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The dissorophoid temnospondyl *Parioxys ferricolus* from the early Permian (Cisuralian) of Texas

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Abstract.—*Parioxys ferricolus* Cope, 1878 is a long-neglected taxon of dissorophid temnospondyls from the early Permian (Cisuralian) of Texas. Reexamination of the original material and preparation of a previously undescribed specimen shed some light on the ontogeny and reveal numerous eucacopine features. *P. ferricolus* is characterized by: (1) a preorbital region 1.5 times as long as the posterior skull table in juveniles and twice as long in adults, (2) a parietal only two-thirds the length of the frontal, (3) interpterygoid vacuities shorter than half the skull length, (4) choanae posteriorly extended, and (5) vomer with enlarged, V-shaped median depression. *P. ferricolus* is found nested with *Kamacops acervalis* Gubin, 1980, with which it shares synapomorphies in the palate, within the dissorophid clade Eucacopinae.

Introduction

Dissorophidae is a Pennsylvanian–Permian clade of temnospondyl stem amphibians that are found in fluvial and floodplain deposits of the southwestern United States, Central Europe, European Russia, and north-central China (Eichwald, 1848; Cope, 1895; Carroll, 1964a; Gubin, 1980; Witzmann, 2005; Schoch and Milner, 2014; Liu, 2018). They belong to the Dissorophoidea, which most authors consider the clade from which some or all extant lissamphibians originated (Bolt, 1969; Anderson et al., 2008a; Pardo et al., 2017). Recently, new dissorophid taxa have been reported and long-known taxa revised, paving the way for phylogenetic analyses of the group (Reisz et al., 2009; Schoch, 2012; Holmes et al., 2013; Maddin et al., 2013; Schoch and Sues, 2013; Gee, 2018; Gee and Reisz, 2018).

Here we focus on a long-neglected dissorophid, *Parioxys ferricolus* Cope, 1878, whose affinities have remained unclear. In a series of publications, Moustafa (1952a, 1955a, b) worked out many anatomical details of this species and considered *P. ferricolus* an eryopiform (in modern parlance). Basing his work largely on *Eryops megacephalus*, he traced in ink what he considered sutures on the roughly prepared adult skull (MCZ 1162; Fig. 1.8, 1.9). Only after much further work on dissorophoids by Carroll (1964a) and later authors did the skeletal features become sufficiently understood to permit referral of *P. ferricolus* to Dissorophoidea, which was first explicitly done by Schoch and Milner (2014), who listed it as a eucacopine dissorophid because of features shared particularly with *Cacops* spp.

The objective of the present study is: (1) to review the existing material of *P. ferricolus*, part of which has been further prepared, with emphasis on previously unreported cranial features and (2) to assess the phylogenetic position of this taxon.

Materials and methods

During this study, material from three institutions was examined.

Material examined.—Four skulls of different sizes (AMNH 2445, 4309; MCZ 1162; USNM 544065), a range of skull fragments (MCZ 1162a, 1162b), and various postcranial bones (MCZ 1162; USNM 544065) form the basis of the present study. Specimens were examined with a WILD M3Z binocular microscope. Illustrations were based on photographs taken with a Panasonic Lumix DMC-TZ22.

The material is moderately well preserved, but preparation is difficult because the bones are covered by a tightly adhering carbonatic crust that cannot be removed entirely without damaging the underlying bone surface. Therefore, sutures are not visible in AMNH 2445 and 4309 (Fig. 1) and only partially exposed in USNM 544065 (Figs. 1, 2). In MCZ 1162, where the dermal ornament and sutures are better exposed, sutures were drawn on the skull by Y.S. Moustafa during his dissertation research; however, some of them could not be confirmed by the present study.

Repositories and institutional abbreviations.—AMNH, American Museum of Natural History, New York; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

In preparing the description, we used the following studies for comparative data: *Actiobates peabodyi* Eaton, 1973 (Gee and

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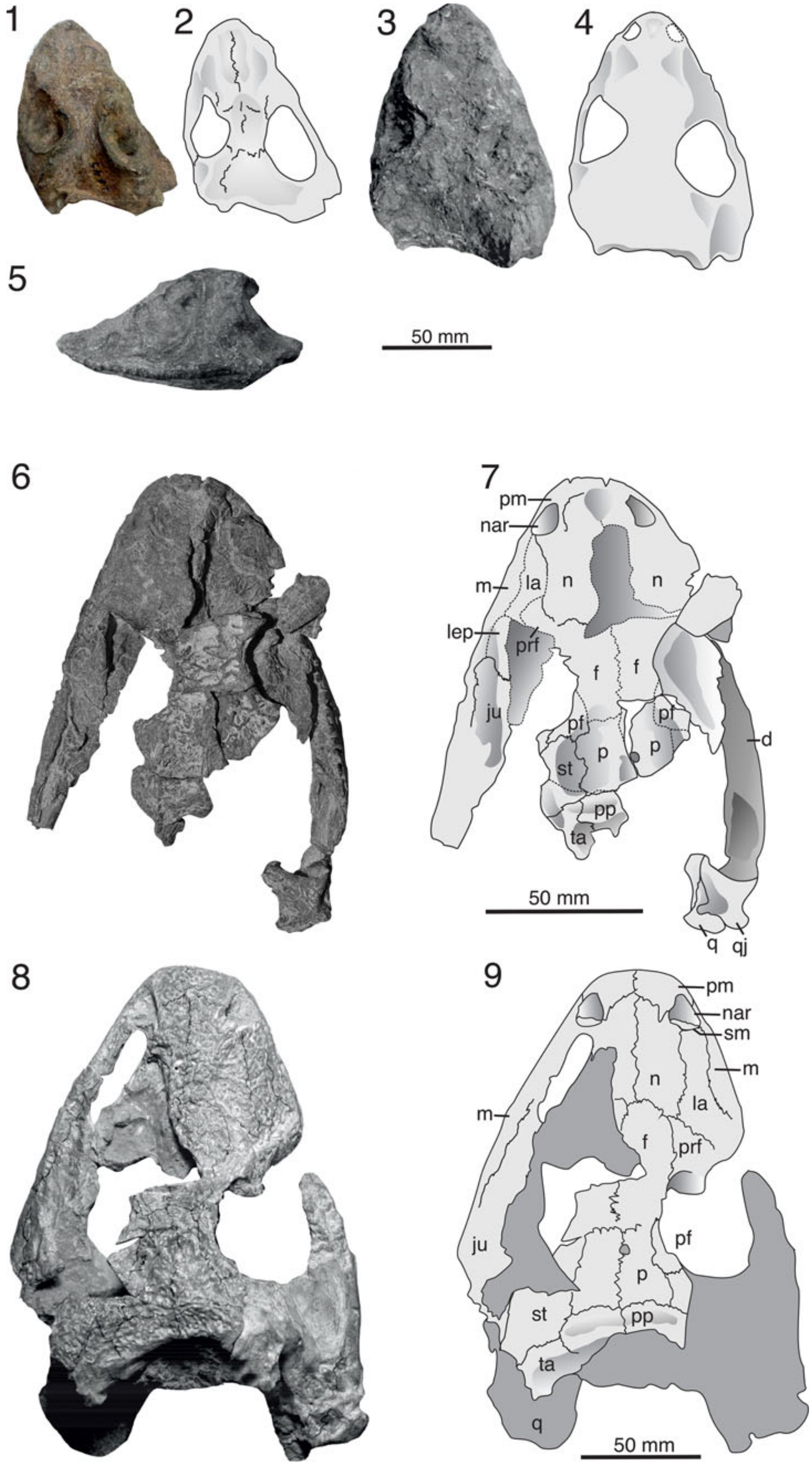

Figure 1. *Parioxys ferricolus* Cope, 1878, skulls. (**1, 2**) AMNH 2445: (**1**) photograph in dorsal view; (**2**) drawing of same specimen. (**3, 4**) AMNH 4309 (holotype): (**3**) photograph; (**4**) drawing. (**5**) AMNH 2445, lateral view. (**6, 7**) USNM 544065: (**6**) photograph; (**7**) drawing. (**8, 9**) MCZ 1162: (**8**) photograph; (**9**) drawing. d = dentary; f = frontal; ju = jugal; la = lacrimal; lep = laterally exposed palatine; m = maxilla; n = nasal; nar = naris; p = parietal; pf = postfrontal; pm = premaxilla; pp = postparietal; prf = prefrontal; q = quadrate; qj = quadratojugal; sm = septomaxilla; st = supratemporal; ta = tabular.

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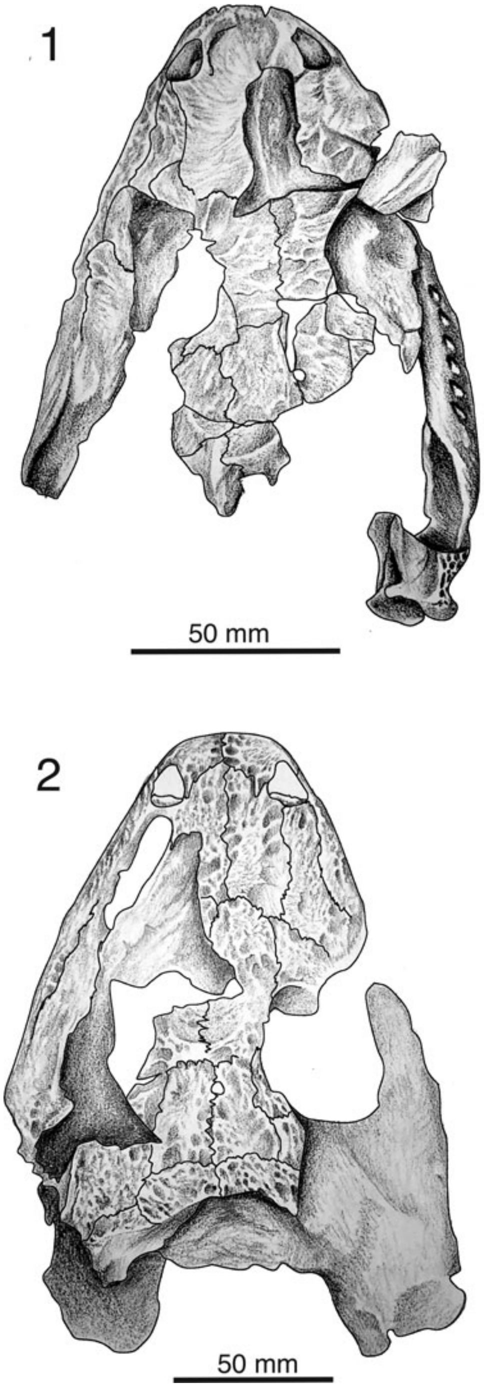

Figure 2. Detailed drawings of *Parioxys ferricolus* Cope, 1878. (**1**) USNM 544065 in dorsal view. (**2**) MCZ 1162 in dorsal view.

Reisz, 2020), *Anakamacops petrolicus* Li and Cheng, 1999 (Liu, 2018), *Broiliellus texensis* Williston, 1914, *Cacops* spp. (Williston, 1910; Reisz et al., 2009; Gee and Reisz, 2018), *Conjunctio multidens* Carroll, 1964a (Schoch and Sues, 2013), *Dissorophus multicinctus* Cope, 1895 (DeMar, 1968; Schoch, 2012), *Kamacops acervalis* Gubin, 1980 (Schoch, 1999), *Mattauschia laticeps* Milner, 2019, *Palodromeus bairdi* Schoch, Henrici, and Hook, 2020, *Scapanops neglecta* Schoch and Sues, 2013, and *Tersomius texensis* Case, 1910 (Carroll, 1964a; Maddin et al., 2013).

Systematic paleontology

Temnospondyli Zittel, 1888
Rhachitomi Watson, 1919 sensu Schoch, 2013
Dissorophoidea Bolt, 1969
Olsoniformes Anderson et al., 2008b
Dissorophidae Boulenger, 1902
Eucacopinae Schoch and Sues, 2013
Parioxys Cope, 1878

Type species.—*Parioxys ferricolus* Cope, 1878.

Diagnosis.—(1) Intercentra closed dorsally to form complete rings, (2) adductor ridge of femur not bifurcated at proximal end, (3) length of tibia 60% of femur length (based on MCZ 2262; Moustafa, 1955a; Carroll, 1964a; Schoch and Milner, 2014).

Occurrence.—Early Permian (Cisuralian); Texas, United States of America.

Remarks.—Moustafa (1955b) named a second species of *Parioxys, P. romeri*, on the basis of the distal end of a humerus (MCZ 1965) from the Petrolia Formation near Dundee, Archer County, Texas. The validity of this taxon is questionable. Carroll (1964b) proposed a third species of *Parioxys*, *P. bolli*, on the basis of a partial postcranial skeleton (AMNH 7118) from the Archer City Formation near Archer City, Archer County, Texas. He noted that only a few features distinguished *Parioxys bolli* from *P. ferricolus.*

Parioxys ferricolus Cope, 1878
Figures 1–4

Holotype.—AMNH 4309, poorly preserved, slightly distorted skull (120 mm length), damaged by crude preparation (Moustafa 1952a, 1955a, b; Schoch and Milner, 2014). Moustafa (1952a) identified this specimen as the lectotype from two specimens that Case (1911) considered syntypes of *Parioxys ferricolus* and referred the other skull (AMNH 4310) to *Eryops*.

Diagnosis.—Autapomorphies: (1) length of preorbital region 1.5 times that of posterior skull table in juveniles and twice that in adults; (2) parietal only two-thirds the length of the frontal; (3) interpterygoid vacuities shorter than half skull length; (4) choana extended posteriorly; (5) vomer with enlarged, V-shaped median depression; (6) palatine ramus of pterygoid anteriorly broadened to wedge between palatine and ectopterygoid.

Synapomorphies with *Cacops* spp. and *Kamacops acervalis*: lacrimal laterally constricted by wide maxillary shelf, narrower than alary process; LEP large, oval feature with concave dorsal surface; and tabular extended posteriorly.

Plesiomorphies (contrasting the condition in *Cacops* spp., *Kamacops acervalis*, and *Anakamacops petrolicus*): interorbital distance of adults wide (0.29); tabular not contacting or fused to quadrate.

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Occurrence.—Near Mt. Barry, Wichita County, Texas, USA; Petrolia Formation, Wichita Group, early Permian (Cisuralian). The referred specimens MCZ 1162 and USNM 544065 were collected from the Petrolia Formation at Dundee in Baylor County, Texas. The tetrapod assemblage from the Petrolia Formation is part of the Seymouran Land Vertebrate Faunachron sensu Lucas (2006).

Description.—*Parioxys ferricolus* has a moderately wide skull (width/length ratio = 0.92), which is narrower than in dissorophines, with relatively large orbits (orbit length/skull length ratio = 0.32) and a tapering preorbital region. The proportions of the skull roof (Figs. 1, 2) are intermediate between those of *Conjunctio multidens* and *Cacops morrisi* Reisz, Schoch, and Anderson, 2009. In the holotype, which is a small juvenile, the preorbital region measures 1.35 times the length of the postorbital skull table. This ratio increases in larger skulls (USNM 544065: 1.5; MCZ 1162: 2.0).

The preorbital region tapers toward the relatively narrow tip, which at the posterior level of the nares measures only 0.55–0.58 times the width of the skull level with the anterior orbital margin. This feature is isometric throughout the preserved size range. The external naris is like that of *K. acervalis* and *Cacops* spp. in being confined to the tip of the snout, contrasting with the much larger opening in *Conjunctio multidens*. There is a shallow depression between the nares in some specimens, but no fontanelle (Figs. 1.7, 4.1). A wedge-shaped septomaxilla is preserved and well exposed on the posterior margin of the naris of MCZ 1162 (Fig. 1.9); it remains unclear whether the bone also included an internal narial portion as in some other temnospondyls.

The premaxilla bears five large teeth. The most completely preserved maxilla has 23 teeth (USNM 544065), with space for 10 additional ones, judging from their relatively equidistant implantation. The nasal, lacrimal, and prefrontal have proportions similar to those in *C. morrisi*, and the concave lateral suture of the lacrimal is particularly similar in these two taxa. A faint central depression is developed on the dorsal surface of the nasals and anterior portion of the frontals, but crushing may have somewhat altered the surface relief.

The pineal foramen is much smaller than in *Cacops morrisi* and *Conjunctio multidens*, and it is emplaced on a gentle eminence at the anterior margin of a medial depression (Fig. 1). The postparietal is short, its dorsal portion reaching only one-third the length of the parietal. In USNM 544065 and AMNH 2445, it bears a transverse ridge along the occipital margin that continues onto the tabular where it ends at the posterior tip of the tabular horn. In AMNH 4309 and MCZ 1162, the ridge is much lower and not continuous (Figs. 1, 2). In USNM 544065, the transverse ridge bifurcates on the tabular, with an anterior branch extending along the supratemporal and postfrontal, similar to the condition in *Cacops morrisi*.

The postorbital region of the skull has a slightly rounded, convex lateral margin. It is shorter and wider than in other eucacopines, with the length/width ratio of the postorbital skull region ranging from 0.43 in juveniles to 0.34 in adults. A contact between the postorbital and squamosal is probably present, considering the proportions of the bones, but not exposed. The supratemporal is longer and the parietal is anteriorly wider than in *C. morrisi*, both having rectangular outlines. The suture between the supratemporal and parietal is markedly curved in double S-shaped fashion in USNM 544065 (Fig. 1).

The squamosal and quadratojugal are not preserved in the larger specimens, but this region is known in AMNH 2445 (Fig. 1). In lateral view, the skull is dorsoventrally deepest at the level of the posterior margin of postparietals and continuously decreases in height toward the tip of the snout. The quadrate has a rudimentary dorsal process, much less developed than in juveniles of *C. morrisi*; thus, a late-ontogenetic closure of the squamosal embayment was absent in *P. ferricolus*, which differs strongly from the condition in *Cacops* spp., *Kamacops acervalis*, *Anakamacops petrolicus*, and *Zygosaurus lucius* Eichwald, 1848.

Palate.—The palate is morphologically intermediate between those of *Cacops* spp. and *Kamacops acervalis* in many features. Its entire preserved ventral surface is covered by closely set, uniformly-sized denticles (Fig. 2). The vomer, palatine, and ectopterygoid are almost completely preserved, but the pterygoid is known only by fragments of its palatine and basipterygoid rami in USNM 544065 and the outline of the quadrate ramus in MCZ 1162. The basal plate of the parasphenoid is well preserved in MCZ 1162a (Fig. 3.5), whereas most of the cultriform process remains unknown. Sutures between any palatal elements cannot be traced in USNM 544065, but there is a fragment of the marginal palate (MCZ 1162b) that preserves sutures well (Fig. 3.6).

The vomer is proportionately longer than in *K. acervalis* and more expanded posteriorly than in any other known dissorophoid except for *Macrerpeton huxleyi* Moodie, 1909 (Schoch and Milner, 2021). In USNM 544065, the complete vomerine dentition is exposed, covering the entire surface of the element. The medial region is strongly concave, spanning the entire length of the vomers. Although probably homologous with the anterior depression in *C. morrisi*, this depression is more comparable in size to the intervomerine depression of zatracheids than to that of dissorophoids (Witzmann and Schoch, 2006). The dentigerous lateral parts of the vomers are gently convex on the ventral side.

The long and narrow choanae are exposed in both MCZ 1162 and USNM 544065 (Fig. 3). This proportionately matches the length of the choana in *K. acervalis* and is much longer than in other eucacopines (Fig. 4).

The interpterygoid vacuity is smaller than in *Cacops* spp. but substantially larger than that in *K. acervalis*. It shares the straight sagittal lateral margin with both. The basipterygoid ramus, which is entirely covered with denticles, is shorter than in *C. morrisi* but not as abbreviated and plate-like as in *K. acervalis*. The dorsal side bears a large, raised socket for the epipterygoid. The palatine ramus of the pterygoid forms a broad, medially expanded plate with the palatine. This region is best preserved in the fragmentary specimen MCZ 1162b (Fig. 3.6), where the sutures are visible. The palatine is an abbreviated element, completely and widely separated from the interpterygoid vacuity by a broadened palatine ramus of the pterygoid (Figs. 3.6, 4.3). This ancestral condition is unparalleled in dissorophids, but a contact between pterygoid and vomer is common in trematopids (Polley and Reisz, 2011; Milner, 2019). However, the marked broadening of the palatine ramus and its wedging between the palatine and ectopterygoid form apomorphic character states. The vomer, palatine, and

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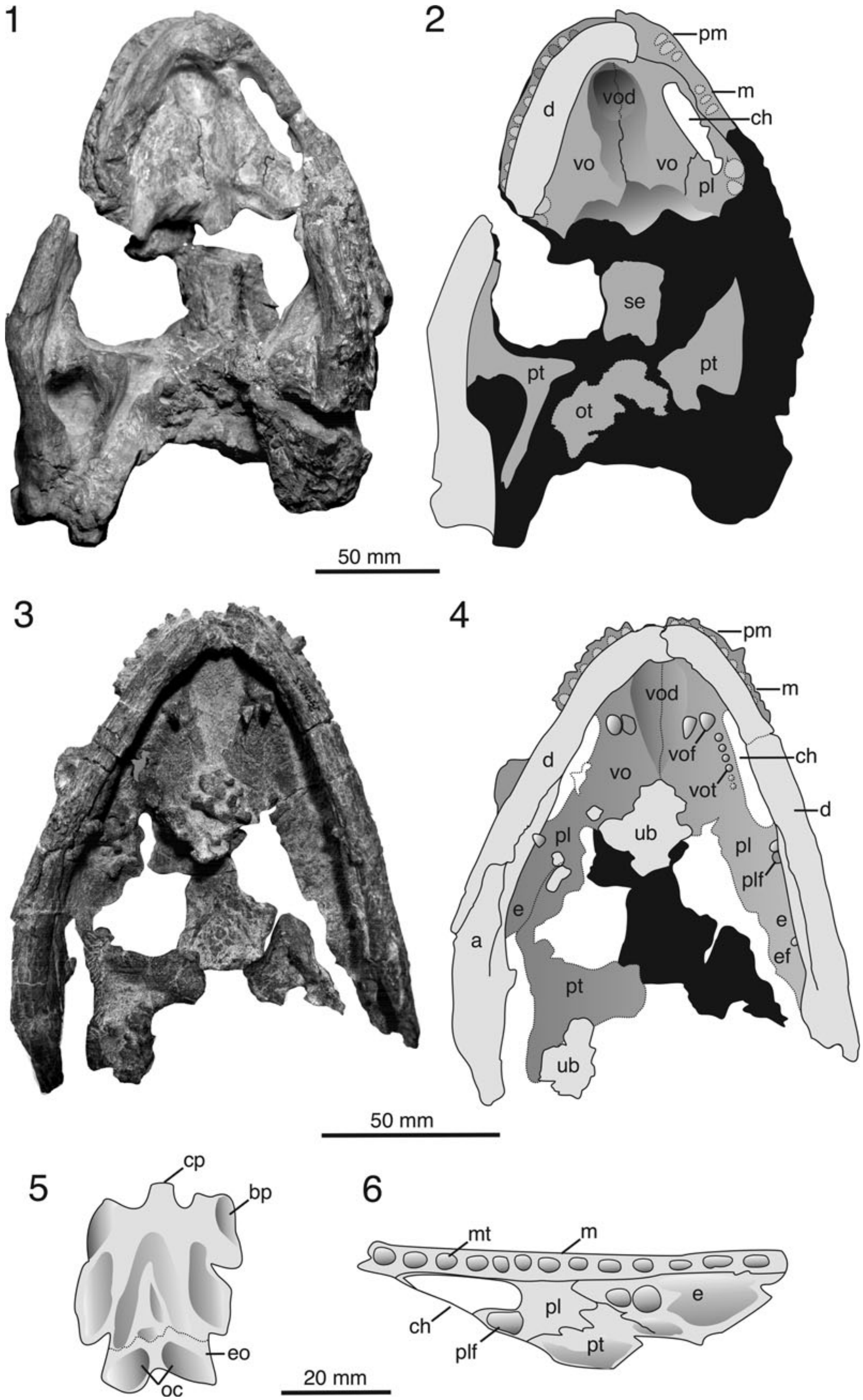

Figure 3. *Parioxys ferricolus* Cope, 1878. (**1, 2**) Palate in ventral view. MCZ 1162: (**1**) photograph; (**2**) drawing. (**3, 4**) USNM 544065: (**3**) photograph; (**4**) drawing. (**5**) MCZ 1162a, drawing of parasphenoid in ventral view. (**6**) MCZ 1162b, drawing of marginal palate in ventral view. a = angular; bp = basipterygoid joint; ch = choana; cp = cultriform process; d = dentary; e = ectopterygoid; ef = ectopterygoid fang; eo = exoccipital; m = maxilla; mt = maxilla tooth; oc = occipital condyle; ot = otic region; pl = palatine; plf = palatine fang; pm = premaxilla; pt = pterygoid; se = sphenethmoid; ub = unidentified bone; vo = vomer; vod = vomerine depression; vof = vomerine fang; vot = vomerine tooth row.

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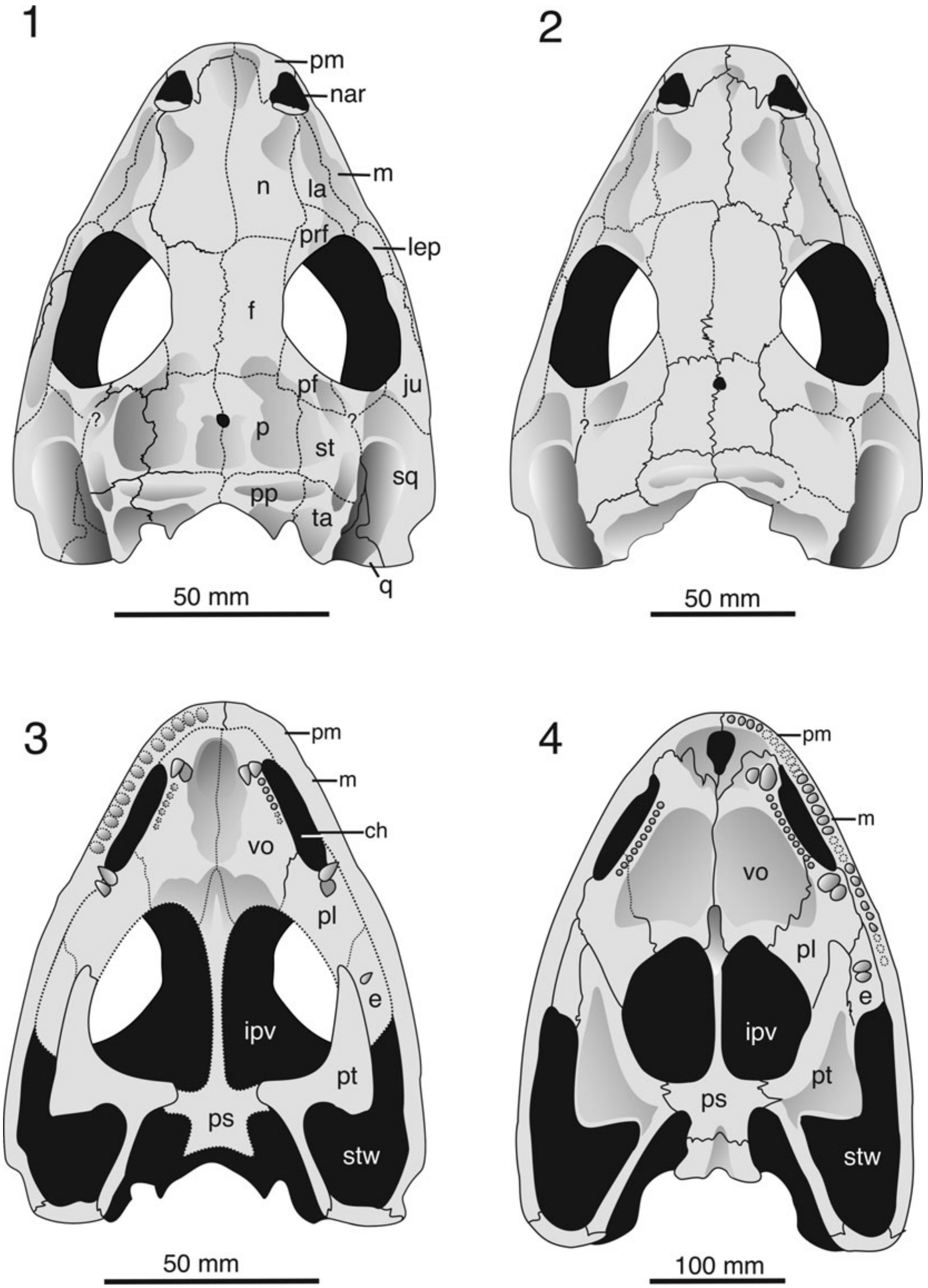

Figure 4. (**1–3**) *Parioxys ferricolus* Cope, 1878. Reconstructions of skulls: (**1**) large juvenile skull based on USNM 544065, dorsal view; (**2**) adult skull based on MCZ 1162, dorsal view; (**3**) Juvenile skull based largely on USNM 544065, supplemented by MCZ 1162, ventral view. (**4**) *Kamacops acervalis*, ventral view (modified from Schoch, 1999). ch = choana; e = ectopterygoid; f = frontal; ipv = interpterygoid vacuity; ju = jugal; la = lacrimal; lep = laterally exposed palatine; m = maxilla; n = nasal; nar = naris; p = parietal; pf = postfrontal; pl = palatine; pm = premaxilla; pp = postparietal; prf = prefrontal; ps = parasphenoid; pt = pterygoid; q = quadrate; sq = squamosal; st = supratemporal; stw = subtemporal window; ta = tabular; vo = vomer.

ectopterygoid all bear large, recurved tusks, with those of the vomer slightly taller than the others (Fig. 4).

The parasphenoid is well preserved in MCZ 1162a, where the base of the very slender cultriform process is present. Consistent with *Kamacops*, the basal plate is very long with pronounced, offset posterolateral wings. Unlike the latter, the suture with the exoccipital is hardly visible, and the ventral surface of the plate bears a large inverted-V-shaped depression. Otherwise,

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this region is smooth without tooth patches, and foramina for the carotid artery are absent. The basipterygoid process is also clearly offset and appears to have been less firmly sutured with the pterygoid than in other eucacopines.

Neurocranium.—The sphenethmoid and otic region are exposed in MCZ 1162 (Fig. 3.2). The sphenethmoid is relatively wide but ends well anterior to the otic region. The otic was fully ossified, without separation into pro- and opisthotic portions.

Visceral skeleton.—The stapes and elements of the hyobranchial apparatus remain unknown.

Mandible.—Moustafa (1955a) figured and described the mandible in detail. The lower jaw agrees in most features with that in *C. morrisi* (Gee and Reisz, 2018). The posterior half of the jaw is lower dorsoventrally than in *C. morrisi*, and its ventral margin is almost straight. The angular is not as expanded dorsally, but the coronoid process is taller and more rounded than in *C. morrisi*, with a continuously sloping anterior margin rather than forming an abrupt edge. The dentary bears at least 26 large conical and recurved teeth. The size of the teeth decreases somewhat posteriorly, where they have broader bases. The adductor fenestra has a low lingual margin formed by the prearticular. The size of the coronoid and splenial was correctly illustrated by Moustafa (1955a).

Postcranial skeleton.—MCZ 1162 comprises a set of at least eight partial skeletons (Moustafa, 1952b). As Moustafa (1955a) already illustrated many postcranial elements in detail, we do not provide figures here. He emphasized the rhachitomous structure of the anterior vertebral column, with semilunar intercentra; in the posterior portion, they are higher and nearly form closed discs, consistent with the condition in other dissorophids (Moustafa, 1955b, pl. 4). The previously undescribed USNM 544065 includes fragments of limb bones and a complete right half of the pelvis. The girdles and limbs include some interesting features that differ from the corresponding ones in *Cacops morrisi*. The scapula is dorsoventrally lower in *P. ferricolus*, dorsally expanded, and co-ossified with the coracoid. The humerus is more robust than in *C. morrisi*, but its articular ends are not as wide as in *C. aspidephorus* Williston, 1910. The supinator process is more clearly defined than in the two species of *Cacops*. In the fully ossified pelvis, the ilium has an anterodorsally expanded portion and the dorsal margin slopes posteroventrally, forming a posterior process. The ischium is elongate and bears a posterolateral process, and the pubis has a slight anterodorsal extension.

Remarks.—None.

Phylogenetic relationships

To assess the phylogenetic position of *Parioxys ferricolus*, we performed a phylogenetic analysis using the character–taxon matrix for dissorophoids recently published by Schoch et al. (2020; see supplementary Appendix).

Phylogenetic analysis.—The analysis was performed using TNT 1.5 (available at https://cladistics.org/tnt/), under the New Technology Search option (Fig. 5). It recovered five equally most parsimonious trees (tree length [TL] = 291 steps; consistency index [CI] = 0.432; retention index [RI] = 0.76). The character descriptions and character–taxon matrix are provided at https://doi.org/10.5061/dryad.tb2rbp02d. All multistate characters were ordered. *Dendrysekos helogenes* Steen, 1934 (=*Dendrerpeton acadianum* Owen, 1853 of many former authors; see discussion in Schoch and Milner, 2014) was used as the outgroup. Scores for the following additional taxa were added: *Anakamacops petrolicus* (Gee and Reisz, 2020), *Kamacops acervalis* (Gubin, 1980; Schoch, 1999), *Scapanops neglecta* (Schoch and Sues, 2013), and *Parioxys ferricolus* (based on the present study).

In a variant analysis, the dissorophoid *Reiszerpeton renascentis* (Maddin et al., 2013) was added, which has recently been found as a potential relative of eucacopines (Gee et al., 2021). This analysis obtained four most parsimonious trees with poorer resolution of eucacopines (TL = 298 steps; CI = 0.42; RI = 0.75).

Phylogenetic position of Parioxys ferricolus.—The topology of the trees is essentially like that found by Schoch (2019) and Schoch et al. (2020). *Perryella olsoni* Carlson, 1987 nests at the base of Dissorophoidea, *Micromelerpeton credneri* Bulman and Whittard, 1926 (representing Micromelerpetidae, which is not further discussed here) is recovered as the basalmost dissorophoid, followed by a clade Amphibamiformes + Olsoniformes. Amphibamiformes comprises four successive clades, Micropholidae (*Eoscopus*, *Tersomius*, *Pasawioops, Micropholis*), Amphibamidae (*Platyrhinops*, *Amphibamus*, *Doleserpeton*), Branchiosauridae (*Apateon*, *Leptorophus*, *Schoenfelderpeton*), and Lissamphibia plus its respective stem groups (*Georgenthalia*, *Gerobatrachus*, *Eocaecilia*, *Karaurus*, *Triadobatrachus*). The internal structure of Olsoniformes is not fully resolved, with *Actiobates*, *Mattauschia*, and *Palodromeus* forming an unresolved polytomy with the rest, followed by a second polytomy with *Ecolsonia* + *Fedexia* and *Tambachia*, *Phonerpeton*, and *Acheloma*, and finally Dissorophidae. The latter comprises two subclades, Dissorophinae with *Broiliellus* and *Dissorophus* and Eucacopinae, with the following branching sequence: (1) *Scapanops neglecta*, (2) *Conjunctio multidens*, (3) *Anakamacops petrolicus*, (4) *Cacops morrisi*, (5) *Parioxys ferricolus*, and (6) *Kamacops acervalis*.

The resolution of eucacopines is lowered when *Reiszerpeton renascentis* is added to the analysis, which results in a polytomy within that clade. In such a variant analysis, *R. renascentis* is not found to nest with dissorophids, but with *Ecolsonia cutlerensis* Vaughn, 1969 within a poorly resolved basal part of the olsoniform tree, which probably highlights our poor knowledge of that taxon.

Discussion

Parioxys ferricolus shares many features with eucacopines and belongs to a more inclusive group of that clade comprising *Cacops* spp. and *Kamacops acervalis*. However, understanding the phylogeny of eucacopines is hampered by the fact that most taxa are still incompletely known: the postcranium is well preserved in only two taxa, *Cacops morrisi* and *C. aspidephorus*; the palate remains unknown in *Scapanops neglecta*; and the

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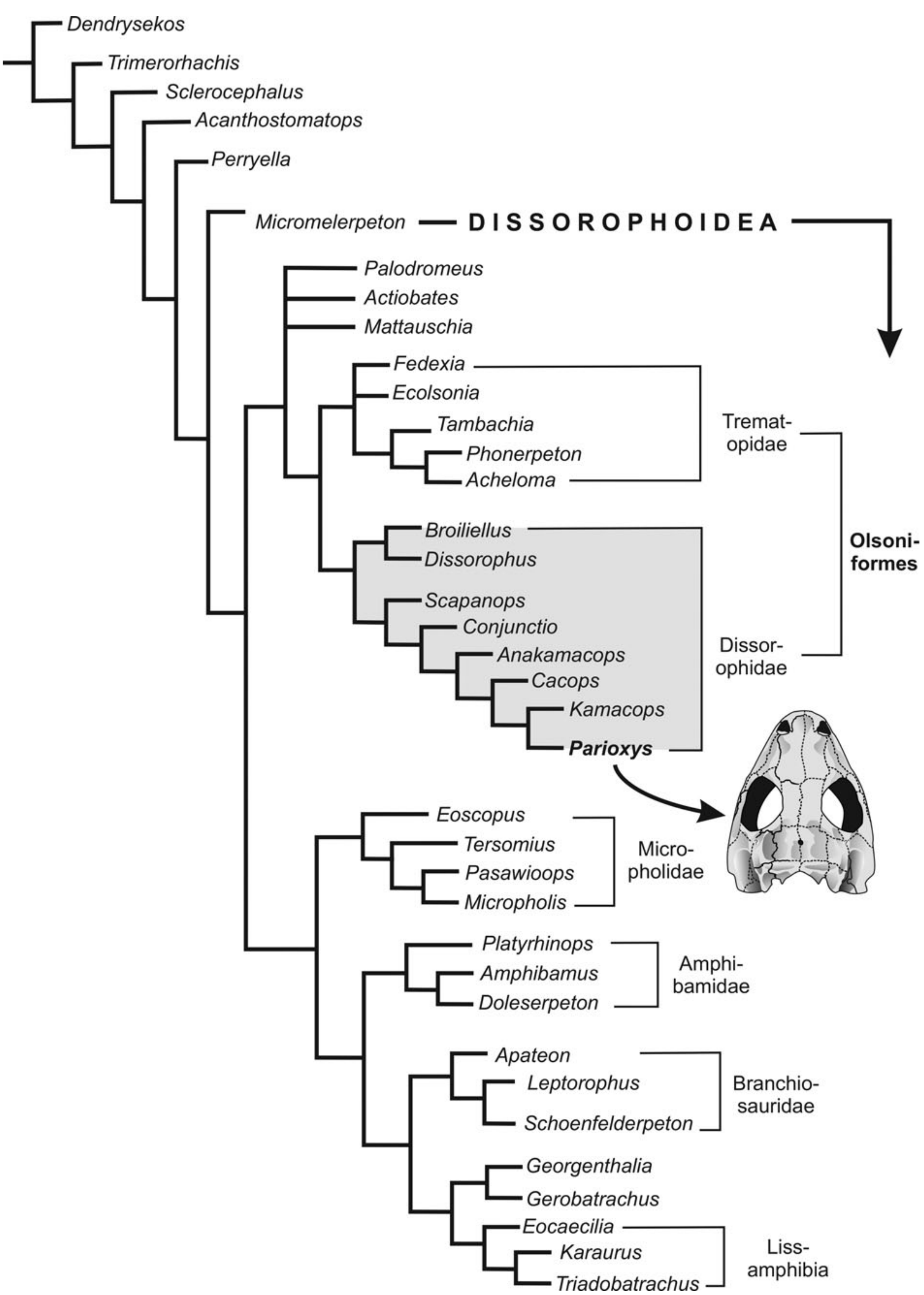

Figure 5. Phylogeny of dissorophoid temnospondyls, with particular emphasis on the Dissorophidae and the position of *Parioxys ferricolus* Cope, 1878.

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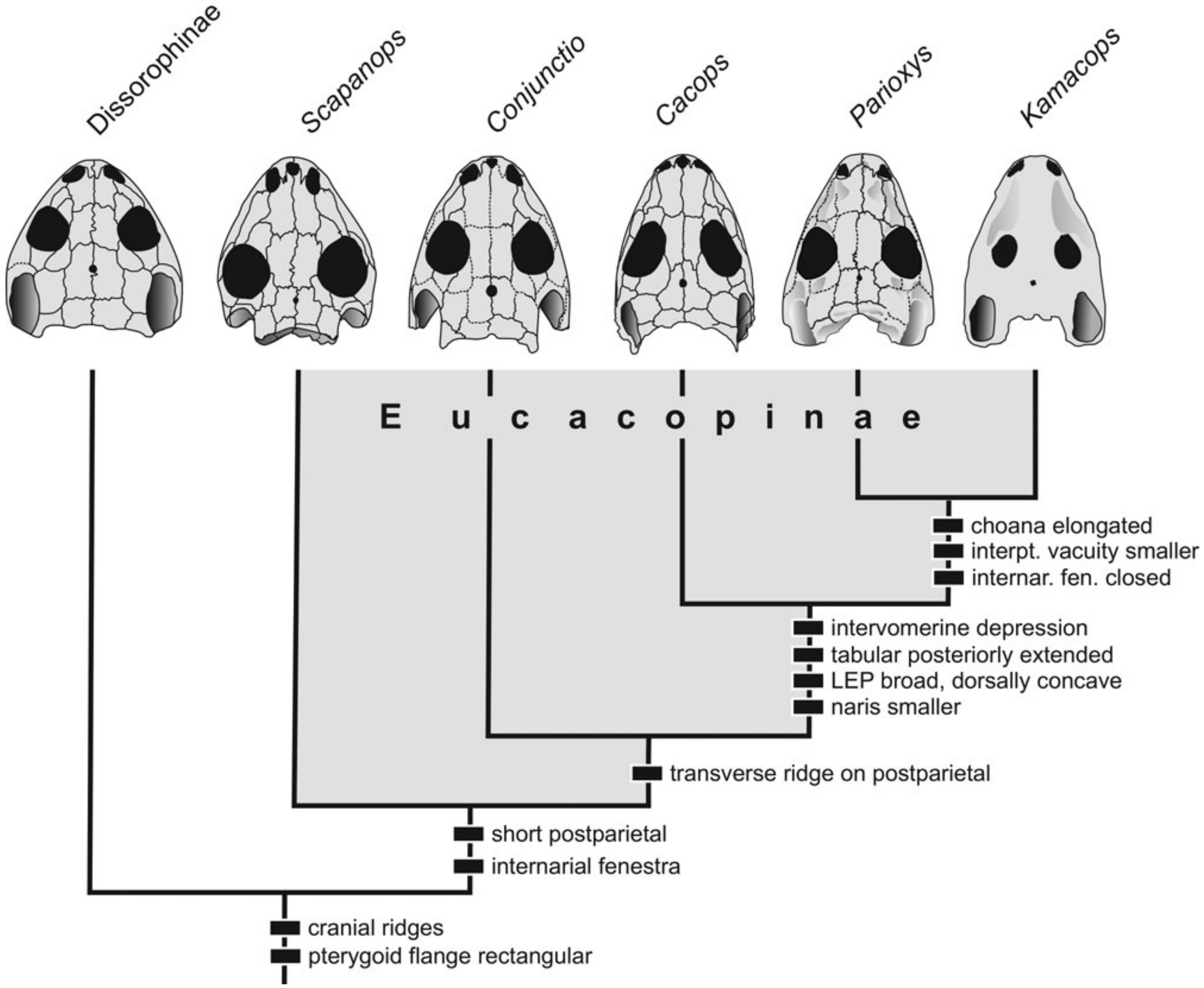

Figure 6. Character evolution in dissorophids, with particular emphasis on the eucacopines and *Parioxys ferricolus*.

sutures are only partially documented for both *Parioxys ferricolus* and *Anakamacops petrolicus* and remain unknown in *Kamacops acervalis*.

The lost holotype of *Zygosaurus lucius*, a steinkern that lacked most of the bone from the middle Permian (Guadalupian) of Bashkortostan (Russia), is rather different from other eucacopines, but its otic notch closely resembles that in *Cacops* spp. (Eichwald, 1848). Unlike all other eucacopines, *Z. lucius* and *A. petrolicus* share an enlarged otic notch that constricts the postorbital skull region laterally, but the orbits differ strongly in size.

Phylogenetic analysis (Fig. 6) indicates that *Scapanops neglecta* may be the basalmost eucacopine, but this remains tentative due to the large amount of missing data. In addition to the many unknown features, *Scapanops neglecta* has a highly autapomorphic skull roof, but it shares with eucacopines the abbreviated postparietal and internarial fenestra. Like *Conjunctio multidens*, it has numerous tiny maxillary teeth, indicating that eucacopines may initially have subsisted on small invertebrate prey, just as the basal olsoniform *Palodromeus bairdi* and amphibamiforms in general. Autapomorphic features of *Scapanops neglecta* are the transverse ridge on the posterior portion of the nasals and the dorsally placed, elongate oval external nares.

A rather well-supported clade encompasses *Conjunctio multidens*, *Cacops* spp., *Parioxys ferricolus*, and *Kamacops acervalis*. *C. multidens* retained a relatively long postorbital skull table, like dissorophines, trematopids, and *Palodromeus bairdi*, but the general proportions of the orbits and snout are like those of *Cacops* spp. and *Parioxys ferricolus*.

Eucacopines more derived than *Conjunctio multidens* have fewer and larger marginal teeth and greatly enlarged, recurved palatal tusks, indicating a change to seizing and swallowing larger prey. *Kamacops acervalis*, the poorly known *Iratusaurus vorax* Gubin, 1980, and *Anakamacops petrolicus* probably had evolved to become major predators in their respective ecosystems.

Eucacopines more derived than *Conjunctio* have more robust skulls with a more pronounced surface relief. The eminences on the skull roof include a prominent ridge connecting the supratemporal with the postfrontal, which is also present in *Dissorophus multicinctus*, *Cacops* spp., and *Parioxys ferricolus*, whereas it extends further laterally across the postorbital in

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Conjunctio multidens. The tabular and postparietal flanges along the occipital margin increase in size from *Conjunctio multidens*, *Cacops* spp., and *P. ferricolus* to *K. acervalis*, *A. petrolicus*, and *Z. lucius*. In all these taxa, except for *P. ferricolus*, the tabular contacts the quadrate; this closure of the otic notch occurred only in late ontogeny in *C. morrisi* (Reisz et al., 2009).

Cacops spp. and *P. ferricolus* share additional apomorphic character states, such as the shorter prefrontal, the smaller external naris, and the enlarged LEP with its concave dorsal surface. These features are possibly shared with *K. acervalis* and others, which remains unclear due to missing data concerning sutures. However, *P. ferricolus* and *K. acervalis* appear to be advanced beyond the condition in *Cacops* spp. in the following character states: (1) smaller interpterygoid vacuities, resulting from the medial expansion of palatine and pterygoid (condition more extreme in *K. acervalis*), (2) the enlarged vomer with the posteriorly elongated, slit-like choana, and (3) the absence of an internarial fenestra. All eucacopines more derived than *Conjunctio multidens* share the tendency to form pronounced dermal sculpture on the skull roof, which usually obscures the sutures in adults.

The large eucacopines probably evolved into niches occupied by trematopids in other ecosystems. It is noteworthy that the former apparently did not co-exist with the latter, and, in at least some assemblages with both trematopids and eucacopines, the latter were substantially smaller, such as the Sakmarian-age fissure fillings at Fort Sill, Oklahoma (Polley and Reisz, 2011; Gee and Reisz, 2018).

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Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tb2rbp02d

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