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The amphibamiform *Nanobamus macrorhinus* from the early Permian of Texas

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Abstract.—*Nanobamus macrorhinus* Schoch and Milner, 2014 is a small amphibamiform temnospondyl from the early Permian Arroyo Formation of Texas. It is most readily characterized by an elongate and partially subdivided naris. This condition is superficially reminiscent of that seen in the coeval trematopids, the group to which *N. macrorhinus* was originally referred to under an interpretation of the holotype as a larval form. This was discounted by later workers, but the amphibamiform affinities of the specimen were not formalized until recently. The specimen has never been described in the context of its amphibamiform affinities and remains poorly characterized, never having been sampled in a phylogenetic analysis. Here we present a complete, updated osteological description of *N. macrorhinus*, including an improved characterization of its unique mosaic of plesiomorphic and apomorphic features and clarification of the taxon's autapomorphies. Our analysis of the taxon's phylogenetic position within Amphibamiformes shows that *N. macrorhinus* was recovered as diverging after basal amphibamiforms, e.g., the micropholids, and before derived amphibamiforms, e.g., the amphibamids. This is supported by the unique mixture of retained plesiomorphies, e.g., nonforeshortened postparietals and an oval choana, and apomorphies, e.g., a narrow interorbital region and slender palatal rami of the pterygoid. These results reflect the complexity of terrestrial amphibamiform diversity and provide further insight into the evolutionary history of the lissamphibian stem in terrestrial environments.

Introduction

Amphibamiforms ('amphibamids' in the traditional sense + branchiosaurids) are a clade of small-bodied dissorophoid temnospondyls that are widely recognized to be closely related to some (e.g., Anderson et al., 2008b; Pardo et al., 2017) or all (e.g., Sigurdsen and Bolt, 2010; Schoch, 2019) of the lissamphibian crown group. These stem lissamphibians occur primarily in Permo-Carboniferous deposits of North America (predominantly terrestrial amphibamiforms) and Europe (primarily branchiosaurids), with the terrestrial *Micropholis stowi* Huxley, 1859 also being known from the early Triassic of South Africa.

Nanobamus macrorhinus Schoch and Milner, 2014 is a poorly known amphibamid represented by a complete but poorly preserved skull (UCLA VP 3686) from the Texas red beds measuring ~2 cm in midline length. The specimen was first described by Olson (1985) as a larval trematopid. Olson's referral was based primarily on two lines of evidence: the elongate naris, which closely resembles that seen in trematopids, and the absence of any dissorophoids from the same stratigraphic context (the middle of the Arroyo Formation) with similar nares. Olson noted many similarities of this specimen to small-bodied dissorophoids (including amphibamiforms) but ultimately argued for its trematopid affinities and concluded that many of the differences between trematopids and other dissorophoids (e.g., reduction of size of the orbits and the interpterygoid vacuities) characterized early trematopid ontogeny.

The specimen was subsequently reappraised by Dilkes (1991) who argued that although the elongate naris bore superficial similarities to that of trematopids, the specific architecture of the elements surrounding the naris was fundamentally different. More specifically, the prefrontal is fully excluded from the posterodorsal margin of the naris, in contrast to all known trematopids. This was later affirmed by the study by Dilkes (1993), which presented a partial ontogenetic series of the narial region in trematopids and which showed no evidence for such an ontogenetic transformation. Dilkes identified UCLA VP 3686 as Dissorophoidea incertae sedis, but he did exclude trematopids from consideration. Dissorophids (which at the time comprised dissorophids and amphibamiforms in the modern framework) were not excluded from consideration.

Dilkes noted that an increased understanding of trematopid anatomy suggested that Olson's (1985) original interpretation might have been inaccurate. By the same token, we note that greatly increased understanding of the Dissorophoidea in the last three decades can inform on the taxonomy of UCLA PV 3686. At the time of Dilkes' (1991) study, the term 'amphibamid' was not even in widespread usage (until it was revived by Daly, 1994), and only a few taxa were well characterized. Since then, eight new terrestrial (i.e., non-branchiosaurid) amphibamiform taxa have been described: *Eoscopus locklardi* Daly, 1994, *Plemmyradytes shintoni* Huttenlocker, Pardo, and Small, 2007, *Georgenthalia clavinasica* Anderson et al., 2008a, *Gerobatrachus hottoni* Anderson et al., 2008b, *Pasawioops mayi* Fröbisch and Reisz, 2008, *Rubeostratilia* *texensis* Bourget and Anderson, 2011, *Platyrhinops fritschi* Werneburg, 2012, and *Tersomius dolesensis* Anderson and Bolt, 2013. Most of the previously described taxa have been re-examined: *Micropholis stowi* (Schoch and Rubidge, 2005), *Platyrhinops lyelli* Wyman, 1858 (Clack and Milner, 2010), *Doleserpeton annectens* Bolt, 1969 (Sigurdsen and Bolt, 2010), and *Tersomius texensis* Case, 1910 (Maddin et al., 2013). The phylogenetic intrarelationships of the clade have been further examined (e.g., Schoch and Milner, 2008; Fröbisch and Schoch, 2009a), leading to revised nomenclature (e.g., restriction of Amphibamidae to the least inclusive clade including *Amphibamus grandiceps* Cope, 1865 and *Doleserpeton annectens*) and the growing consensus that Branchosauridae nests within Amphibamiformes. Schoch (2002, p. 319) mentioned that UCLA VP 3686 represented a mature amphibamid (in the historic use of the term), but the taxonomy of UCLA VP 3686 was not formalized until it was erected as the holotype of *Nanobamus macrorhinus* by Schoch and Milner (2014), who presented only a taxonomic diagnosis and reconstructed line drawing derived largely from the study by Dilkes (1991). Here, we present a complete comparative anatomical description of UCLA VP 3686 and place it using a phylogenetic analysis that properly compares and contextualizes it within amphibamiform evolution.

Materials and methods

Phylogenetic analysis.—To test the relationships of *Nanobamus macrorhinus* within Dissorophoidea at large and more specifically within Amphibamiformes, we utilized the matrix of Schoch (2019), which originally included 34 taxa and 108 characters. *Nanobamus* could be coded for 65 of the total 108 characters (60% completeness); no postcranial characters could be coded. One coding was changed from that of Schoch (2019): for character 39 (external narial opening), we changed *Georgenthalia clavinasica* from 0 to 1, reflecting the ‘keyhole-shaped’ naris described by Anderson et al. (2008a) that is shared with *N. macrorhinus*. We performed a maximum parsimony analysis in PAUP 4.0b164 for Macintosh (Swofford, 2002) with multistate characters ordered, a heuristic search, simple stepwise addition, and *Dendrysekos helogenes* Steen, 1934 as the outgroup. As with Schoch (2019), changing all multistate characters to be unordered did not produce any changes to the strict consensus, so these characters were maintained as ordered in all subsequent permutations and in the supplemental data matrix. Following a reviewer’s suggestion, we also ran the analysis with random addition sequence stepwise addition (10,000 reps), which resulted in the strict consensus tree remaining the same. A bootstrap analysis with 1,000 replicates was also performed. Following Schoch (2019), three permutations with slightly reduced character sampling were performed: (1) the removal of character 17 (postparietal length); (2) the removal of character 30 (a second postparietal length character); and (3) the removal of both characters, with bootstrap analyses performed on each permutation. Schoch’s original analysis examined these permutations because of previous concerns over the independence or redundancy of these characters. The NEXUS file is available as a supplemental datafile to this paper.

Repositories and institutional abbreviations.—MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts, USA; UCLA VP = University of California Los Angeles, Vertebrate Paleontology, Los Angeles, California, USA. The specimen is now reposited at the UCMP = University of California Museum of Paleontology, Berkeley, California, USA.

Systematic paleontology

Superfamily Dissorophoidea Bolt, 1969
Unranked clade Xerodromes Schoch and Milner, 2014
Unranked clade Amphibamiformes Schoch, 2019
Genus *Nanobamus* Schoch and Milner, 2014

1985 Trematopidae indet. Olson, p. 1176, 1177, figs. 1–6.
1991 Dissorophoidea incertae sedis Dilkes, p. 1491, fig. 1.

Type species.—*Nanobamus macrorhinus* Schoch and Milner, 2014 from the Arroyo Formation of Texas, by original designation.

Revised diagnosis.—As for the type species, by monotypy.

Remarks.—We have slightly modified the diagnosis from that of Schoch and Milner (2014) to clarify a number of features.

Nanobamus macrorhinus Schoch and Milner, 2014
Figures 1–5

Holotype.—Complete skull with associated left mandible (UCLA VP 3686) from the Arroyo Formation, Baylor County, Texas (Schoch and Milner, 2014, p. 60, 61, fig. 29G). This specimen is now catalogued as UCMP 203686 and is referred to as such for the remainder of the paper.

Revised diagnosis.—Small amphibamiform characterized by the following combination of characters: (1) posteriorly expanded external naris that partially incises the anteroventral portion of the lacrimal and that is partially subdivided by a ventral extension of the nasal and by the lacrimal, forming a keyhole-shaped outline superficially resembling that of trematopids (shared with *Georgenthalia clavinasica*); (2) interorbital width narrow, being less than the width of the orbit in dorsal profile (shared with most post-Carboniferous terrestrial amphibamiforms); (3) frontals that taper posteriorly to a width half that of the anterior region (shared with *Rubeostratilia texensis*); (4) presence of denticle field extending onto the posterior third of the cultriform process; (5) large postfrontal with long circumorbital processes anteriorly and laterally and prominent postermedial expansion that constricts the parietal anteriorly; and (6) slender basipterygoid processes of the pterygoid extending far medially onto the basal plate of the parasphenoid.

Occurrence.—Olson (1985) stated that the specimen came from the Arroyo Formation of the Clear Fork Group in Baylor County, Texas. Per Olson (1985, p. 1173), “the site from which it was taken lies about two-tenths of a mile south of the Wilbarger County line and five miles west of the Seymour-Vernon road

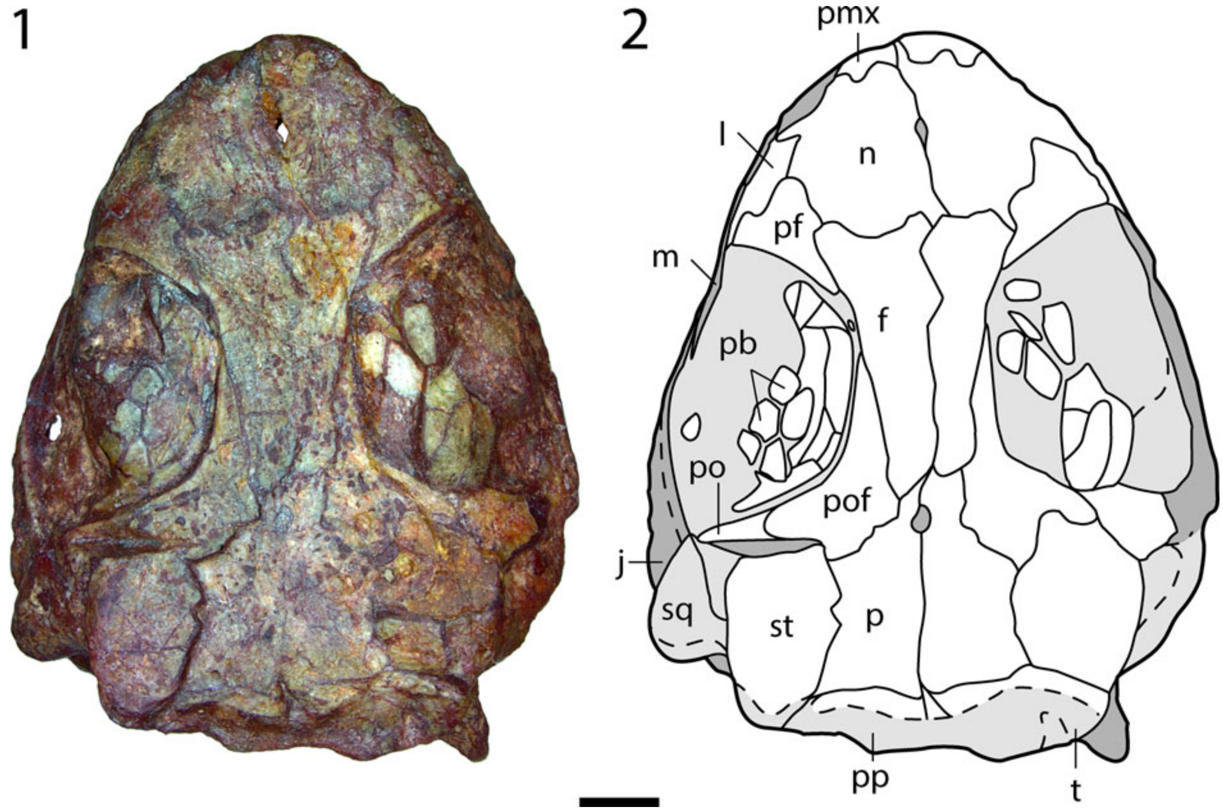

Figure 1. Dorsal profile of the holotype of *Nanobamus macrorhinus*, UCMP 203686: (**1**) photograph; (**2**) line drawing. f = frontal; j = jugal; l = lacrimal; m = maxilla; n = nasal; p = parietal; pb = palpebral bone; pf = prefrontal; pmx = premaxilla; po = postorbital; pof = postfrontal; pp = postparietal; sq = squamosal; st = supratemporal; t = tabular. Shading utilized to indicate relative depth. Scale bar = 2 mm.

(U.S. 283). Coordinates are approximately 33°49′N, 99°14′W." This was maintained by Dilkes (1991). However, this provenance is at odds with that listed by Schoch and Milner (2014, p. 61), who stated that the type locality is the Archer City bonebed in Archer County, immediately to the east of Baylor County. These authors did not comment on this apparent disparity and have since indicated that the original provenance should be retained (personal communication to BMG, R.R. Schoch, 2019).

Description.—The skull of UCMP 203686 is relatively long for an amphibamiform, with a gently rounded snout and gradual expansion of the posterior skull table. The orbits are proportionately large, being closer to both the naris and the otic notch than in most amphibamiforms. The skull is only slightly distorted, although some palatal elements have been slightly dislodged, and the left lower jaw has been displaced medially into the palatal region. Overpreparation has occurred in some areas (e.g., the snout) such that the specimen is nearly translucent in these regions due to its thinness and without ornamentation that would be predicted based on other amphibamiforms and dissorophoids.

The premaxilla is a subtriangular element. The alary process appears blunter and with a more rounded termination than the narrowly tapering process seen in many other dissorophoids, but it is not identifiable on the right side, and the dorsal exposure of the left premaxilla appears to be slightly dislodged and possibly slightly damaged (Fig. 1). The premaxilla frames the external naris anteriorly and for a short distance ventrally and dorsally. There is no internarial fontanelle (Fig. 1).

The maxilla is a slender element extending from the external naris to an indeterminate position near the posteroventral corner of the skull (Fig. 2). It is low in height for most of its length but expands dorsally between the naris and the orbit (Fig. 2). Teeth are not identifiable. Anterior sutural relationships (e.g., anteriorly to the premaxilla, medially to the septomaxilla) are identifiable, but posterior contacts are not defined.

The septomaxilla is partially preserved at its base as part of the floor of the anterior half of the external naris (Fig. 2).

The nasal is a broad, plate-like element that forms most of the dorsal narial margin together with the premaxilla and the lacrimal (Fig. 1). It is mostly flat throughout but curves slightly ventrolaterally at its midlength to form a ventral inflection into the naris, creating a partially subdivided profile (Fig. 2).

The lacrimal is a subtriangular element that frames the naris posteriorly (Fig. 2). On the left lacrimal, two large sediment grains are adhered to the posterodorsal narial margin, artificially producing a jagged contour, but the undisturbed right naris is clearly smoothly curved along this region. The lacrimal is anteriorly excavated as a result of the elongation of the naris, and there are long processes extending along both dorsal and ventral margins of the naris (Fig. 2). The ventral process lies mostly internal to the maxilla and thus gives the impression of a short process in lateral view.

The prefrontal is a subtriangular element that frames the orbit anteriorly and medially (Fig. 1). It is widely separated

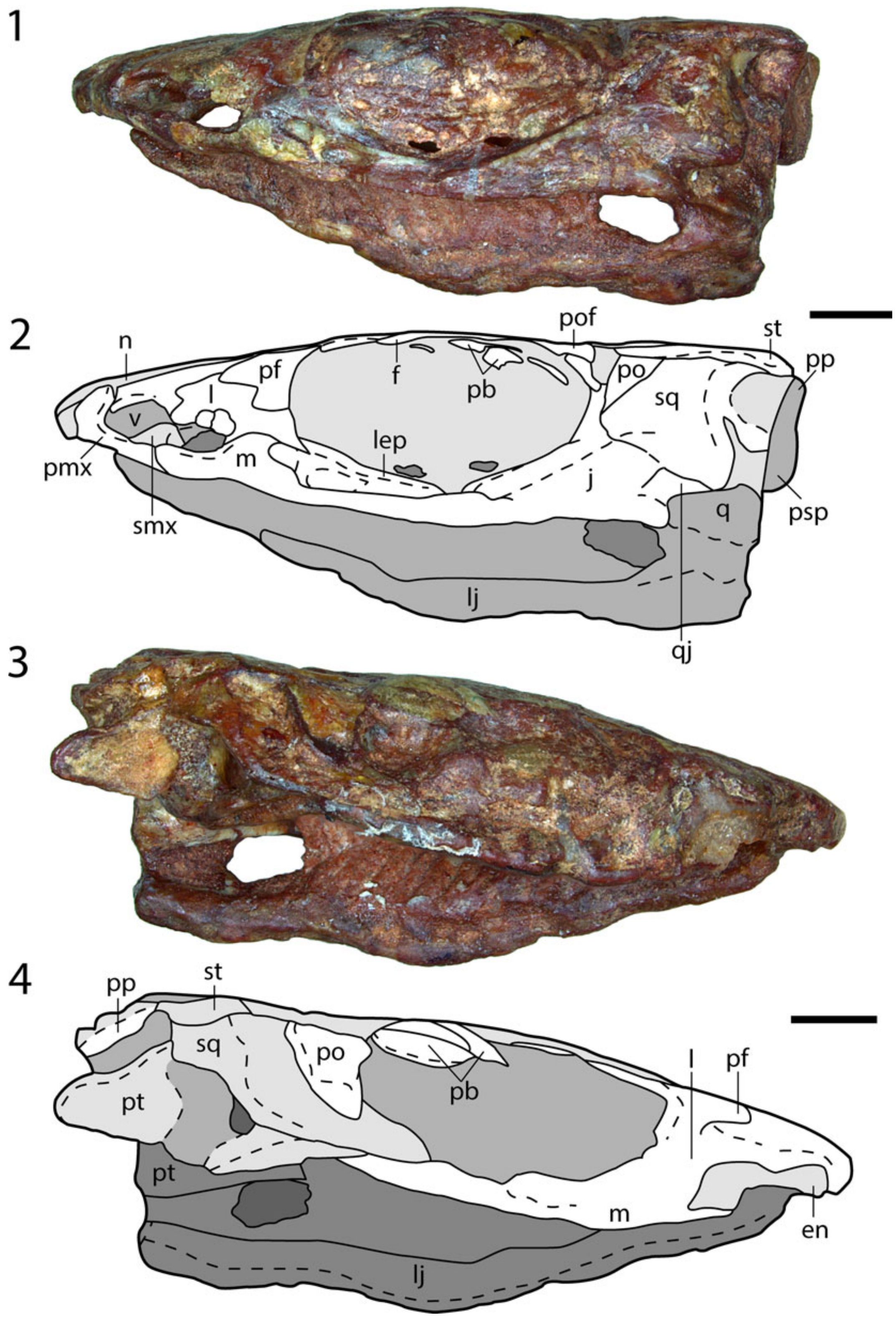

Figure 2. Lateral profiles of the holotype of *Nanobamus macrorhinus*, UCMP 203686: (**1**) photograph in left lateral profile; (**2**) line drawing of Figure 2.1; (**3**) photograph in right lateral profile; (**4**) line drawing of Figure 2.3. en = external naris; f = frontal; j = jugal; lep = lateral exposure of the palatine; l = lacrimal; lj = lower jaw; m = maxilla; n = nasal; pb = palpebral bone; pf = prefrontal; pmx = premaxilla; po = postorbital; pof = postfrontal; pp = postparietal; psp = parasphenoid; pt = pterygoid; q = quadrate; qj = quadratojugal; smx = septomaxilla; sq = squamosal; st = supratemporal; v = vomer. Shading utilized to indicate relative depth. Scale bars = 2 mm.

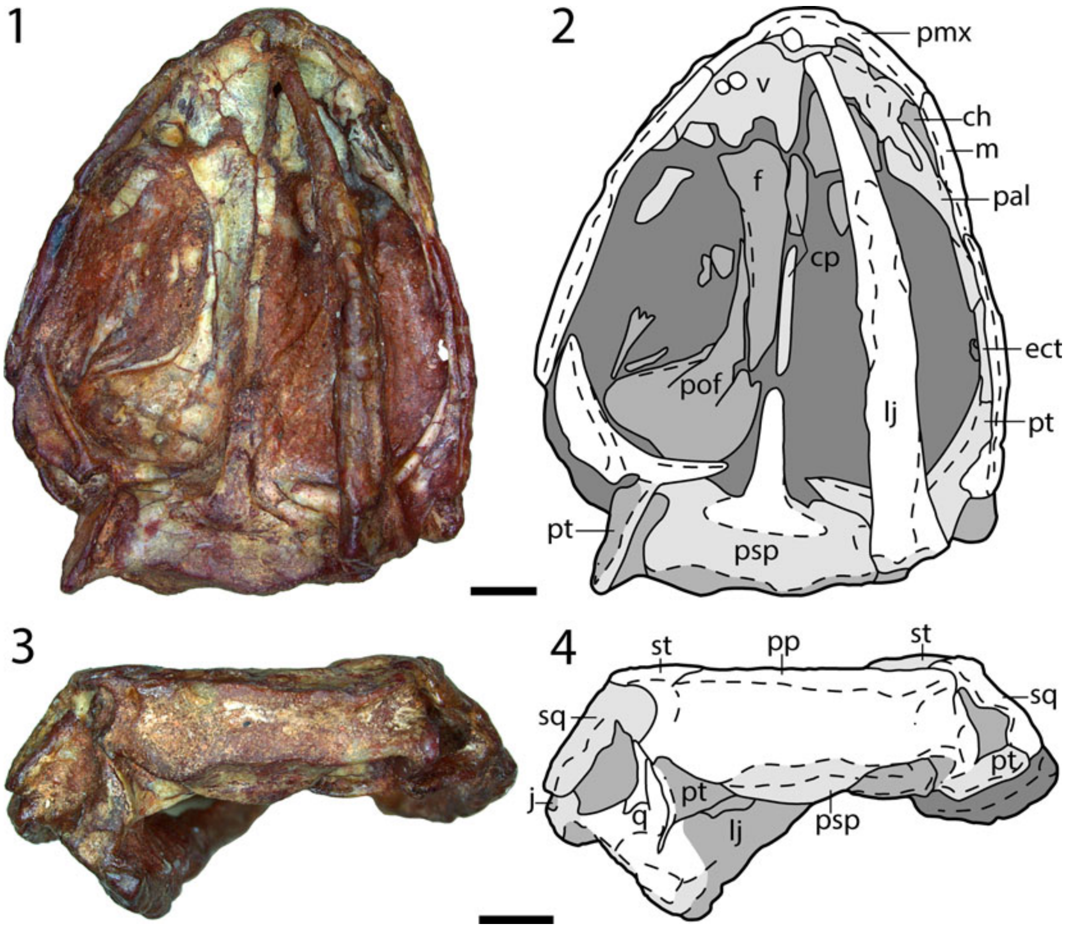

Figure 3. Ventral and occipital profiles of the holotype of *Nanobamus macrorhinus*, UCMP 203686: (**1**) photograph in ventral profile; (**2**) line drawing of Figure 3.1; (**3**) photograph in occipital profile; (**4**) line drawing of Figure 3.4. ch = choana; cp = cultriform process; ect = ectopterygoid; f = frontal; lj = lower jaw; j = jugal; m = maxilla; pal = palatine; pmx = premaxilla; pof = postfrontal; pp = postparietal; psp = parasphenoid; pt = pterygoid; q = quadrate; sq = squamosal; st = supratemporal; v = vomer. Shading utilized to indicate relative depth. Scale bars = 2 mm.

from the naris by the lacrimal and the nasal (Fig. 2). It is widely separated from the postfrontal along the medial orbital margin (Fig. 1), contrary to the reconstruction by Schoch and Milner (2014). A minute bone posterior to the prefrontal and along the left orbital margin (Fig. 1) might have been interpreted as a broken and isolated fragment of the prefrontal. However, it is small, flat, lacks distinctive morphological features, and is closer to the postfrontal than to the prefrontal, making it impossible to identify it as belonging to any particular element. The right prefrontal has a posterior process along the orbit similar to that of the left prefrontal.

The frontal is a broad trapezoidal element that contributes to the medial orbital margin in the absence of prefrontal-postfrontal contact (Fig. 1). The element is broadest anteriorly and tapers gradually posteriorly, producing a relatively narrow interorbital region, especially in comparison to Carboniferous amphibamiforms. The midline contact between frontals is sinuous in the anterior half.

A large number of palpebral bone fragments is visible in both orbits (Figs. 1, 2). They are of various sizes and shapes, similar to those of other dissorophoids, suggesting that they originally formed a single ossification. Several of them feature faint pitting similar to that of some of the cranial elements.

The postfrontal is a large subtriangular element that contributes to the medial and posterior orbital margins (Fig. 1). It is expanded posteromedially, closely approaching the pineal foramen, and is characterized by large processes extending far anteriorly and laterally around the orbit. As noted above, despite its anterior elongation, it is widely separated from the prefrontal.

The postorbital is incomplete ventrally on both sides (Figs. 1, 2). It contributes to the posterior orbital margin with the jugal.

The parietal is a large trapezoidal element that is markedly constricted anteriorly to accommodate the expansion of the postfrontal, resulting in a narrow, squared-off process that meets the frontal (Fig. 1). The pineal foramen is small and situated far anterior along the midline suture of the parietals, approximately at the level of the posterior orbital margin.

The postparietal is a rectangle that appears essentially complete; a shallowly angled, unornamented surface at the posterior edge of the skull probably represents a weathered or overprepared surface, rather than nearly horizontal occipital flanges, which are unknown in amphibamiforms (Fig. 1). Based on this interpretation, the postparietals are only slightly wider than they are long.

The right tabular is inferred to be partially complete based on the presence of an ossification immediately posterior to the

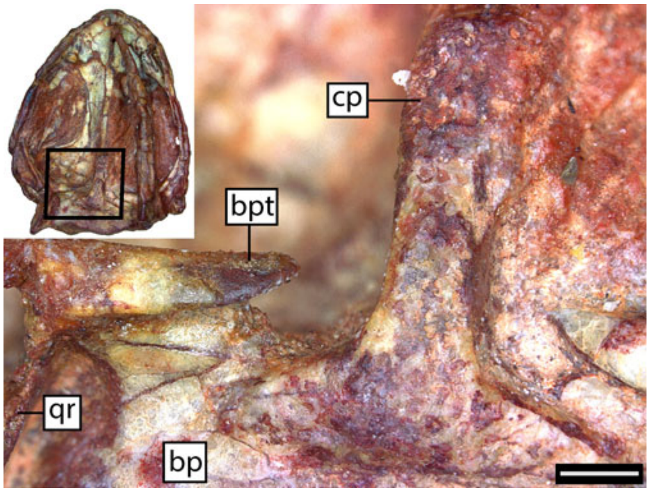

Figure 4. Photograph of the parasphenoid of the holotype of *Nanobamus macrorhinus*, UCMP 203686, showing the dentition on the posterior part of the cultriform process. Inset indicates location of close-up. bp = basal plate of the parasphenoid; bpt = basipterygoid process of the pterygoid; cp = cultriform process; qr = quadrate ramus of the pterygoid. Scale bar = 750 μm.

supratemporal, the lateral edge of which appears to be unbroken (Fig. 1). However, the lateral suture with the postparietal is unclear; this surface is not well preserved and has many fractures that cannot be plausibly inferred to represent breakage along a sutural contact. It is highly unlikely that this ossification is part of the postparietal because the postparietal does not extend to the otic notch in any dissorophoid.

The supratemporal is a flat rectangular element that tapers slightly posteriorly (Fig. 1). The lateral and medial margins are straight and mostly parallel to each other. It has been slightly uplifted, in place, above the plane of the skull, and overlies part of the otic notch (inferred to be the real relationship).

The jugal is well defined only anteriorly, where a long process extends along the posteroventral margin of the orbit (Fig. 2). Sutures with the incomplete postorbital (dorsally), the squamosal and the quadratojugal (posteriorly), and the maxilla (ventrally) are not well defined.

The squamosal is poorly defined except in its relation to other elements and by the otic notch (Fig. 2). The supratympanic flange is similar to those of other amphibamiforms, with a short vertically oriented flange extending anteroposteriorly beneath the supratemporal and a posteroventrally descending flange with a broad, unornamented surface.

The quadratojugal is at least partially preserved as a fragment positioned posterior to the jugal and below the supratympanic flange of the squamosal (Fig. 2). It appears to have been largely lost, and little more can be said about it.

As previously noted, the ornamentation of the skull is not well preserved, probably having been overprepared in some areas (e.g., snout) where ornamentation might be predicted to have occurred. In places where it is preserved, e.g., the frontals and the postfrontals (Fig. 1), the ornamentation consists of small, shallow pitting similar to that found in other amphibamiforms.

Palate.—The parasphenoid is formed by the large quadrangular basal plate and the slender cultriform process, broken into several fragments in the specimen (Fig. 4). The basal plate is wider than it is long and expands posterolaterally toward the quadrate rami of the pterygoid. The cultriform process is transversely slender and dorsoventrally flat, extending anteriorly to meet the vomers (Fig. 3.1, 3.2). The base of the process is ventrally depressed to produce a prominent offset from the basal plate. A large patch of denticle sockets is present at the base of the process that extends onto the posteriormost third of the process (Fig. 4).

The vomer is a broad, flat element without any anteromedial depression (Fig. 3.1, 3.2). It meets the cultriform process posteromedially and the palatine posterolaterally around the choana. The choana is long and slender with a smooth oval contour, broadening only slightly anteromedially. Two broken vomerine fangs are identified on the right vomer near the anteromedial corner of the choana (Fig. 3.1, 3.2). A ventral bulge in the corresponding position on the left vomer probably represents the paired sockets on this element, but the outlines of these sockets cannot be precisely defined. No other teeth are clearly preserved. The presence of a vomerine septum cannot be determined.

The palatine is a long element that frames the choana anteriorly with the vomer and that meets the slender ectopterygoid posteriorly (Fig. 3.1, 3.2). It has a sizeable lateral exposure along the anteroventral corner of the orbit that separates the lacrimal from the jugal, although this region is also damaged and might have lost parts of the maxilla and the prefrontal along the anteroventral orbital margin (Fig. 2.1, 2.2). If this interpretation is correct, then the lateral exposure of the palatine would have been confined to the ventral orbital and of a more typical size for dissorophoids. Neither denticles nor fangs are preserved.

The ectopterygoid is a narrow strut sutured to the palatine anteriorly and to the pterygoid posteriorly (Fig. 3.1, 3.2). Neither denticles nor fangs are preserved. It does not appear to have a lateral exposure.

The pterygoid is a slender triradiate element. The basipterygoid ramus is relatively long and slender, which produces a prominent medial extent that broadly overlaps the basicranial processes of the basal plate of the parasphenoid and that closely approaches the cultriform process (Figs. 3.1, 3.2, 4). The ascending flange of the pterygoid overlies the ramus and continues posteriorly along the dorsal margin of the quadrate ramus, remaining in contact with the skull roof throughout its extent. The palatal ramus is a long, slender process with a distinct ridge extending medially along its long axis. It appears to be anteroposteriorly short and widely separated from the vomer. However, the anteriormost tip of the left palatal ramus is displaced beneath the ectopterygoid (Fig. 3.1, 3.2), suggesting that the pterygoid contributed more substantially to the lateral margin of the vacuities than appears in its present state. However, it is not likely that it extended sufficiently far to meet the palatine. There is also minimal development of the transverse flange, resulting in a lateral margin that is curved and parallel to the medial margin (Fig. 3.1, 3.2). No denticles are preserved on the pterygoids.

Occiput.—The occiput is very poorly preserved and even major landmark features (e.g., foramen magnum, occipital condyles) are too poorly preserved to be identified (Fig. 3.3, 3.4). It is mostly informative for showing the

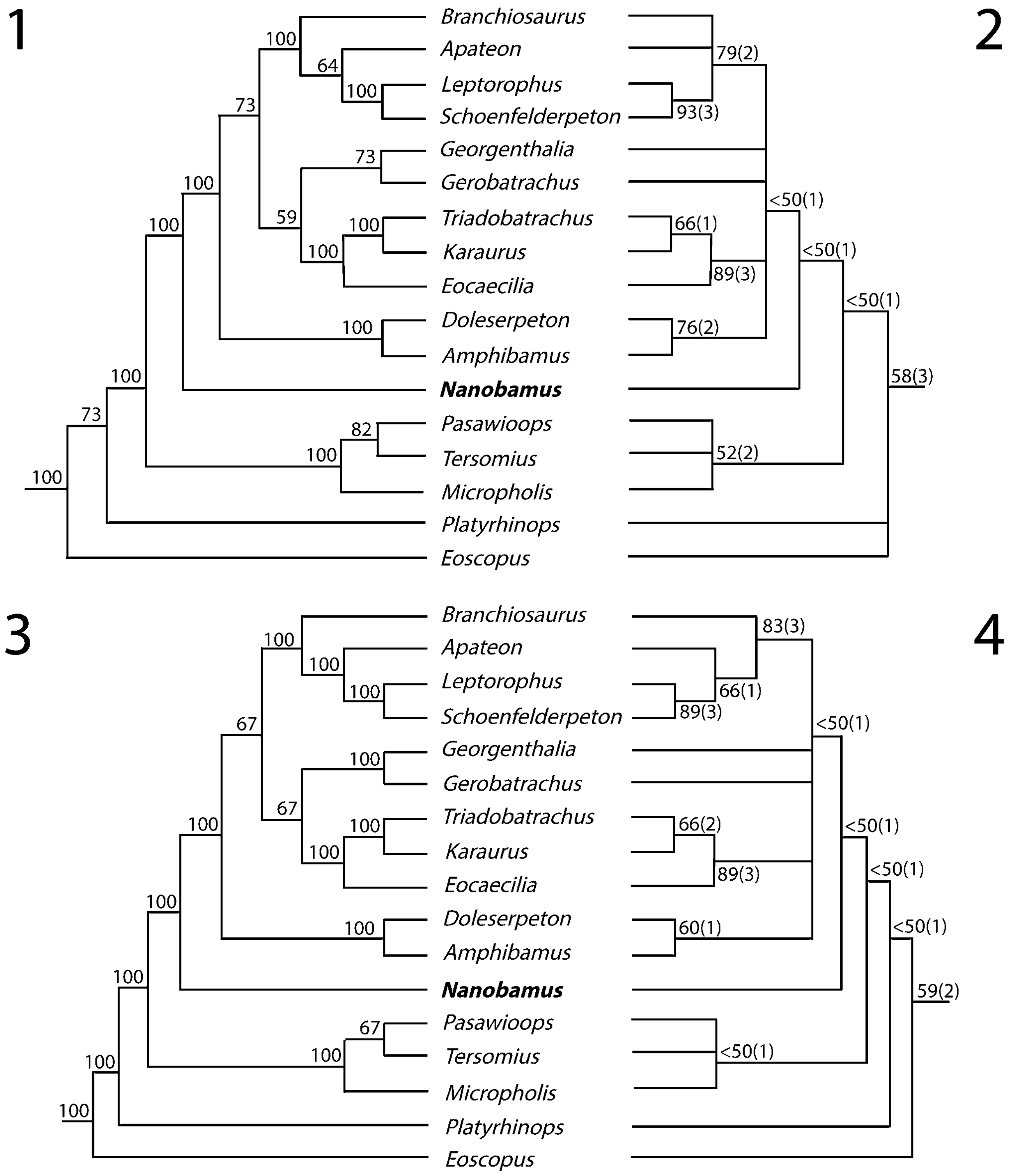

Figure 5. Results of phylogenetic analysis of *Nanobamus macrorhinus* in the matrix of Schoch (2019) (35 taxa, 108 characters); trees visually pruned to focus on amphibamiforms: (**1**) majority rule consensus of the full-character sampling permutation; (**2**) strict consensus tree of the same permutation with bootstrap support and Bremer decay indices (the latter in parentheses); (**3**) majority rule consensus of the 106-character sampling (removal of characters 17 and 30) permutation; (**4**) strict consensus tree of the same permutation with bootstrap support and Bremer decay indices.

general profile of the skull, being flat along the dorsal margin of the roof and with steeply angled cheeks. The posterior margin of the skull roof is fully defined along its transverse extent.

Lower jaw.—Virtually nothing can be said about the lower jaw (Figs. 1–4). It is nearly complete, but teeth are either unexposed or not preserved. The variable topography of the external surfaces does not clearly conform to sutural contacts and is best interpreted as the result of taphonomic damage. Ornamentation is totally absent.

Remarks.—The species diagnosis is amended as listed above.

Discussion

Phylogenetic analysis.—The initial analysis (full character sampling) recovered 198 most parsimonious trees (MPTs) with a length of 304 steps. As noted in Materials and methods, leaving multistate characters unordered did not produce changes to the strict consensus topology (as with Schoch, 2019), although it recovered 198 MPTs with a length of 300 steps (four fewer steps than with ordered multistate characters). *Nanobamus macrorhinus* was recovered as diverging after the Micropholidae (*Eoscopus* Daly, 1994, *Micropholis* Huxley, 1859, *Pasawioops* Fröbisch and Reisz, 2008) and before the Amphibamidae (*Amphibamus* Cope, 1865, *Doleserpeton* Bolt, 1969) (Fig. 5.1, 5.2; Supp. Fig. 1). The three permutations with removal of character 17 (postparietal length; 72 MPTs, 296 steps), removal of character 30 (postparietal length, distinct from character 17; 144 MPTs, 298 steps), and removal of both characters (54 MPTs, 291 steps), produced similar topologies with comparable bootstrap and Bremer support for major nodes. The consensus trees for the permutation without characters 17 and 30 is presented in the main text (Fig. 5.3, 5.4); the single character removal permutations are included in Supplemental Figure 1. The overall consistency between permutations suggests that including both characters 17 and 30 at least does not exert substantial influence on the tree topology, but the characters both refer to proportions of the postparietal and are thus not fully independent. As such, we recommend that they either be combined into a single character modeled after character 30 (the more quantitative and binary of the two) or more clearly defined in a way that makes them fully independent in future analyses. In none of the permutations is there strong support for the position of *N. macrorhinus*. Our character change for the naris of *Georgenthalia clavinasica* did not affect the tree topology compared to analyses where it was coded for the primitive condition as by Schoch (2019).

These results, including the instabilities and variable position of some taxa, are consistent with the findings of Schoch (2019). Formally defined clades (e.g., amphibamids, branchiosaurids) are the best supported. Here, *Georgenthalia clavinasica* was always recovered as the sister taxon to *Gerobatrachus hottoni* but with weak support in all permutations (Fig. 5.1, 5.2). *Platyrhinops lyelli* was always recovered as an early diverging amphibamiform rather than at the base of the Amphibamidae, a position found in some MPTs from Schoch's analysis. *Tersomius texensis* was recovered as the sister taxon to *Pasawioops mayi,* with this pair being sister to *Micropholis stowi* (Fig. 5.1, 5.2). This differs slightly from the results of Schoch (2019) in which *Pa. mayi* and *Micropholis stowi* formed the sister clade to *T. texensis*. Instabilities in some parts of the amphibamiform tree likely reflect widespread convergence and variable combinations of retained plesiomorphic states. Although the position of *Nanobamus macrorhinus* was not strongly supported, it was recovered as the sister taxon to micropholids and as diverging prior to amphibamids in all permutations of the analysis. Weak support for *N. macrorhinus* was likely driven by incompleteness of the coding, specifically with respect to many features of greater informative value among amphibamids (e.g., many features of the palate and the dentition). The recovered position is unsurprising based on the combination of retained plesiomorphies (many of which are plesiomorphic for Dissorophoidea at large [e.g., nonposteriorly-truncated postparietals]) and derived features (often shared only with derived amphibamiforms [e.g., slender palatal rami of the pterygoid]).

It is important to note the continued instability in certain areas of the amphibamiform phylogeny, as evidenced by disparity between studies of the past decade (e.g., Fröbisch and Reisz, 2008; Anderson and Bolt, 2013; Maddin et al., 2013). For example, *Georgenthalia clavinasica* has been variably recovered as: (1) stemward of *Eoscopus locklardi* and most other amphibamids (Fröbisch and Reisz, 2008); (2) the sister taxon of branchiosaurids (Maddin et al., 2013); (3) the sister taxon to a grouping of *Plemmyradytes shintoni* and *Tersomius dolesensis* (Anderson and Bolt, 2013); (4) the sister taxon to the amphibamids sensu stricto (Sigurdsen and Bolt, 2010); and (5) the sister taxon of the stem batrachian *Gerobatrachus hottoni* (see Schoch, 2019). This might in part relate to incomplete taxon sampling within and between analyses and a correspondingly low number of parsimony-informative characters for differentiating the terrestrial nonlissamphibian amphibamiforms (27 in this analysis). The matrix of Schoch (2019) that we used in this study does not include the poorly known amphibamiform genera, e.g., *Rubeostratilia texensis* (see Bourget and Anderson, 2011) and *P. shintoni* (see Huttenlocker et al., 2007), which Schoch (2019) suggested as possible micropholids, or the poorly known species *Tersomius mosesi* Olson, 1970 and *Platyrhinops fritschi*. Instability could also relate to the various combinations of retained plesiomorphies and apomorphies within the terrestrial amphibamiforms. For example, *Geo. clavinasica* and *Nanobamus macrorhinus* were not recovered as closely related, but this result poses an intriguing evolutionary scenario in which narial elongation evolved in an identical but apparently independent morphological fashion. Further work to assess the mosaicism and potential parallelism seen in amphibamiforms will be important for further resolution of their phylogenetic relationships.

Comparative amphibamiform morphology.—*Nanobamus macrorhinus* is characterized by a unique combination of retained plesiomorphies and derived features. The particular combination observed in *N. macrorhinus* fills a morphological gap between primitive and derived amphibamiforms. For example, the postparietals (as interpreted here) are relatively long anteroposteriorly, the choana forming a long oval slit without prominent medial expansion along its length, and there is at least one pair of vomerine 'fangs' (Figs. 1, 3.1, 3.2). This is in contrast to more derived amphibamiforms and lissamphibians, which have foreshortened postparietals, more circular and medially expanded choanae, and vomers lacking 'fangs' (e.g., Sigurdsen and Bolt, 2010; Schoch, 2019). However, *N. macrorhinus* also shares a number of features with more derived amphibamiforms. Examples include a posterolaterally expanded parasphenoid with denticles extending onto the cultriform process and a slender palatal ramus of the pterygoid without a developed transverse flange.

Other than the elongate naris (discussed below), most differences between the skull roof of *Nanobamus macrorhinus* and those of other amphibamiforms pertain to minor variation in the proportions of elements and the composite effect that this has on overall skull shape and profile. Individual features that are rare among amphibamiforms but shared with at least one other taxon include: (1) narrow, posteriorly tapering frontals (shared with *Rubeostratilia texensis*; Bourget and Anderson, 2011); (2) excavation of the lacrimal by a posteriorly expanded naris (shared with *Georgenthalia clavinasica*; Anderson et al., 2008a); and (3) prominent posteromedial expansion of the postfrontal to markedly constrict the parietals anteriorly (most similar to *R. texensis* and *Platyrhinops lyelli* in this regard; Clack and Milner, 2010; Bourget and Anderson, 2011). Collectively, this produces a relatively long and slender skull with a narrow interorbital region, in contrast to most other amphibamiforms (but similar in this regard to, e.g., *Plemmyradytes shintoni* and *R. texensis*). The orbits are proportionately large relative to the skull and noticeably longer than they are wide. They are similar in this regard to derived amphibamiforms, being slightly larger than those of *Doleserpeton annectens* and slightly smaller than those of *G. clavinasica*.

The palate of *Nanobamus macrorhinus* is most comparable to that of the amphibamids, with a large patch of denticles extending from the base of the cultriform process onto the process itself (Fig. 4). The extent (posterior third of the process) is similar to that of *Doleserpeton annectens*, whereas *Amphibamus grandiceps* also has a large patch anteriorly where the process meets the vomers. The pterygoids are slender and without a posterolaterally flaring transverse flange (in contrast to the plesiomorphic condition). The ectopterygoid is a long and narrow strut, although whether it was edentulous (as in, e.g., *D. annectens*) is unknown. The basal plate of the parasphenoid is much wider than it is long and expands prominently posterolaterally to closely approach the quadrate ramus of the pterygoid. However, the choana is not expanded anteromedially, forming a plesiomorphic elongate oval, and *N. macrorhinus* retains at least one pair of vomerine 'fangs.'

Narial elongation in dissorophoids.—The most conspicuous feature of *Nanobamus macrorhinus* is the elongate external naris, which is matched only by those of some trematopids in its length relative to the overall skull (Fig. 2). Although the external naris is superficially similar to that of trematopids, the construction in UCMP 203686 is fundamentally different. As in the amphibamiform *Georgenthalia clavinasica*, the posterior elongation excavates only the lacrimal (Anderson et al., 2008a), which widely separates the short prefrontal from the opening. As with *G. clavinasica*, this particular construction indicates nontrematopid affinities. In trematopids, both the prefrontal and the lacrimal are truncated as a result of the narial elongation, the lacrimal does not extend along the dorsal margin of the naris, and the prefrontal contributes substantially to the posterior narial margin. The prefrontal is highly variable among amphibamiforms in both total length and in relative anterior and posterior extents, but it is always widely separated from the naris, as in most temnospondyls. It should be noted that the prefrontal is narrowly excluded from the naris in a partial trematopid snout (MCZ 2531) described by Dilkes (1993), the preserved length of which is already longer than UCMP 203686. The naris extends posterior to the septomaxilla in MCZ 2531, but it does not have the keyhole-shaped profile in lateral view that is formed by the dorsal inflection of the maxilla in larger trematopids, instead being uniformly oval. In UCMP 203686, the inflection into the naris is along the dorsal margin, formed by a ventral inflection of the nasal and the lacrimal. The maxilla is dorsally expanded in UCMP 203686, but this occurs posterior to the naris (Fig. 2). This underscores the point that superficial similarities in anatomy can result from distinct, nonhomologous modifications to the skeleton that could influence phylogenetic analyses based on character construction and coding (Simões et al., 2017).

Among nontrematopid dissorophoids, elongate nares are also noted in the slender-headed morph of the micropholid *Micropholis stowi* from the early Triassic of South Africa (Schoch and Rubidge, 2005) and the branchiosaurid *Leptorophus* Schönfeld, 1911 from the early Permian of Germany (Boy, 1985; Schoch, 2014). In neither of these taxa does the naris approach either the full length or the subdivided condition seen in *Nanobamus macrorhinus*, and only in *Georgenthalia clavinasica* is the construction similar, where anteriorly extensive processes frame the naris posteroventrally and posterodorsally. As previously noted, the phylogenetic (and geographic) separation of *N. macrorhinus* and *G. clavinasica* complicates a fuller understanding of this type of narial elongation. The lacrimal of *Leptoropus tener* (Schönfeld, 1911) is more abruptly truncated by the naris, and it lacks these circumnarial processes (Schoch, 2014). The branchiosaurid *Schoendfelderpeton prescheri* Boy, 1986 is more similar to *N. macrorhinus* and *G. clavinasica* in having these processes, but that taxon has a more typical, circular naris. The narial elongation of *Micropholis stowi* is found only in the slender-headed morph of the taxon, and the lacrimal is either truncated abruptly or only slightly contacts the naris (e.g., Schoch and Rubidge, 2005).

The presence of narial elongation within dissorophoids thus continues to be an intriguing yet enigmatic feature. Notwithstanding the longstanding interpretations of *Mordex calliprepes* Steen, 1938 and *Ecolsonia cutlerensis* Vaughn, 1969 as dissorophids (both are now widely accepted to be trematopids), the aforementioned amphibamiforms represent the presence of an enlarged narial opening outside of Trematopidae. *Nanobamus macrorhinus* is the most extreme example of narial elongation in a nontrematopid, with the relative proportions closely approaching those of substantially larger trematopids, e.g., *Acheloma* Cope, 1882, which represents an extreme end member on the trematopid spectrum. Regardless of the exact configuration, the functional import of elongation of the external naris in dissorophoids remains unresolved. It has only been explored in trematopids (e.g., Dilkes, 1993), and the question remains open at present. The fact that narial elongation evidently evolved independently in both large- and small-bodied taxa and in both terrestrial and aquatic settings only confounds the issue further, because previous hypotheses of potential soft tissue structures (e.g., salt gland, Jacobson's organ) would not intuitively predict the absence of any clear ecological pattern or signal.

Ontogenetic maturity and Nanobamus.—A consideration that merits brief discussion is whether ontogeny can be implicated in either the architecture of the naris or the broader mosaicism of cranial features in *Nanobamus macrorhinus*. It must be noted that this discussion is largely cursory because the ontogeny of most amphibamiforms is poorly known. This has produced uncertainty regarding the inferred maturity of other taxa (e.g., Bolt, 1977, 1979) that can only be more conclusively resolved when a large proportion of the skeletal anatomy is known from specimens spanning a broad size range (e.g., Schoch and Rubidge, 2005; Clack and Milner, 2010; Sigurdsen and Bolt, 2010). As a result, it is difficult to precisely determine the maturity of UCMP 203686 because of the paucity of information for amphibamiforms and the absence of postcranial material associated with the specimen. It is relatively small (midline skull length of ∼2 cm), although size is not a precise determiner of development maturity, and it is not the smallest known amphibamiform. Some aspects of the skull proportions, e.g., the relatively large orbits and narrow interorbital region, could suggest a degree of immaturity, at least in comparison to larger amphibamiform specimens. Conversely, other features, e.g., the presence of the palpebral ossifications, a relatively small pineal foramen, and prominent interdigitation along some sutural contacts (e.g., frontal-parietal suture; Fig. 1A), indicate a degree of maturity. Comparisons with the known ontogenetic sequences of other amphibamiforms are limited to a few taxa and are largely restricted to features that are not preserved in UCMP 203686, e.g., the relative ossification of the neurocranium and otic capsule (e.g., Sigurdsen and Bolt, 2010) or the pelvic girdle (e.g., Clack and Milner, 2010). Clack and Milner (2010) did indicate that posterior expansion of the postfrontal (which is large for an amphibamiform in *N. macrorhinus*) characterized advanced ontogeny in *Platyrhinops lyelli*. Features that are applied to the ontogenetic maturity of temnospondyls more broadly (e.g., position of the pineal foramen) must be more carefully considered until they are assessed in amphibamiforms. At present, our interpretation of *N. macrorhinus* is that it undoubtedly represents a postmetamorphic individual that was probably relatively, but not fully, mature.

Based on our interpretation, it should be considered that incomplete ontogenetic maturation at the time of death could have produced the anatomy of *Nanobamus macrorhinus*. More precisely, differential timing of ossification and development of the different cranial regions and features, which does occur in temnospondyls more broadly (e.g., Boy and Sues, 2000), could have produced the combination of retained plesiomorphies and apomorphies that characterizes the taxon. This could apply to other amphibamiforms, particularly those for which no ontogenetic sequence is available. However, we reiterate that this requires additional material beyond the handful of taxa characterized from many specimens to be more precisely identify ontogenetic patterns among the terrestrial amphibamiforms. This also applies to the unusual narial architecture seen in *N. macrorhinus*, for which there is no evidence at present to support an ontogenetic influence. The most compelling evidence for an ontogenetic influence on the narial morphology comes from the long-snouted early Permian trematopid *Phonerpeton* Dilkes, 1990 in which small individuals have circular, undivided nares that transition to elongate, 'keyhole-shaped' openings in larger individuals (Dilkes, 1993). However, in *Micropholis stowi*, arguably the amphibamiform with the best-known ontogenetic trajectory (Schoch and Rubidge, 2005), there is no evidence for either pronounced elongation or late-stage subdivision of the naris (or the opposite, transformation toward a circular, undivided naris). Both *Georgenthalia clavinasica* and *N. macrorhinus* are known only from the type specimens, so it is not possible to evaluate any hypothesis of ontogenetic transformation in these taxa.

Amphibamiform biogeography.—Amphibamiforms have long been of interest in the context of lissamphibian origins, resulting in a substantial amount of work regarding their morphology, ontogeny, phylogeny, taxonomy, and ecology. One key outcome of previous work is the growing consensus that branchiosaurids are a neotenic branch within Amphibamiformes that secondarily transitioned to an aquatic lifestyle (with occasional metamorphosis to terrestrial adults; e.g., Schoch and Milner, 2008; Fröbisch and Schoch, 2009a; Maddin et al., 2013; Schoch, 2019). An interesting aspect of this is the noticeable disparity in the relative abundance and geographical distribution of terrestrial amphibamiforms (predominantly found in North America) and branchiosaurids (predominantly found in Europe) in approximately coeval early Permian environments. There are only two terrestrial amphibamiforms found in Europe: *Georgenthalia clavinasica* from the upland early Permian Bromacker locality and *Platyrhinops fritschi* from the Carboniferous of Nýřany (see Clack and Milner, 2010 for discussion of the ecology of *Platyrhinops*). Conversely, only two branchiosaurids have been found in North America (*Eumicrerpeton parvum* Moodie, 1909, *Milnererpeton huberi* Hunt, Lucas, and Berman, 1996), and both are from the Carboniferous. Previous workers (e.g., Schoch and Fröbisch, 2006; Schoch and Milner, 2008) have suggested that elevational disparity between environments inhabited by dissorophoids produced this pattern. Branchiosaurids are often found in high-elevation lake deposits of the Variscian orogen, which have been interpreted to be more seasonally disparate (e.g., Clausing and Boy, 2000). Lakes would have offered a relatively stable environment compared to lowland fluvial systems that would have produced strong selection pressures for alternative life strategies such as neoteny (e.g., Fröbisch and Schoch, 2009b; Sanchez et al., 2010). Conversely, dissorophoids in lowland environments (e.g., the Texas red beds) would not have experienced the same physiological constraints of pronounced elevation and thus radiated in terrestrial settings. A similar lack of constraints probably applied to so-called 'upland localities,' e.g., the Richards Spur (Oklahoma) and Bromacker (Germany), which might have been better drained than lowland sites but not at high elevations.

Recent work by Pardo et al. (2019) on global patterns of the Carboniferous-Permian transition (CPT) sheds further light on the geographic disparity. The divergence between branchiosaurids and terrestrial amphibamiforms can be constrained to the late Carboniferous. The fossil record of this time is dominated by wetland environments, including coal swamps, and members of both groups appeared in North America and Europe (e.g., *Eoscopus locklardi, Platyrhinops lyelli, Apateon pedestris* von Meyer, 1844). The late Carboniferous also marks the onset of a geographically diachronous climate transition across Pangea: the Carboniferous-Permian Transition (CPT), in which dryland environments replaced coal swamps. An onset of the spread of dryland environments in North America during the CPT (Pardo et al., 2019) would have favored the radiation of terrestrial amphibamiforms relative to neotenic branchiosaurids, which thus explains the total absence of the latter in the Permian of North America. In contrast to, but concurrent with, this development in North America, the delayed replacement of wetland environments and the presence of high-elevation aquatic habitats in Europe would have favored the radiation of branchiosaurids. This pattern likely accounts for similar patterns seen in the larger, fully terrestrial olsoniforms, in particular the dissorophids, of which virtually all of the early Permian members (> 20 species) are found in North America. Further exploration of the environmental factors that influenced dissorophoid evolution will be necessary for a more complete appreciation of the ecological context in which crown lissamphibians evolved.

Conclusions

The history of study of *Nanobamus macrorhinus* encapsulates one of the longstanding challenges in the study of dissorophoid evolution and taxonomy, namely how to differentiate small-bodied, paedomorphic adults of some taxa from small-bodied, immature juveniles of other taxa (e.g., Anderson et al., 2008a, p. 71). The longstanding challenge in the identification of this specimen is the absence of larval olsoniforms (e.g., Schoch and Milner, 2014, p. 54; Milner, 2018, p. 20–21). As with *Georgenthalia clavinasica,* various features of *N. macrorhinus* (e.g., ossified septomaxilla) indicate that it is a relatively mature adult amphibamiform (Boy and Sues, 2000) rather than a markedly immature trematopid (Olson, 1985). Despite substantial improvements in our knowledge of dissorophoids in recent decades, unequivocal larval forms of olsoniforms remain virtually unknown (see Milner, 2018 for further discussion and an example of a larval specimen), and juvenile forms are rare in comparison to more mature ('adult') stages. Although various specimens of small-bodied (presumably juvenile) trematopids have been described (see, e.g., Olson, 1941; Dilkes, 1993; Gee et al., 2019), they are much larger than UCMP 203686 and are clearly postmetamorphic.

The typical depositional environments in which olsoniforms have been found are primarily fluvial systems that were probably both biologically and taphonomically inhospitable to aquatic larval forms of these large-bodied dissorophoids, if in fact members of the clade underwent metamorphosis (e.g., Schoch, 2002). Carboniferous localities in Europe (e.g., Nýřany) represent one of the few environments that would likely capture both olsoniform larvae naturally residing in low-energy freshwater bodies and their adult forms that were likely inadvertently captured through drowning or postmortem transport of remains along the shore (e.g., Milner, 2018). Similar settings are rarer in the Permo-Carboniferous of North America (e.g., Linton, Ohio and Mazon Creek, Illinois) and they do not preserve evidence of olsoniforms. Characterizations of early ontogeny in olsoniforms and differentiation of putative olsoniform larvae from small-bodied adult xerodromes remains an important area of ongoing research. Reexamination of historic specimens (e.g., Maddin et al., 2013; this study) and further testing of amphibamiform intrarelationships will be essential for an improved understanding of the evolution and diversification of stem lissamphibians in terrestrial environments.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mq385f0

Supplemental information

Supplemental Figure 1. Results of phylogenetic analysis of *Nanobamus macrorhinus* in the matrix of Schoch (2019) (35 taxa, 108 characters); tree visually pruned to focus on Amphibamiforms: (**1**) majority rule consensus of the first 107-character (removal of character 17) sampling permutation; (**2**) strict consensus tree of the same permutation with bootstrap support and Bremer decay indices (the latter in parentheses); (**3**) majority rule consensus of the second 107-character sampling (removal of character 30) permutation; (**4**) strict consensus tree of the same permutation with bootstrap support and Bremer decay indices.

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