

GEORGENTHALIA CLAVINASICA, A NEW GENUS AND SPECIES OF DISSOROPHOID TEMNOSPONDYL FROM THE EARLY PERMIAN OF GERMANY, AND THE RELATIONSHIPS OF THE FAMILY AMPHIBAMIDAE

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ABSTRACT—*Georgenthalia clavinasica*, a new genus and species of amphibamid dissorophoid temnospondyl, is represented by a small, complete, postmetamorphic skull from the Lower Permian Bromacker locality, Germany. It is only the third non-amniote of an assemblage of 12 terrestrial tetrapod taxa known from this locality. It is characterized by a broadly rounded skull with large orbits, a short postorbital length, and a unique keyhole-shaped external naris superficially resembling that of trematopid dissorophoids. New features that help to discriminate between amphibamid species are highlighted. Phylogenetically informative characters present in *G. clavinasica* include: anterolateral flaring of the lateral margin of frontals; narrow interorbital width; ventral orbital process of the prefrontal contacts palatine; palatine exposed on lateral surface of ventral rim of orbit; large otic notches closely approach the orbits; absence of a supratympanic flange of otic notch; long supratympanic process of squamosal with flange-like process that underlaps the midcentral portion of supratemporal. Several features support a highly terrestrial habitus of *G. clavinasica*, which is consistent with the interpretation of the fossiliferous beds of the Bromacker quarry as representing an upland terrestrial environment in which limnic conditions were characterized by ephemeral lakes and ponds.

A new clade, Olsoniformes, is named for Dissorophidae and Trematopidae (dissorophoids exclusive of Amphibamidae), and new phylogenetic definitions for Amphibamidae, Trematopidae, and Dissorophidae are presented. The small neotenic Micromelerpetontidae, and presumably also the neotenic and larval Branchiosauridae, fall within the newly defined clade Amphibamidae in the current study, and future work should focus on clarifying the nature of this relationship.

INTRODUCTION

The Bromacker quarry in the Thuringian Forest of central Germany is the only Early Permian site in Europe to produce a diverse assemblage of terrestrial tetrapods and as a result has become an important locality for understanding the distribution and composition of Early Permian terrestrial vertebrate faunas of Euramerica (Boy and Martens, 1991; Berman and Martens, 1993; Sumida and Berman, 1994; Sumida et al., 1996; Berman et al., 1998, 2000a,b, 2001, 2004a,b; Sumida et al., 1998; Eberth et al., 2000). Whereas the Bromacker assemblage consists almost entirely of taxa shared with, or closely related to, those of Early Permian assemblages of North America, all species are unique to Europe. Herbivores dominated the vertebrate assemblage in both size and abundance and include the diadectomorphs *Diadectes* (Berman et al., 1998) and the recently described *Orobates* (Berman et al., 2004b), and an undescribed basal synapsid caseid (Berman et al., 2004b). Medium-to-large-sized predators are relatively scarce, and include the basal synapsids *Dimetrodon teutonius* and an undescribed varanopid (Eberth et al., 2000; Berman et al., 2001, 2004a,b). Also included in the Bromacker assemblage is *Thuringothyris malhendorffae*, a captorhinomorph

(Boy and Martens, 1991; Müller et al., 2006) and the bolosaurid parareptile *Eudibamis cursoris*, the earliest known bipedal animal (Berman et al., 2000b). Non-amniote Bromacker tetrapods include numerous specimens of the seymouriamorph *Seymouria sanjuanensis* that is represented by a widely spaced growth series (Berman and Martens, 1993; Berman et al., 2000a; Klembara et al., 2001, 2005, 2006, 2007) and rare occurrences of the trematopid temnospondyl *Tambachia trogallas* Sumida et al. (1998). Here we report the presence of a second dissorophoid temnospondyl, a small amphibamid recovered from the Bromacker quarry in 2002, which possesses a unique keyhole-shaped naris that is superficially similar to the elongate naris of trematopids. The present paper focuses on the cranial anatomy only, as description of the poorly preserved postcranial skeleton necessitates postponement until additional specimens are found.

Amphibamidae

Amphibamids are small, generalized dissorophoids that are paedomorphic with respect to dissorophids, trematopids, and more basal temnospondyls. They are characterized by a broadly rounded skull in dorsal view, gastrocentric vertebrae, closely placed orbits, and an extremely shortened skull with highly reduced tabulars and postparietals that are restricted to a narrow exposure on the occipital margin of the skull table (Fig. 1). Cur-

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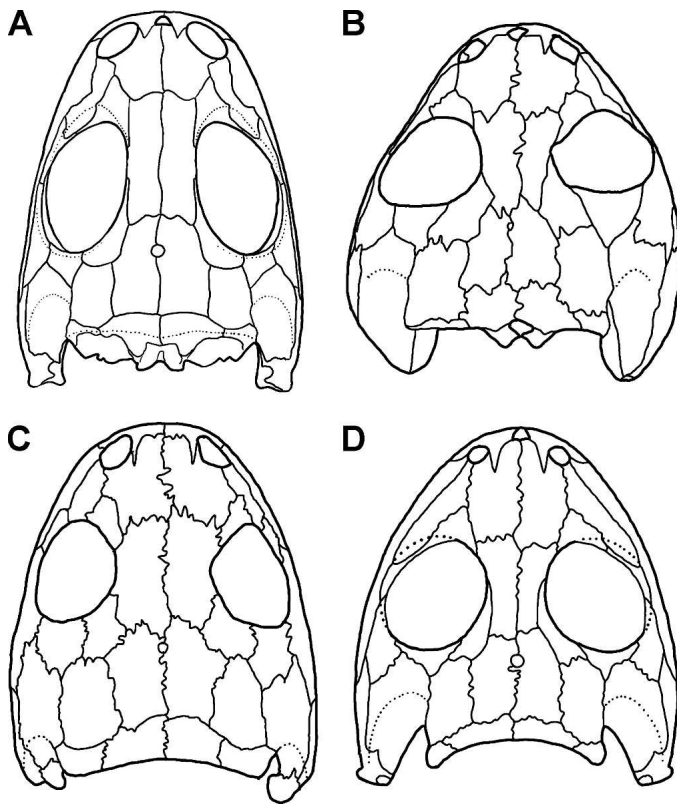


FIGURE 1. Amphibamids. **A**, *Doleserpeton*, modified from Bolt (1969); **B**, *Tersomius*, modified from Carroll (1964); **C**, *Micropholis* (broad-headed morph), modified from Schoch and Rubidge (2005); **D**, *Eoscopus*, modified from Daly (1994).

rently recognized amphibamid genera include *Amphibamus* (Bolt, 1979; Milner, 1982), *Platyrhinops* (Carroll, 1964; Clack and Milner, 1993), *Eoscopus* (Daly, 1994), *Doleserpeton* (Bolt, 1969, 1977), *Micropholis* (Boy, 1985; Schoch and Rubidge, 2005), *Tersomius* (Carroll, 1964; Anderson and Bolt, 2005), the newly described *Plemmyradytes shintoni* Huttenlocker et al. (2007), and possibly *Milnererpeton*, although this genus may turn out to be a branchiosaurid (Hunt et al., 1996, 2002; R. Werneberg, pers. com. to JSA 2006). Amphibamids have frequently been cited as associated with the origin of modern amphibians (see Schoch and Milner, 2004 for a summary of the current views on this problem) because of their nearly unipartite vertebrae, large 'otic notches', and, in some species, the presence of bicuspid, pedicellate teeth (Bolt, 1969, 1977, 1991; Trueb and Cloutier, 1991). Therefore, additional knowledge about this important clade may have implications for our understanding of the origins of frogs, salamanders, and caecilians.

Amphibamids are difficult to analyze phylogenetically because they are small, have a generalized morphology, and retain features known to change ontogenetically in other, larger, temnospondyls. This has led some workers (Bolt, 1977, 1979) to suggest that they represent the juvenile stages of larger dissorophoids. Clack and Milner (1993) rejected this view because no growth series possessing shared, unique derived characters exists between the small unarmored amphibamids and larger armored dissorophoids or unarmored trematopids. They reestablished the name Amphibamidae and diagnosed the family as "small dissorophoid temnospondyls with highly abbreviated skull tables, elongate humeri, and bicuspid teeth" (p. 188). They also listed a number of shared, primitive features that distinguish amphibamids from other dissorophoids, but admitted that the number of

diagnostic features is limited and that the family may be paraphyletic with respect to Lissamphibia. To this family they assigned the genera *Tersomius*, *Amphibamus*, *Doleserpeton*, and *Platyrhinops* ("*Amphibamus*" *lyelli* from Linton, Ohio and Nýřany, Czech Republic). Daly (1994) expanded the concept of Amphibamidae to include the new genus *Eoscopus*, which lacks bicuspid teeth, and, tentatively, Micromelerpetontidae and the later occurring Triassic-aged *Micropholis* from South Africa. She recognized Amphibamidae as small temnospondyls possessing expanded pleurocentra that nearly articulate with immediately preceding and succeeding pleurocentra, short, undifferentiated ribs posterior to the pectoral girdle, and a host of shared, primitive traits. Schoch and Rubidge (2005) provided the most thorough argument for the monophyly of Amphibamidae, assigning *Micropholis*, which they divided into broad- and narrow-headed morphs, to the family. They also recognized several new synapomorphies uniting amphibamids: (1) palatine and ectopterygoid reduced to extremely slender rods, creating broad interpterygoid vacuities; (2) pterygoid with a short, anteriorly reduced, laterally directed palatine process; and (3) vomers with a widened lateral portion framing an elongated, medially expanded choana.

Despite this recent work, there remains a lack of clarity regarding apomorphies distinguishing individual species and internal clades of amphibamids, because of their generalized morphology and the ontogenetic nature of many of their most distinguishing characteristics. The present description of a new species of amphibamid addresses this problem.

Anatomical Abbreviations—**ang**, angular; **art**, articular; **as**, adsymphyseal bone; **ch**, choana; **cp**, cultriform process of parasphenoid; **d**, dentary; **dsq**, dorsal process of squamosal; **inf**, internarial fenestra; **IOW**, interorbital width; **j**, jugal; **l**, lacrimal; **lep**, lateral exposure of palatine; **n**, nasal; **m**, maxilla; **nlc**, nasolacrimal canal; **OL**, orbital length; **OT-O**, distance from anterior margin of otic notch to posterior margin of orbit; **OW**, orbital width; **p**, parietal; **pal**, palatine; **pf**, parietal foramen; **po**, postorbital; **PoL**, postorbital skull length; **PoW**, postorbital skull table width measured at level of tabulars; **pp**, postparietal; **ppb**, palpebral cup elements; **PreL**, preorbital skull length; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **ptf**, postfrontal; **q**, quadrate; **Q-Ot**, distance from quadrate to anterior margin of otic notch; **qj**, quadratojugal; **SkL**, midline skull length; **sm**, septomaxilla; **sp**, splenial; **sp2**, postsplenial; **sq**, squamosal; **st**, supratemporal; **t**, tabular; **v**, vomer; **vpprf**, ventral process of prefrontal.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **CM**, Carnegie Museum of Natural History, Pittsburgh; **FMNH**, Field Museum of Natural History, Chicago; **LFUM**, Landesamt für Geowissenschaften, Johannes Gutenberg University, Mainz, Germany; **MB**, Museum für Naturkunde, Humboldt Universität, Berlin; **MCZ**, Museum of Comparative Zoology, Harvard University; **MNG**, Museum der Natur, Gotha, Germany; **NSM**, Nova Scotia Museum, Halifax; **YPB** Yale Peabody Museum, New Haven.

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1888
EUSKELIA Yates and Warren, 2000
DISSOROPHOIDEA Bolt, 1969
AMPHIBAMIDAE Moodie, 1909
GEORGENTHALIA n. gen.
(Figs. 2–6)

Type Species—*Georgenthalia clavinasica*, new species

Etymology—Genus indicates the proximity of the Bromacker quarry to the village of Georgenthal.

Diagnosis—As for type and only species.

GEORGENTHALIA CLAVINASICA n. sp.

Etymology—Latin, *clavis*, key, and *nasica*, nostril, an epithet referring to the unique keyhole-shaped external naris.

Holotype—MNG 11135, skull and partial postcranium.

Type Locality and Horizon—Uppermost level of the 60 m thick middle sandstone unit of the Early Permian, Upper Rotliegend, Tambach Formation. The Bromacker quarry locality is an area of about 0.5 km² in the Thuringian Forest that comprises abandoned and intermittently active sandstone quarries about 20 km south of Gotha, central Germany, and 1.5 km north and 3.0 km southeast of the villages of Tambach-Dietharz and Georgenthal, respectively.

Diagnosis—Amphibamid dissorophoid temnospondyl with the following autapomorphies: embayment of narial margin of lacrimal; short, pointed, dorsal exposure of squamosal on skull roof over otic notch; dorsal process of squamosal narrowly exposed on lateral skull roof with medial flange that underlaps supratemporal. Synapomorphy with *Amphibamus* and *Doleserpeton*: short parasphenoid basal plate with wide lateral extensions; synapomorphy with *Amphibamus*, *Doleserpeton*, and *Platyrhinops*: anteroposteriorly shortened supratemporal; synapomorphies with *Amphibamus*, *Doleserpeton*, *Platyrhinops*, and *Eoscopus*: shortened squamosal-supratemporal suture; large squamosal embayment (otic notch) closely approaching orbit; amphibamid or dissorophoid synapomorphies with ambiguous optimization: large orbits, narrow interorbital width, short tabular horns, falciform postfrontal with long anterior processes, anterolaterally flaring lateral margins of frontals, and two vomerine fangs.

DESCRIPTION

General

The nearly complete skull MNG 11135 exhibits variable bone preservation, from well consolidated and preserving minute surface features to a soft, spongy consistency with loss of surface features. The poorly preserved bone is not thought to be the result of incomplete ossification, as this type of preservation also occurs in unambiguously mature vertebrates from the Bromacker quarry, but rather is most likely due to postdepositional, subaerial chemical dissolution. Areas of the skull particularly affected by dissolution include the left temporal, the tabular-postparietal-occipital, the left quadratojugal and quadrate, and the palate.

The skull (Figs. 2, 3) was dorsoventrally compressed, resulting in a very low profile and some distortion. The left side of the skull is splayed outward, so that most of the orbital and pre- and postorbital bones occupy a single horizontal plane. Distortion is greatest on the right side of the skull, resulting in some overlapping of the anterior and posterior circumorbital and postorbital cheek bones. The skull is depressed along its midlength, producing longitudinally oriented cracks that run through the specimen in several areas, especially in the postorbital region, and a narrow midline gap between the premaxillae.

In dorsal view (Figs. 2, 3) the skull widens from the broadly rounded snout to approximately the level of the posterior extent of the orbits, and then gradually narrows posteriorly to the jaw articulations, which occupy a level just posterior to the occiput. The external narial openings are oval shaped and exhibit a small but well-defined embayment on their posterior margins, on the rostral edge of the lacrimal. The length and width of the large, circular orbits are subequal (Table 1), at least in the less distorted left orbit, and their length is greater than either the pre- or postorbital regions of the skull. The interorbital width is very narrow. The preorbital and postorbital skull lengths, measured along the midline, are subequal, with the postorbital length being slightly more abbreviated. The nasals are slightly shorter in



FIGURE 2. *Georgenthalia clavinasica*, gen. et sp. nov., photograph of holotype MNG 11135 in dorsal view.

length than the parietals, whereas both are shorter than the frontals. The otic notches are anteroposteriorly deep, closely approaching the orbits. Although crushing has distorted their shape somewhat, the angle formed by the squamosal embayment is acute but probably greater than 45° in the undistorted skull. Sculpturing is variably developed as a delicate pattern of longitudinal ridges and grooves radiating from a central area of growth, and appears to be undergoing replacement by a pit and ridge pattern. In some bones (for example, the nasals, frontals, and parietals) the pit and ridge sculpturing occurs mainly at the center of the bones with the longitudinal ridges and grooves being restricted to their periphery. The sutures are mostly simple, lacking a pattern of complex interdigitation.

Dental Arcade

The premaxilla has the standard temnospondyl morphology, possessing a tooth-bearing maxillary process, which contacts the maxilla in a posteroventrally oblique suture at about the midlength of the subnarial bar, and a narrow, posterodorsally directed process. Together these processes form the anterior margin of the external naris. The posterodorsally directed processes are widely separated from the midline by, and appear to overlap the lateral margins of, the nasals, a morphology typically seen temnospondyls and referred to as 'alary processes' (to distinguish them from 'dorsal' or 'nasal processes' that contact one another along the midline). The rounded distal ends of the alary processes and a short, longitudinally oriented impression on the dorsal surface of the left nasal just posterior to the alary process suggest that the full extent of the processes, which terminate in a pointed margin in all other amphibamids, have been lost. At the midline intersection of the premaxillae and nasals is an internarial fontanelle, similar to those seen in *Doleserpeton*, *Ter-somius*, and *Eoscopus* (Fig. 1).

The slender maxilla extends to a level approximately midlength between the orbit and otic notch. The maxilla has a rela-

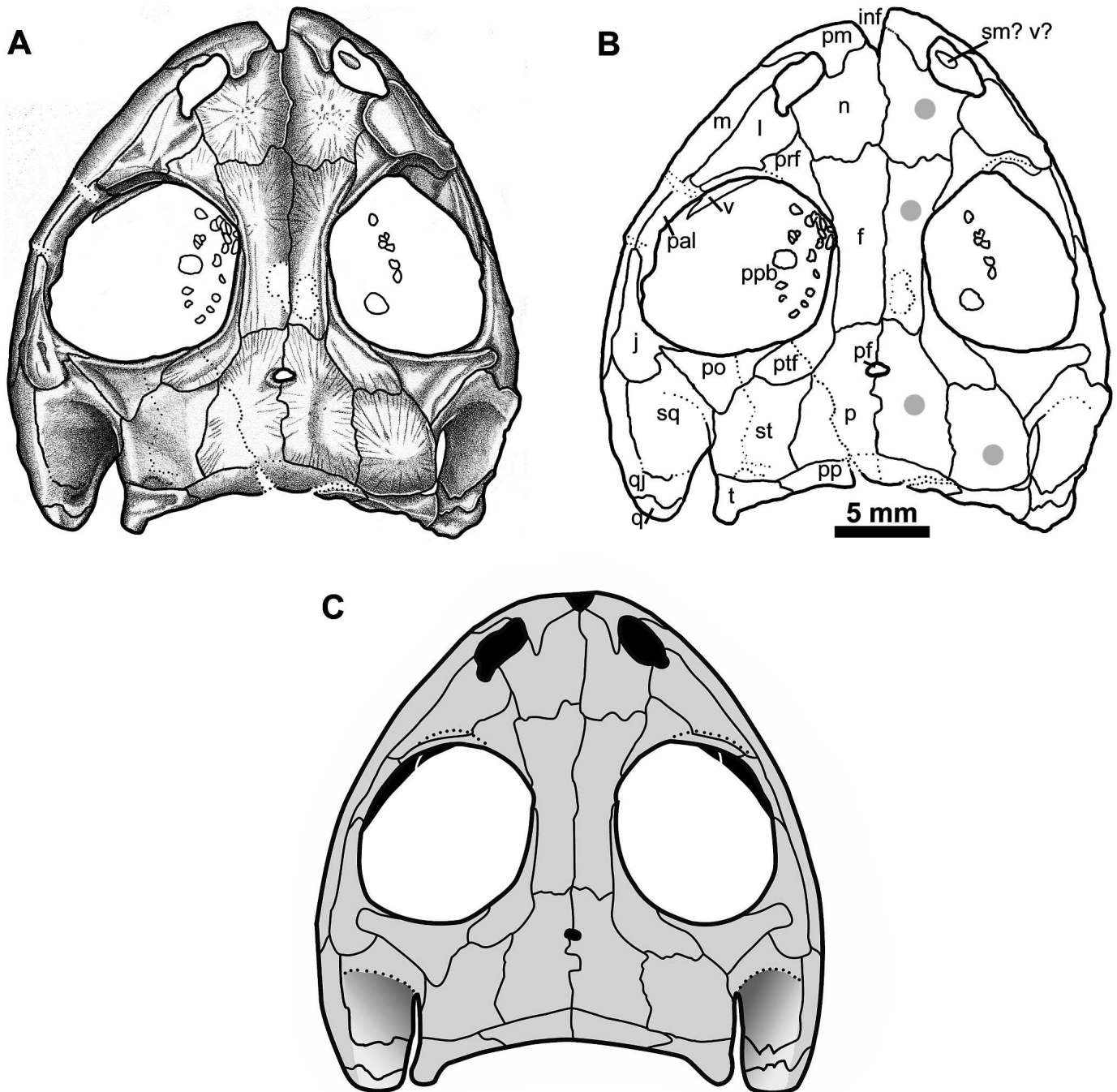


FIGURE 3. *Georgethalia clavinasica*, gen. et sp. nov., holotype MNG 11135 in dorsal view. **A**, interpretive drawing, **B**, sutures and homologies, **C**, reconstruction. Grey dots on **B** indicate centers of dermal ornamentation radiation and, presumably, ossification.

tively prominent facial lamina, and has a sharp decrease in its dorsoventral height at the anterior orbital margin ventral to the suborbital process of the lacrimal, although this decrease is more gradual on the right side (Fig. 4). From this point, the maxilla

gradually tapers in height until its posterior termination. The premaxillary-maxillary dentition consists of small, narrowly cylindrical, sharply pointed, non-labyrinthine teeth that serially decrease slightly in size posteriorly. Longitudinal sections of some

TABLE 1. Measurements and proportions for the skull of *Georgethalia*.

	SkL	PreL	PoL	PoW	IntW	OL	OW	PreL/SkL	OL/SkL	PoL/SkL
MNG 11135	28.3	9.3	9.1	17.3	4.5	10.6	11.2	.33	.32	.37

All measurement in millimeters. Skull length measurements made along midline of skull.

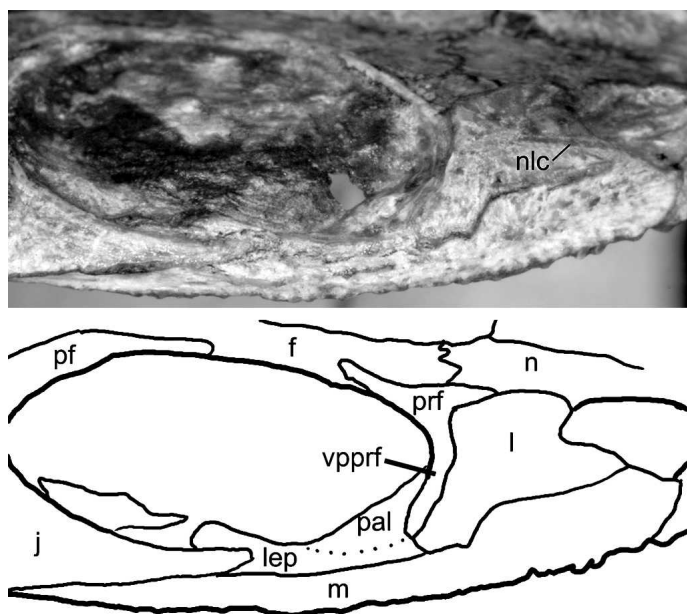


FIGURE 4. *Georgethalia clavinastica*, gen. et sp. nov., holotype MNG 11135 in oblique right lateral view. Photograph and interpretive drawing of suborbital anatomy, including the ventral prefrontal process articulating with the palatine, the lateral exposure of the palatine, and the superficial trace of the nasolacrimal canal (photo).

of the teeth indicate they are not pedicellate. It is estimated that the premaxilla had 10–15 and the maxilla 30–40 teeth.

Skull Roof

The paired, quadrangular nasals expand greatly posterolaterally as they extend beneath the alary processes of the premaxillae and form almost the entire posteromedial margin of the external nares, and then converge to a transverse but irregular contact with the frontals. The frontals, whose lengths are contained within the anteroposterior extent of the orbits, have a subrectangular outline that gradually expands anteriorly to a width that is nearly twice that of the posterior ends. The lateral margins of the nasals continue this anterolateral flaring to the external nares. The lateral margin of the anterior third of the parietal expands posterolaterally along its contact with the posterior half of the medial margin of the postfrontal. The remaining lateral margin of the parietal maintains a course essentially parallel to the skull midline as it contacts the medial margin of the supratemporal. The moderately sized parietal foramen, which bears a raised rim along its posterior margin, is located one third of the length of the interparietal suture from its anterior end. The interparietal suture exhibits a couple of deep curves just posterior to the parietal foramen, similar to, but not as highly developed as, those seen in other amphibamids (i.e., *Eoscopus* and some specimens of *Micropholis*; Daly, 1994; Schoch and Rubidge, 2005; Fig. 1C, D).

The supratemporal occupies a large subrectangular area with a slight narrowing of its lateral margin anteriorly. Its lateral margin forms most of the central portion of the horizontal shelf-like dorsal margin of the otic notch without contributing to a vertical supratympanic flange, as is typical of dissorophids and trematopids (Bolt, 1974a), and some specimens of the amphibamid *Eoscopus* (Daly, 1994). The tabulars and postparietals form a narrow band along the occipital margin of the skull table. Although the right tabular and a small adjoining portion of the postparietal are displaced a short distance anteroventrally beneath the supratem-

poral of the skull table, the contact between the nondisplaced portion of the right postparietal and the parietal is faintly visible. The postparietals are broadest in anteroposterior width along their midline suture, and narrow laterally to contact the tabulars and posteromedial corner of the supratemporals. The tabulars exhibit a modestly developed, rounded, tab-like posterolateral projection at their contribution to the posterodorsal margin of the otic notch. Medially, they narrow slightly to their contact with the postparietal. The tabulars also do not contribute to a supratympanic flange of the otic notch. Although the occipital margins of the postparietals and tabulars are incomplete, they obviously formed a slightly concave occipital margin of the skull table.

Circumorbital and Temporal Bones

Among the circumorbital bones only the margins of the prefrontals, frontals, postfrontals, and postorbitals are moderately elevated into a nonsculptured, rounded ridge (Figs. 2, 3). The triangular prefrontal wedges anteriorly between the nasal and lacrimal, but remains widely separated from the external naris. The posterodorsal corner of the prefrontal forms a narrow, tapering orbital process that contacts the anterior third of the lateral margin of the frontal. Whereas the posteroventral corner of the prefrontal has an abbreviated lateral exposure (Fig. 4), it continues as a ventral process along the anterior orbital wall, medial to the orbital margin of the lacrimal, to contact the palatine. The lacrimal extends between the ventral half of the anterior orbital margin and the posterior margin of the external naris, with the right lacrimal being slightly displaced dorsomedially onto the dorsal surface of the nasal and prefrontal. A narrow, posteriorly directed, hemispherical embayment on the narial margin of the lacrimal gives the external nares a keyhole-shaped outline, unknown in any other amphibamid. A nasolacrimal canal is evident as a thin white trace on the external surface of both lacrimals, extending directly between the dorsoventral midpoint of the orbital margin of the lacrimal to the narial margin just ventral to its posterior embayment (Figs. 3A, 4). The palatine and its lateral suborbital exposure are best exemplified by the right, whereas the left has been displaced slightly into the orbit and is not laterally exposed. The lateral, suborbital exposure of the palatine consists of a narrow strip extending between contacts with the narrow distal ends of the orbital processes of the lacrimal and jugal.

The postfrontal is falciform in outline with a narrow, attenuate anterior extension that excludes the posterior half of the lateral margin of the frontal from the orbit. The remainder gently follows the orbital margin and ends ventrally in a bluntly rounded process that extends between a wedge-shaped, dorsal orbital process of the postorbital and the transverse anterior margin of the supratemporal. The triangular postorbital forms almost the entire posterior margin of the orbit, from which it extends posteriorly to a level just dorsal to the anterior margin of the otic notch in a sharply pointed apex that wedges between the anterior portions of the supratemporal and squamosal. The distal end of its ventral orbital process overlaps the dorsal orbital process of the jugal, but is narrowly separated from the orbital rim. The suborbital process of the jugal, best exemplified by the right, narrows anteriorly along the dorsal margin of the maxilla to the midlength of the suborbital bar, where its distal end wedges a short distance beneath the posterior end of the laterally exposed palatine. Posteriorly the jugal ends in a broadly rectangular projection that narrowly contacts the quadratojugal but deeply incises the ventral anterior margin of the squamosal (Fig. 5). The orbital margin of the jugal has a short, splint-like dorsal orbital process that intervenes between the acute ventral process of the postorbital and the orbit.

The squamosal, the largest of the postorbital temporal bones,

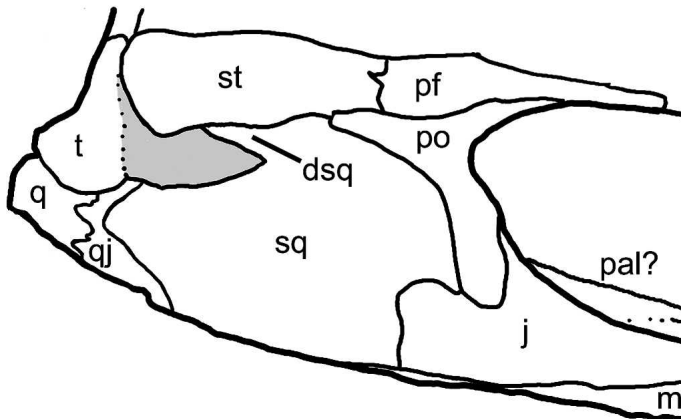
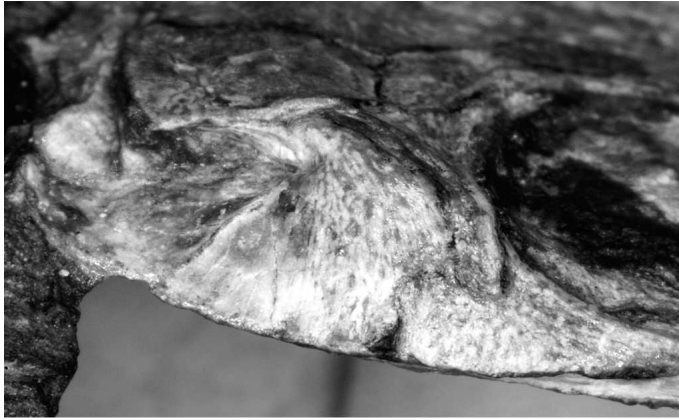


FIGURE 5. *Georgethalia clavinastica*, gen. et sp. nov., holotype MNG 11135 in right lateral view. Photograph and interpretive drawing of right otic notch, showing the supraotic process of the squamosal underlapping and supporting the supratemporal.

forms the anterior, much of the ventral, and a portion of the dorsal margins of the large otic notch (Fig. 5). Along the ventral border of the notch a wide margin of the squamosal curves strongly medially to face posterodorsally. A narrow portion of the squamosal on the dorsal border of the otic notch tapers to a sharp, posteriorly directed apex that contacts the midlateral margin of the supratemporal (Fig. 5); this projection also appears as a short, narrow splint of bone in dorsal view of the skull (Figs. 2, 3). This portion of the dorsal squamosal also extends medially in the form of a horizontal flange that contacts the ventral surface of the supratemporal to support the skull roof. The squamosal does not contribute to a supratympanic flange, as is typical of dissorophids, trematopids, and the amphibamid *Eoscopus* (Bolt, 1974a; Daly, 1994).

The quadratojugal is folded under the right side of the skull and is only visible in the otic notch in dorsal view (Fig. 3). On the left side of the skull the quadratojugal is seen as an elongate, rectangular ossification spanning from the posterior notch in the jugal to the quadrate. Poor preservation has obscured the suture between the quadratojugal and the squamosal so that it is not easily traceable on the left side, but the right side shows that the quadratojugal underlapped, and passed medially to, the posterior margin of the squamosal (Figs. 3, 5). A suture between the quadratojugal and the quadrate is clearly visible on the right side of the skull, and faintly on the left, which shows the quadrate has a broad dorsal exposure at the jaw articulation unlike other amphibamids where it is dorsally covered by the medial projection of the quadratojugal (Fig. 1). The dorsal process of the quadrate, if present, is covered by the quadratojugal.

Two additional small features seen in dorsal view (Figs. 2, 3) are: (1) a small, bone with a tear-drop outline in the right narial opening that is most likely part of the dorsal surface of the vomer but may represent the septomaxilla; and (2) a mosaic of poorly preserved bones occupying most of the dorsomedial half of each orbit that quite likely represents a palpebral cup.

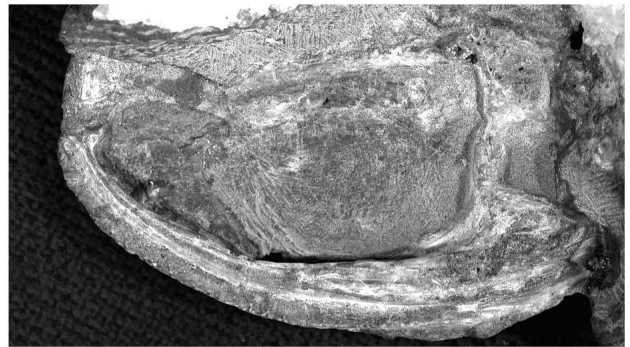
Occiput

At least the right occipital condyle is present and possibly a portion of the left. On the right side of the skull the occipital flanges of the tabular and postparietal are preserved, but the suture between them is visible only at the dorsal edge of the occiput. The remainder of the occiput is obscured by dorsoventral compression.

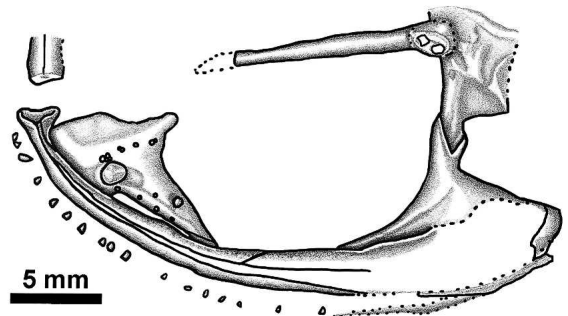
Palate

The palate was only prepared on the right side of the skull, and the tightly occluded lower jaw obscures the lateral-most portion of the palate in ventral view (Fig. 6). The interpterygoid vacuities are large and extend almost the full width of the palate. Al-

A



B



C

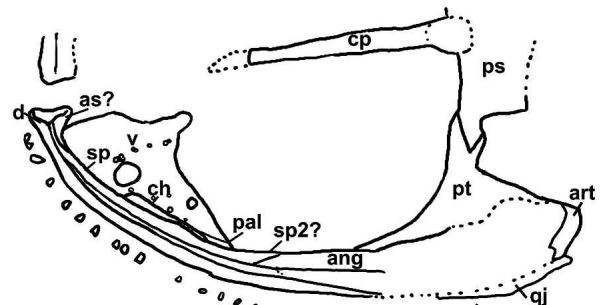


FIGURE 6. *Georgethalia clavinastica*, gen. et sp. nov., holotype MNG 11135 in palatal view. A, photograph, B, specimen drawing, C, sutures.

though the choana is not exposed along its lateral margin, it can be determined by the placement of the maxilla that it is longer than the external naris and most likely has a greater length than width.

The vomer forms a straight medial border of the internal naris. It cannot be determined how much the palatine contributed to the medial narial border, because the suture between the palatine and vomer is not obvious. A suture can be detected between the vomer and palatine at the posterior margin of the choana. Ridges are present running from the posteromedial margin anterolaterally, and along the medial border of the choana, although compression has somewhat flattened these ridges. The vomer bears two fang-pit pairs, one on the medial border of the internal naris at its anterior terminus and the other on the long, slender, distally tapering process that articulates with the palatine. A shagreen of denticles covers the ventral surface of the vomer, and a row of larger denticles are present on the two aforementioned ridges. Along the median suture between the vomers there appears to be a slight depression of the surface of the vomer (Fig. 6b). This is interpreted to be an intervomerine depression, although compression flattens this area substantially.

Only a small anterior portion of the palatine is visible in ventral aspect, and the ectopterygoid is not exposed. Because the narrow lower jaw prevents these bones from being visible in ventral aspect, it is assumed that they are mediolaterally slender.

Most of the triradiate pterygoid is visible in ventral aspect. The palatal ramus is exposed along its medial and dorsal edge and extends to the midlength level of the orbit, and thus could not reach the vomer to articulate with it. Denticles extend along the exposed ventral palatal ramus, suggesting that it is covered with a shagreen. The short quadrate ramus is mostly ventrally covered by the lower jaw. The medial ramus, the shortest of the three, bears a V-shaped socket for reception of the basiptyergoid process to form a mobile basicranial joint.

The poorly preserved basal plate of the parasphenoid is transversely expanded, giving it a subrectangular shape. A raised triangular field of denticles lies at the junction of the cultriform process and the basal plate. The anterior extent of the slender cultriform process cannot be confidently determined, though it appears to reach the posterior border of the midline union of the vomers. A shagreen of teeth does not occur on the cultriform process, nor do they appear to be present on the basal plate, but the bone surface is very poorly preserved here.

Mandible

Only the left mandible was prepared, and because it is preserved tightly adjoined to the skull, only the ventral surface and some of the lateral and medial faces could be exposed (Fig. 6). In ventral view the crescentic jaw is extremely slender just posterior of the symphysis and becomes wider posteriorly. Sculpturing is not present on any of the mandibular bones. The dentary has become disarticulated with the splenial and postsplenial along their lengths. The splenial passes posteriorly from the symphysis to a suture found posterior to the level of the palatine process of the vomer. It is possible that this represents the suture between the postsplenial and angular, which would mean that the suture between the splenial and postsplenial is obscured due to damage. Alternatively, this suture is between the splenial and postsplenial, which would make the splenial one of the longest known among amphibamids. We prefer the former interpretation. The angular forms an anteriorly projecting wedge between the dentary and splenial. Posteriorly the bones are too eroded to make out sutures, except for the articular, which forms the entire posterior margin of the posterior lower jaw.

At the symphysis the jaw flares anteroposteriorly to form a broad articulation surface. In most amphibamids this flaring is attributed to the dentary (e.g., Bolt, 1969; Daly, 1994). However,

the splenial appears to be narrowly compressed at its anterior end, reaching the symphysis only by a tiny sliver of bone on the ventral surface of the mandible, although this area is difficult to interpret with certainty. If the latter interpretation were correct, the majority of the posterior symphysis would be composed of an adsymphyseal (parasymphyseal of others, Bolt and Lombard, 2001), only recently identified in a temnospondyl (Anderson, 2005, 2006). Because this expansion, whatever its homology, is only visible in ventral view it is unknown whether it bears teeth or fangs as is typical in more basal taxa (Bolt and Lombard, 2001).

PHYLOGENETIC ANALYSIS

Amphibamids have figured prominently in discussions of the origins of lissamphibians (frogs, salamanders, and caecilians), and it is in this context that most phylogenetic analyses of the group have been performed (Bolt, 1991; Trueb and Cloutier, 1991; Milner, 1993; Ruta et al., 2003; Anderson, 2007; Ruta and Coates, 2007). These analyses vary in taxonomic inclusiveness but usually find that amphibamids are paraphyletic with respect to some, or all, lissamphibians, although ingroup relationships among dissorophoids are generally poorly resolved (but see Vallin and Laurin, 2004, for another view). Most recently, Anderson (2007) performed an analysis of basal tetrapod relationships, in a study of developmental characters cited as important to the question of the origins of modern amphibians. Preliminary information on *Georgenthalia* (Anderson et al., 2004) was incorporated in this study, the results of which are in Figure 7C. It was found that *Georgenthalia* fell into a polytomy that includes all dissorophoids. However, this analysis was too broad in taxonomic scope to answer specific questions regarding amphibamid relationships.

Studies of amphibamid in-group relationships began with the analysis of Milner (1988). In a discussion of the competing hypotheses of a mono-, para-, or polyphyletic Lissamphibia, Milner presented a hypothesis of relationships of selected temnospondyls and lissamphibians. Two amphibamids were included, '*Amphibamus*' (*Platyrhinops*) *lyelli* and *Doleserpeton*, along with successively more basal taxa such as *Trematops*, *Eryops*, *Archegosaurus*, and *Dendrerpeton*. He found Lissamphibia to be the sister taxon to *Doleserpeton*, with '*Amphibamus*' as its next closest outgroup. Trueb and Cloutier (1991) also examined relationships among temnospondyls in an exploration of the origin of Lissamphibia. They found (Fig. 7A) that the amphibamids *Tersomius*, *Doleserpeton*, and *Amphibamus* formed the sister taxon to a clade composed of *Micromelerpeton*, a number of branchiosaurid taxa, and a monophyletic Lissamphibia. Clack and Milner (1993) looked exclusively at the relationships within Amphibamidae (a name they reinstated over *Doleserpetontidae*). Their result (Fig. 7B) clustered *Tersomius* and *Doleserpeton*, with *Amphibamus* and *Platyrhinops* successively more basal taxa, but unfortunately they assumed the monophyly of the family. The first computer assisted analysis of amphibamid relationships after that of Trueb and Cloutier (1991) was that of Schoch and Rubidge (2005). They included a host of out-group taxa, and included in the ingroup exemplars of all dissorophoids except branchiosaurids: *Micromelerpeton*, *Trematopidae*, *Ecolsonia*, *Dissorophinae*, *Cacopinae*, and the amphibamids *Micropholis*, *Eoscopus*, *Platyrhinops*, *Doleserpeton*, and *Amphibamus*. They removed *Tersomius* from the analysis because of concerns that it is a composite taxon, which improved resolution of the phylogenetic hypothesis and increased the consistency index. In their tree *Doleserpeton* and *Amphibamus* formed the terminal dichotomy, and *Platyrhinops*, *Eoscopus*, and *Micropholis* fell to successively more basal positions, in general agreement with the topology of Clack and Milner, although the latter study placed *Tersomius* in the terminal dichotomy. The remainder of the dis-

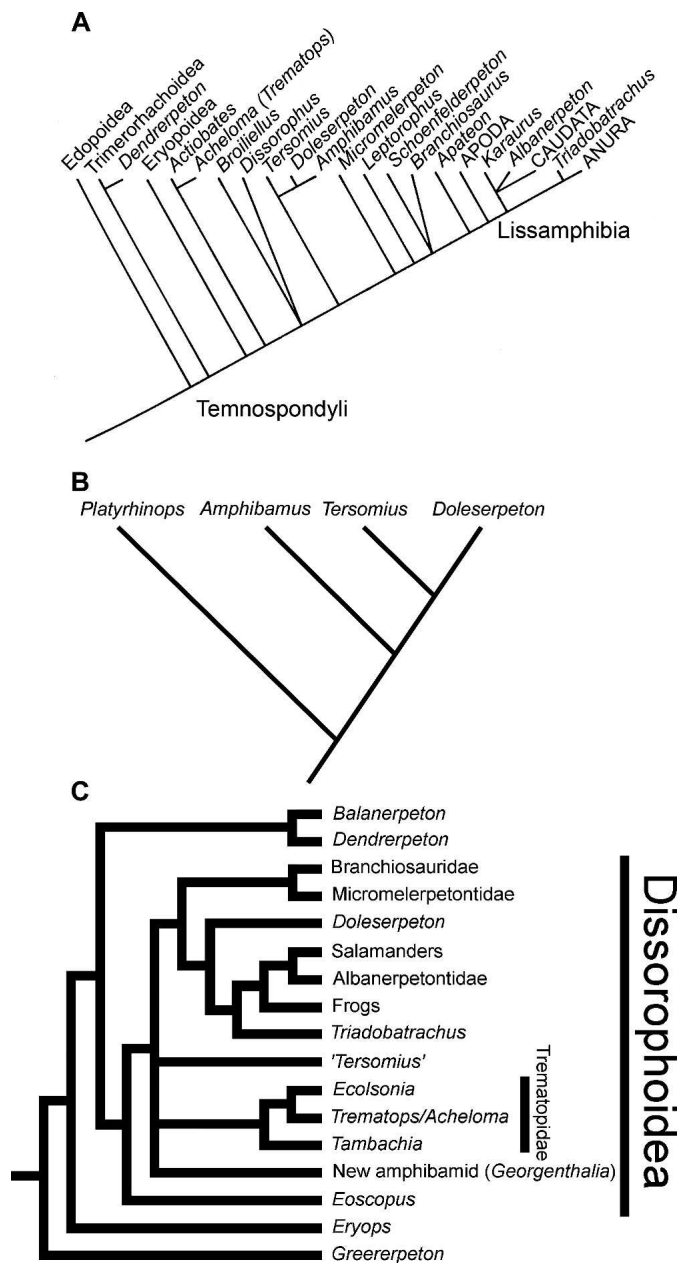


FIGURE 7. Previous hypotheses of amphibamid relationships. **A**, from Trueb and Cloutier (1991), where amphibamids are sister taxa to a “branchiosaur”-lissamphibian clade. **B**, from Clack and Milner (1993), which only included amphibamids. **C**, from Anderson (2007), only the temnospondyl portion of the tree, which placed *Doleserpeton* as sister taxa to Batrachia (frogs and salamanders), while the remaining amphibamids fell to a polytomy with other dissorophoids, and *Eoscopus* was the basalmost dissorophoid. This analysis was testing the placement of lissamphibians among a large group of Paleozoic tetrapods, rather than investigating details of amphibamid relationships.

sorophoids assumed a pectinate structure, basal to Amphibamidae.

To discover *Georgenthalia*'s place among amphibamids a new analysis was performed, using the matrix of Schoch and Rubidge (2005) as the basis for further exploration. We modified their matrix in a number of ways (Appendices 1 and 2: all changes to the codings of Schoch and Rubidge [their numbering was retained in our analysis to facilitate communication] and all new

characters are indicated by boldface text). To begin, we recoded character 5 so that taxa identified in character 4 as having an entirely smooth parasphenoid plate (Dissorophinae, Cacopinae) were scored as ‘inapplicable’ for further discussions of parasphenoid denticle field morphology. Next, we rephrased character 17 by eliminating the phrase “with labyrinthine infolding of enamel and dentine” (Schoch and Rubidge, 2005:521) for two reasons. Firstly, the presence of labyrinthine infolding is accounted for in character 19, thus we removed a potential source of nonindependence. Second, the presence or absence of labyrinthodonty is not directly related to the presence or absence of pedicely—most taxa that lack labyrinthodonty also lack pedicely—so including labyrinthodonty in the description of pedicely is irrelevant to the derived state being captured by that character. We changed the coding of character 30 for *Eoscopus* (from 0 to 0&1).

We also added six new characters. To capture the derived falciform (sickle-shaped) postfrontal morphology we added character 48. Character 49 records the presence or absence of an internarial fontanelle. The anterolateral flaring of the frontals seen in some amphibamids is included as character 50. The rounded skull shape is included as the derived state of character 51.

New characters 52 and 53 document the relatively narrow interorbital width and large otic notches seen in some amphibamids, respectively. Both of these characters required taking measurements from published reconstructions (Table 2; Fig. 8). The narrow interorbital width was described as a ratio of the minimal interorbital width and the length of the median skull table. This feature is not correlated with the absolute size of the skull; taxa with both absolutely large and small skulls showed this feature. Taxa with an interorbital distance of less than 25% of the median skull roof length were scored as narrow; all others were scored as wide. Outgroup taxa *Eryops* and *Sclerocephalus*, which are semiaquatic taxa with a crocodylian-like cranial construction with small dorsomedially placed orbits, were scored as possessing a different state from the large orbited amphibamids despite having the requisite ratio because of their overall different morphology. Character 53 captured the large otic notch size by creating a ratio of the distance from the anterior margin of the notch to the posterior margin of the orbit against the distance from the quadrate to the anterior margin of the notch (Fig. 8). Three states capture the three clusters of ratios found: large otic notches closely approaching the posterior margin of the orbit (postorbital area less than 50% of the length of the notch), a moderate distance from the orbit (postorbital area 50–70% the length of the notch), or far from the orbit (over 70%).

We searched using the branch and bound algorithm (stepwise, furthest addition sequence) in PAUP*4b10 (Swofford, 2002). Tree statistics were calculated, and topology and character distribution explored, using MacClade 4.08 (Maddison and Maddison, 2005).

Results

Analysis of all taxa produces 3 most parsimonious trees (116 steps, consistency index 0.71, and retention index 0.81; Figure 9). These trees vary in the placement of *Georgenthalia* within the amphibamid clade ((*Tersomius* + *Micromelerpeton*) (*Eoscopus* (*Platyrrhinops* (*Doleserpeton* + *Amphibamus*))); it is placed as sister taxon to the crown dichotomy, or a step or two more basal from it. *Georgenthalia* is always placed crownward of the clade of *Tersomius* and *Micromelerpeton*. *Micromelerpeton* is found to be the basalmost amphibamid in all trees. *Ecolsonia* is placed as outgroup to crown Dissorophidae (Cacopinae + Dissorophinae) as originally suggested by Berman et al. (1985).

TABLE 2. Ratios of interorbital width and orbital length to basal skull length, and size of otic notch to distance to posterior orbital margin for the taxa included in the phylogenetic analysis.

Taxon	Spec. #	IOW Ratio	OL:SkL	State	OT-O Ratio	State	Source of reconstruction
<i>Dendrerpeton</i>	NSM 978 GF33.1	0.25	0.26	Wide	1.22	Far	Godfrey et al., 1987
<i>Dendrerpeton</i>	NSM 987 GF99.1	0.29	0.19	Wide	1.00	Far	Holmes et al., 1998
<i>Eryops</i>	Composite reconstruction	0.22	0.12	Narrow*	0.71	Far	Holmes, 2000
<i>Sclerocephalus</i>	Juvenile skull reconstruction	0.21	0.31	Narrow*	2.00	Far	Schoch, 2003
<i>Sclerocephalus</i>	Adult skull reconstruction	0.16	0.16	Narrow*	0.86	Far	Schoch, 2004
<i>Dissorophus</i>	MCZ 2122-1	0.28	0.24	Wide	0.95	Far	DeMar, 1968
<i>Tambachia</i>	MNG 772	0.25	0.28	Wide	1.03	Far	Sumida et al., 1998
<i>Ecolsonia</i>	CM 41703	0.25	0.29	Wide	0.88	Far	Berman et al., 1985
<i>Amphibamus grandiceps</i>	YPM 794/FMNH UR2000	0.33	0.43	Wide	0.47	Near	Milner, 1982
<i>Platyrhinops lyelli</i>	MB 1888-1456	0.37	0.40	Wide	0.53	Medium	Milner, 1982
<i>Platyrhinops lyelli</i>	Composite reconstruction	0.40	0.30	Wide	0.53	Medium	Clack and Milner, 1993
<i>Eoscopus lockardi</i>	Composite reconstruction	0.19	0.35	Narrow	0.48	Near	Daly, 1994
<i>Tersomius texensis</i>	AMNH 4719 (holotype)	0.23	0.30	Narrow	1.64	Far	Carroll, 1964
<i>Tersomius texensis</i>	MCZ 1912 (large adult skull)	0.20	0.27	Narrow	0.60	Medium	Carroll, 1964
<i>Doleserpeton</i>	Composite reconstruction	0.19	0.42	Narrow	0.42	Near	Bolt, 1969
<i>Micromelerpeton credneri</i>	Premetamorphic	0.22	0.34	Narrow	1.17	Far	Boy and Sues, 2000
<i>Micromelerpeton credneri</i>	Postmetamorphic reconstruction	0.18	0.36	Narrow	0.75	Far	Boy and Sues, 2000
<i>Apateon gracilis</i>	Premetamorphic reconstruction	0.20	0.50	Narrow	1.33	Far	Schoch and Fröbisch, 2006
<i>Apateon gracilis</i>	LFUM-SS 13612 (adult)	0.21	0.38	Narrow	0.38	Near	Schoch and Fröbisch, 2006
<i>Micropholis</i>	Broad morph reconstruction	0.28	0.31	Wide	2.00	Far	Schoch and Rubidge, 2005
<i>Micropholis</i>	Narrow morph reconstruction	0.27	0.30	Wide	0.88	Far	Schoch and Rubidge, 2005
<i>Georgenthalia</i>	MNG 11135	0.16	0.40	Narrow	0.39	Near	Present study

*Indicates alternate coding. See text for details.

DISCUSSION

Georgenthalia and Amphibamidae

Georgenthalia is nested deep within Amphibamidae, but the uncertainty over its precise placement underscores the difficulty of analyzing this group. Various characters support its placement at each of the three possible nodes (Fig. 9), and we fully expect that the description of the postcrania of *Georgenthalia*, and the

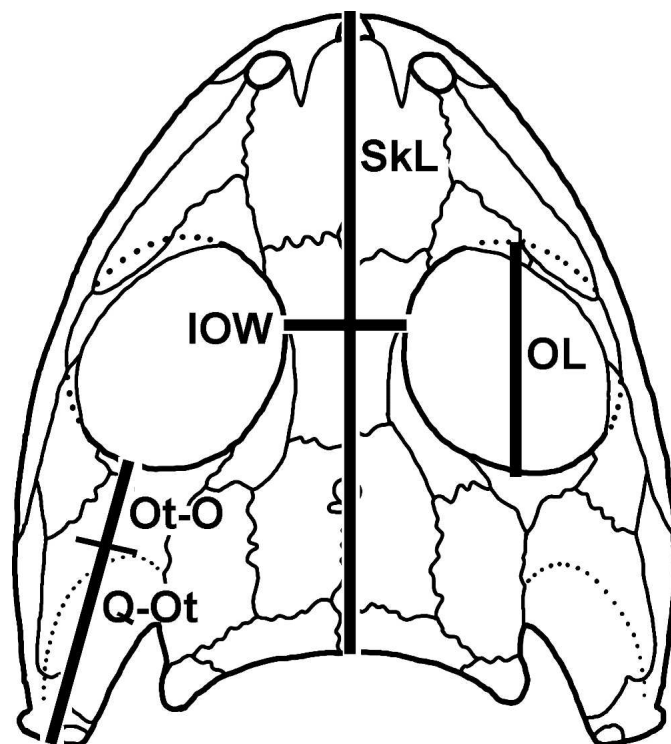


FIGURE 8. Measurements used to examine interorbital width and size of the otic notch and its proximity to the orbital margin. Modified from Daly (1994). See Table 2 and text for discussion.

description of new amphibamids and consequent discovery of new characters, will resolve its placement. It is also anticipated that the solution of the ‘*Tersomius* problem’ will help solidify the placement of *Georgenthalia*. Currently, *Tersomius* includes a number of distinct, different amphibamids. The larger specimens described by Carroll (1964), which we used for coding our new characters, show features quite close to *Micropholis*, which is reflected by their clustering in the present analysis, but others appear similar to some of the more derived amphibamids. Revision of this genus should greatly improve our understanding of amphibamid relationships.

Features present in the branchiosaurid *Apateon* after its rapid metamorphosis that are shared with amphibamids include large orbits and a large increase in the size of the otic notch—both features associated with an ecologic shift toward terrestriality (Schoch and Fröbisch, 2006). In general, for the temnospondyls measured the interorbital width appears to be set early in ontogeny, and the ratio of interorbital distance measured (Table 2) does not change substantially with growth; even in *Sclerocephalus*, with its smaller orbits, this ratio holds constant (although with a broad range; Schoch, pers. comm. 2006). The orbital length compared to the total skull length does change drastically with growth; compare the juvenile and adults of *Sclerocephalus* for instance. Again, however, in amphibamids and branchiosaurs (sensu lato) the orbit begins larger early in ontogeny and remains larger (compared with the out-groups) with growth despite the overall negative allometry of this feature. The size of the otic notch also changes dramatically through ontogeny in *Apateon* (ratio of the postorbital bar to size of otic notch changing from 1.33 to 0.38; Table 2; Schoch and Fröbisch, 2006), becoming larger with the posterior extension of the quadrate during growth. It also changes in *Micromelerpeton* (1.17 to 0.75), *Tersomius* (1.64 to 0.60), and *Sclerocephalus* (2.00 to 0.86), but interestingly, in none of these taxa does the size of the otic notch achieve the size seen in *Apateon*, *Eoscopus*, *Amphibamus*, or *Georgenthalia*. In these derived taxa, the otic notch is large early in ontogeny and becomes even larger with growth, similar to the orbital length.

Perhaps related to this, with respect to *Micromelerpeton*, is the recent finding in an analysis of branchiosaur relationships (Schoch and Milner, in press) that it is a stem dissorophoid and

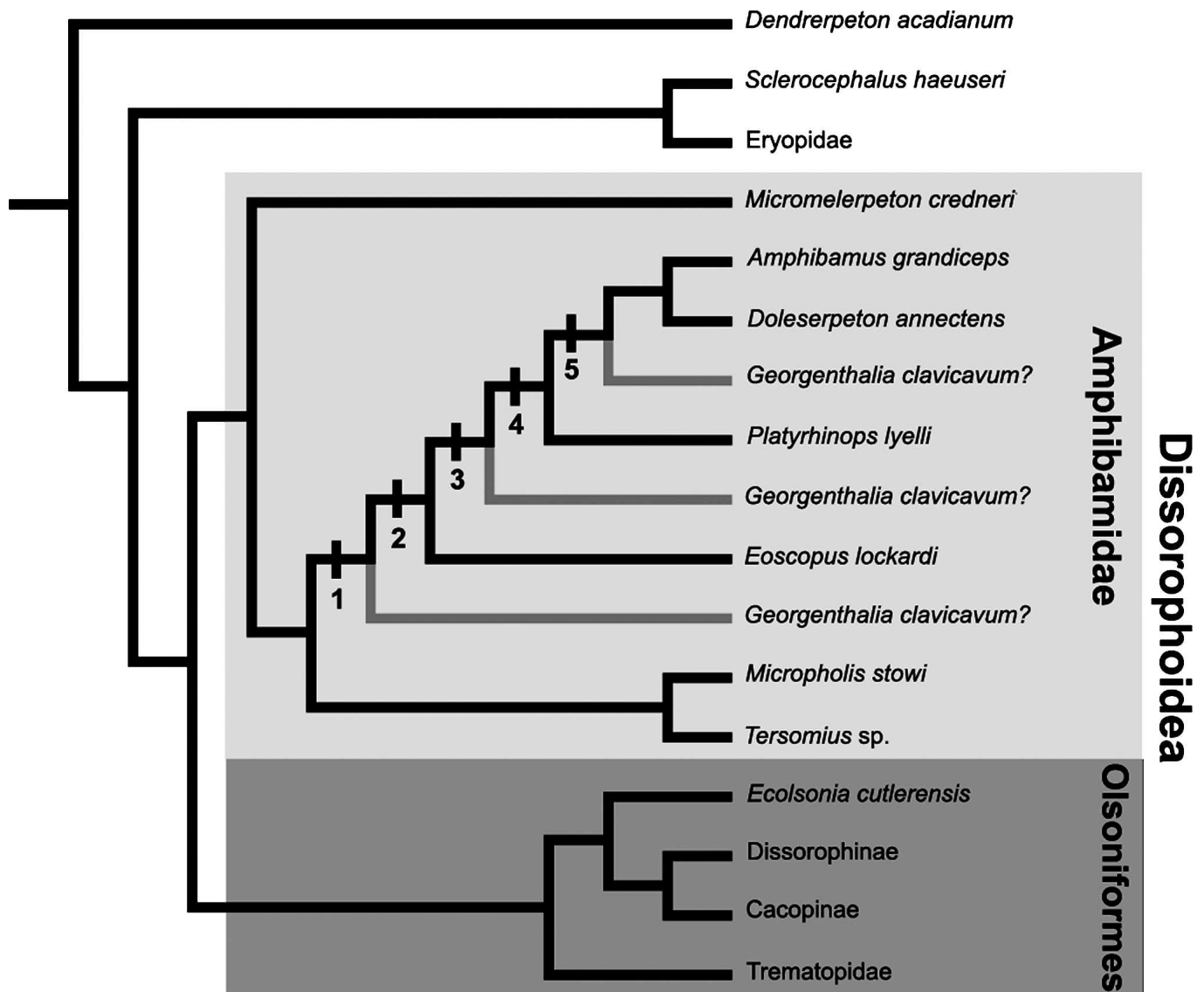


FIGURE 9. Summary of three most parsimonious trees found in the present analysis, with the boundaries of the definitions of Amphibamidae and Olsoniformes indicated in grey. *Georgethalia* is placed in the three indicated positions (grey branches). Character support for each position given as follows, by names and numbered nodes (positive numbers represent derived state, negative reversal, parenthetical for multistate characters): Dissorophoidea: 1, 2, 20, 21; Amphibamidae: 11 (parallel in Dissorophidae), 31, 43, 49 (reversed in *Platyrhinops* and *Micropholis*); Olsoniformes: 23, 26, 28, 34, 36; **1**) -3, 25, 32, 53(2); **2**) 22 (*Georgethalia* has state 0 so is a reversal of this character in the two higher positions); **3**) 10, 13, 19, 27 (*Georgethalia* is unknown for 10, 13, and 19); **4**) 18, 35; **5**) 6.

not an amphibamid as we found. Our matrix has some conflicting signals on this point; while we have several characters supporting our Amphibamidae (11, also seen in Dissorophidae, 21, 43, and 49 in all but *Platyrhinops* and *Micromelerpeton*), quite a number of other characters support all other amphibamids to the exclusion of *Micromelerpeton* (12 and 15 in parallel with Dissorophidae, 34 (2), 36 (2), 38, 42, 45 except *Amphibamus*, 47, 51). On the other hand, this would be expected in a more plesiomorphic amphibamid as well, but we expect future work should clarify the nature of relationships between branchiosaurs, micromelerpetontids, and Amphibamidae.

This study suggests additional characters that can distinguish between amphibamid taxa. Discussed above are: pedicellate teeth (and bicuspid teeth should be a separate character; Anderson and Bolt, 2005), the large otic notches, and narrow interorbital width. Also, the postfrontal of *Georgethalia* is a narrow, falciform (crescent-shaped) element, which is a feature shared

with a number of amphibamids (*Eoscopus*, *Amphibamus*, *Platyrhinops*, and some specimens attributed to *Tersomius*). *Georgethalia* has frontals that are rostrally expanded, also seen in *Platyrhinops*, *Tersomius*, and *Eoscopus*. *Georgethalia* and other amphibamids have an internarial fontanelle, which is also seen convergently in other clades of temnospondyls such as zatrachydids (Schoch, 1997).

It is striking that *Georgethalia* should have such large orbits and otic notches postmetamorphically, which strongly supports a highly terrestrial nature and fits with the overall environmental interpretation of the Bromacker locality. The Tambach Formation appears to have been deposited in a small, upland, internally-drained paleogaben (Eberth et al., 2000), and the Bromacker locality within it preserves a rare, strictly terrestrial assemblage. This interpretation is reinforced by the complete absence of fish and aquatic to semi-aquatic tetrapods, despite over a century of collection of both trackway and skeletal ma-

terial. A significant portion of the fossils recovered at the locality are characterized by their remarkable completeness which Eberth et al. (2000) interpreted as the result of death and burial being coeval events, mostly likely caused by sheet floods.

Georgenthalia and Ontogeny

Georgenthalia is best interpreted as an early postmetamorphic amphibamid, meeting a number of the criteria for metamorphosis of Boy and Sues (2000) and Schoch (2002). First, its dermal bone ornamentation is in the process of transforming from the lighter ridge and groove pattern to the more pronounced reticulated ridges and pits seen in adult temnospondyls, a transformation of stage three of Boy and Sues (2000). There are no ceratobranchials present, nor are there any traces of lateral line canal grooves. A septomaxilla may have been present, which is usually a late-ossifying bone among aquatic temnospondyls (Boy and Sues, 2000). The nasolacrimal groove, which runs longitudinally along the lacrimal in larvae, has been fully walled over, forming a canal. This event occurs around the time of metamorphosis. The parietal foramen is of reduced size, a sign of advanced development (Carroll, 1964). The quadrate is ossified, an event correlated with ‘metamorphosis’ in temnospondyls (Boy and Sues, 2000; Schoch and Fröbisch, 2006). Finally, the dorsal process of the palatine is present and it has a lateral exposure. However, evidence against *Georgenthalia* being fully adult include the aforementioned pattern of dermal bone ornamentation, simple sutures, the rather indistinct possible septomaxilla, and jaw articulations only slightly posterior to the level of the occiput.

Given that *Georgenthalia* is not fully adult, is there a possibility that it might mature into another recognized taxon of dissorophoid? The difficulty of discerning between pedomorphic taxa and juveniles of another taxon is a pressing problem in amphibamid taxonomy, because many of the features characteristic of amphibamids (large orbits, shortened ant- and postorbital skulls) are also known from allometric studies to change to more typical temnospondyl morphologies with larger size (Boy and Sues, 2000 and citations therein; Schoch, 2002; Steyer, 2000; Schoch and Fröbisch, 2006). The difficulty is succinctly stated by Bolt’s (1977) speculation that *Doleserpeton* may be a juvenile of *Tersomius*.

This is analogous to the situation that plagued studies of ‘branchiosaurs’ for many years. ‘Branchiosaurs’ were originally a collection of all small larvae found primarily in Lagerstätten in southwestern Germany and the Czech Republic. Whereas different growth series came to be recognized, the tendency was to group these growth series with adults from the same locality—for instance, Romer (1939) attributed branchiosaurs to be the larvae of the large (2–3 m) *Sclerocephalus*. However, more careful study, beginning in the 1970s (e.g., Boy, 1972), led to a better understanding of these important early ontogenetic stages. Actual larvae and growth series were discovered for *Sclerocephalus*. Other ‘branchiosaurs’ were recognized to belong to specific groups based on apomorphies: *Discosauriscus* to Seymouriamorpha, for instance, and Branchiosauridae and Micromelerpetontidae to Dissorophoidea. It is now widely accepted that branchiosaurs themselves are neotenic temnospondyls—despite a rich fossil record (with thousands of specimens for some species) and a depositional environment that is capable of preserving larger animals, no fully adult branchiosaurs were ever found (Boy, 1972; Schoch, 1992, 2002, 2004; Boy and Sues, 2000). Nevertheless, negative evidence such as this always leaves room for doubt; perhaps there was a dramatic metamorphosis at some point that was not preserved due to ecological factors.

Recently Schoch and Fröbisch (2006) described a fully adult, metamorphosed branchiosaurid of the species *Apateon gracilis*. Their description was of a rapid metamorphosis, with many de-

velopmental events occurring nearly simultaneously, similar to modern salamanders. Unlike modern salamanders, however, the skull does not undergo major remodeling during metamorphosis. Furthermore, it compares more closely with the amphibamids *Amphibamus* and *Doleserpeton* in its adult morphology than with any other temnospondyl. It retains, however, a palatal ramus of the pterygoid, to which the palatine and ectopterygoid are primarily attached, which extends much further rostrally than is seen in most amphibamids, a synapomorphy of branchiosaurids and micromelerpetontids (Schoch and Fröbisch, 2006; pers. comm. to JSA 2006). So, while it seems certain that amphibamids are not juveniles of larger dissorophoids as previously thought, ironically they may be ‘adult branchiosaurids’. *Micromelerpeton*’s placement as a basal amphibamid in this analysis is consistent with other recent studies of larger scale phylogeny (Ruta et al., 2003; Anderson, 2007; Ruta and Coates, 2007), which suggest that micromelerpetontids and branchiosaurids are nested within Amphibamidae, although a recent study suggests that micromelerpetontids are placed more basally within Dissorophoidea (Schoch and Milner, in press). This question should be examined in greater detail subsequent to the detailed description of the fully transformed branchiosaurid *Apateon gracilis* (Schoch and Fröbisch, 2006, pers. comm. to JSA, 2006).

Georgenthalia and Trematopidae

The most striking feature of *Georgenthalia* is the apomorphic external naris. This shape is reminiscent of the keyhole shape characteristic of the relatively closely related Trematopidae, which has been the subject of previous study (Olson, 1941, 1985; Bolt, 1974b; Dilkes, 1991, 1993). With the trematopid *Tambachia* also occurring at the Bromacker quarry, and given the late metamorphic stage of the holotype, it could be argued that *Georgenthalia* is a juvenile form of the latter. Ontogenetic studies offer a solution to this problem since juvenile trematopids are known from the fossil record (Olson, 1941, 1985; Dilkes, 1991, 1993). Dilkes (1993) assembled a growth series of a trematopid (probably *Phonerpeton*) demonstrating that the posterior continuation of the naris runs between the nasal and lacrimal, along the suture, even in juvenile forms. In *Georgenthalia*, in contrast, the smaller posterior extension is excavated into the large lacrimal. Additionally, juvenile (and adult) trematopids have a more pointed rostrum, and have narrower skulls than the broadly rounded *Georgenthalia*, which is otherwise typically amphibamid in cranial morphology.

What is similar between trematopids and *Georgenthalia* is the fact that the posterior extension of the external naris does not appear to be associated with the nasal capsule. Dilkes (1993) observed that the septomaxilla, which represents a cup-like ossification of the nasal capsule, is placed just anterior to a dorsoventral constriction of the narial margin present in trematopids. From the shape and orientation of the trematopid septomaxilla, it is clear that this represents the posterior portion of the nasal capsule. Similarly, in *Georgenthalia* the nasolacrimal canal (itself a feature associated with terrestriality; Boy and Sues, 2000:1159) bypasses the posterior extension ventrally and enters the external naris in its main, rounded, region. Were this embayment simply to be the result of a displaced septomaxilla, we would expect to see the nasolacrimal canal pass directly to it (and thus to Jacobson’s organ), as in modern amphibians (Jurgens, 1971). This means that whatever the function performed by the posterior extension of the external naris, whether to house a salt gland or other soft tissue structure (Bolt, 1974b) or as a functional adaptation to stresses associated with feeding (Dilkes, 1993), it was probably not associated with olfaction or respiration.

Nomenclatural Implications

Dissorophoidea has for many years served as a taxon to receive difficult to categorize, generalized temnospondyls. The

larger members of Trematopidae and Dissorophidae have long been affiliated with one another, whereas amphibamids, branchiosaurs, and micromelerpetontids have been added to the superfamily over time, partially on the assumption that they represent juveniles of the latter two families. With the emerging consensus that Amphibamidae itself is a distinct clade, we are presented with a nomenclatural issue: how can one easily discuss trematopids and dissorophids exclusive of amphibamids? 'Non amphibamid dissorophoids' simply does not roll off the tongue and it does not accommodate the possibility that micromelerpetontids are basal dissorophoids.

We suggest the following new taxon name for trematopids and dissorophids: Olsoniformes. We define it as dissorophoid temnospondyls that share a more recent common ancestor with *Acheloma* and *Dissorophus* than *Amphibamus*, a stem-based definition. In the current analysis, Olsoniformes is diagnosed by: contact between the tabular and squamosal; a supratemporal flange; a semilunar flange of the squamosal; straight distal ribs; and a long, rodlike humerus. Amphibamidae is defined recursively as dissorophoid temnospondyls that share a more recent common ancestor with *Amphibamus* than with *Acheloma* or *Dissorophus*. It could be argued that the definition of Amphibamidae should use *Micromelerpeton* as an out-group specifier taxon, but this would preclude the possibility that micromelerpetontids and branchiosaurs are deeply nested within Amphibamidae, as has been suggested recently (Ruta et al., 2003; Anderson, 2007; Ruta and Coates, 2007). *Dissorophus* and *Amphibamus* were chosen as specifier taxa since they are the type genera for Dissorophidae and Amphibamidae. *Trematops* however has been found to be synonymous with *Acheloma* (Dilkes and Reisz, 1987), which we select as specifier.

Following Sereno (1999), Dissorophoidea would be a logical choice for a node-based definition, completing a 'node-stem triplet'. However, an equally valid approach would be to define Dissorophoidea as a stem-based taxon with external reference taxon located within Eryopoidea or Zatrachyidae, or both, and possibly establishing another name for the node in question. The strength of the latter approach is that it would preserve the attribution of micromelerpetontids as dissorophoids should they fall stem-ward of the amphibamid-olsoniform dichotomy. We decline to define this clade at present, but suggest that the spirit of inclusiveness of the previous taxonomic context be preserved in converting this name.

We attempted to avoid confusing nomenclature with our choices. Dissorophoidea has included Dissorophidae, Trematopidae, and Amphibamidae (then Doleserpetontidae) for nearly 40 years (Bolt, 1969), so restricting Dissorophoidea to Dissorophidae and Trematopidae made little sense, although it would be equally logical. We believe that the insertion of a phylogenetically defined Olsoniformes, well set off from Linnean taxonomy with a unique suffix not used for a rank in the International Code of Zoological Nomenclature (ICNZ), will cause less confusion than restricting Dissorophoidea counter most recent usage and establishing a new rank above superfamily to include Amphibamidae, Dissorophidae, and Trematopidae.

CONCLUSIONS

Georgenthalia is an amphibamid temnospondyl that is placed higher than the basal *Micropholis-Tersomius* clade. Characters that allow discrimination of relationships within the clade are becoming clearer, but greater resolution requires discovery of additional characters, revision of problematic taxa, and additional study of other dissorophoid groups. *Micromelerpeton*, and by extension Branchiosauridae, are basal amphibamids, which is consistent with other studies that have found a close relationship between branchiosaurs *sensu lato* and amphibamids. Amphibamids are not juvenile stages of other larger temnospondyls, but

represent a distinct assemblage that may be affiliated with the origins of some, or all, extant amphibians. Both *Georgenthalia* and trematopids had a superficially similar posterior extension of the external naris for reasons unrelated to the nasal capsule. Phylogenetic definitions are offered for the constituent dissorophoid clades, although a definition for Dissorophoidea is not offered at present, until a consensus is reached with respect to internal relationships.

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LITERATURE CITED

- Anderson, J. S. 2005. On the skull of *Cacops aspidephorus* Williston (Tetrapoda: Temnospondyli: Dissorophidae) from the Lower Permian of Texas. Part 1: Lower jaw anatomy; pp. 15 in S. G. Lucas and K. E. Zeigler (eds.), *The Nonmarine Permian*. Albuquerque: New Mexico Museum of Natural History and Science.
- Anderson, J. S. 2006. On the skull of *Cacops aspidephorus* Williston (Tetrapoda; Temnospondyli; Dissorophidae) from the Lower Permian of Texas. *Journal of Vertebrate Paleontology* 26 (supplement to 3):36A.
- Anderson, J. S. 2007. Incorporating ontogeny into the matrix: a phylogenetic evaluation of developmental evidence for the origins of modern amphibians; pp. 182–227 in J. S. Anderson and H.-D. Sues (eds.), *Major Transitions in Vertebrate Evolution*. Bloomington: Indiana University Press.
- Anderson, J. S., and J. R. Bolt. 2005. A nearly complete amphibamid skull from Richards Spur (Ft. Sill), Oklahoma, and its implications for interpretation of dental characters related to the origin of modern amphibians. *Journal of Vertebrate Paleontology* 25 (supplement to 3):31A.
- Anderson, J. S., S. S. Sumida, D. S. Berman, A. C. Henrici, and T. Martens. 2004. The dissorophoid temnospondyls from the Early Permian of Bromacker, Germany. *Journal of Vertebrate Paleontology* 24 (supplement to 3):34A.
- Berman, D. S., and T. Martens. 1993. First occurrence of *Seymouria* (Amphibia: Batrachosauria) in the Lower Permian Rotliegend of Central Germany. *Annals of Carnegie Museum* 62:63–79.
- Berman, D. S., R. R. Reisz, and D. A. Eberth. 1985. *Ecolsonia cutlerensis*, an Early Permian dissorophid amphibian from the Cutler Formation of north-central New Mexico. *New Mexico Bureau of Mines and Mineral Resources Circular* 191:1–31.
- Berman, D. S., S. S. Sumida, and T. Martens. 1998. *Diadectes* (Diadectomorpha: Diadectidae) from the Early Permian of Central Germany, with description of a new species. *Annals of Carnegie Museum* 67:53–93.
- Berman, D. S., A. C. Henrici, S. S. Sumida, and T. Martens. 2000a. Re-description of *Seymouria sanjuanensis* (Seymouriamorpha) from the Lower Permian of Germany based on complete, mature specimens with a discussion of paleoecology of the Bromacker locality assemblage. *Journal of Vertebrate Paleontology* 20:253–268.
- Berman, D. S., R. R. Reisz, T. Martens, and A. C. Henrici. 2001. A new species of *Dimetrodon* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside of North America. *Canadian Journal of Earth Science* 38: 803–812.

- Berman, D. S., A. C. Henrici, S. S. Sumida, and T. Martens. 2004a. New materials of *Dimetrodon teutonius* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany. *Annals of Carnegie Museum* 73:48–56.
- Berman, D. S., A. C. Henrici, R. A. Kissel, S. S. Sumida, and T. Martens. 2004b. A new diadectid (Diadectomorpha), *Orobates pabsti*, from the Early Permian of central Germany. *Bulletin of the Carnegie Museum of Natural History* 35:1–36.
- Berman, D. S., R. R. Reisz, D. Scott, A. C. Henrici, S. S. Sumida, and T. Martens. 2000b. Early Permian bipedal reptile. *Science* 290:969–972.
- Bolt, J. R. 1969. Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science* 166:888–891.
- Bolt, J. R. 1974a. A trematopsid skull from the Lower Permian, and analysis of some characters of the dissorophoid (Amphibia: Labyrinthodontia) otic notch. *Fieldiana* 30:67–79.
- Bolt, J. R. 1974b. Osteology, function, and evolution of the trematopsid (Amphibia: Labyrinthodontia) nasal region. *Fieldiana* 33:11–30.
- Bolt, J. R. 1977. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. *Journal of Paleontology* 51:235–249.
- Bolt, J. R. 1979. *Amphibamus grandiceps* as a juvenile dissorophid: evidence and implications; pp. 529–563 in M. H. Nitecki (ed.), *Mazon Creek Fossils*. New York: Academic Press.
- Bolt, J. R. 1991. Lissamphibian origins; pp. 194–222 in H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Ithaca and London: Comstock Publishing Associates.
- Bolt, J. R., and R. E. Lombard. 2001. The mandible of the primitive tetrapod *Greererpeton*, and the early evolution of the tetrapod lower jaw. *Journal of Paleontology* 75:1016–1042.
- Boy, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). *Abhandlungen des Hessischen Landesamtes für Bodenforschung* 65:1–137.
- Boy, J. A. 1985. Über *Micropholis*, den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1985:29–45.
- Boy, J. A., and T. Martens. 1991. A new captorhinomorph reptile from the Rotliegende of Thuringia (Lower Permian; eastern Germany). *Paläontologische Zeitschrift* 65:363–389.
- Boy, J. A., and H.-D. Sues. 2000. Branchiosaurs: larvae, metamorphosis and heterochrony in temnospondyls and seymouriamorphs; pp. 1150–1197 in H. Heatwole and R. L. Carroll (eds.), *Amphibian Biology Vol. 4: Paleontology: the Evolutionary History of Amphibians*. Chipping Norton: Surrey Beatty & Sons.
- Carroll, R. L. 1964. Early evolution of the dissorophid amphibians. *Bulletin of the Museum of Comparative Zoology* 131:161–250.
- Clack, J. A., and A. R. Milner. 1993. *Platyrhinops* from the Upper Carboniferous of Linton and Nyrany, and the family Peliontidae (Amphibia; Temnospondyli); pp. 185–192 in D. Schweiss and U. Heidtke (eds.), *New Results on Permo-Carboniferous Fauna*. Bad Dürkheim.
- 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.
- Dilkes, D. W. 1991. Reinterpretation of a larval dissorophoid amphibian from the Lower Permian of Texas. *Canadian Journal of Earth Science* 28:1488–1492.
- Dilkes, D. W. 1993. Biology and evolution of the nasal region in trematopid amphibians. *Palaeontology* 36:839–859.
- Dilkes, D. W., and R. R. Reisz. 1987. *Trematops milleri* Williston, 1909 identified as a junior synonym of *Acheloma cumminsi* Cope, 1882, with a revision of the genus. *American Museum Novitates* 2902: 1–12.
- Eberth, D. A., D. S. Berman, S. S. Sumida, and H. Hopf. 2000. Lower Permian terrestrial paleoenvironments and vertebrate paleoecology of the Tambach Basin (Thuringia, Central Germany): the upland Holy Grail. *Palaos* 15:293–313.
- Hunt, A. P., S. G. Lucas, and D. S. Berman. 1996. A new amphibamid (Amphibia: Temnospondyli) from the Late Pennsylvanian (Middle Stephanian) of central New Mexico, USA. *Paläontologische Zeitschrift* 70:555–565.
- Hunt, A. P., S. G. Lucas, and D. S. Berman. 2002. *Milnererpeton*, a replacement name for the temnospondyl amphibian *Milneria*. *Paläontologische Zeitschrift* 76:125.
- Huttenlocker, A. K., B. J. Small, and J. D. Pardo. 2007. *Plemmyradytes shintoni*, gen. et sp. nov., an Early Permian amphibamid (Temnospondyli: Dissorophoidea) from the Eskridge Formation, Nebraska. *Journal of Vertebrate Paleontology* 27:316–328.
- Jurgens, J. D. 1971. The morphology of the nasal region of Amphibia and its bearing on the phylogeny of the group. *Annale Universiteit Van Stellenbosch* 46 (2):1–146.
- Klembara, J., T. Martens, and I. K. Bart. 2001. The postcranial remains of a juvenile seymouriamorph tetrapod from the Lower Permian Rotliegende of the Tambach Formation of central Germany. *Journal of Vertebrate Paleontology* 21:521–527.
- Klembara, J., D. S. Berman, A. C. Henrici, and A. Cernansky. 2005. New structures and reconstructions of the skull of seymouriamorph *Seymouria sanjuanensis* Vaughn. *Annals of Carnegie Museum* 74: 217–224.
- Klembara, J., D. S. Berman, A. C. Henrici, A. Cernansky, and R. Werneburg. 2006. Comparison of cranial anatomy and proportions of similarly sized *Seymouria sanjuanensis* and *Discosauriscus austriacus*. *Annals of Carnegie Museum* 75:37–49.
- Klembara, J., D. S. Berman, A. C. Henrici, A. Cernansky, R. Werneburg, and T. Martens. 2007. First description of skull of Lower Permian *Seymouria sanjuanensis* (Seymouriamorpha: Seymouridae) at an early juvenile growth stage. *Annals of Carnegie Museum* 76:53–72.
- Maddison, D. R., and W. P. Maddison. 2005. *MacClade*. 4.08. Sinauer Associates, Sunderland, Massachusetts.
- Milner, A. R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology* 25:635–664.
- Milner, A. R. 1988. The relationships and origin of living amphibians; pp. 59–102 in M. J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods*. Oxford: Clarendon Press.
- Milner, A. R. 1993. The Paleozoic relatives of lissamphibians. *Herpetological Monographs* 7:8–27.
- Moodie, R. L. 1909. A contribution to a monograph of the extinct Amphibia of North America. New forms from the Carboniferous. *Journal of Geology* 17:38–82.
- Müller, J., D. S. Berman, A. C. Henrici, T. Martens, and S. S. Sumida. 2006. The basal reptile *Thuringothyris mahlendorffae* (Amniota: Eureptilia) from the Lower Permian of Germany. *Journal of Paleontology* 80:726–739.
- Olson, E. C. 1941. The Family Trematopsidae. *Journal of Geology* 49: 149–176.
- Olson, E. C. 1985. A larval specimen of a trematopsid (Amphibia: Temnospondyli). *Journal of Paleontology* 59:1173–1180.
- Romer, A. S. 1939. Notes on branchiosaurs. *American Journal of Science* 237:748–761.
- Ruta, M., and M. I. Coates. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. *Journal of Systematic Palaeontology* 5:69–122.
- Ruta, M., M. I. Coates, and D. L. Quicke. 2003. Early tetrapod relationships revisited. *Biological Reviews* 78:251–345.
- Schoch, R. R. 1992. Comparative ontogeny of Early Permian branchiosaurid amphibians. *Developmental stages*. *Palaeontographica, Abteilung A* 222:43–83.
- Schoch, R. R. 1997. Cranial anatomy of the Permian temnospondyl amphibian *Zatrachys serratus* Cope 1887, and the phylogenetic position of the *Zatrachyidae*. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 206:223–248.
- Schoch, R. R. 2002. The evolution of metamorphosis in temnospondyls. *Lethaia* 35:309–327.
- Schoch, R. R. 2004. Skeleton formation in the Branchiosauridae: a case study in comparing ontogenetic trajectories. *Journal of Vertebrate Paleontology* 24:309–319.
- Schoch, R. R., and N. B. Fröbisch. 2006. Metamorphosis and neoteny: alternative pathways in an extinct amphibian clade. *Evolution* 60: 1467–1475.
- Schoch, R. R., and A. R. Milner. 2004. Structure and implications of theories on the origin of lissamphibians; pp. 345–377 in G. Arratia, M. V. H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*. München: Verlag Dr. Friedrich Pfeil.
- Schoch, R. R., and A. R. Milner. In press. The interrelationships and evolutionary history of the temnospondyl family Branchiosauridae. *Journal of Systematic Palaeontology*.
- Schoch, R. R., and B. S. Rubidge. 2005. The amphibamid *Micropholis* from the *Lystrorhynchus* Assemblage Zone of South Africa. *Journal of Vertebrate Paleontology* 25:502–522.

- Sereno, P. C. 1999. Definitions in phylogenetic taxonomy: critique and rationale. *Systematic Biology* 48:329–351.
- Steyer, J. S. 2000. Ontogeny and phylogeny in temnospondyls: a new method of analysis. *Zoological Journal of the Linnean Society* 130: 449–467.
- Sumida, S. S., and D. S. Berman. 1994. Correlation between the Lower Permian of North America and Central Europe using the first record of an assemblage of terrestrial tetrapods. *Geological Society of America Abstracts with Programs, Cordilleran Section*:97.
- Sumida, S. S., D. S. Berman, and T. Martens. 1996. Biostratigraphic correlations between the Lower Permian of North America and central Europe using the first record of an assemblage of terrestrial tetrapods from Germany. *PaleoBios* 17:1–12.
- Sumida, S. S., D. S. Berman, and T. Martens. 1998. A new trematopid amphibian from the Lower Permian of central Germany. *Palaeontology* 41:605–629.
- Swofford, D. L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Trueb, L., and R. Cloutier. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli); pp. 175–193 in H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. London: Comstock Publishing Associates.
- Vallin, G., and M. Laurin. 2004. Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology* 24:56–72.
- Yates, A. M., and A. Warren. 2000. The phylogeny of the ‘higher’ temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* 128:77–121.
- Zittel, K. v. 1888. *Handbuch der Palaeontologie*. 1. Abteilung Palaeozoologie. III. Band (Pisces, Amphibia, Reptilia, Aves). Oldenbourg, München und Leipzig, 971 pp.
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- APPENDIX 1. Character and state names used in phylogenetic analysis. Characters 1–47 are from Schoch and Rubidge (2005), and characters 48–53 are additional characters added for this study.
- (1) Laterally exposed palatine: palatine overplated by jugal and lacrimal and with no dorsal exposure (0); palatine wedging between lacrimal and jugal to make contribution to skull roof and orbit margin (1).
 - (2) Dorsal quadrate process: quadrate with smooth posterodorsal side (0); quadrate with prominent dorsoposterior process (1).
 - (3) Vomerine depression: ventral surface of vomers flat and elements divided into anterior and posterior portion by transverse ridge that may or may not bear transverse tooth row (0); single unpaired depression in anterior portion of vomers that may or may not house an opening (1).
 - (4) Parasphenoid dentition: basal plate of parasphenoid bearing shagreen of small teeth (denticles) anteromedially (0); plate entirely smooth (1).
 - (5) Parasphenoid denticle field: parasphenoid denticle field well established, with triangular outline with apex reaching onto base of cultriform process (0); denticle field greatly expanded anteriorly to cover most of cultriform process (1).
 - (6) Parasphenoid basal plate: basal plate roughly quadrangular, as long as wide (0); basal plate much shorter than wide, reaching about half the width (1).
 - (7) Vomerine denticle field: vomer covered with more or less dense shagreen of teeth in addition to obligatory fang pair (0); shagreen confined to juvenile stages and/or absent throughout ontogeny (1).
 - (8) Vomerine fangs: vomer lacking fangs in its medial portion, outside lateral tooth arcade, but may have smaller accessory teeth in that position (0); vomer with additional fang-pairs posterior to mid-vomerine depression (1).
 - (9) Palatine fangs: palatine with one fang pair in its anterior third (0); palatine fangs replaced by patch of small, equally sized teeth (1).
 - (10) Ectopterygoid fangs: one fang pair at about mid-level (0); no fangs present (1).
 - (11) Pterygoid-vomer: retention of suture between pterygoid (palatine ramus) and vomer (0); pterygoid contacting only posteriormost portion of palatine and lacking suture with vomer (1).
 - (12) Pterygoid flange: palatine ramus of pterygoid merging continuously into basipterygoid ramus (0); palatine ramus broadening abruptly to form transverse flange (1).
 - (13) Pterygoid-palatine: pterygoid (palatine ramus) reaching and suturing to palatine (0); pterygoid contacting only ectopterygoid, or, when latter absent, maxilla (1).
 - (14) Palatine, ectopterygoid: much wider than maxilla (0); reduced to narrow struts not wider than adjoining maxilla (1).
 - (15) Interpterygoid vacuity: round or longitudinally oval in outline (0); greatly expanded laterally at mid-level (1).
 - (16) Choana: narrow, forming elongated oval with parallel, parasagittal lateral and medial margins (0); expanded anteromedially (1).
 - (17) Pedicely: marginal jaw and palatal dentition consisting of conical, fully mineralised teeth (0); jaw and/or palatal teeth subdivided by unmineralized zone forming separate tooth crown (1).
 - (18) Bicuspidality: larval and adult teeth conical or needle-shaped with single point (monocuspid) (0); jaw and/or palatal teeth bicuspid (1).
 - (19) Labyrinthodonty: jaw and palatal teeth labyrinthodont at least in adult stages (0); teeth never labyrinthodont at any stage of development (1).
 - (20) Narial flange: ventral (inner) side of prefrontal, lacrimal, and nasal smooth (0); inner side of these bones forming complicated bar-like structure (narial flange), permitting contact with antorbital bar (1).
 - (21) Prefrontal process: prefrontal forming simple suture with lacrimal laterally (0); prefrontal underplating lacrimal widely by means of ventral prefrontal process contacting palatine (1).
 - (22) Tabular size: narrower than postparietal, but reaching almost same size as latter (0); minute and laterally constricted by unique enlargement of otic notch (1).
 - (23) Tabular-squamosal: widely separated by supratemporal (0); squamosal meeting tabular, excluding supratemporal from otic notch (1).
 - (24) Postparietal length: postparietal forming transversely rectangular or quadrangular element (0); postparietal abbreviated and reduced to narrow, poorly ornamented strut at posterior margin of skull table (1).
 - (25) Squamosal-supratemporal: suture between supratemporal and squamosal nearly as long as supratemporal itself (0); foreshortened squamoso-supratemporal suture reaching only one third or less length of supratemporal (1).
 - (26) Semilunar flange: squamosal continuously ornamented around margin of otic notch (0); squamosal having dorsally exposed and ornamented area (semilunar flange) stepping abruptly into steeply aligned, poorly ornamented portion (1).
 - (27) Supratemporal and parietal length: elongated, having similar length, reaching more than double length of all other bones in posterior skull table (0); posteriorly abbreviated, supratemporal markedly shorter than parietal (1).
 - (28) Supratemporal flange: supratemporal without ventral projection into otic notch (0); supratemporal forming marked ventral flange participating in medial bordering of otic notch (1).
 - (29) Prefrontal-postfrontal: firmly sutured, excluding frontal from orbital margin (0); separated by frontal, at least dorsally (1).
 - (30) Skull width: moderately wide skull with jugals, postorbitals, and medial skull roofing series usually longer than wide (0); skull table and cheek overall broadened, most elements being as wide as long or wider (1).
 - (31) Palpebral ossifications: ossifications in orbit restricted to sclerotic ring (0); numerous palpebral ossicles at medial margin of sclerotic ring, made up of polygonal platelets that may be ornamented (1).
 - (32) Stapes: pronounced dorsodistal curvature directed towards dorsally located otic notch (0); abbreviated without dorsodistal curvature, directed laterally towards vertically aligned otic notch (1).
 - (33) Pleurocentra: paired, dorsally separated elements failing to reach ventral level of adjunct intercentrum (0); approaching each other on ventral side (1); fused ventrally to form large element that has become main bearer of vertebral centrum, intercentra much smaller than in plesiomorphic condition (2).
 - (34) Rib length: moderately elongated thoracic ribs in adult stage, may or may not bear uncinat processes and usually curved distoventrally (0); without distal curvature, but may bear uncinat processes (1); very short, forming simple rods (2).
 - (35) Anterior rib morphology: larger and more solid than following

- ones, having massive proximal and distal ends (0); not longer than succeeding ones (1).
- (36) Humerus shaft: short and broad (0); substantially longer and more like rod than blade (1).
- (37) Humerus, supinator process: rising from humerus in adults (0); absent throughout ontogeny (1).
- (38) Humerus head: irrespective of length and slenderness of shaft, humeral condyles and head generally massive and widened (0); in adult amphibamids and branchiosaurids, condyles minute and usually poorly ossified, giving only slightly broadened proximal head region having reduced deltopectoral buttress rather than crest (1).
- (39) Interclavicle: rhomboidal, at least two times longer than wide (0); with abbreviated anterior and posterior ends and as wide as long (1); much shorter than wide, without anterior process (2).
- (40) Ilium: with thin dorsal shaft, much higher than wide (0); dorsally abbreviated, with dorsoposterior process (1); very short, only as high as wide (2).
- (41) Cleithrum, head: aligned along anterior rim of scapula (0); head posterodorsally enlarged, wrapping around scapula dorsally (1).
- (42) Cleithrum, size: with large dorsal head much wider than shaft (0); simple rod, without any head (1).
- (43) Scapula: forming low or moderately high element, depending on degree of ossification, about two times longer than wide (0); dorsally much extended, being three to four times longer than wide (1).
- (44) Presacral count: 24–25 (0); only 20 presacral vertebrae or fewer (1).
- (45) Ventral scutes: spindle-shaped (0); entirely absent (1).
- (46) Carapace: dorsal scutes either absent or small, oval or round, loosely set (0); heavily ossified, forming transversely broadened osteoderms making up strongly ornamented carapace (1).
- (47) Tail: long, reaching at least length of trunk, often exceeding length of trunk and skull (0); foreshortened, markedly shorter than trunk (1).
- (48) Postfrontal shape: broadly quadrangular (0); falciform, or narrowly sickle-shaped (1).
- (49) Internarial fontanelle: absent (0); present (1).
- (50) Frontals: parallel sided (0); flares widely anterolaterally (1).
- (51) Skull shape, dorsal view: triangular (0); rounded (1).
- (52) Interorbital width: wide (0); narrow (1); narrow, small orbits (2).
- (53) Otic notch to orbit: far (0); medium (1); near (2).

APPENDIX 2. Taxon by character matrix used in phylogenetic study. Numbering follows Schoch and Rubidge (2005), and bold text represents changes or additions to their matrix.

Character	<i>Denderpeton acadianum</i>	<i>Scelerocephalus haeuseri</i>	Eryopidae	<i>Micromelerpeton credneri</i>	<i>Amphibamus grandiceps</i>	<i>Platyrhinops lyelli</i>	<i>Dolesepeton annexens</i>	<i>Eoscopus lockardi</i>	<i>Micropholis stowi</i>	<i>Tersomius</i> sp.	<i>Ecolsonia cutlerensis</i>	Trematopidae	Dissorophinae	Cacopinae	<i>Georgenthalia clavinasica</i>
1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
2	0	0	0	?	1	1	1	1	1	1	1	1	1	1	1
3	0	0	0	1	0	0	0	0	1	1	1	1	0&1	1	0/1
4	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
5	0	0	0	0	1	0&1	0	0	1	0	0	0	—	—	0
6	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1
7	0	1	1	0&1	0	0	0	0&1	1	1	1	0	0	0	0
8	0	0	0&1	0&1	0	0&1	0	0&1	0&1	1	0	0	0	0	1
9	0	0	0	0	1	0	1	0	0	0	0	0	0	0	?
10	0	0	0	0	1	1	1	0	0	0	0	0	0	0	?
11	0	0	0	1	1	1	1	1	1	1	0	0	1	1	1
12	0	0	0&1	0&1	1	1	1	1	1	1	0	0	1	1	1
13	0	0	0	0	1	1	1	0	0	0	0	0	0	0	?
14	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1
15	0	0	0	0	1	1	1	1	1	1	0	0	1	1	1
16	0	0	0	0	1	0	1	0	1	1	0	0	0	0	?
17	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
18	0	0	0	0	1	1	1	0	0	1	0	0	0&1	0	0
19	0	0	0	0	1	1	1	0	0	0	0	0	0	0	?
20	0	0	0	?	?	?	1	1	1	1	1	1	1	1	?
21	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
22	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0&1	0	1	1	1	1	0
24	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1
25	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1
26	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
27	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1
28	0	0	0	0	0	0	0	0&1	0	0	1	1	1	1	0
29	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
30	0	0	0	1	1	0	0	0&1	0&1	0	1	0	1	1	0&1
31	0	0	0	1	1	1	1	1	1	1	0	0	0	0	1
32	0	0	0	0	1	1	1	1	0	?	0	0	0	0	?
33	0	0	0	0	2	1	2	1	1	1	0	0	0	0	?
34	0	0	0	0	2	2	2	2	2	?	1	1	1	1	?
35	0	0	0	0	1	1	1	0	0	?	0	0	0	0	?
36	0	0	0	0	2	2	2	2	2	?	1	1	1	1	?
37	0	0	0	0&1	1	1	1	1	1	?	0	0	1	1	?
38	0	0	0	0	1	1	1	1	1	?	0	0	0	0	?
39	0	0	0	1	1	1	1	1	1	?	1	1	2	2	?
40	0	0	0	0	1	1	?	1	1	?	1	1	2	2	?
41	0	0	0	0	0	0	0	0	0	0	0	0	1	1	?
42	0	0	0	0	1	1	1	1	1	?	0	0	0	0	?
43	0	0	0	0	0	0	0	0	0	?	1	1	1	1	?
44	0	0	0	0	1	0	0	0	1	?	?	0	1	1	?
45	0	0	0	0	0	1	1	1	1	?	0	0	0	0	?
46	0	0	0	0	0	0	0	0	0	?	0	0	1	1	?
47	0	0	0	0	1	1	1	1	1	?	1	0	1	1	?
48	0	0	0	1	1	1	1	1	0	0&1	0	0	0	0	1
49	0	0	0	1	1	0	1	1	0	1	0	0&1	0	?	1
50	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1
51	0	0	0	0	1	1	1	1	0&1	1	0	0	0	0	1
52	0	2	2	1	0	0	1	1	0	1	0	0	0	0	1
53	0	0	0	0	2	1	2	2	0	0/1	0	0	0	0	2