. Hyphens mean that the specimen had yet to be entered into the literature as a dissorophid (not applicable); question marks mean that the taxonomy of this specimen is unclear in a given study. Schoch (2012) listed UCMP 40103 as both "A." novomexicanus and "B." novomexicanus in addition to the "Rio Arriba Taxon." Holmes et al. listed UCMP 40103 as both "B." novomexicanus and the "Rio Arriba Taxon." Only temnospondyl-focused studies are listed; see the Systematic Paleontology section for full list of synonyms.

Study	YPM VP 810	FMNH UC 673	FMNH UC 744	UCMP 40103
Williston (1911)	Aspidosaurus novomexicanus	-	-	-
Case & Williston (1913)	Aspidosaurus novomexicanus	Aspidosaurus novomexicanus	-	-
Romer (1947)	"Broiliellus" novomexicanus	"Broiliellus" novomexicanus	-	-
Langston (1953)	Broiliellus novomexicanus	Broiliellus novomexicanus	Broiliellus novomexicanus	Broiliellus novomexicanus
Carroll (1964)	Aspidosaurus novomexicanus	Conjunctio multidens	?	Conjunctio multidens
DeMar (1966b)	"Aspidosaurus" novomexicanus	"Aspidosaurus" novomexicanus	?	"Aspidosaurus" novomexicanus
Schoch (2012)	?	Conjunctio multidens	"Broiliellus" novomexicanus	Rio Arriba Taxon
Holmes et al. (2013)	"Broiliellus" novomexicanus	?	?	Rio Arriba Taxon
Schoch and Milner (2014)	Aspidosaurus novomexicanus	Conjunctio multidens	Conjunctio multidenss	Conjunctio multidens
This study	"Aspidosaurus novomexicanus"	Conjunctio multidens	Conjunctio multidens	Conjunctio multidens

specimen may not be accurate, but the resemblance of the parts preserved, especially the skull, is so close that it seems best to use the earlier name [A. novomexicanus], provisionally, until more material can be obtained" (ironically, the following sentence emphasized a strong resemblance to Cacops aspidephorus). Similar to Williston's (1911) original description, Case and Williston made sparse mention of Aspidosaurus and 'A.' novomexicanus (and no mention of Aspidosaurus chiton). The referral of FMNH UC 673 was more explicitly made on the basis of postcranial differentiation from Cacops and Dissorophus, echoing Williston's (1911) referral of YPM VP 810 to Aspidosaurus. Langston (1953) then referred a third (UCMP 40103) and fourth (FMNH UC 744) specimen from the Abo Formation exposures at Arroyo del Agua, New Mexico. Langston highlighted three features of the two new specimens that were shared with the previously described material: (1) concavity of the skull roof; (2) tabulars forming rounded tabular horns; and (3) otic notch open due to the absence of ventral expansion of the tabulars, features that are shared with the holotype and the referred specimen of Case and Williston (1913).

On the basis of UCMP 40103, Langston (1953) also transferred 'Aspidosaurus' novomexicanus to Broiliellus on the basis of relative dissimilarity to Aspidosaurus chiton and relative similarity to Broiliellus texensis Williston, 1914. Langston's taxonomy was predicated on conspecificity between YPM VP 810 and UCMP 40103, which was subsequently challenged by Carroll (1964), who returned 'A.' novomexicanus to Aspidosaurus but restricted it to the holotype (YPM VP 810), with the three previously referred specimens (Case and Williston, 1913; Langston, 1953) being placed into the novel Conjunctio multidens Carroll, 1964, for which FMNH UC 673 is the holotype. Carroll aptly noted the severely limited taxonomic framework of the early 20th century and the practice of using non-holotype specimens in making taxonomic placements of species. Carroll's basis for returning 'A.' novomexicanus to Aspidosaurus comprised both differentiation from Broiliellus, Cacops, and Dissorophus and variation in dimensions of osteoderms in YPM VP 810 that was purportedly shared with Aspidosaurus chiton.

Carroll's (1964) classification of the four specimens (YPM VP 810, FMNH UC 673, FMNH UC 744, UCMP 40103) is still considered valid today (e.g., Schoch and Milner, 2014), although the lengthy history of specimen referral and taxonomic instability has resulted in some contemporary authors using Langston's concept of "Broiliellus novomexicanus" (e.g., Berman and Lucas, 2003; Lucas et al., 2005, 2010; Holmes et al., 2013; Berman et al., 2015; Table 1). In these instances, most taxonomic and anatomical arguments usually reference the holotype of Conjunctio multidens (FMNH UC

673, mainly for postcrania) or the best-preserved, referred cranium (UCMP 40103, sometimes referred to as the Rio Arriba Taxon; e.g., Schoch, 2012). Because of this, much of the discussion that either separated 'Aspidosaurus' novomexicanus from alreadyknown species or that argued for placement in Broiliellus has actually been based on comparison with C. multidens. For example, Holmes et al. (2013) list a long preorbital region as a feature shared between 'A.' novomexicanus [their 'B.' novomexicanus] and their novel Broiliellus reiszi Holmes et al., 2013, even though the preorbital region is entirely unknown in YPM VP 810 (but essentially complete in FMNH UC 673 and UCMP 40103). This underscores the challenges of poorly preserved holotypes, as a subsequently referred specimen, whose conspecificity with the holotype is sometimes tenuous, often becomes the 'proxy holotype' (e.g., Parker, 2012) against which other specimens and taxa are compared, even after conspecificity with the holotype has been challenged or disproven.

With the recent restriction of Aspidosaurus to the type species (Gee et al., 2025b), the validity and placement of 'Aspidosaurus' novomexicanus is an open question. Schoch and Milner (2014) is the most recent work to provide a diagnosis for the species, with a singular feature that only separates it from one other questionably valid species (dermal scutes flatter and with finer sculpture than in 'Aspidosaurus' glascocki Case, 1910). Dissorophids are relatively rare in New Mexico, despite the abundant record of other clades of non-marine Permo-Carboniferous tetrapods. Beyond 'A.' novomexicanus, only Broiliellus reiszi (Holmes et al., 2013), Conjunctio multidens (Case and Williston, 1913; Langston, 1953). and Platyhystrix rugosa Case, 1910 (Williston, 1911) have been recovered from this region. Werneburg et al. (2010) also described a large dissorophoid snout from the Pennsylvanian of Cañon del Cobre, which is probably a dissorophid if it is a dissorophoid based on its size (complete cranium estimated to 20 cm in length) and non-elongated external nares in contrast to trematopids (Schoch and Milner, 2014); it is potentially a novel taxon based on the paired vomerine depressions for the symphyseal 'fangs,' which are otherwise not documented in Olsoniformes (Werneburg et al., 2010). Resolving the status of 'A.' novomexicanus is thus important not only for further clarifying the alpha taxonomy of Aspidosaurus but also for understanding the degree to which dissorophids may have exhibited geographic provincialism within a relatively localized region in the present-day American southwest and mid-continent (Gee et al., 2021).



Geological setting

YPM VP 810 was collected from the El Cobre Canyon Formation of the Cutler Group in Cañon del Cobre, New Mexico. As the specimen was collected well over a century ago, specifics of its collection (e.g., whether it was found in situ, details on the encapsulating lithology if so) are not available. Some workers (Williston, 1911; Langston, 1953) suggested that it was collected near a specimen of *Limnoscelis paludis* Williston, 1911 (MCZ 1948, formerly YPM 809), but the exact location and thus the relative stratigraphic level, are unknown. The age or age range of the El Cobre Canyon Formation in this collecting area has long been debated (e.g., Case and Williston, 1913; Vaughn, 1963; Fracasso, 1980; Lucas *et al.*, 2010; Berman *et al.* 2015), so the specimen and taxon are traditionally regarded as Permo-Carboniferous.

Materials and methods

Repositories and institutional abbreviations

The holotype of 'Aspidosaurus' novomexicanus is reposited at the Yale Peabody Museum, Vertebrate Paleontology Collection (YPM VP), New Haven, Connecticut, USA. Comparative material was examined at the American Museum of Natural History, Fossil Amphibians, Reptiles, and Birds Collection (AMNH FARB), New York, New York, USA; the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania, USA; the Field Museum of Natural History (FMNH), Chicago, Illinois, USA; the Sam Noble Oklahoma Museum of Natural History (OMNH), Norman, Oklahoma, USA; the Texas Memorial Museum (TMM), Austin, Texas, USA; the University of Michigan Museum of Paleontology (UMMP), Ann Arbor, Michigan, USA; and the United States National Museum of Natural History (USNM), Washington, D.C., USA. IGCAGS stands for Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; MCZ stands for Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

Systematic paleontology

Order **Temnospondyli** Zittel, 1888 Superfamily **Dissorophoidea** Bolt, 1969 Family **Dissorophidae** Boulenger, 1902 Dissorophidae indet.

'Aspidosaurus novomexicanus' Williston, 1911, nomen dubium 1913 Aspidosaurus novomexicanus; Case and Williston, p. 7–9, fig.

1947 "Aspidosaurus" novomexicanus; Romer, p. 160 1953 Broiliellus novomexicanus; Langston, p. 380 1963 Broiliellus novomexicanus; Vaughn, p. 284 1964 Aspidosaurus novomexicanus; Carroll, p. 214-216, fig. 17 1966 "Aspidosaurus" novomexicanus; DeMar, p. 74 1968 Aspidosaurus novomexicanus; DeMar, p. 1234 1974 Aspidosaurus novomexicanus; Bolt, Table 1 1980 Aspidosaurus novomexicanus; Fracasso, Table 1 1993 Aspidosaurus novomexicanus; Berman, p. 15 2003 Broiliellus novomexicanus; Berman and Lucas, p. 259 2010 Broiliellus novomexicanus; Lucas et al., p. 117 2011 "Aspidosaurus" novomexicanus; May et al., p. 910 2013 'Broiliellus' novomexicanus; Holmes et al., p. 430 2014 Aspidosaurus novomexicanus; Schoch and Milner, p. 78 2015 Broiliellus novomexicanus; Berman et al., p. 67 2018 "Aspidosaurus" novomexicanus; Gee, p. 667 2019 Aspidosaurus novomexicanus; Gee et al., p. 15

2020 Aspidosaurus novomexicanus; Dilkes, p. 2 2021 Aspidosaurus novomexicanus; Gee, Table 1 2025 "Aspidosaurus" novomexicanus; Gee et al., p. 28

Holotype. Partial skeleton consisting of a partial cranium articulated with the presacral column and portions of the pectoral girdle and of the forelimbs (YPM VP 810). The specimen is divided among four blocks: (1) the cranium, not embedded in matrix but with some remnants of matrix throughout; (2) presacral positions 2–10, the pectoral girdle and forelimb; (3) presacral positions 11–19; and (4) presacral positions 20–21 and putative pelvic material. The last block is attached to the underlying plaster mount that was used for display purposes and cannot be removed.

Type locality. The type and only known specimen was collected from Cañon del Cobre, New Mexico, USA. As with many historic specimens from this locality, the exact stratigraphic position within the El Cobre Canyon Formation of the Cutler Group, and thus the general age, is unclear. This taxon is often treated as being from around the Permo-Carboniferous boundary.

Phylogenetic analysis

'Aspidosaurus' novomexicanus has only been incorporated into one phylogenetic analysis (Gee, 2021) due to its incompleteness and the use of 'Aspidosaurus' binasser Berman and Lucas, 2003, as the representative of the genus in other work (e.g., Berman et al., 2010, 2011; Schoch, 2012; Holmes et al., 2013; Maddin et al., 2013; Schoch and Sues, 2013; Liu, 2018; Dilkes, 2020). In Gee (2021), 'A.' novomexicanus was only tested in an expansive sampling of most nominal olsoniforms, which included many other poorly known taxa, and thus the results of that study contribute little more than phylogenetic verification of the dissorophid affinities of the taxon.

The matrix of Gee (2021) was recently modified and analyzed with a more restricted taxon sample comprising only the better-known dissorophids (Gee *et al.*, 2025b; see also Werneburg *et al.*, 2025). One of these derivates (Gee *et al.*, 2025a) was modified slightly here with respect to addition of several characters (Gee, 2025), with '*Aspidosaurus*' *novomexicanus* rescored for all characters based on the redescription performed here (previously it was scored based only on the literature). The matrix (114 characters, 31 taxa; Gee, 2025) was edited in Mesquite v.4.0 (Maddison and Maddison, 2025), and the analysis was performed in TNT v.1.6 (Goloboff and Morales 2023). YPM VP 810 could only be scored for 34 of the 114 characters (~30%). Nineteen select multistate characters [listed in the character appendix and encoded in the matrix file] were ordered; all characters were equally weighted.

The effects of taxon sampling in dissorophoid matrices have been well-demonstrated by previous studies (e.g., Schoch, 2019; Gee, 2021; Gee et al., 2025b), and the focus of this new analysis is mainly to attempt to best infer the position of YPM VP 810, not to revise dissorophid phylogeny. Therefore, following an initial run with the same taxon sample (plus YPM VP 810), the taxon sample was restricted to the following for a second iteration: the operational (designated) outgroup of *Greererpeton burkemorani* Romer, 1969; two non-operational outgroups (*Dendrerpeton helogenes* Steen, 1934, *Eryops megacephalus* Cope, 1878); three non-olsoniform dissorophoids (*Doleserpeton annectens* Bolt, 1969, *Eoscopus lockardi* Daly, 1993, *Micromelerpeton credneri* Bulman and Whittard, 1926); four trematopids (*Anconastes vesperus* Berman et al., 1987, *Acheloma cumminsi* Cope, 1882, *Ecolsonia cutlerensis* Vaughn, 1969, *Phonerpeton pricei* [Olson, 1941]); and the following



dissorophids (in alphabetical order): Anakamacops petrolicus Li and Cheng, 1999; Aspidosaurus chiton; 'Broiliellus' brevis Carroll, 1964; 'Broiliellus' reiszi; Broiliellus texensis; Cacops aspidephorus; Cacops morrisi Reisz et al., 2009; Cacops woehri Fröbisch and Reisz, 2012; Conjunctio multidens; Dissorophus multicinctus; and Parioxys ferricolus Cope, 1878. This excludes more fragmentary dissorophids that were previously sampled by Gee (2021) and Gee et al. (2025b; e.g., 'Broiliellus' olsoni DeMar, 1967, Kamacops acervalis Gubin, 1980), most of which can be readily differentiated from YPM VP 810 on qualitative attributes (e.g., osteoderm morphology). The newly described Buxierophus pouilloni Werneburg et al., 2025, is not added here since it is anatomically disparate to YPM VP 810 (e.g., osteoderm morphology), and this analysis is only intended to test the position of YPM VP 810 in a 'favorable' setting (taxon sample restricted to the best-known taxa).

A heuristic search ('traditional search') with the following parameters and room for 50,000 trees was employed: 5,000 random addition sequence (RAS) replicates, holding 10 trees at each step, and tree-bisection-and-reconnection (TBR). The set of trees recovered by the initial analysis was then used as the starting trees for a second round of branch swapping to obtain the final set of most parsimonious trees (MPTs). Default settings of TNT (e.g. rule 1 for branch collapsing: min. length = 0) were otherwise maintained. I also performed 25,000 bootstrap replicates with a heuristic search to assess absolute nodal support.

Results

Description

YPM VP 810 is preserved as four blocks that are either mounted onto, or embedded into, an underlying plaster mount on the ventral surface of the skeleton (Fig. 1). Williston (1911) noted that when collected, the cranium was originally oriented at a 90-degree angle (snout pointing upwards) relative to the postcranium and was subsequently separated in order for repositioning into the approximate biological position in which it is now arranged. There is a short gap between the cranium, which can be detached, and the postcranium. The axial column is nearly complete, and the postcranium shows no significant distortion. The cranium has been distorted in some areas and is discussed further below.

Cranium. The cranium is incomplete anteriorly, with the anteriormost preserved extent likely representing a level at or nearly at the anteriormost extent of the orbits (Figs. 1-3). Whether the anteriormost preserved margin of the frontals is their true anterior margin is unclear, but most to all of the medial orbital margin appears to be preserved. The cranium measures about 6.75 cm along the midline, in contrast to the estimate of a complete cranial length of 6.2 cm that was reported by Bolt (1974:table 1), who did not examine the specimen first-hand. This discrepancy appears to result from Bolt using a second-hand postorbital measurement of 2.19 cm (for which measurement landmarks are unclear) and a coarse linear regression based on plotted data for select dissorophid specimens in DeMar (1968:fig. 1). Based on the data available for other dissorophids, YPM VP 810 is probably between 60 to 70% complete in midline cranial length (complete length estimated to between 9.5 and 11 cm). The maximum preserved width is about 7.6 cm; this is probably close to the true value of the undistorted cranium.

The cranium has a box-like construction when viewed from behind (tall, relatively vertical cheek region; Fig. 2C-D) despite transverse compression that has mostly affected the left side of the cranium, causing the temporal region to be partially folded under the roof (Fig. 2A-D); the right side is probably close to the biological condition. As noted by previous workers (e.g., Langston, 1953; Carroll, 1964), there is a marked depression in the cranial roof, forming a longitudinal trough, but this is almost certainly the result of post-mortem distortion since the cranium is hardly symmetrical across the midline in this region (Fig. 2A-D), and such a condition has never been identified in undistorted specimens of other olsoniforms. If the right side is viewed from behind (Fig. 2C-D) and then mirrored, the cranial roof would be nearly flat. Ornamentation is essentially weathered off across the dorsal surface, with only sparse patches of circular pitting visible on the left jugal and the right postfrontal and some vestiges of pitting on the frontals and the parietals (Fig. 3). The presence of any topography on the roof, such as ridges common to many dissorophids or protuberances found on various elements in dissorophines (e.g., DeMar, 1967; Schoch, 2012; Dilkes, 2020), also cannot be confidently determined, although if it is assumed that weathering was uniform across the cranium (unclear given its distortion), there do not appear to have been any marked elevations.

Because of the weathering, the cranial sutures are especially stark in most places, but there is also extensive fracturing of the roof, and some encrusting matrix creates ambiguity in certain areas (Fig. 3). In some areas (e.g., lateral margins; Fig. 2C-D), the contour of the surface approximates the expected cranial outline, but it is unclear whether the surface has been abraded off, with the underlying matrix contoured to it, or if the surface is intact but covered in a thin matrix layer. What can be confidently discerned is relatively uninformative, as the postorbital region of dissorophids varies little beyond relative proportions. It is important to note that many of the sutures depicted by Carroll (1964; Fig. 1C) cannot be revalidated here, especially on the left side of the cranium (Fig. 3). These may have been inferred rather than identified since both his redescription and Williston's (1911) original description make scant reference of individual elements; there is no indication that the specimen has undergone preparation since Carroll's redescription. The frontals are rectangular and have a wide contribution to the orbits (Fig. 3). The postfrontal is broadly crescentic but does not markedly indent the lateral margin of the parietal as in some other taxa (Fig. 3). The posterior margin of the right postfrontal is clearly defined and does not appear to have separated the postorbital from the supratemporal (Fig. 3); a postorbital-supratemporal contact is found in most dissorophids but not in Cacops aspidephorus and Cacops morrisi (Reisz et al., 2009; Anderson et al., 2020). The right postorbital is incomplete anteromedially and laterally, so no determination about its overall morphology can be made (Fig. 3). The parietals are more pentagonal in shape and without an abrupt step in the lateral margin. The postparietals are difficult to fully define (Fig. 3). Carroll figured marked asymmetry (more equant on the left side), but the sutures on the left side are completely indiscernible as assessed here, and a partial suture on the right side can only be tentatively identified due to the presence of an interdigitated crack that reaches the occipital margin. A linear crack closer to the midline is interpreted as a fracture. As interpreted here, the postparietal was distinctly longer than wide, of a similar degree to 'Broiliellus' brevis (Carroll, 1964), but not guite to the degree of marked foreshortening observed in most aspidosaurines like Cacops spp. and Parioxys ferricolus (e.g., Fröbisch and Reisz, 2012; Gee and Reisz, 2018a; Anderson et al., 2020; Schoch and Sues, 2022). The shapes and sutures of the supratemporal, tabular, squamosal, jugal, and quadratojugal are essentially unknown. At



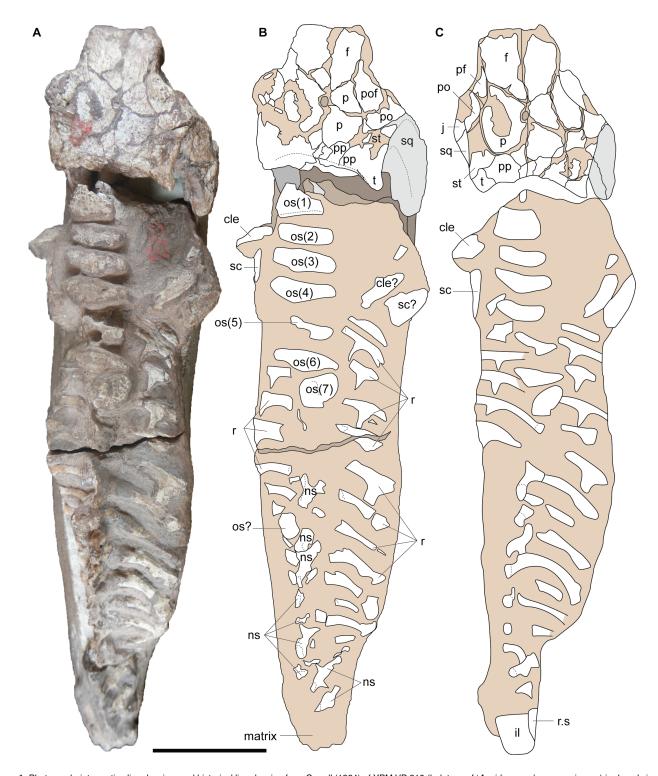


Figure 1. Photograph, interpretive line drawing, and historical line drawing from Carroll (1964) of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus) in dorsal view. A, photograph; B, new interpretive line drawing of the same; C, reproduction of the line drawing of Carroll (1964), which was likely made in a slightly different profile, accounting for some of the discrepancies. Labeling (or lack thereof) in part C mirrors the original figure. Abbreviations: cle, cleithrum; f, frontal; il, ilium; ns, neural spine; os (#), osteoderm (position); p, parietal; po, postorbital; pof, postfrontal; pp, postparietal; r, rib; r.s., sacral rib; sc, scapula/scapulocoracoid; sq, squamosal; st, supratemporal; t, tabular. Scale bars equal to 5 cm.



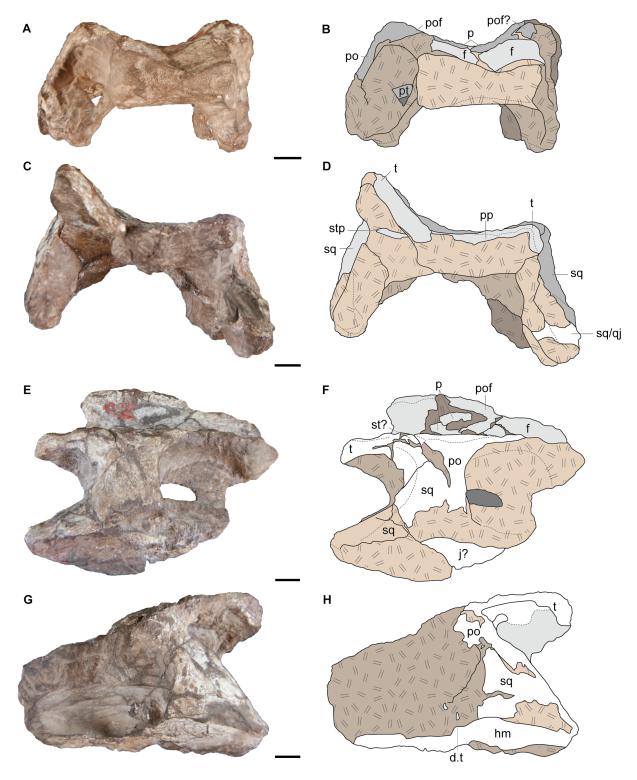


Figure 2. Photographs and interpretive line drawings of the cranium of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus) in various views. A, photograph in anterior view; B, interpretive line drawing of the same; C, photograph in posterior (occipital) view; D, interpretive line drawing of the same; E, photograph in right lateral view; F, interpretive line drawing of the same. Although the right lateral view appears angled from the side and slightly to the front, the visibility of the dorsal surface of the left side of the cranium is due to post-mortem deformation; this view is taken perpendicular to the plane of the right side of the cranium. Abbreviations: d.t, dentary tooth; f, frontal; hm, hemimandible; j, jugal; p, parietal; po; postorbital; pof, postfrontal; pp, postparietal; pt, pterygoid; qj, quadratojugal; sq, squamosal; st, supratemporal; stp, stapes; t, tabular. Scale bars equal to 1 cm.



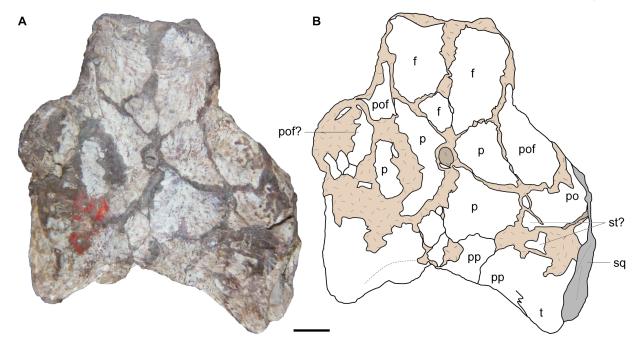


Figure 3. Photograph and interpretive line drawing of the cranium of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus) in dorsal view. **A**, photograph; **B**, interpretive line drawing of the same. Abbreviations: f, frontal; po, postforbital; pof, postfrontal; pp, postparietal; sq, squamosal; st, supratemporal; t, tabular. Scale bar equal to 1 cm.

least some of the sutures on the left temporal region that Carroll figured are clearly cracks that extend past the inferred sutures, although they could approximate the region of the suture or occur along a portion of it; his figured jugal-squamosal suture would be typical for a dissorophid, for example. However, other sutures cannot be substantiated; the sutural relationships between the squamosal, supratemporal, and tabular would only be defined on the upper flank of the unornamented supratympanic flange (Fig. 2E-H), and this region is either not preserved or not exposed.

The overall construction of the otic notch is typical for dissorophids, with the supratympanic flange extending horizontally below the cranial roof, with a slight overhang by a supratympanic shelf, and posteroventrally towards the quadrate (Fig. 2E-H). No semilunar curvature is evident. Neither tabular horn is definitively complete, but there is also no obvious evidence for the loss of a well-developed ventrally-directed tabular horn that would extend towards the quadrate. Similarly, the quadrate must be preserved on at least the right side because the jaw articulation and the quadrate ramus of the pterygoid appear nearly complete posteriorly (Figs. 2E-F, 4), but the preservation is so poor that the quadrate cannot be defined, and there appears to have been no marked dorsal process compared to taxa like *Cacops* spp. or *Dissorophus multicinctus* with closed otic notches (e.g., Reisz *et al.*, 2009; Anderson *et al.*, 2020; Dilkes, 2020).

The palate is poorly preserved, similar to the cranial roof (Fig. 4), and most identifiable features are generic attributes of dissorophids. The parasphenoid is largely complete, although the sutures with the pterygoids are not definable. There is a marked depression in the center of the basal plate, with a transverse ridge spanning the basicranial articulations in front of it. A perforation near the left basicranial articulation may have been a foramen for the carotid artery. There appear to have been posterolateral wings of the parasphenoid, but their full extent is unclear posteriorly and laterally. The cultriform process forms a narrow rod or strip; its ventral surface

is mostly damaged. The main body of the pterygoids is complete on each side, with portions of the posteriorly directed quadrate ramus, the medially directed basipterygoid ramus, and the anterolaterally directed palatine ramus all identifiable on at least one side. The basicranial articulation forms a firm contact, but whether it was sutured or fused is uncertain. There is a transverse flange of the pterygoid that expanded posteriorly from the palatine ramus, and it appears to have descended below the plane of the palate as in other dissorophids. Denticles cannot be identified on any of the surfaces, but dissorophids lack denticles on the parasphenoid, and poor preservation likely contributes to their apparent absence on the pterygoid. The exoccipitals appear to have been entirely lost, which may have accounted for the original dislodgement of the cranium relative to the postcranium.

A thin, rectangular element is visible on the left side of the cranium in occipital and palatal views, with one end pointing laterally and slightly dorsally towards the otic notch (Figs. 2C-D, 4). The orientation is appropriate for an articulated stapes, but no information can be discerned from it. There are no other elements of the neurocranium that appear to be preserved. The occipital flanges of the roofing elements are either absent or were entirely vertically oriented and remain partially obscured.

Hemimandible. The hemimandibles are extremely poorly preserved on each side (Figs. 2E-H, 4). Elements from the posterior region must be present, but the external surfaces have been largely lost, and no sutures can be identified. The dentary is partially preserved on the left side, including the single tooth that Carroll (1964) used to estimate the marginal tooth count.

Postcranium. The postcranium forms the only potential basis for diagnosing this taxon and for recognizing it confidently as a dissorophid. Most of the preserved or exposed postcranium pertains to the axial column, which is only exposed dorsally and laterally (Figs. 1, 5–7).



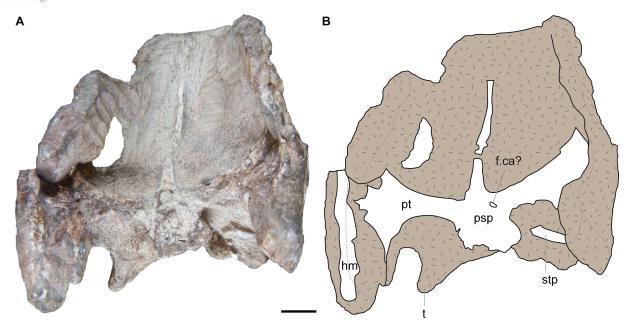


Figure 4. Photograph, interpretive line drawing, and historical line drawing from Carroll (1964) of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus) in ventral view. A, photograph; B, interpretive line drawing of the same. Abbreviations: f.ca, foramen for carotid artery; hm, hemimandible; psp, parasphenoid; pt, pterygoid; stp, stapes; t, tabular. Scale bar equal to 1 cm.

Vertebrae. The vertebrae are only represented by the neural arches and spines, although the centra are probably present within the matrix. The atlas appears to have been lost based on the incomplete preservation of the anteriormost osteoderm (Fig. 5), which normally covers the axis, the loss of the exoccipitals, and the gap between the postcranium and the cranium (Fig. 1). There is at least no observable element with the characteristic two dorsal prongs with finished bone surfaces that would not articulate with an osteoderm (e.g., Williston, 1910a; Gee and Reisz, 2018b), although there is an undiagnostic fragment of bone between the cranium and the anteriormost osteoderm (Fig. 1). The vertebrae are bestexposed in the posterior half of the presacral column where the separation between them is more definitive (Fig. 6A-B). They are characterized by a typical morphology for dissorophids; the spines appear relatively short in height, less than the maximum width across the transverse processes; bear no apparent ornamentation or external projections like tubercles; and are longer sagittally than they are wide transversely. The presumed axis is partially exposed anteriorly underneath the anteriormost osteoderm and shows only a slight dorsal expansion at the apex to contact the osteoderm. It is unclear whether a ventral flange might mediate the contact, and the articulation between any other pair of vertebrae and osteoderms is not exposed. Based on where Carroll (1964) marked the pelvis (Fig. 1C), there would have been 21 presacral positions, including the now-lost atlas, the same presacral count as in Cacops aspidephorus (Williston, 1910a), but as discussed further below, whether any part of the pelvis is truly identifiable is questionable.

Osteoderms. The osteoderms have traditionally been the most informative attribute of this specimen. There are probably eight osteoderms preserved (Figs. 1, 5–7), not seven as stated by Carroll (1964), with seven covering the first seven vertebral positions posterior to the atlas. The probable eighth osteoderm is a small ornamented fragment adjacent to the 12th and 13th presacral positions (Figs. 6A-B; 7A). It does not preserve clear features of an

osteoderm (e.g., a ventral flange), so in theory, this could represent a cranial fragment, but given the articulation of the specimen, a partial osteoderm seems more likely. The first osteoderm (corresponding to the axis, presacral position 2) is longer than the rest despite being incomplete anteriorly (Figs. 5, 7C). It was sub-triangular, tapering in width anteriorly, which is common for the anteriormost position in aspidosaurines (e.g., Anakamacops petrolicus, Aspidosaurus chiton, Cacops aspidephorus, Cacops morrisi; Dilkes and Brown, 2007; Dilkes, 2009; Liu, 2018; Gee et al., 2025b) and in contrast to the broader, more parabolic first position in certain dissorophines like Broiliellus texensis and Dissorophus multicinctus (e.g., Williston, 1914; DeMar, 1966b, 1968; Dilkes, 2009; Gee et al., 2019). The ornamentation on this osteoderm consists of small circular pits; it is not clear whether it might have had a facet along the posterior margin for articulation with another osteoderm, but this surface appears to be sloped. The next three osteoderms (presacral positions 3-5) are largely complete but badly weathered dorsally such that very little ornamentation is preserved anywhere (Fig. 5). which questions Carroll's (1964) assertion that the osteoderms were fully ornamented dorsally and without facets for a potential overlying series of osteoderms. These osteoderms are probably about as wide or a little wider than the transverse processes of the underlying vertebrae and are anteroposteriorly short. The fifth osteoderm (presacral position 6) is very badly preserved, with only a small portion of the ornamentation identified at the lateralmost edge on the right side (Fig. 5). The sixth osteoderm (presacral position 7) is mostly incomplete on the left side (Fig. 5); some faint pitting can be identified, but, again, it is not clear that the ornamentation extended across the entire surface, and, in fact, there appears to be an unornamented strip posteriorly, although this could also be the outcome of less developed ornamentation and weathering. The seventh osteoderm (presacral position 8) is only preserved on the right side (Figs. 5, 7B). It overlaps the preceding osteoderm, but there is matrix separating them vertically, hence why they appear fully separated in both Carroll's (1964) illustration and





Figure 5. Photograph and interpretive line drawing of the anterior half of the postcranium of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus') in dorsal view. A, photograph; B. interpretive line drawing of the same. Arrow points anteriorly. The posteriormost region shown in the photograph is not drawn here since it overlaps with the region of Figure 6. Abbreviations: cle, cleithrum; ns, neural spine; os (#), osteoderm (position); r, rib; sc, scapula/scapulocoracoid. Scale bar equal to 5 cm.

the line drawing here. This osteoderm is interesting because it is anteroposteriorly longer than the preceding positions and because of the overlap. It suggests, at minimum, that the osteoderm was not tightly articulated with the spine and potentially that it was not articulated at all (i.e., that it is an external osteoderm). The ornamented fragment interpreted as the posteriormost preserved osteoderm (presacral positions 12–13) is relatively uninformative (Figs. 6A-B, 7A). All of the definitive osteoderms have a gentle dorsal convexity (Fig. 7D) more like that common to aspidosaurines like Cacops spp. and dissorophines than to the marked inverted-V morphology of Aspidosaurus chiton (e.g., Gee, 2018; Gee et al., 2019, 2025b) or Scapanops neglectus Schoch and Sues, 2013. None of the osteoderms abut each other (Figs. 1, 5-6), as would be expected for a taxon with a single series based on taxa like Broiliellus texensis, Conjunctio multidens, Diploseira angusta (Carroll, 1964; posterior presacral region only), and S. neglectus (Case and Williston, 1913; Williston, 1914; Carroll, 1964; Dilkes, 2020). In these taxa, successive positions are in contact along nearly their entire width, not only at the midline.

Ribs. The ribs are mostly incomplete but are essentially fully articulated throughout the presacral column (Figs. 1, 5-6). They are relatively flat in cross-section, do not have bifurcated or markedly expanded proximal or distal ends, and bear short spikelike uncinate processes; it is unclear whether all presacral positions had these processes. There is some indication that the processes become broader posteriorly, but the more posterior ribs are mostly incomplete. Williston (1911) stated that there were two sacral ribs, while Carroll (1964) stated that there is only one. Much of this uncertainty relates to their identification of the pelvis. Most of the area that Carroll figured as part of the left ilium is covered by airscribe marks or by matrix (Fig. 6C-D). From a right lateral view, only parts of three vertebrae are identifiable in this region (Fig. 6). There is a rib that extends ventrally at the end of the block (Fig. 6D), but it is not well-exposed, appears to be relatively slender compared to the more anterior positions (and in contrast to the typically robust sacral rib of other dissorophids; e.g., Williston, 1910a; DeMar, 1968; Berman et al., 1981) and shows no features clearly identifying it as a sacral rib. The matrix in this region does form a ridge dorsally (Fig. 6C), but this could easily be following the



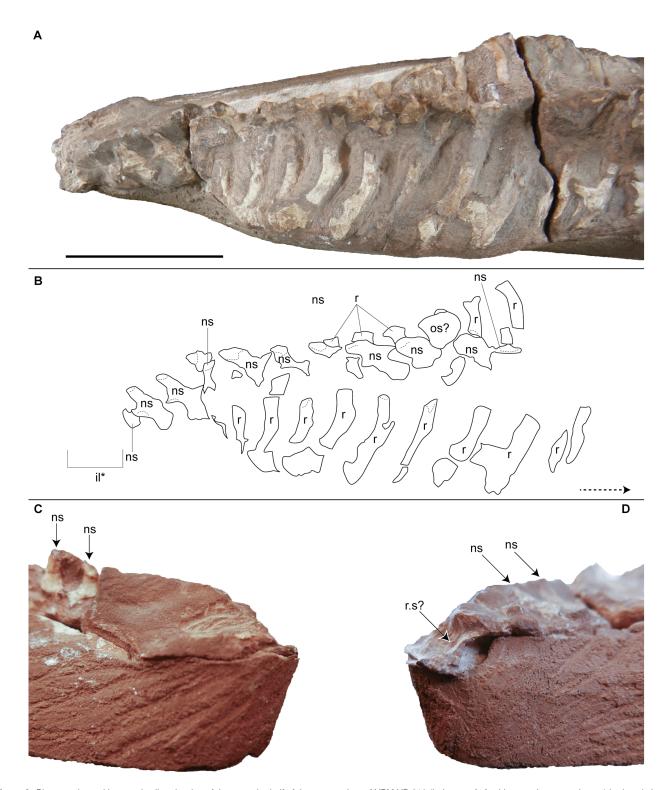


Figure 6. Photographs and interpretive line drawing of the posterior half of the postcranium of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus) in dorsal view. A, photograph; B, interpretive line drawing of the same; C, photograph of the purported pelvic region in left lateral view; D, photograph of the purported pelvic region in right lateral view. Arrow for parts A and B points anteriorly; arrows for parts C and D are used as label markers. The two neural spines marked in parts C and D are intentionally out of focus and are only labelled to help orient the reader to the focal feature (the putative sacral rib); these positions correspond to the two mostly complete positions at the end of the preserved column. The anteriormost region shown in part A is not drawn here since it overlaps with the region of Figure 5. Abbreviations: il*, purported region of the illium per Carroll (1964); ns, neural spine; os?, osteoderm (?); r, rib; r.s., sacral rib. Scale bar equal to 5 cm.



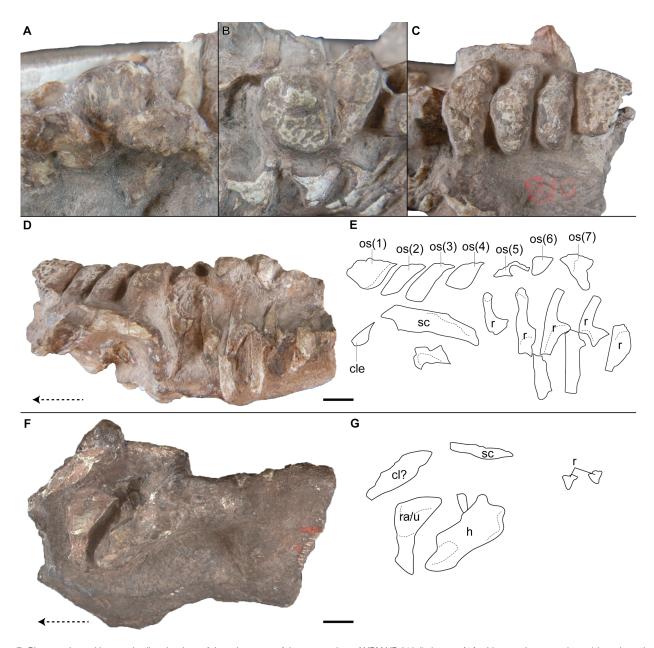


Figure 7. Photographs and interpretive line drawings of the select parts of the postcranium of YPM VP 810 (holotype of 'Aspidosaurus' novomexicanus) in various view. **A**, photograph of the tentatively identified eighth osteoderm in dorsal view; **B**, photograph of the seventh osteoderm in dorsal view; **C**, photograph of the four anteriormost osteoderms in dorsal view; **D**, photograph of the anterior postcranium in left lateral view; **E**, interpretive line drawing of the same; **F**, photograph of the anterior postcranium in ventral view; **G**, interpretive line drawing of the same. Arrow for parts E-G points anteriorly. Abbreviations: cl, clavicle; cle, cleithrum; h, humerus; ns, neural spine; os (#), osteoderm (position); r, rib; r.s., sacral rib; ra, radius; sc, scapula/scapulocoracoid; u, ulna. Scale bar equal to 1 cm.



contour of the neural spines or merely a taphonomic or preparatory artifact. The cross-sectional view exposed in the gap between the blocks in this region also provides no evidence for any portion of the pelvis. It is hardly unreasonable to predict the pelvis to be partially preserved – the identifiable presacral count is again within a typical range for dissorophids – but I could not find any positive evidence for the ilium specifically, which should contribute to the acetabulum and form a well-developed process that rises above the vertebral column. Although the ribs appear to become distinctly shorter in the region of the putative pelvic girdle, it is important to emphasize that the ribs are mostly incomplete distally, and the impression of shortening results from tapering of the matrix block.

Pectoral girdle and forelimb. Portions of the pectoral girdle and the forelimb are identified on each side of the skeleton (Figs. 1, 7D-G). They are more or less articulated but partially folded under the vertebral column, especially on the left side (similar to the compression of the cranium). As noted by Carroll (1964), most of the surface is lost on all of these elements, complicating their identification, but the general position of the exposed fragments is used to tentatively make identifications. On the left side (Fig. 7D-G), portions of the cleithrum, scapula/scapulocoracoid, humerus, and either the radius or ulna are preserved. None of these appear to be complete, and they are mainly identified by general shape and relative position. Two elements on the right side (Fig. 1) are probably two of the cleithrum, scapula/scapulocoracoid, and interclavicle. None of these elements confer any information to confirm dissorophid affinities or to differentiate the specimen from other taxa.

Phylogenetic analysis

The analysis with all taxa included recovered 21 MPTs with a length of 345 steps (CI = 0.397; RI = 0.556; Fig. 8A). As with similar permutations in Gee (2021) that included numerous poorly known taxa, Olsoniformes is poorly resolved, with a giant polytomy comprising individual branches for most dissorophids (including YPM VP 810), one branch for Trematopidae, one branch for the three species of *Cacops*, and one branch for *Anakamacops petrolicus* + *Kamacops acervalis*. This iteration does little more than demonstrate that YPM VP 810 can be scored for a sufficient number of informative characters to establish olsoniform affinities. Bootstrap support is generally modest within the resolved olsoniform nodes and is poor outside of Olsoniformes.

The analysis with selective taxon sampling (20 OTUs) recovered 2 MPTs with a length of 260 steps (CI = 0.527; RI = 0.737; Fig. 8B). The strict consensus topology is predictably more resolved, with dissorophoid relationships as historically recovered (Micromelerpetidae at the base, followed by a branching between Amphibamiformes and Olsoniformes). Dissorophidae and Trematopidae are monophyletic. Within Dissorophidae, Aspidosaurinae and Dissorophinae are recovered. Dissorophinae comprises a resolved clade with *Dissorophus multicinctus* at the base, followed by 'Broiliellus' brevis and then 'Broiliellus' reiszi + Broiliellus texensis. Aspidosaurinae is partially resolved and includes YPM VP 810. There is a polytomy with individual branches for *Anakamacops* petrolicus, Aspidosaurus chiton, YPM VP 810, Conjunctio multidens, Parioxys ferricolus and Cacops spp., with Ca. aspidephorus and Ca. morrisi recovered as sister taxa within Cacops. Bootstrap support is relatively weak (<50%) for most dissorophid nodes, including Aspidosaurinae inclusive of YPM VP 810.

Discussion

The concept of 'Aspidosaurus' novomexicanus

As noted in the Introduction, much of the uncertainty regarding the validity and placement of this species results from differing concepts of the species that are based on differing sets of assigned specimens (Table 1). Langston's (1953) concept in which four specimens - YPM VP 810, UCMP 40103, FMNH UC 673, and FMNH UC 744 - form the species, is the most expansive. Since then, different combinations of referrals of these specimens, and thus of the nomenclature around 'Aspidosaurus' novomexicanus, have been variably created. The concept of these specimens has also been muddled in phylogenetic analyses. Schoch (2012), which provided the first comprehensive phylogenetic analysis of Dissorophidae, referred to FMNH UC 744 as a specimen of "Broiliellus" novomexicanus following Langston; FMNH UC 673 as the holotype of Conjunctio multidens following Carroll (1964); and UCMP 40103 as the "Rio Arriba Taxon" / "Aspidosaurus" novomexicanus / "Broiliellus" novomexicanus, which was treated as a separate OTU in his analysis. It is unclear why UCMP 40103 was separated from C. multidens in this analysis, although it did not cluster with FMNH UC 673 in the analysis, but UCMP 40103 was re-assigned to C. multidens in short order by Schoch and Sues (2013). However, because of the treatment of UCMP 40103 as a separate operational taxonomic unit (OTU) by Schoch (2012), a number of analyses that were part of the same festschrift as Schoch and Sues (2013) and that used the original matrix of Schoch (2012) thus maintained the separation of UCMP 40103 as the "Rio Arriba Taxon" (Holmes et al., 2013; Maddin et al., 2013). It took several years for UCMP 40103 to be reincorporated into C. multidens in phylogenetic derivates by Liu (2018) and Dilkes (2020), and the "Rio Arriba Taxon" was still utilized as a separate OTU as recently as Atkins et al. (2019). UCMP 40103 was intentionally scored separately by Gee et al. (2021) and Gee (2021) for the express purpose of testing monophyly and ontogeny, respectively. Carroll's (1964) framework for these specimens has largely been adopted (e.g., Schoch and Milner, 2014) and is maintained here, but there continues to be usage of Langston's (1953) framework (e.g., Berman and Lucas, 2003; subsequently propagated by Lucas et al., 2005, 2010; May et al., 2011; Berman et al., 2015) and thus instability in the genus-level placement of the taxon.

Comparison with other dissorophids

Comparisons are inhibited by poor preservation of the cranium (Figs. 1-4), which remains the predominant source of differential information for temnospondyls. What is preserved of the cranium in YPM VP 810 is stereotypical for dissorophids. For example, the cranium is tall in the temporal region, with laterally facing otic notches (Figs. 2-3; typical for olsoniforms); the frontal enters the orbital margin (Fig. 3; found in all dissorophids); the postorbital contacts the supratemporal (Fig. 3; found in most dissorophids except for Conjunctio multidens (polymorphic), Cacops aspidephorus, and Cacops morrisi; Reisz et al., 2009; Schoch and Sues, 2013; Anderson et al., 2020); and the postparietals are not markedly foreshortened (Fig. 3; found in most non-aspidosaurine dissorophids except for 'Broiliellus' brevis, but see also Aspidosaurus chiton and Parioxys ferricolus; Carroll, 1964; Schoch and Sues, 2022; Gee et al., 2025b). Closure of the otic notch is certainly ontogenetic in at least some olsoniforms (e.g., Ca. morrisi, Acheloma cumminsi; Olson, 1941; Reisz et al., 2009), and YPM VP 810 is not an exceptionally large specimen in the known context of dissorophids, so immaturity may explain



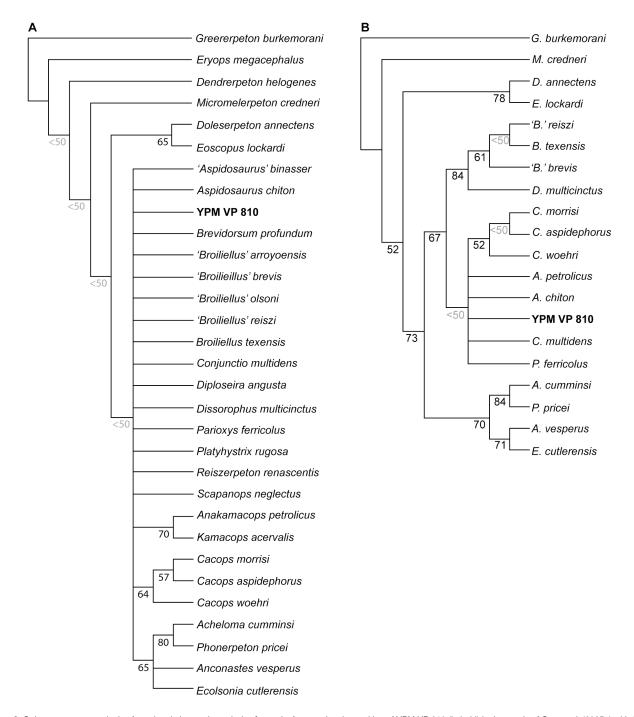


Figure 8. Strict consensus topologies from the phylogenetic analysis. A, results from testing the position of YPM VP 810 (in bold) in the matrix of Gee *et al.* (2025a) with 31 OTUs; B, results from testing the position of YPM VP 810 in the same matrix with 20 OTUs. Absolute bootstrap values are depicted underneath branches, with values of 50% or higher in black color and values below 50% in lighter gray.



this feature. However, there may be some taxonomic signal for dissorophids that were relatively small (<15 cm cranial length) since the otic notch is wide open in specimens of Aspidosaurus chiton (Gee et al., 2025b) and Parioxys ferricolus (Schoch and Sues, 2022) that are similarly sized to specimens of other dissorophids with closed otic notches (e.g., Reisz et al., 2009) and that exhibit at least some features of relative maturity (e.g., sphenethmoid ossification). Assessing the relative maturity of YPM VP 810 is complicated by its poor preservation; common indicators such as ossification of the sphenethmoid or co-ossification of the opisthotic and prootic cannot be confidently assessed. Ornamentation is of questionable value given the extreme abrasion of YPM VP 810, but there is at least enough preserved to indicate that the ornamentation comprised circular pits (Fig. 3), rather than the less common condition of ridges (Cacops woehri, Scapanops neglectus; Fröbisch and Reisz, 2012; Schoch and Sues, 2013).

Carroll (1964) estimated a total upper jaw tooth count of 45–55 positions, which puts it in the same range as 'Broiliellus' reiszi, contra Holmes et al. (2013), who cited the higher tooth count of UCMP 40103 as a differentiating feature. However, only one marginal tooth is exposed (on the dentary) in YPM VP 810 (Fig. 2G-H). Carroll's estimate thus relies upon certain implied assumptions (e.g., that all teeth are as large as the single preserved tooth), ambiguous assumptions (e.g., how far the marginal tooth row extended), and unstated estimates of how long the cranium and hemimandible would have been when complete. Dissorophids show a range of preorbital-postorbital length ratios, and there is likely to be some ontogenetic influence based on the largest known taxa (e.g., Anakamacops petrolicus, Kamacops acervalis; Gubin, 1980; Liu, 2018), ontogenetic data from the closely related amphibamiforms (e.g., Werneburg, 2020; Schoch, 2022; Schoch and Werneburg, 2023), and ontogenetic trends in other Paleozoic temnospondyls with doliocephalic crania (e.g., Sequeira, 2004; Witzmann, 2005b; Witzmann and Scholz, 2007; Schoch, 2021). Circular logic should be avoided in assuming similar proportions to an inferred close relative (e.g., Aspidosaurus chiton), especially when close relatedness is not well-supported. The single marginal tooth is relatively small, so it is reasonable to infer that the marginal tooth count was probably similar to the more common plesiomorphic condition (>45 marginal teeth) in contrast to some highly nested aspidosaurines with reduced counts (e.g., Cacops spp.; Reisz et al., 2009; Fröbisch and Reisz, 2012; Gee and Reisz, 2018a). In spite of the relatively limited cranial data, from the above discussion, it is possible to exclude most aspidosaurines, including Cacops aspidephorus, Cacops morrisi, Cacops woehri, Conjunctio multidens, and some post-Cisuralian dissorophids (An. petrolicus, K. acervalis) from consideration.

The morphology of the osteoderms (Figs. 5–7) is more informative and further restricts the potential for 'Aspidosaurus' novomexicanus to be conspecific with another taxon. Their relatively short width differentiates YPM VP 810 from dissorophines with wide osteoderms (e.g., Broiliellus texensis, Dissorophus multicinctus; Williston, 1914; DeMar, 1966b, 1968). They are proportionately more rectangular than the relatively equant osteoderms of Aspidosaurus chiton and Scapanops neglectus (Broili, 1904; Schoch and Sues, 2013; Gee et al., 2025b). Assuming the positions are essentially complete mediolaterally, they are most similar in proportions to 'Broiliellus' reiszi, Cacops aspidephorus, and Conjunctio multidens, (Case and Williston, 1913; Dilkes and Brown, 2007, Dilkes, 2009; Holmes et al., 2013). It bears noting that there is probably some ontogenetic influence in osteoderm width (e.g.,

the osteoderms of immature *Cacops morrisi* are narrower than in larger specimens of *Ca. aspidephorus*; Dilkes and Brown, 2007; Dilkes, 2009; Gee and Reisz, 2018a; Gee *et al.*, 2019).

While the number of osteoderm series is historically a common differentiator, a crucial uncertainty is whether YPM VP 810 had only a single series of osteoderms, as characterized by previous workers (e.g., Carroll, 1964), or if a second series was present but lost postmortem. Carroll (1964) specifically argued that the osteoderms were entirely ornamented dorsally and thus lack the predicted facets for any second, overlying series, but as shown here, the osteoderms are very poorly preserved (Figs. 5-7), with little discernible ornamentation on the most complete positions. The anteriormost position confirms the inference that the ornamentation should be well-developed and consist of the typical circular pitting that probably characterized the cranium and that the more posterior positions (2-4) that barely show any pitting are likely badly weathered. It is thus impossible to confidently state that facets for overlying positions were not present, and the posterior margin of the anteriormost osteoderm appears to have a posteroventrally sloping surface without ornamentation. I favor a hypothesis that a second series was present but lost based on observations from other dissorophids and explain this rationale below. Firstly, only seven articulated positions are preserved (Fig. 1), and no dissorophid is known to have a large section of the presacral region that lacks osteoderms. If an internal osteoderm that is normally more tightly articulated with the spine could be dislodged, an external osteoderm only connected to other elements via soft tissue could also be lost. Documented occurrences of single osteoderms that are referred to taxa with a double series (e.g., Anakamacops petrolicus, Cacops sp., Dissorophus multicinctus; Bolt, 1974; Liu, 2018; Gee et al., 2019) demonstrate that the two sets in a double series of osteoderms can be separated from each other post-mortem. Secondly, the articulated osteoderms in YPM VP 810 do not contact successive positions (Figs. 5-7), in contrast to taxa with a single series (e.g., Broiliellus texensis, Conjunctio multidens; Case and Williston, 1913; Williston, 1914). The lack of contact in Platyhystrix rugosa is clearly related to the distinctive sail formed by the curved, bladelike osteoderms (e.g., Lewis and Vaughn, 1965). The apparent absence of an external series in the 'type 1' osteoderms attributed to 'Aspidosaurus' binasser (Berman and Lucas, 2003) should be regarded as ambiguous as well; Berman and Lucas noted that there are smooth surfaces along the anterior and posterior margins that could be interpreted as evidence for a detached external series. Even in *Diploseira angusta*, which transitions from a double series anteriorly to a single series posteriorly, the region with the single series has the osteoderms in abutting contact with adjacent positions along their entire width (Dilkes, 2020). As dissorophid osteoderms have been interpreted as an adaptation for increasing rigidity of the spine (e.g., Dilkes and Brown, 2007; Dilkes, 2009), each osteoderm would be expected to be in extensive contact with another osteoderm regardless of the number of series (excluding P. rugosa). This consistent pattern of contact between successive positions in dissorophids with a single series (also seen in the convergent carapaces of chroniosuchians; e.g., Buchwitz et al., 2012) further suggests that YPM VP 810 had an external series of osteoderms that were dislodged and not preserved. It bears noting that we still know very little of the origins and anatomy of the earliest dissorophids. Dissorophids are almost entirely known from lower Permian deposits despite a predicted appearance in the Carboniferous based on the earliest appearances of trematopids, so it remains possible that early-appearing dissorophids lacked contact



between osteoderms and instead mediated trunk rigidity through soft tissue connections. However, this is only speculative, whereas available data for other dissorophids with single osteoderm series suggests consistent contact between positions, which is why I favor a hypothesis of a double series, with one series lost, in YPM VP 810. Regardless of the number of series, the osteoderms lack the autapomorphic morphology and overlap of successive positions that is found in *Aspidosaurus chiton* (Gee *et al.*, 2025b), and the specimen cannot be referred to *Aspidosaurus* based on the present genus-level diagnosis. Likewise, it can only be referred to *Broiliellus* if that genus is treated in an even more (overly) expansive fashion than it is at present; the osteoderms, particularly the anteriormost position, are very distinct from the genotype, *Broiliellus texensis*.

Is 'Aspidosaurus' novomexicanus a valid taxon?

The frequent confusion over which specimens constitute the known body of 'Aspidosaurus' novomexicanus means that some previous comparisons with other taxa, specifically those arguing for taxonomic distinctiveness of either 'A.' novomexicanus or another taxon, are not accurate. This muddles the question of whether YPM VP 810 represents a distinct, diagnosable taxon. For example, Holmes et al. (2013) named 'Broiliellus' reiszi based on a partial skeleton from the El Cobre Canyon Formation exposures in Cañon del Cobre, the same collecting area and geologic unit that produced YPM VP 810. Their comparisons (section 5.3 and sporadic references throughout the text) to 'Broiliellus novomexicanus' are based on Langston's (1953) outdated concept, as they refer to various cranial features (e.g., narial and orbital size, overall cranial proportions, internarial fontanelle) that are largely or entirely unknown in YPM VP 810 but known in both of the two most complete specimens of Conjunctio multidens (FMNH UC 673, UCMP 40103) that were referred to Langston's (1953) 'B. novomexicanus.' Their comparison thus demonstrates the separation of C. multidens and 'B.' reiszi (not disputed here) but does not address the status of YPM VP 810. The incompleteness, poor preservation, and uncertainty over certain features (e.g., number of osteoderm series) only further complicates matters.

In my opinion, YPM VP 810 lacks sufficient features to be regarded as diagnostic, either autapomorphies or a unique combination of features. The most recent diagnosis by Schoch and Milner (2014:78) included only one feature: "dermal scutes flatter and with finer sculpture than in Aspidosaurus glascocki." This feature obviously differentiates only two species and presumes placement in Aspidosaurus, which is not supported by more recent revision (Gee et al., 2025b). The previous diagnosis by Carroll (1964) listed several features, some of which are not individually diagnostic (e.g., single series of osteoderms) and others of which have been challenged upon restudy (e.g., one sacral rib, estimate of 45–55 marginal teeth, separation of adjacent osteoderms). I therefore designate 'Aspidosaurus novomexicanus' as a nomen dubium. This does not preclude the possibility that YPM VP 810 is conspecific with a known dissorophid. Although YPM VP 810 can be reliably differentiated from *Conjunctio multidens* and Platyhystrix rugosa, two of the other three dissorophids known from New Mexico, proper separation from 'Broiliellus' reiszi is less clear. The holotypes occur in the same geographic area (Cañon del Cobre), the same geologic unit (El Cobre Canyon Formation), and are not clearly distinct in areas where the anatomy of YPM VP 810 is more certain. For example, the osteoderms are of moderate width and comparable size; Holmes et al. (2013) argued that the osteoderms of YPM VP 810 were substantially larger than those of

CM 41705 (citing Williston, 1911, and thus contrasting with YPM VP 810), but having examined both specimens myself, I do not consider the difference in size to be particularly appreciable, and the proportions are similar. If my suspicion that YPM VP 810 originally had two osteoderm series is correct, that would only further align the specimens. What little information can be discerned from the cranium of YPM VP 810 is at least not in conflict with CM 41705, and the weakly supported placement of the former in Aspidosaurinae in the results of this analysis (Fig. 7B) should not be afforded substantial weight for taxonomic distinctiveness given the extensive amount of missing data for the OTU (~70% of characters left as unknown). This hypothesis can likely only be fully tested through collection of additional specimens referable to 'B.' reiszi, which even then might still be insufficient. If conspecificity of these specimens could be more demonstrably shown, 'Aspidosaurus novomexicanus' would have precedence but must likely remain a nomen dubium due to the absence of sufficient diagnostic information (i.e., the holotype is insufficient to serve as the bearer of a valid name). I present this possibility mainly to indicate that I believe that it can only be confidently stated that at least three ('B.' reiszi, C. multidens, P. rugosa), not four, distinct dissorophids are known from the Paleozoic of New Mexico at present. The partial dissorophoid snout of Werneburg et al. (2010), also from Cañon del Cobre, may represent another taxon, as it is clearly not a trematopid based on narial morphology. It cannot be compared to YPM VP 810 given the lack of skeletal overlap and probably also pertains to a much larger individual.

The problem of proxy holotypes for dissorophids

The previous discussion about the possible conspecificity of YPM VP 810 with CM 41705 prompts a short discussion of 'proxy holotypes,' a situation where a more informative referred specimen is treated as the functional name-bearing specimen for taxonomic comparisons (e.g., Parker, 2012). Even if these two specimens could be demonstrated to be conspecific, 'Aspidosaurus novomexicanus' should not be reinstated (priority over 'Broiliellus' reiszi) because the holotype of the former (YPM VP 810) is unlikely to ever be diagnostic, a requirement for maintaining the validity of the name. Many other dissorophids are known from holotypes collected between the late 19th century and the early 20th century, and their completeness and quality of preservation, either due to taphonomy or preparation, is often subpar in comparison to more recently discovered or prepared material. As a result, comparisons are often drawn from skeletally equivalent materials (e.g., a holotype cranium versus a referred cranium) or skeletally expanded materials (e.g., a holotype cranium versus a referred complete skeleton) that are better preserved. In some instances, this can lead to the use of a referred specimen as a 'proxy holotype' that serves as the reference point for a given taxon, even though the true holotype is the name-bearing specimen.

While it is typical for the osteology and diagnosis of a given taxon to be expanded as new material is discovered, the name remains affixed to the holotype, and both conspecificity of new material with the holotype and continued diagnostic value of the holotype must be maintained. For example, what was originally identified as an autapomorphy of a single species may be proven to instead be a synapomorphy of a clade based on discovery of additional material that warrants revisiting of the original species diagnosis. One case study in this is the systematics of *Cacops*. Gee and Reisz (2018a) re-diagnosed *Cacops morrisi* to include (among other features) a lacrimal excluded from the orbit as an autapomorphy. At the time, no data on cranial sutures for *Cacops aspidephorus* were available



(Williston, 1910a), and this morphology was definitively not found in *Cacops woehri* (Fröbisch and Reisz, 2012). Subsequent description of better-preserved material of *C. aspidephorus* (Anderson *et al.*, 2020) and a larger specimen of *C. woehri* (Gee *et al.*, 2019) revealed that this lacrimal-orbit separation actually occurs in all three species and thus would be an autapomorphy of the genus, not of *C. morrisi* specifically, had this separation not also been subsequently reported in *Anakamacops petrolicus* and *Aspidosaurus chiton* (Liu, 2018; Gee *et al.*, 2025b).

Similar considerations apply to the use of non-type species as representative of a genus. For example, 'Aspidosaurus' binasser was often the representative for Aspidosaurus in phylogenetic work, which is now convoluted by the probable chimerism of the holotype (Gee, 2021) and the uncertain genus-level placement of the taxon if it is valid in some form (Gee et al., 2025b). This practice is not intrinsically problematic, but it can become so when working with species-rich genera that are potentially wastebasket taxa (as Aspidosaurus was prior to work by Gee et al., 2025b).

In the context of 'Aspidosaurus novomexicanus,' most characterizations and comparisons to this taxon, including in works published in the 21st century, have been based on the use of FMNH UC 673 or UCMP 40103 as 'proxy holotypes,' which were referred to the taxon by Langston (1953) but which are now uncontroversially identified as Conjunctio multidens (following Carroll, 1964). Even were they conspecific, those referred specimens would still not be the name-bearing type. The use of 'proxy holotypes' concerns other dissorophids as well. The holotypes of Cacops aspidephorus (FMNH UC 647) and Parioxys ferricolus (AMNH FARB 4309) are both badly preserved crania with essentially no visible sutures, and recent redescriptions have relied on other specimens in order to identify some of the diagnostic features (Anderson et al., 2020; Schoch and Sues, 2022). A similar situation concerns Dissorophus multicinctus, whose holotype (AMNH FARB 4593) is a set of osteoderms in articulation with vertebrae but without any cranial material (or the diagnostic enlarged first osteoderm); and Anakamacops petrolicus, whose holotype (IGCAGS V365) is the left side of a snout (Li and Cheng, 1999) without skeletal overlap with subsequently referred cranial and postcranial material (Liu, 2018). 'Fayella chickashaensis' Olson, 1965, based on an isolated braincase (FMNH UR 1004), is a final example of a 'proxy holotype' situation in which a much more substantial skeleton from another locality and without skeletal overlap (Olson, 1972) served as the 'proxy holotype' until the latter was split out into a novel taxon by Gee et al. (2018). These examples highlight the need for express justification of conspecificity and the challenges of highly incomplete holotypes. For example, there is no clear justification as to why the specimen that Moustafa (1952) designated as the holotype of P. ferricolus (AMNH FARB 4309), which is taphonomically deformed, without sutures, and much smaller than better-preserved, subsequently described and figured specimens (Sues and Schoch, 2022:fig. 1.1-1.4), could not be immature individuals of another dissorophid like Cacops or why the larger specimens are conspecific with the holotype. Contemporary workers often cannot do anything to directly improve the informativeness of poorly preserved or fragmentary holotypes, but they can uphold a high standard for maintaining species diagnoses and for making referrals of additional specimens to known taxa. Critical examination of exclusively the holotypes of several taxa might reveal that they are in fact no longer diagnostic, even if they are probably or demonstrably conspecific with more informative referred specimens.

Conclusions

Despite an extensive amount of anatomical, taxonomic, and phylogenetic work in the 21st century, a holistic understanding of dissorophids remains encumbered by a lack of information and clarity on more poorly known specimens and taxa. In some instances, restudy demonstrates the validity and distinctiveness of taxa (e.g., Diploseira angusta, Parioxys ferricolus; Dilkes, 2020; Schoch and Sues, 2022), and in others, restudy demonstrates either a lack of diagnosability or synonymy with another taxon (e.g., 'Alegeinosaurus aphthitos' Case, 1911, 'Fayella chickashaensis,' 'Longiscitula houghae' DeMar, 1966a; Milner, 2003; Gee, 2018; Gee et al., 2018). This study continues the work of attempting to resolve one of two wastebasket genera within Dissorophidae, Aspidosaurus (Gee, 2021; Gee et al., 2025b), and concludes that the holotype of 'Aspidosaurus novomexicanus' (YPM VP 810) is not sufficiently diagnostic to merit being retained as a valid taxon. It may, however, be the same taxon as 'Broiliellus' reiszi, but even in the event of more demonstrable conspecificity, 'A. novomexicanus' must likely remain a nomen dubium due to the lack of diagnostic features.

Data availability

The phylogenetic matrix and sets of recovered MPTs are available on MorphoBank (Gee, 2025).

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Author contributions

Bryan M. Gee contributed to the Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, and Writing (original draft and review & editing) of this manuscript.

Competing interests

The author declares no conflicts of interests.

Ethics and Al use

This study followed all standard legal and ethical norms for study of museum specimens; no special regulatory approval was necessary for its conduct. All was not utilized for any component of this research.

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References

Anderson, J.S. 2005. On the skull of *Cacops aspidephorus* Williston (Tetrapod; Temnospondyli; Dissorophidae) from the Lower Permian of Texas. Part 1. Lower jaw anatomy. *New Mexico Museum of Natural History and Science Bulletin* 30, 15.

Anderson, J.S., Scott, D. and Reisz, R.R. 2020. The anatomy



- of the dermatocranium and mandible of *Cacops aspidephorus* Williston, 1910 (Temnospondyli: Dissorophidae), from the Lower Permian of Texas. *Journal of Vertebrate Paleontology* 40:2, e1776720. https://doi.org/10.1080/02724634.2020.1776720
- Atkins, J.B., Reisz, R.R. and Maddin, H.C. 2019. Braincase simplification and the origin of lissamphibians. *PLOS ONE* 14:3, e0213694. https://doi.org/10.1371/journal.pone.0213694
- Berman, D.S. 1993. Lower Permian vertebrate localities of New Mexico and their assemblages. *New Mexico Museum of Natural History and Science Bulletin* 2, 11–21.
- Berman, D.S. and Lucas, S.G. 2003. *Aspidosaurus binasser* (Amphibia, Temnospondyli), a new species of Dissorophidae from the lower Permian of Texas. *Annals of Carnegie Museum* 72:4, 241–262.
- Berman, D.S., Henrici, A.C. and Lucas, S.G. 2015. Pennsylvanian-Permian red bed vertebrate localities of New Mexico and their assemblages. *New Mexico Museum of Natural History and Science Bulletin* 68, 65–76.
- Berman, D.S., Henrici, A.C., Brezinski, D.K. and Kollar, A.D. 2010. A new trematopid amphibian (Temnospondyli: Dissorophoidea) from the Upper Pennsylvanian of western Pennsylvania: earliest record of terrestrial vertebrates responding to a warmer, drier climate. *Annals of Carnegie Museum* 78:4, 289–318. https://doi.org/10.2992/007.078.0401
- Berman, D.S., Henrici, A.C., Martens, T., Sumida, S.S. and Anderson, J.S. 2011. *Rotaryus gothae*, a new trematopid (Temnospondyli: Dissorophoidea) from the lower Permian of Central Germany. *Annals of Carnegie Museum* 80:1, 49–65. https://doi.org/10.2992/007.080.0106
- Berman, D.S., Reisz, R.R. and Eberth, D.A. 1987. A new genus and species of trematopid amphibian from the Late Pennsylvanian of north-central New Mexico. *Journal of Vertebrate Paleontology* 7:3, 252–269. https://doi.org/10.1080/02724634.1987.10011659
- Berman, D.S., Reisz, R.R., and Fracasso, M.A. 1981. Skull of the Lower Permian dissorophid amphibian *Platyhystrix rugosus. Annals of Carnegie Museum* 50:17, 391–416.
- Bolt, J.R. 1969. Lissamphibian origins: Possible protolissamphibian from the Lower Permian of Oklahoma. *Science* 166:3907, 888–891. https://doi.org/10.1126/science.166.3907.888
- Bolt, J.R. 1974. Armor of dissorophids (Amphibia: Labyrinthodontia): An examination of Its taxonomic use and report of a new occurrence. *Journal of Paleontology* 48:1, 135–142.
- Boulenger, G. 1902. Amphibia. In *Encyclopaedia Britannica* (10th ed., Vol. 1, pp. 381–384). Adam and Charles Black.
- Broili, F. 1904. Permische stegocephalen und reptilien aus Texas. *Palaeontographica* 51, 1–120.
- Buchwitz, M., Foth, C., Kogan, I. and Voigt, S. 2012. On the use of osteoderm features in a phylogenetic approach on the internal relationships of the Chroniosuchia (Tetrapoda: Reptiliomorpha). *Palaeontology* 55:3, 623–640. https://doi.org/10.1111/j.1475-4983.2012.01137.x
- Bulman, O.M.B. and Whittard, W.F. 1926. On *Branchiosaurus* and allied genera (Amphibia). *Proceedings of the Zoological Society of London* 96:2, 533–579. https://doi.org/10.1111/j.1469-7998.1926.tb08112.x
- Carroll, R.L. 1964. Early evolution of the dissorophid amphibians. *Bulletin of the Museum of Comparative Zoology* 131:7, 161–250.
- Case, E.C 1910. New or little known reptiles and amphibians from the Permian (?) of Texas. *Bulletin of the American Museum of Natural History* 28, 163–181. http://hdl.handle.net/2246/1394
- Case, E.C. 1911. Revision of the Amphibia and Pisces of the Permian of North America. *Publications of the Carnegie Institution of Washington* 146, 1–179.
- Case, E.C. and Williston, S.W. 1913. A description of *Aspidosaurus novomexicanus* Williston. *Publications of the Carnegie Institution of Washington* 181, 7–9.
- Cope, E.D. 1878. Descriptions of extinct Batrachia and Reptilia from the Permian formation of Texas. *Proceedings of the American Philosophical*

- Society 17, 505-530. https://doi.org/10.5962/bhl.title.104569
- Cope, E.D. 1882. Third contribution to the history of the Vertebrata of the Permian formation of Texas. *Proceedings of the American Philosophical Society* 20, 447–461.
- Cope, E.D. 1895. A batrachian armadillo. *The American Naturalist* 29, 998. https://doi.org/10.1086/276277
- Daly, E. 1994. The Amphibamidae (Amphibia: Temnospondyli), with a description of a new genus from the Upper Pennsylvanian of Kansas. *The University of Kansas Museum of Natural History Miscellaneous Publications* 85, 1–59.
- DeMar, R. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the Family Dissorophidae. *Journal of Paleontology* 42:5, 1210–1242.
- DeMar, R.E. 1966a. *Longiscitula houghae*, a new genus of dissorophid amphibian from the Permian of Texas. *Fieldiana: Geology* 16:2, 45–53. https://doi.org/10.5962/bhl.title.5215
- DeMar, R.E. 1966b. The phylogenetic and functional implications of the armor of the Dissorophidae. *Fieldiana: Geology* 16:3, 55–88. https://doi.org/10.5962/bhl.title.5351
- DeMar, R.E. 1967. Two new species of *Broiliellus* from the Permian of Texas. *Fieldiana: Geology* 16:5, 117–129. https://doi.org/10.5962/bhl.title.5190
- Dilkes, D. and Brown, L.E. 2007. Biomechanics of the vertebrae and associated osteoderms of the Early Permian amphibian *Cacops aspidephorus. Journal of Zoology* 271:4, 396–407. https://doi.org/10.1111/j.1469-7998.2006.00221.x
- Dilkes, D.W. 1990. A new trematopsid amphibian (Temnospondyli: Dissorophoidea) from the Lower Permian of Texas. *Journal of Vertebrate Paleontology* 10:2, 222–243. https://doi.org/10.1080/02724634.1990.10011809
- Dilkes, D.W. 2009. Comparison and biomechanical interpretations of the vertebrae and osteoderms of *Cacops aspidephorus* and *Dissorophus multicinctus* (Temnospondyli, Dissorophidae). *Journal of Vertebrate Paleontology* 29:4, 1013–1021. https://doi.org/10.1671/039.029.0410
- Dilkes, D.W. 2020. Revision of the early Permian dissorophid 'Dissorophus' angustus (Temnospondyli: Dissorophoidea). Journal of Vertebrate Paleontology 40:4, e1801704. https://doi.org/10.1080/02724634.2020.1801704
- Fracasso, M.A. 1980. Age of the Permo-Carboniferous Cutler Formation vertebrate fauna from El Cobre Canyon, New Mexico. Journal of Paleontology 54:6, 1237–1244.
- Fröbisch, N.B. and Reisz, R.R. 2012. A new species of dissorophid (*Cacops woehri*) from the Lower Permian Dolese Quarry, near Richards Spur, Oklahoma. Journal of Vertebrate Paleontology 32:1, 35–44. https://doi.org/10.1080/02724634.2012.633586
- Fröbisch, N.B., Brar, A. and Reisz, R.R. 2015. New specimen of *Cacops woehri* indicates differences in the ontogenetic trajectories among cacopine dissorophids. Fossil Record 18:1, 73–80. https://doi.org/10.5194/fr-18-73-2015
- Gee, B.M. 2018. Reappraisal of the early Permian dissorophid *Alegeinosaurus* from Texas, USA. *PalZ* 92:4, 661–669. https://doi.org/10.1007/s12542-018-0421-9
- Gee, B.M. 2021. Returning to the roots: Resolution, reproducibility, and robusticity in the phylogenetic inference of Dissorophidae (Amphibia: Temnospondyli). *PeerJ* 9, e12423. https://doi.org/10.7717/peerj.12423
- Gee, B.M. 2025. Phylogenetic dataset for: Revision of 'Aspidosaurus' novomexicanus, a Permo-Carboniferous dissorophid from New Mexico [Dataset]. MorphoBank. http://dx.doi.org/10.7934/P5973
- Gee, B.M. and Reisz, R.R. 2018a. Cranial and postcranial anatomy of *Cacops morrisi*, a eucacopine dissorophid from the early Permian of Oklahoma. *Journal of Vertebrate Paleontology* 38:2, e1433186. https://doi.org/10.1080/02724634.2018.1433186
- Gee, B.M. and Reisz, R.R. 2018b. Postcrania of large dissorophid temnospondyls from Richards Spur, Oklahoma. *Fossil Record* 21:1, 79–91.



https://doi.org/10.5194/fr-21-79-2018

- Gee, B.M., Berman, D.S., Henrici, A.C., Pardo, J.D. and Huttenlocker, A.K. 2020. New information on the dissorophid *Conjunctio* (Temnospondyli) based on a specimen from the Cutler Formation of Colorado, U.S.A. *Journal of Vertebrate Paleontology* 40:6, e1877152. https://doi.org/10.1080/02724634.2020.1877152
- Gee, B.M., Bevitt, J.J. and Reisz, R.R. 2019. Dissorophid diversity at the early Permian cave system near Richards Spur, Oklahoma, USA. *Palaeontologia Electronica* 22:2, 46A:1–32. https://doi.org/10.26879/976
- Gee, B.M., Mann, A. and Sues, H.-D. 2025a. Phylogenetic datasets for: A reassessment of *Aspidosaurus chiton* Broili, 1904 (Temnospondyli: Dissorophoidea) based on a new skeleton from the early Permian of Texas [Dataset]. *MorphoBank*. https://doi.org/10.7934/P5866
- Gee, B.M., Mann, A. and Sues, H.-D. 2025b. A reassessment of *Aspidosaurus chiton* Broili, 1904 (Temnospondyli: Dissorophoidea) based on a new skeleton from the early Permian of Texas. *Zoological Journal of the Linnean Society* 204:3, zlaf046. https://doi.org/10.1093/zoolinnean/zlaf046
- Gee, B.M., Scott, D. and Reisz, R.R. 2018. Reappraisal of the Permian dissorophid *Fayella chickashaensis*. *Canadian Journal of Earth Sciences* 55:10, 1103–1114. https://doi.org/10.1139/cjes-2018-0053
- Goloboff, P.A. and Morales, M.E. 2023. TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics* 39:2, 144–153. https://doi.org/10.1111/cla.12524
- Gubin, Y.M. 1980. [New Permian dissorophoids of the Ural forelands]. *Paleontologicheskii Zhurnal* 1980:3, 82–90. [Russian]
- Holmes, R., Berman, D.S. and Anderson, J.S. 2013. A new dissorophid (Temnospondyli, Dissorophoidea) from the Early Permian of New Mexico (United States). *Comptes Rendus Palevol* 12:7–8, 419–435. https://doi.org/10.1016/j.crpv.2013.07.002
- Langston, W. Jr. 1953. Permian amphibians from New Mexico. *University of California Publications in Geological Sciences* 29, 346–416.
- Lewis, G.E. and Vaughn, P.P. 1965. Early Permian vertebrates from the Cutler Formation of the Placerville Area Colorado. *US. Geological Survey Professional Paper* 503C, 1–50.
- Li, J.-L. and Cheng, Z.-W. 1999. New anthracosaur and temnospondyl amphibians from Gansu, China-the fifth report on Late Permian Dashankou lower tetrapod fauna. *Vertebrata PalAsiatica* 37, 242–248.
- Liu, J. 2018. Osteology of the large dissorophid temnospondyl *Anakamacops petrolicus* from the Guadalupian Dashankou Fauna of China. *Journal of Vertebrate Paleontology* 38:5, e1513407. https://doi.org/10.1080/02724634.2018.1513407
- Lucas, S.G., Harris, S.K., Spielmann, J.A., Berman, D.S., Henrici, A.C., Heckert, A.B., Zeigler, K.E. and Rinehart, L.F. 2005. Early Permian vertebrate assemblage and its biostratigraphic significance, Arroyo del Agua, Rio Arriba County, New Mexico. New Mexico Geological Society, Guidebook, 56th Field Conference, 288–296. https://doi.org/10.56577/FFC-56.288
- Lucas, S.G., Harris, S.K., Spielmann, J.A., Rinehart, L.F., Berman, D.S., Henrici, A.C. and Krainer, K. 2010. Vertebrate paleontology, biostratigraphy, and biochronology of the Pennsylvanian-Permian Cutler Group, Cañon del Cobre, northern New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 49, 115–124.
- Maddin, H.C., Fröbisch, N.B., Evans, D.C. and Milner, A.R. 2013. Reappraisal of the Early Permian amphibamid *Tersomius texensis* and some referred material. *Comptes Rendus Palevol* 12:7–8, 447–461. https://doi.org/10.1016/j.crpv.2013.06.007
- Maddison, W.P. and Maddison, D.R. 2025. *Mesquite: Mesquite: a modular system for evolutionary analysis* (Version 4.0). https://www.mesquiteproject.org
- May, W., Huttenlocker, A.K., Pardo, J.D., Benca, J. and Small, B.J. 2011. New Upper Pennsylvanian armored dissorophid records (Temnospondyli, Dissorophoidea) from the U.S. midcontinent and the stratigraphic distributions of dissorophids. *Journal of Vertebrate Paleontology* 31:4, 907–912. https://doi.org/10.1080/02724634.2011.582532

- Milner, A.R. 2003. Longiscitula houghae DeMar, 1966 (Amphibia: Temnospondyli), a junior synonym of Dissorophus multicinctus Cope, 1895. Journal of Vertebrate Paleontology 23:4, 941–944. https://doi.org/10.1671/18
- Moustafa, Y.S. 1952. The type of *Parioxys ferricolus*, Cope. *Bulletin de l'institut d'Egypte* 33, 295–300.
- Moustafa, Y.S. 1955. The skeletal structure of *Parioxys ferricolus*, Cope. *Bulletin de l'institut d'Egypte* 36, 41–76.
- Olson, E.C. 1941. The family Trematopsidae. *The Journal of Geology* 49:2, 149–176. https://doi.org/10.1086/624952
- Olson, E.C. 1965. Chickasha vertebrates. *Oklahoma Geological Survey Circular* 70. 1–70.
- Olson, E.C. 1972. Fayella chickashaensis, the Dissorophoidea and the Permian terrestrial radiations. Journal of Paleontology, 46:1, 104–114.
- Parker, W.G. 2012. Redescription and taxonomic status of specimens of *Episcoposaurus* and *Typothorax*, the earliest known aetosaurs (Archosauria: Suchia) from the Upper Triassic of western North America, and the problem of proxy "holotypes." *Earth and Environmental Science Transactions of The Royal Society of Edinburgh* 103:3–4, 313–338. https://doi.org/10.1017/S1755691013000212
- Reisz, R.R., Schoch, R.R. and Anderson, J.S. 2009. The armoured dissorophid *Cacops* from the Early Permian of Oklahoma and the exploitation of the terrestrial realm by amphibians. *Naturwissenschaften* 96:7, 789–796. https://doi.org/10.1007/s00114-009-0533-x
- Romer, A.S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology* 99:1, 1–368.
- Romer, A.S. 1969. A temnospondylous labyrinthodont from the Lower Carboniferous. *Kirtlandia* 6, 1–20.
- Schoch, R.R. 2012. Character distribution and phylogeny of the dissorophid temnospondyls. *Fossil Record* 15:2, 121–137. https://doi.org/10.1002/mmng.201200010
- Schoch, R.R. 2019 (online 2018). The putative lissamphibian stem-group: Phylogeny and evolution of the dissorophoid temnospondyls. *Journal of Paleontology* 93:1, 137–156. https://doi.org/10.1017/jpa.2018.67
- Schoch, R.R. 2021. The life cycle in late Paleozoic eryopid temnospondyls: developmental variation, plasticity and phylogeny. *Fossil Record* 24:2, 295–319. https://doi.org/10.5194/fr-24-295-2021
- Schoch, R.R. 2022. Phylogeny of the amphibamiform temnospondyls: the relationship of taxa known by adults, larvae and neotenes. *Journal of Systematic Palaeontology* 20:1, 1–30. https://doi.org/10.1080/14772019.2022.2113831
- Schoch, R.R. and Milner, A.R. 2014. *Handbook of Paleoherpetology, Part 3A2: Temnospondyli I.* Verlag Dr. Friedrich Pfeil. 150 pp.
- Schoch, R.R. and Sues, H.-D. 2013. A new dissorophid temnospondyl from the Lower Permian of north-central Texas. *Comptes Rendus Palevol* 12:7–8, 437–445. https://doi.org/10.1016/j.crpv.2013.04.002
- Schoch, R.R. and Sues, H.-D. 2022. The dissorophoid temnospondyl *Parioxys ferricolus* from the early Permian (Cisuralian) of Texas. *Journal of Paleontology* 96:4, 950–960. https://doi.org/10.1017/jpa.2022.10
- Schoch, R.R. and Werneburg, R. 2023. Adult branchiosaurid temnospondyls: the life cycle of *Xerodromeus gracilis*. *Papers in Palaeontology* 9(4), e1513. https://doi.org/10.1002/spp2.1513
- Sequeira, S.E.K. 2004 (for 2003). The skull of *Cochleosaurus bohemicus* Frič, a temnospondyl from the Czech Republic (Upper Carboniferous) and cochleosaurid interrelationships. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh* 94:1, 21–43. https://doi.org/10.1017/S0263593300000511
- Steen, M.C. 1934. The Amphibian Fauna from the South Joggins. Nova Scotia. *Proceedings of the Zoological Society of London* 104:3, 465–504. https://doi.org/10.1111/j.1096-3642.1934.tb01644.x
- Vaughn, P.P. 1963. The age and locality of the late Paleozoic vertebrates



from El Cobre Canyon, Rio Arriba County, New Mexico. *Journal of Paleontology* 37:1, 283–286.

Vaughn, P.P. 1969. Further evidence of close relationship of the trematopsid and dissorophid labyrinthodont amphibians with a description of a new genus and new species. *Bulletin of the Southern California Academy of Sciences* 68:3, 121–130.

Werneburg, R. 2020. On the morphology of large branchiosaurids (Amphibamiformes) from the Rotliegend (Lower Permian) of the Saar-Nahe basin, Germany. *Semana* 35, 39–54.

Werneburg, R., Berman, D.S. and Lucas, S.G. 2010. Dissorophoid record from the Upper Pennsylvanian of Cañon del Cobre, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 49, 125–128.

Werneburg, R., Logghe, A. and Steyer, J.-S. 2025. *Buxierophus pouilloni* n. gen. n. sp., a new dissorophid temnospondyl from the Lower Permian of France (Allier). *Journal of Paleontology* 99:2, 382–402. https://doi.org/10.1017/jpa.2025.10112

Williston, S.W. 1910a. Cacops, Desmospondylus; new genera of Permian vertebrates. *Geological Society of America Bulletin* 21:1, 249–284. https://doi.org/10.1130/GSAB-21-249

Williston, S.W. 1910b. Dissorophus Cope. *The Journal of Geology* 18:6, 526–536. https://doi.org/10.1086/621768

Williston, S.W. 1914. Broiliellus, a new genus of amphibians from the Permian of Texas. *The Journal of Geology* 22:1, 49–56. https://doi.org/10.1086/622132

Williston, S.W. 1911. *American Permian Vertebrates*. The University of Chicago Press. 144 pp.

Witzmann, F. 2005a. A dissorophid temnospondyl in the Upper Permian Kupferschiefer of Germany. Neues Jahrbuch Für Geologie Und Paläontologie – Monatshefte 2005:5, 289–300. https://doi.org/10.1127/njgpm/2005/2005/289

Witzmann, F. 2005b. Cranial morphology and ontogeny of the Permo-Carboniferous temnospondyl *Archegosaurus decheni* Goldfuss, 1847 from the Saar–Nahe Basin, Germany. Earth and *Environmental Science Transactions of The Royal Society of Edinburgh* 96:2, 131–162. https://doi.org/10.1017/S0263593300001279

Witzmann, F. and Scholz, H. 2007. Morphometric study of allometric skull growth in the temnospondyl *Archegosaurus decheni* from the Permian/Carboniferous of Germany. *Geobios* 40:4, 541–554. https://doi.org/10.1016/j.geobios.2006.07.001

Zittel, K.A. von. 1888. *Handbuch der Palaeontologie. 1. Abtheilung: Palaeozoologie. 3. Band: Vertebrata (Pisces, Amphibia, Reptilia, Aves).* Oldenbourg. 900 pp. ['Temnospondyli' was named on p. 384; p. 257–436 were issued in 1888.]