A NEW TREMATOPID AMPHIBIAN FROM THE LOWER PERMIAN OF CENTRAL GERMANY

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ABSTRACT. A new genus and species of trematopid amphibian, *Tambachia trogallas*, is described on the basis of the greater portion of a skeleton, including the skull. The holotype was collected from the Early Permian Tambach Formation, the lowermost unit of the Upper Rotliegend, of the Bromacker locality in the midregion of the Thuringian Forest near Gotha, central Germany. Not only is this the first trematopid to be reported outside the United States, but it is the first specimen to include the greater portion of the postcranial skeleton. Analysis of the interrelationships of the trematopids agrees with the results of other recent studies: (1) *Tambachia* and the Late Pennsylvanian *Anconastes*, on the one hand, and the Early Permian *Acheloma* and *Phonerpeton* on the other, form sister clades of the monophyletic Trematopidae; and (2) *Actiobates*, although almost certainly a trematopid, is too poorly known to determine its intrafamilial relationships.

The Bromacker locality is the only Early Permian site in Europe to produce a diverse assemblage of terrestrial or semi-terrestrial tetrapods, several of which are known otherwise only from the Upper Pennsylvanian and Lower Permian of the United States. The Bromacker assemblage is, therefore, of great interest in indicating: (1) an earliest Permian Wolfcampian age for the Tambach Formation, the basal unit of the Upper Rotliegend of the Thuringian Forest. This in turn suggests a Late Pennsylvanian age for all or most of the underlying Lower Rotliegend, rather than the widely accepted Early Permian; (2) a cosmopolitan, Euramerican distribution of Early Permian terrestrial or semi-terrestrial tetrapods previously reported only from the United States. This suggests an absence of any strong physical barriers to tetrapod dispersal across Euramerica during the Early Permian.

MOST terrestrial members of the widely diverse late Palaeozoic amphibian order Temnospondyli belong to the families Dissorophidae and Trematopidae, united by Bolt (1969) under the superfamily Dissorophoidea. The close relationship between these two families was originally recognized by Olson (1941). Later descriptions (DeMar 1966; Vaughn 1969; Eaton 1973; Berman *et al.* 1985) of forms exhibiting a combination of 'dissorophid' and 'trematopid' features has since justified their unification into a superfamily. Dissorophidae contains a larger number of taxa (16 or more genera) and has a greater temporal and spatial range, occurring in the Upper Pennsylvanian and Lower Permian of the United States (Carroll 1964; Berman and Berman 1975; Berman *et al.* 1985) to the lower Upper Permian of the cis-Uralian forelands of Russia (Gubin 1980). However, the family is difficult to define, and its ingroup relationships are not well understood (Berman *et al.* 1985, 1987; Dilkes 1990; Daly 1994). Conversely, the more conservative Trematopidae is composed of only four genera, not including the new genus described here, and, except for a single specimen from the Lower Permian of Ohio (Olson 1970), all known are from the Upper Pennsylvanian and Lower Permian of the midcontinental and south-western regions of the United States (Berman *et al.* 1987; Dilkes 1990). Recent analyses of the family have yielded very consistent conclusions (Dilkes 1990; Daly 1994), that recognized only three genera: the Late Pennsylvanian *Anconastes* and the Early Permian *Acheloma* and *Phonerpeton*. On the basis of a restudy of the holotypes of the type species of the well-known *Acheloma* and *Trematops*, Dilkes and Reisz (1987) identified the latter as a subjective junior synonym of the former, but retained the family name Trematopidae. Although Berman *et al.* (1987) considered the Late Pennsylvanian *Actiobates* as a trematopid (originally described as a dissorophid by Eaton 1973), Dilkes (1990) and Daly (1994) assigned it only tentatively to the Trematopidae.

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A new genus and species of trematopid, *Tambachia trogalles*, based on a skull and the greater portion of the postcranium of a single individual is described here. The specimen is from the Early Permian Tambach Formation, lowermost unit of the Upper Rotliegend, of the well-known Bromacker locality (Pabst 1896; Martens 1980, 1988; Berman and Martens 1993) in the midregion of the Thuringian Forest of central Germany.

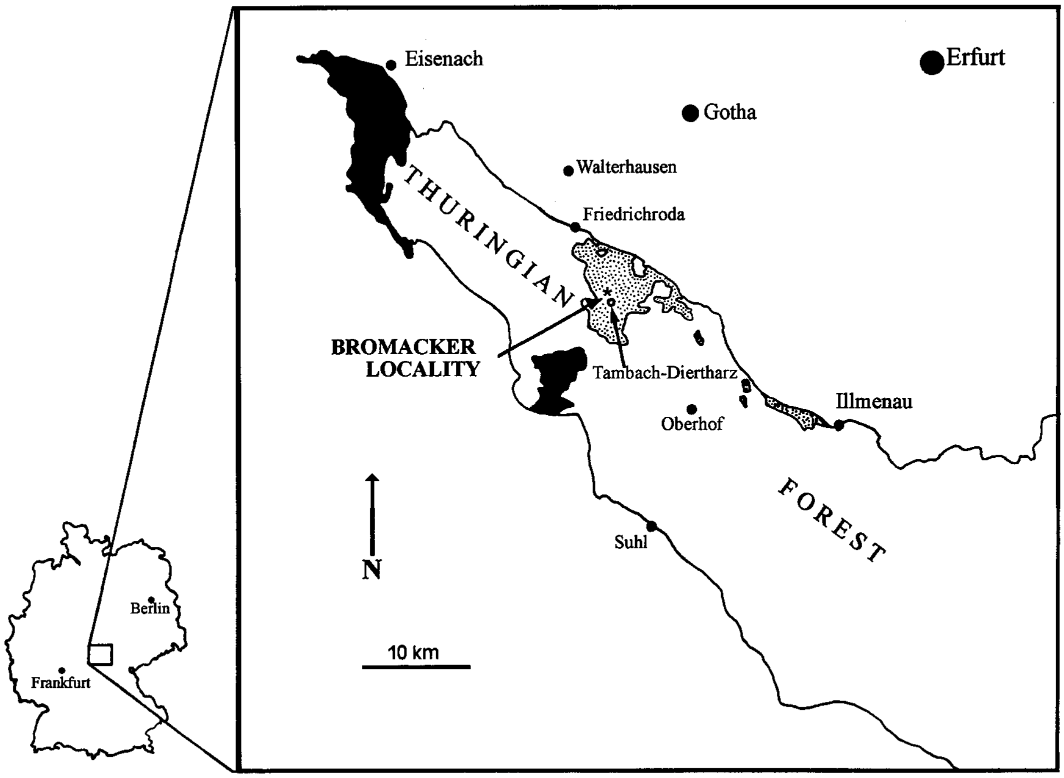
Abbreviations used in figures are as follows: a, angular; ac, acetabulum; clt pr, cultriform process; cr, caudal rib; cv, caudal vertebra; d, dentary; ec, ectopterygoid; f, frontal; fe, femur; fi, fibula; h, humerus; ic, interclavicle; il, ilium; imf, inframeckelian foramen; j, jugal; l, lacrimal; m, maxilla; n, nasal; na, neural arch; p, parietal; pa, palatine; paf, para-articular foramen; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; ps, parasphenoid; psp, postsplenial; pt, pterygoid; q, quadrate; qj, quadratojugal; r, radius; s1, s2, sacral vertebrae; sa, surangular; sf, supratympanic flange; sm, septomaxilla; sp, splenial; sq, squamosal; sr, sacral rib; st, supratemporal; t, tabular; tk, tusk; u, ulna; v, vomer; I–IV, metapodials and digits.

BROMACKER QUARRY VERTEBRATE ASSEMBLAGE

Principally a commercial quarry for the sandstones of the Early Permian Tambach Formation, which is the lowermost formational unit of the Upper Rotliegend near Tambach–Dietharz, central Germany, the Bromacker locality has been an important source of excellent tetrapod trackways for a century (Pabst 1896, 1908; Mueller 1954, 1969; Haubold 1971, 1973). More recently, however, the Bromacker locality has yielded a diverse assemblage of articulated skeletal remains of terrestrial or semi-terrestrial amphibians and reptiles (Martens 1980, 1988; Boy and Martens 1991; Berman and Martens 1993; Sumida *et al.* 1996), as well as some invertebrates (conchostracans, insects and myriapods). Among the vertebrate taxa already described from the Bromacker locality are the seymouriamorph amphibian *Seymouria* cf. *sanjuanensis* (Berman and Martens 1993) and the protorothyridid reptile *Thuringothyris mahlendorffae* (Boy and Martens 1991). Bromacker specimens currently being described or prepared include: a complete skeleton (more than 1 m long), an isolated skull, and the greater portion of the postcranium of a new species of the diadectomorph *Diadectes*; a complete skeleton (nearly 1 m long) of a new, primitive diadectomorph that is closely related to *Diadectes*; and a complete skeleton (about 0·3 m long) of a small, possible neodiapsid.

Apart from the Bromacker locality, the Early Permian trematopids *Seymouria*, and *Diadectes* are known only from the United States, where they are frequently encountered. The Bromacker locality is also unique as the only European site to have yielded a large assemblage of Early Permian terrestrial or semi-terrestrial tetrapods. Vertebrates of this type and age from central and western Europe are very rare, are typically found as isolated specimens varying in completeness from fragments to partial skeletons, and occur at widely distant locales and various stratigraphical levels (Berman and Martens 1993; Sumida *et al.* 1996). An explanation of why Early Permian terrestrially adapted vertebrates are so rare in Europe, despite a long history of intensive prospecting of the highly productive Rotliegend and equivalent-aged deposits, has been offered by Martens (1988, 1989) and Berman and Martens (1993). They suggested that this is due to a bias in exploration which has traditionally ignored the fluvial, red-bed deposits where such discoveries are most likely to be made. Poor exposures of sedimentary rocks of this type in the Lower Permian of Europe and the long-standing, widely accepted misconception that they represent an inhospitable, dry climate in which preservation of vertebrate skeletal remains would have been unlikely, discouraged interest in their exploration. The result has been a paucity of vertebrates collected from the terrestrial red-beds and an overwhelming concentration by palaeontologists on the lacustrine grey sediments and black shales in which have been found highly productive sites characteristically yielding obligatory aquatic amphibians.

Two obvious conclusions can be drawn from the above observations: (1) the similarity between the widely separated Early Permian assemblages of the Bromacker locality and those of the United

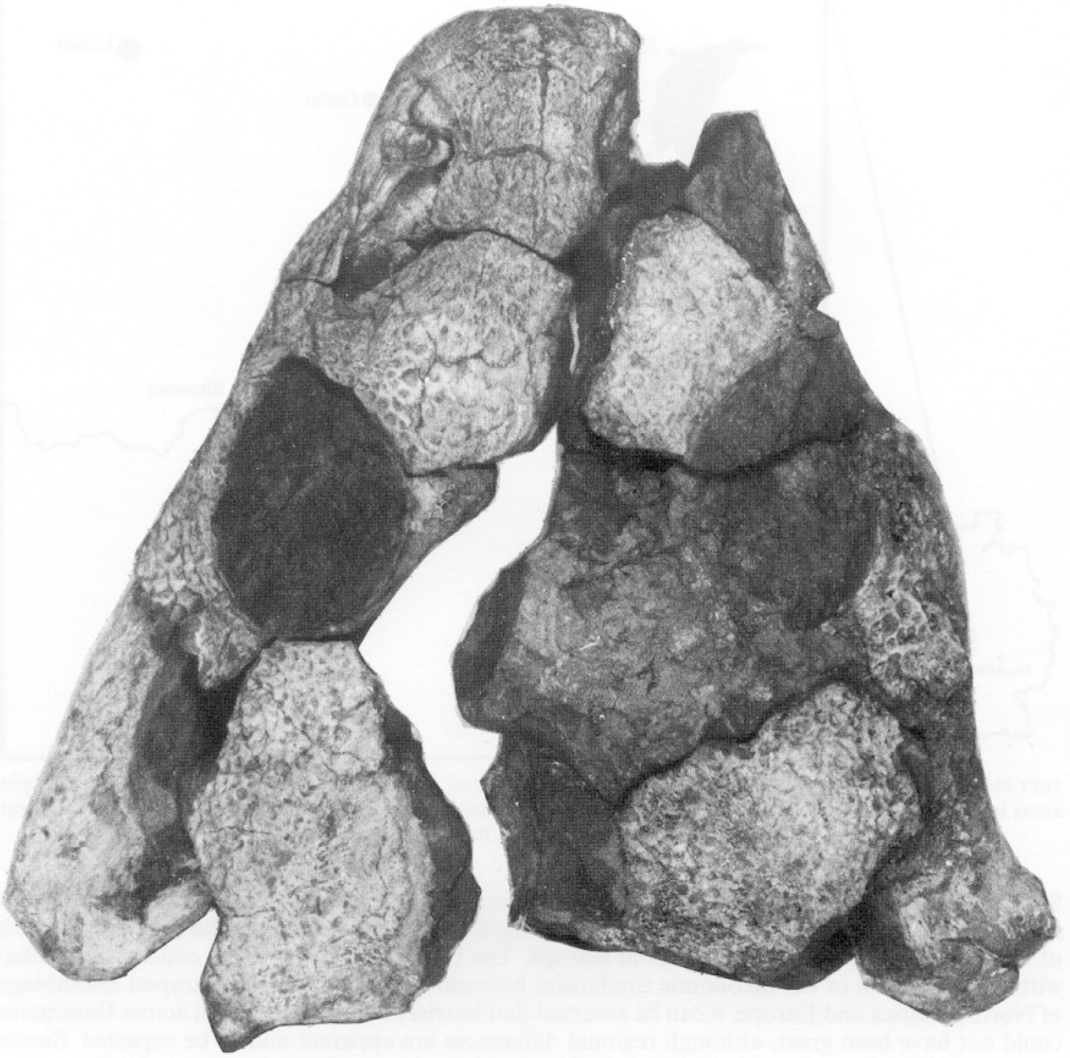


TEXT-FIG. 1. Map of Germany with inset showing Thuringian Forest area and Bromacker locality. Stippled areas indicate the extent of the Tambach Formation and solid areas the extent of other Early Permian strata (primarily Eisenach Formation) in the Thuringian Forest.

States can be attributed to a sampling of similar environments of deposition (Sumida *et al.* 1996); and (2) fluvial red-bed deposits, such as those at the Bromacker locality, are the most likely source of Early Permian terrestrial tetrapods in Europe. The broader aspect of these conclusions is that, with the expansion of the taxonomic similarities between the Early Permian tetrapod assemblages of North America and Europe, it can be assumed that barriers to faunal dispersal across Euramerica could not have been great, although regional differences are apparent and to be expected. Similar interpretations were offered by Milner (1993) based on similar taxa; however, the Bromacker assemblage offers the first example of a European assemblage that includes both similar genera as well as taxa congeneric with those found in North America.

GEOLOGY AND AGE OF THE BROMACKER LOCALITY

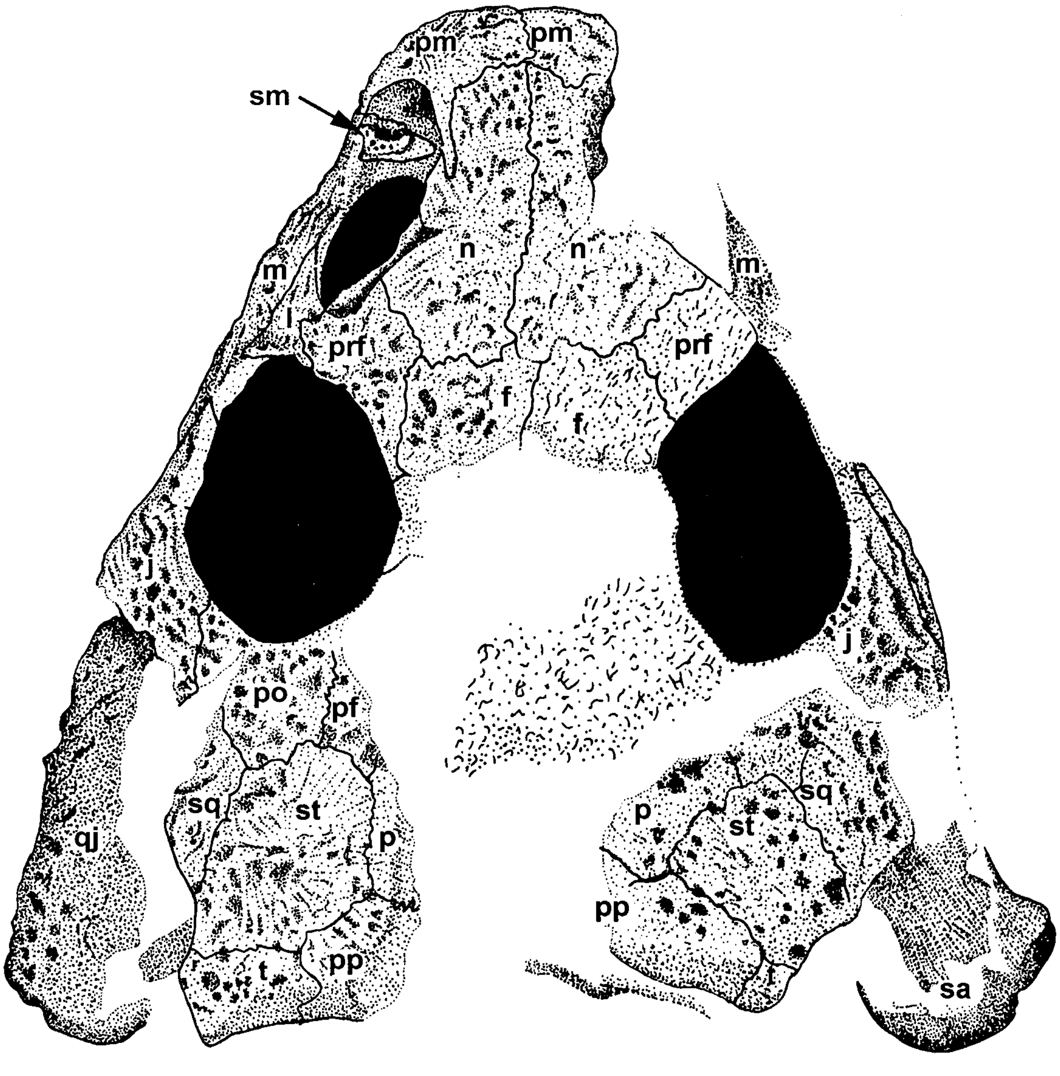
The Bromacker sandstone quarry is located near the village of Tambach–Dietharz, approximately 20 km south of the town of Gotha in the midregion of the Thuringian Forest (Text-fig. 1). The quarry is in the Tambach Formation, which in the Thuringian Forest is the lowermost unit of the Early Permian Upper Rotliegend, and is part of a sequence of terrestrial formations dated as Late Carboniferous (Stephanian) and Early Permian (Lower and Upper Rotliegend). The Stephanian–Rotliegend sediments of the Thuringian Forest were deposited in the south-western portion of the north-east-trending, intramontane Saale Basin which extends about 200 km to the north-east to include also the Halle Basin. The Saale Basin is one of many intramontane basins in central and



TEXT-FIG. 2. *Tambachia trogallas* gen. et sp. nov.; holotype, MNG 7722; skull in dorsal view; ×2.

western continental Europe that formed in close association with the Hercynian Orogeny. The basin sediments, originating mainly from the erosion of areas uplifted during the Hercynian Orogeny and filling associated with subsiding basins and fault blocks, lie disconformably on crystalline basement rocks of the uplift. They are overlain in places by the Late Permian marine Zechstein.

Exposures at the Bromacker locality are limited to the Tambach Formation, which consists of typical red-bed fluvial deposits that can be divided into three units: a basal streamflood-dominated conglomerate unit; a 60 m thick sandstone unit; and an overlying sheetflood-dominated fanglomerate unit (Berman and Martens 1993). An 8 m section of the upper level of the middle sandstone unit is exposed at the Bromacker locality. Within this section three distinct fluvial facies can be recognized, each containing particular types of fossils. The lower half of the section consists



TEXT-FIG. 3. *Tambachia trogallas* gen. et sp. nov.; holotype, MNG 7722; illustration of skull in dorsal view as seen in Text-figure 2. Scale bar represents 10 mm.

of thick-bedded sandstones containing thin intercalations of silty mudstones originating from (possibly seasonal) floods, with mudcracks and numerous vertebrate trackways (Haubold 1971, 1973). In the middle portion of the section are flat-bedded channel fills composed primarily of mudstones and thin layers of unconsolidated clay pebbles. The channels are generally well consolidated and have yielded isolated insect and tetrapod remains the latter ranging from isolated bones to partially or completely articulated skeletons, including the new trematopid described here, and previously described tetrapods (Martens 1980, 1988, 1989; Boy and Martens 1991; Berman and Martens 1993).

Rock samples associated with the Bromacker trematopid were subjected to thin sectioning and microscopic examination. They agree with the gross, sedimentological features of this level, revealing a brown to red-brown, silty claystone that is well cemented and contains small micaceous flakes. Cementation of the grains is indicative of a depositional environment of relatively low energy, possibly a flood plain or flood basin.

Determining the precise age of the Bromacker locality, as well as the stratigraphical levels of any of the Permian basinal sections of central or western Europe, is difficult for several reasons. The Rotliegend is strictly a lithostratigraphical term which refers to sediments that are underlain by the uppermost part of the Carboniferous (i.e. Stephanian C) and overlain by marine beds of the Zechstein (i.e. Upper Permian); the Rotliegend, therefore, cannot be considered to be either a biostratigraphical or chronostratigraphical unit. The same applies to the two divisions of the Rotliegend, the Lower, also called the Autunian (derived from the Permian basin in Autun, France) and the Upper, also called the Saxonian (derived from the Sachsen region in central Germany). The Carboniferous–Permian (C–P) boundary has traditionally been established on the basis of the lowest stratigraphical occurrence of a macroflora, the most important elements of which are *Callipteris conferta* and *C. naumanni*. However, the irregular occurrence of this in different basins or even within the same basin has made recognition of the C–P boundary difficult. In such instances the C–P boundary, as well as that between the Lower and Upper Rotliegend, has been identified by lithostratigraphical marker beds, in most cases conglomerates, which indicate the beginning of a rejuvenation of the Hercynian Orogeny. The absence of interbedded, easily dated marine sediments also makes it difficult to recognize a precise C–P boundary in the terrestrial sections of Europe. In several reviews of these problems, Kozur (1984, 1988, 1989) has rejected the widely accepted notion that the Rotliegend marks the base of the Lower Permian and can be recognized by the first appearance of certain plant fossils. Alternatively, Kozur redefined the C–P boundary in central Germany to agree with published accounts of abrupt changes in the flora and fauna that occur at a high level in the Lower Rotliegend (i.e. within the Lower Oberhof Formation in the Saale Basin of the Thuringian Forest). Furthermore, Kozur's reassignment of the C–P boundary agrees with the Early Permian Wolfcampian age assessment of the Bromacker locality based on the recently discovered tetrapod assemblage that includes the protorothyridid *Thuringothyris*, the seymouriamorph *Seymouria sanjuanensis*, and the diadectomorph *Diadectes* (Berman and Martens 1993; Sumida *et al.* 1996). The new trematopid described here also supports this age estimate for the Bromacker locality, as all known trematopids are from deposits ranging from the Late Pennsylvanian to Early Permian (Wolfcampian).

SYSTEMATIC PALAEONTOLOGY

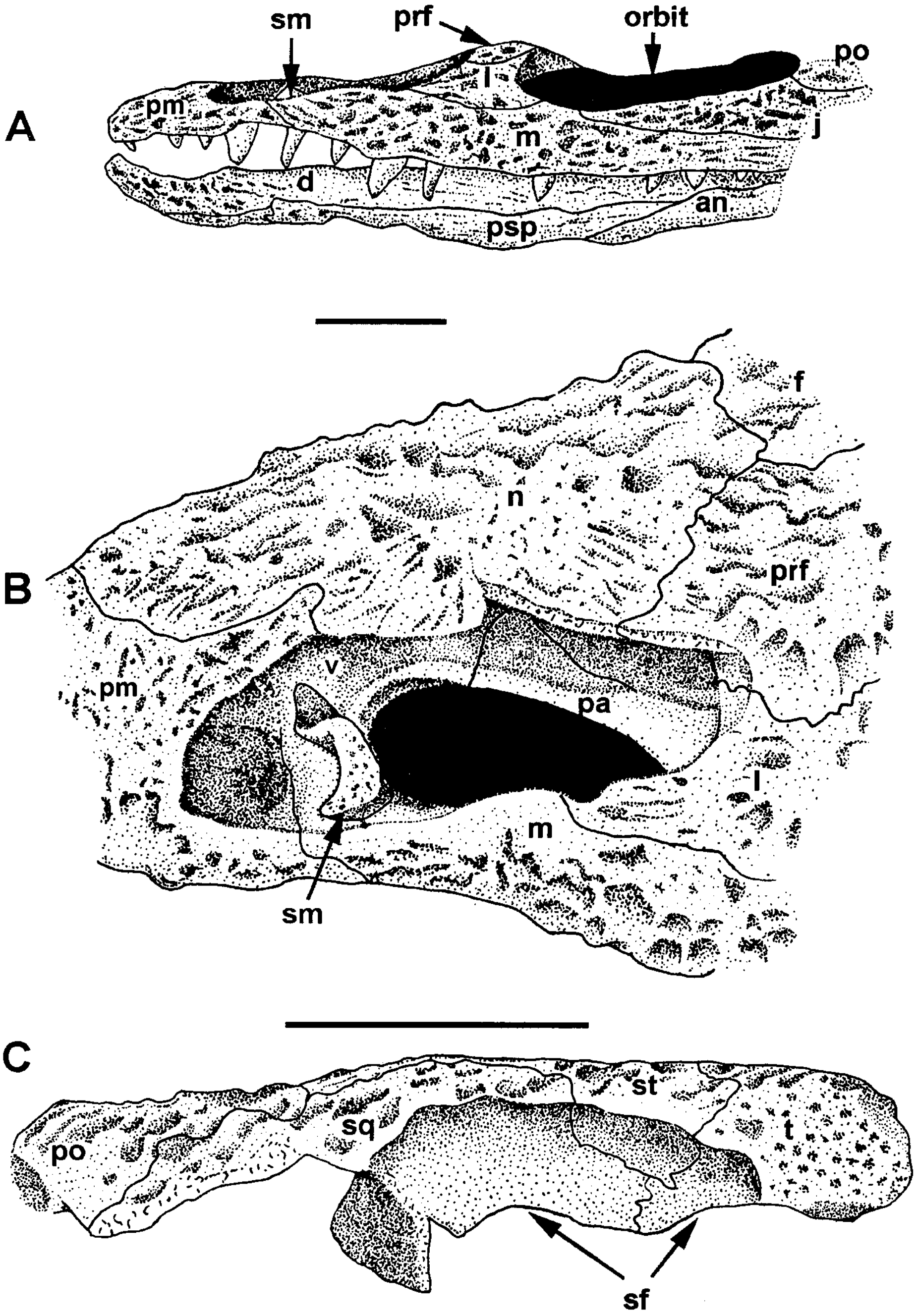
Class AMPHIBIA Linnaeus, 1758
Order TEMNOSPONDYLI Zittel, 1888
Superfamily DISSOROPHOIDEA Bolt, 1969
Family TREMATOPIDAE Williston, 1910

Genus TAMBACHIA gen. nov.

Derivation of name. Refers to the formational unit in which the holotype was found.

Type species. Tambachia trogalles sp. nov.

Diagnosis. Trematopid temnospondyl amphibian that can be distinguished from all other members of the family by the following unique features: (1) subnarial process of lacrimal very short; (2) dorsal margin of otic notch extended posteriorly by a sculptured, downturned lateral expansion of the tabular; (3) the midline, occipital margin of the skull roof lies at a level nearly equal to the posteroventral corner of the skull roof; (4) a deep channel on the ventral surface of the parasphenoid separates the basipterygoid process from the body of the braincase; (5) the width of



TEXT-FIG. 4. *Tambachia trogallas* gen. et sp. nov.; holotype, MNG 7722. A, snout region of skull and lower jaw in lateral view; B, left narial region of skull in dorsolateral view (lower jaw omitted); C, partial left otic region in lateral view. Scale bars represent 10 mm.

the basipterygoid process is extremely broad, extending along almost the entire lateral margin of the parasphenoid, and slightly exceeds the width of the internal process of the pterygoid.

Tambachia trogallas sp. nov.

Text-figures 2–9

Derivation of name. From the Greek *trogo*, munch or nibble, and *allas*, sausage, referring to the Thuringian bratwurst eaten frequently by the authors at Bromacker quarry.

Holotype. Museum der Natur Gotha, MNG 772; consists of isolated or displaced articulated portions of a skeleton, representing all major regions except the presacral column.

Horizon and locality. Uppermost level of the 60 m thick middle sandstone unit of the Early Permian Tambach Formation, Upper Rotliegend. The locality is a reactivated sandstone quarry known as the Bromacker locality near the village of Tambach–Dietharz, approximately 20 km south of the town of Gotha, in the Thuringian Forest of central Germany.

Diagnosis. As for genus.

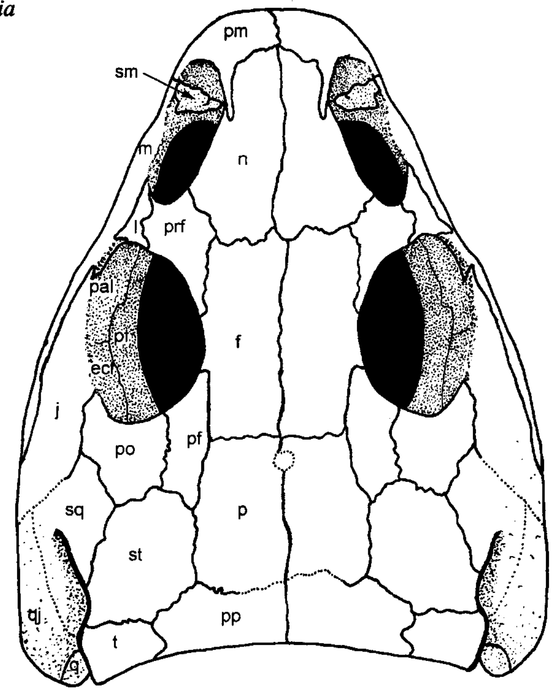
DESCRIPTION

General. The only major portion of the skeleton of *Tambachia trogallas* MNG 772 not represented is the presacral column. The rest of the skeleton is preserved as isolated or displaced articulated portions that were distributed over an area of *c*. 0·02 m^2 and includes: the skull with the right interclavicle (Text-figs 2–3, 6–7), the greater portion of the tail (not figured), portions of the right and left forelimbs and manus without the carpals (Text-fig. 8), the right femur and portions of the sacral region (Text-fig. 9A), and the right hindlimb and pes, without femur and tarsals (Text-fig. 9B). It is difficult to assess the maturity of MNG 7722. On the one hand, the non-ossification of the carpals, tarsals, and endochondral portion of the braincase, and the absence of most of the detailed structures of the limb elements suggest an early stage of development. However, the pronounced sculpturing and the tightly closed sutures of the skull roofing bones suggests a mature specimen. This combination of developmental features probably indicates an early adult stage of development.

Skull roof. Most of the bones of the skull roof of *Tambachia trogallas* MNG 7722 are well represented, with the primary exception being a wide midline area that extends from between the orbits to the occipital margin and includes much of the frontals, parietals, postfrontals, and postparietals (Text-figs 2–3). During the course of preparation, the skull was separated grossly from the matrix covering its dorsal roof. The area of the bone-matrix contact was preserved in a shallow, natural, mould-like depression that contained the skull as a very light-green, reduced area which clearly defines most of the skull-roof margins against an otherwise red-brown matrix (Text-fig. 6). Whereas the orbit and external naris are preserved accurately, the skull width and curvature, particularly in the posterior region have been distorted severely by post-mortem, dorsoventral crushing. In dorsal view the restored skull (Text-fig. 5) appears sub-triangular in outline, with the ventrolateral margins of the postorbital cheek region being nearly parallel and the straight or slightly concave ventrolateral margins of the preorbital region converging strongly on a broad, blunt snout whose tip is truncated. It is impossible to determine the exact angle between the skull roof table and postorbital cheek region, but it must have approached at least 120°, giving the posterior half of the skull a box-like morphology. The occipital margin of the skull table is slightly concave and lies at a level nearly equal to the posteroventral corner of the cheek region. The left external naris and orbit are well preserved. Of the otic notches, only the horizontal dorsal border of the left is well preserved, and determination of the posteroventral slope of the ventral border cannot be determined due to crushing and loss of bone. Much of the dermal sculpturing of the skull roof is badly eroded, but enough remains to indicate that it was strongly developed. Preserved portions typically exhibit a pattern of shallow pits that are occasionally elongated into short furrows. On some of the larger dorsal roofing bones the sculpturing radiates from what were presumably centres of ossification.

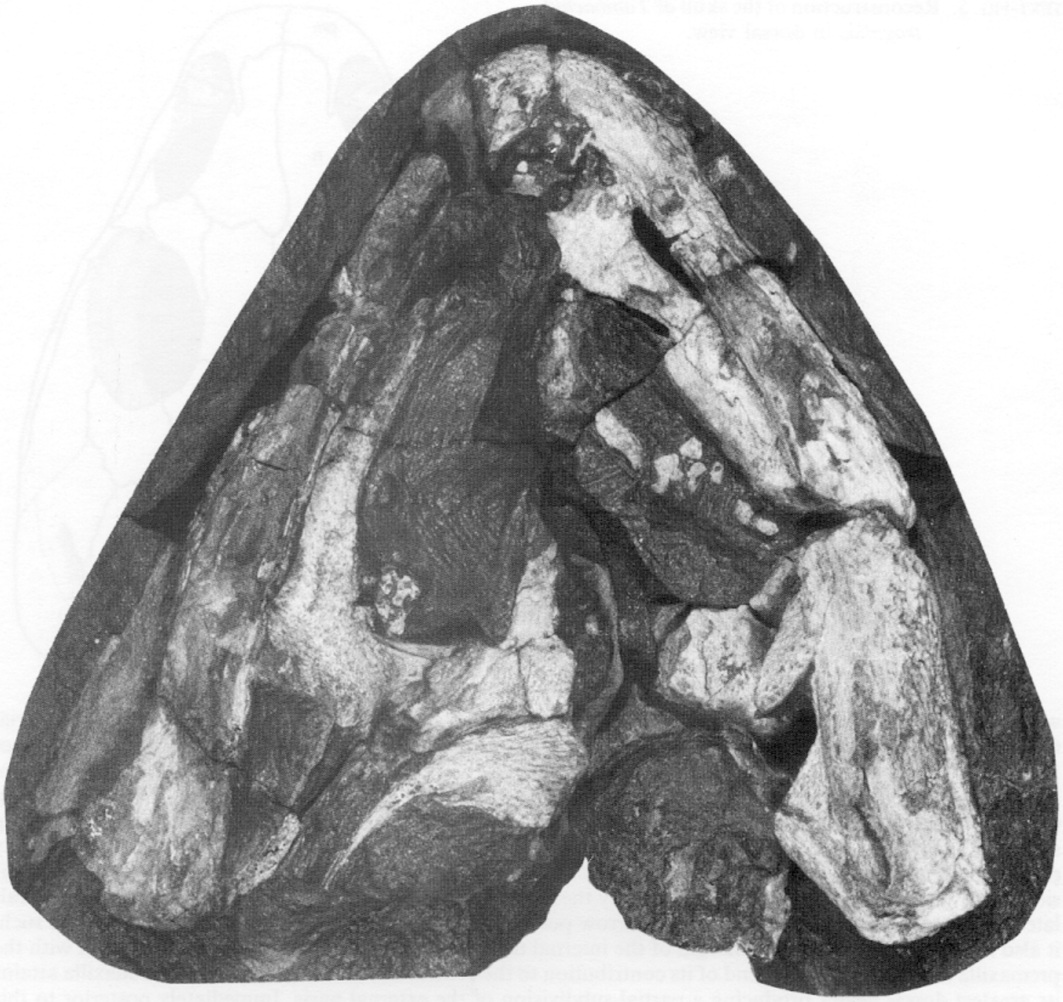
The stoutly constructed premaxilla forms the anterior margin of the external naris, as well as the anterior and lateral walls of the rostral end of the nasal chamber. Its posterodorsal process is a narrow splint of bone

TEXT-FIG. 5. Reconstruction of the skull of *Tambachia trogallas* in dorsal view.



whose distal end penetrates the anterolateral margin of the nasal. There is no evidence of an internarial foramen at the junction of the premaxillae and nasals, as reported in some trematopids (Bolt 1974*a*; Dilkes 1990). Determination of the exact number of premaxillary teeth is difficult, due to incomplete preservation. Partial remains of four teeth and spaces for four more are evident in the left premaxilla, giving a minimum count of eight. The preserved series of teeth increase in size posteriorly, with the posteriormost being significantly larger and having a 'caniniform' appearance. They are blunt cones, but were undoubtedly sharply pointed and possibly recurved slightly in life. The long, slender maxilla can be observed clearly only on the left side of the skull. Anteriorly, it overlaps dorsally the maxillary process of the premaxilla as it forms the central-lateral border of the external naris and a narrow portion of the lateral floor of the narial chamber. As such, it also forms most of the lateral margin of the internal naris. A short distance posterior to its contact with the premaxilla and at the posterior end of its contribution to the ventral rim of the external naris the maxilla attains its greatest dorsal height producing a partial subdivision of the external naris. Immediately posterior to this point there is an abrupt, but slight reduction in the height of the maxilla, which is essentially maintained until just behind the antorbital bar. Here, the maxilla makes a very small entrance into the ventral margin of the orbit before steadily narrowing posteriorly; although not complete posteriorly, it undoubtedly tapered to a very thin splint that ended at a level well behind the orbit. The left maxilla possesses nine teeth identical in shape to those of the premaxilla, with spaces for approximately 12 or more teeth; an exact count is impossible due to poor preservation and the extremely small size of the posteriormost teeth, but is estimated as well over 20. The third preserved tooth, probably representing the fifth tooth position, is clearly the largest of the series, and thus, as in the similarly sized posteriormost premaxillary tooth, has a 'caniniform' appearance.

As in other trematopids, the external naris (Text-fig. 4A–B) is elongated and subdivided into two portions by the low, broad, dorsal expansion of the maxilla a short distance posterior to the septomaxilla. Bolt (1974*a*) described the division in trematopids as being formed by the dorsal expansion of the maxilla and a ventrolateral process of the nasal. That the anterior, sub-circular division of the external naris was the true or functional narial opening has been generally accepted (Bolt 1974*a*; Berman *et al.* 1987; Dilkes 1993). Bolt (1974*a*) interpreted the longer posterior division of the external naris as probably having accommodated a specialized gland, possibly a salt gland that developed lateral to the nasal capsule and homologous to the external nasal gland found in most living reptiles. On the other hand, Dilkes (1993) argued convincingly that, if the trematopids possessed a salt gland like that found in modern reptiles, it would not account for the posterior

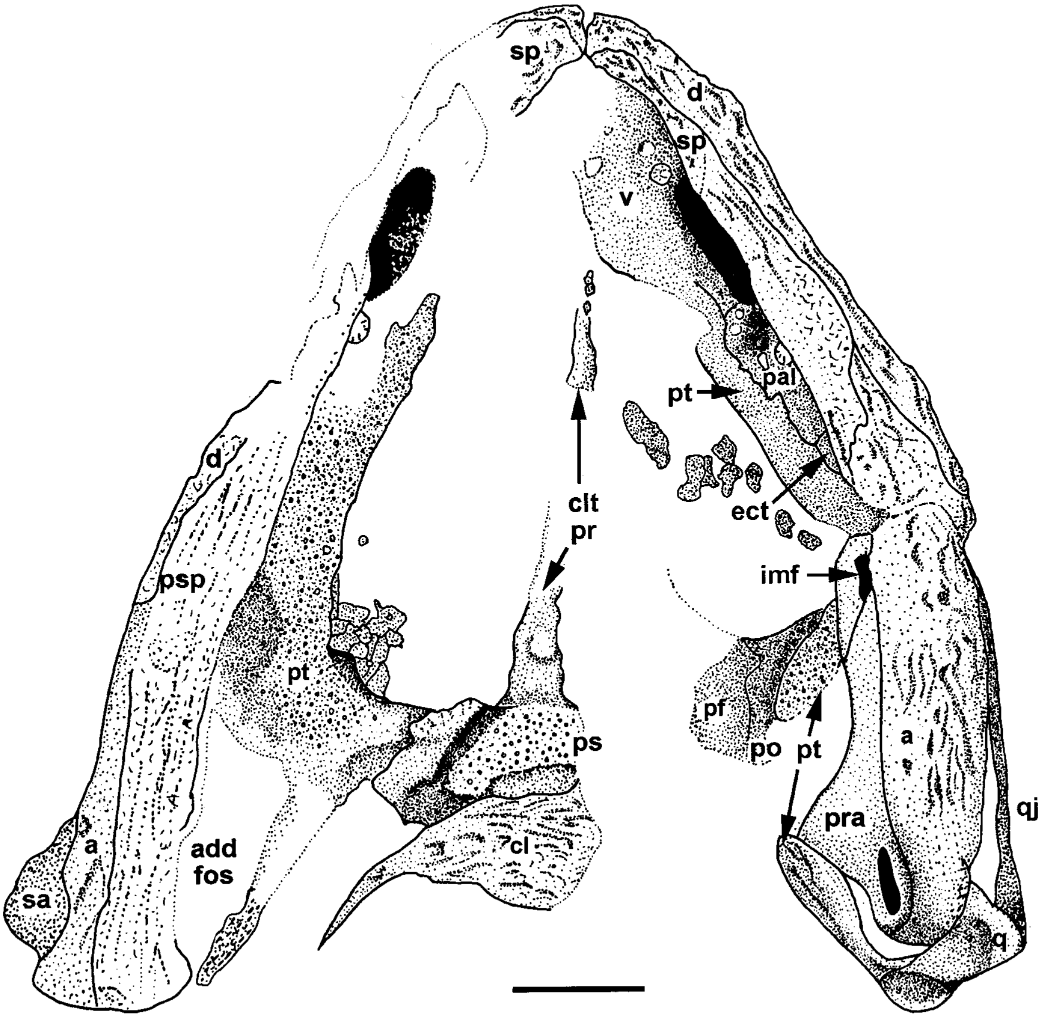


TEXT-FIG. 6. *Tambachia trogallas* gen. et sp. nov.; holotype, MNG 7722; skull in ventral view with right clavicle covering posterior margin of braincase; skull has been replaced in a natural, mould-like depression from which it was removed during preparation; × 1·74.

expansion of the external naris. The existence of the salt gland is equivocal, and although Dilkes (1993) suggested that the posterior expansion is possibly related to alterations of cranial stresses during feeding, the function remains unclear. The anterior portion of the external narial opening, the true external naris, is floored by the vomer, whereas the posterior portion directly overlies the internal naris.

Only the left septomaxilla is preserved and appears to occupy nearly its correct position. It is supported by the anterior end of the maxilla along the ventral margin of the external naris, but has apparently tilted inward on its base at *c.* 45° from a nearly vertical orientation which would have brought it into close proximity and, possibly even contact with, the lateral margin of the nasal. A helical twisting of the septomaxilla divides it into two components: a ventral portion consisting of an externally sculptured, laterally directed, lunate flange and a smaller dorsal portion that has the form of a triangular process.

Of the medial roofing bones, only the nasals are well represented. Although their margins bordering the external nares are incomplete, enough remains to suggest the absence of the triangular, ventrolateral projection



TEXT-FIG. 7. *Tambachia trogallas* gen. et sp. nov.; holotype, MNG 7722; illustration of skull and right clavicle in ventral view as seen in Text-figure 6. Scale bar represents 10 mm.

that partially divides this opening in some trematopids (Bolt 1974*a*; Dilkes and Reisz 1987; Dilkes 1990). A pronounced lateral expansion of the nasals as they extend posteriorly along the margin of the external naris gives them a pentagonal outline and a combined transverse width that is slightly greater than their midline length. The left frontal indicates that this bone had a moderate entrance into the orbit. What remains of the parietals indicates no deviation from the expected trematopid pattern. The sub-rectangular postparietals have a combined transverse width that is approximately four times their midline length. Although their occipital margins are poorly preserved and the posteroventral projecting occipital flanges are absent, the postparietals clearly define a very shallow, concave occipital margin of the skull roof.

The left and only preserved lacrimal is complete and forms the lower half of the very narrow antorbital bar. From its base it sends forward a very short, stout subnarial process along the ventral margin of the posterior portion of the external naris. The subnarial process ends at the posterior margin of the low, anterior dorsal expansion of the maxilla. There is almost no posterior extension of the base of the lacrimal in the form of a suborbital process. The left prefontal is essentially complete and exhibits the general pattern for dissorophoids, whereas the right is missing the posterior extension along the orbital margin. A ventral process of the prefontal, extending along the anterior wall of the orbit medial to the lacrimal in various dissorophoids (Bolt 1974*b*; Dilkes 1990), is not evident in MNG 7722. Projecting from the ventral surfaces of the nasal, prefrontal and lacrimal just medial to the dorsal rim of the external naris is a vertical flange (not visible in the Text-figures given here) designated as the nasal flange by Bolt (1974*a*) and the narial flange by Dilkes (1990, 1993). For most of its anterior length the narial flange is oriented in a parasagittal plane. Posteriorly, the flange gradually deepens ventrally, then curves abruptly laterally to merge with the medial surface of the antorbital bar.

Only small portions of the postfrontals remain, and their relationships to neighbouring elements remain mostly undeterminable. The nearly complete left postorbital is like that in all dissorophoids.

Only the left supratemporal and tabular bones of the temporal series are well preserved, including their contributions to the otic notch, but the posteroventrally projecting occipital flange of the tabular is missing. The supratemporal is large, with a greatest width-to-length ratio of approximately 0·72. The sculptured, dorsal-roof portion of the tabular is rectangular; its lateral margin curves abruptly downward to form a large, rectangular sculptured area at the posterior end of the dorsal margin of the otic notch; clearly the posterolateral corner of the tabular was not drawn out into a horn-like extension as in some trematopids (Olson 1941; Dilkes and Reisz 1987). The otic notch is represented only by the complete dorsal margin of the left otic region (Text-fig. 4C). The ventral margin of the notch, which was presumably formed by the squamosal and quadratojugal and sloped posteroventrally, is not preserved on either side of the skull. The greater anterior portion of the vertical shelf of bone forming the dorsal margin of the otic notch consists of a broad, well-defined smooth or unsculptured area, the supratympanic flange, which compares closely to that of other trematopids (Bolt 1974*b*; Berman *et al.* 1987; Dilkes 1990). As the supratympanic flange extends posteriorly it gradually narrows, with its slightly dorsally convex margin curving downward to the otic notch to form the anterior border of the laterally downturned, sculptured portion of the tabular. The squamosal, supratemporal, and tabular portions of the supratemporal flange are clearly visible. There is a substantial contact between the squamosal and tabular that excludes a subrounded supratemporal portion, the 'semilunar flange of the supratemporal' of Bolt (1974*b*), from the ventral margin of the supratympanic shelf. At the level of this contact the squamosal and tabular contribute to a short, broadly convex process of the ventral margin of the supratympanic flange which projects into the otic notch. This flange, designated the 'semilunar curvature' by Bolt (1974*b*), is present in dissorophids (Carroll 1964; DeMar 1968; Bolt 1974*c*; Berman *et al.* 1985) and the trematopid *Phonerpeton* (Dilkes, 1990).

Palatal complex. Not only are large portions of the palate missing or poorly preserved, but its description is also limited by the tightly attached lower jaws (Text-figs 6–7). However, enough of the palate remains to give a reasonable account, with the added advantage that a small portion of it can be seen in dorsal view through the left external naris and orbit (Text-fig. 4B). Almost the entire left vomer is visible, and the portion bounding the anterior end of the internal naris is visible through the external naris. The area of the medial union of the vomers is too poorly preserved to indicate whether they formed a deep, wide internarial pit on their ventral surface, as is typical in trematopids (Olson 1941; Dilkes 1990). A palatine process of the vomer appears to form almost the entire narrow, lateral border of the internal naris before contacting the anterior end of the pterygoid to exclude the palatine from the widely expanded interpterygoid vacuity. A moderately sized tusk and matching socket is located on the vomer near the anterior margin of the internal naris. Viewed through the left external naris (Text-fig. 4B) the vomer can be seen to form much of the floor and medial wall of the nasal chamber. Anteriorly, at the level of the anterior portion of the true external naris, the medial wall curves laterally and appears to extend dorsally to the ventral surface of the nasal. Posteriorly, at the level of the internal naris, the medial wall lies medial to the narial flange, is oriented anteroposteriorly, and slopes dorsomedially to an undetermined height. The vomerine medial wall of the nasal chamber was described by Dilkes (1990, p. 230) in the trematopid *Phonerpeton* as the 'median bony lamina' of the vomer. In addition, he referred to the paired medial laminae of the vomers as a single structure, the median vomerine septum. Bolt (1974*a*) and Olson (1941) described the same structure in trematopids, but used different terminologies.

All but the lateral margin of the left palatine is exposed in palatal view. Anteriorly it forms the posterior margin of the internal naris, and its posterior extent and level of contact with the ectopterygoid is also comparable to that of other trematopids. A short distance posterior to the internal naris the palatine bears a large tooth; it probably was associated with a socket of equal size. Only a very small portion of the anterolateral margin of the left ectopterygoid is visible. Neither the ectopterygoid nor the palatine has an exposure on the dorsal or lateral surface of the ventral orbital rim, as is common in dissorophoids (DeMar 1968; Bolt 1974*b*; Dilkes 1990).

Although neither pterygoid is complete, the combined features of both exhibit the standard temnospondyl form that can be divided into palatal (anterior) and quadrate rami, and a basipterygoid region. The palatal ramus and basipterygoid region form most of the lateral and posterior margins of the heart-shaped interpterygoid vacuity. The ventral surface of the right pterygoid is well enough preserved to indicate a dense shagreen covering of tiny denticles on the palatal ramus and the base of the basipterygoid region. The medially directed, process-like basipterygoid region, referred to here by Daly's (1994) designation as the internal process, is a very stoutly built, broad, flat structure that is directed medially and slightly dorsally to its distal articulation with the basipterygoid process of the braincase. An articular facet extends as a broad band across the entire ventral width of the distal end of the internal process, faces ventromedially, and appears to have a very shallow, concave surface. The basicranial joint was clearly open and mobile. The narrow quadrate ramus bordered the sub-triangular subtemporal fossa medially.

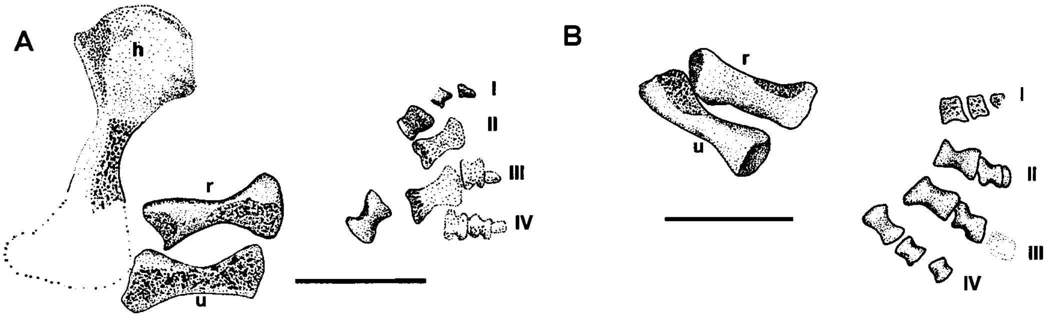
The only preserved and visible portion of the quadrates is the ventral surface of the left condyle. Although its posterior margin is incompletely preserved, what remains indicates a typical bicondylar structure. It is not possible to determine whether a posterodorsal process of the quadrate was present, as in other dissorophoids (Bolt 1977*a*).

Within the interpterygoid vacuity and occupying the same level as the palate are numerous, small, widely distributed, irregularly shaped plates. Most are scattered, but along the posterolateral margin of the right pterygoid they are arranged in a tightly fitting mosaic, with some appearing to possess minute denticles. The plates are interpreted as remnants of a mosaic of tight-fitting, denticulated ossifications which lay within the skin covering the palate, but were restricted to the area of the interpterygoid vacuity. Similar structures have been reported in other dissorophoids. Carroll (1964) described an ossified 'skin' membrane covering the entire palate of *Amphibamus lyelli*, whereas Berman and Berman (1975) noted the presence of an ossified, denticulated 'skin' covering the interpterygoid vacuity region of the palate in *Broiliellus hektotopos*.

Braincase. The only visible and presumably preserved portion of the braincase is the parasphenoid, which is visible in the ventral view of the skull (Text-figs 6–7). A large, central portion of the narrow, anteriorly tapering cultriform process is missing. The process obviously extended to at least the posterior, midline union of the vomers. Near the base of the process is a small, hemispherical protuberance. Its function is unknown, but Clack and Holmes (1988) have noted paired depressions in the same location in anthracosaurian amphibians which they suggest may have provided for attachment of extraoccular muscles. Although the left side of the body of the parasphenoid is missing and its posterior margin is concealed by the right clavicle, it obviously had the outline of a laterally expanded quadrangle whose lateral margins angled anteromedially. In the anteromedial region is a slightly raised, triangular field of denticles of the same size as those of the pterygoid. A conspicuously deep furrow separates the right margin of the field and the smoothly surfaced, basipterygoid process. The basipterygoid process is unusual in being extraordinarily broad, having a width that extends across the entire lateral margin of the body of the parasphenoid and slightly exceeds the width of the distal portion of the internal process of the pterygoid. The basipterygoid process of the braincase is directed slightly ventrally, and its dorsal articular surface faces dorsolaterally and has a slightly convex surface that fits snugly into the concave articular surface on the internal process of the pterygoid.

Lower jar. The mandible is firmly attached to the skull, with only the left rami being preserved well enough to allow substantial description of the ventral portions of the lateral and medial surfaces (Text-figs 4A, 6–7). The jaw shows no strong deviation from the general trematopid pattern (Berman *et al.* 1987; Dilkes 1990), and only a few comments are necessary. Much of the sculpturing, which is mainly limited to the lateral surface of the jaw, has been severely damaged due to weathering. What remains indicates a coarse texture of irregular, longitudinal grooves which are replaced by small oval to circular pits near the symphysis. Although both the dentary and splenial enter the symphysis, the former element is the dominant contributor. An inframeckelian foramen is located on the ventromedial margin of the jaw at the posterior end of the postsplenial and adjacent to the angular-prearticular suture. At the posterior end of the medial rim of the adductor fossa there is a pronounced, medially directed, flange-like inflection of the prearticular. A large, oblong para-articular foramen penetrates the prearticular near its posteriormost margin.

Axial skeleton. Very little remains of the axial skeleton. Remnants of a string of three poorly preserved vertebrae are exposed in dorsal view between the dorsal blades of the associated ilia (Text-fig. 9A). The anterior two vertebrae are too fragmentary to comment upon, except to note that the configuration of the second suggests that it is a true sacral vertebra. The much better preserved third vertebra of the series, represented by the neural arch in dorsal view, is therefore believed to be the first caudal. Its short, stout neural spine appears circular in horizontal section. The buttresses of the prezygapophyses slope ventrally as they diverge anteriorly



TEXT-FIG. 8. *Tambachia trogallas* gen. et sp. nov.; holotype MNG 7722; partial right, A, and left, B, forelimbs and manus. Scale bars represent 10 mm.

from the base of the spine, producing a shallow V-shaped depression between them. Short, broad transverse processes are directed laterally and slightly posteriorly. What is undoubtedly the right sacral rib exposed in posterior view is closely associated with the vertebrae. The broadly expanded head tapers quickly to the thin, arcuate posterior edge of the shaft. A confusion of remnants of several unidentified bones is also preserved in close association with the sacral elements.

A large portion of the tail (not shown) is represented by an impression of an articulated series of vertebrae that has been displaced several tens of millimetres from the first caudal vertebra described above. The impression is 85 mm long and very faint, and the only structures that can be discerned clearly are short neural spines and haemal arches of the anterior 6 mm of the series. They attain a maximum length of approximately 4 mm at the anterior end of the series.

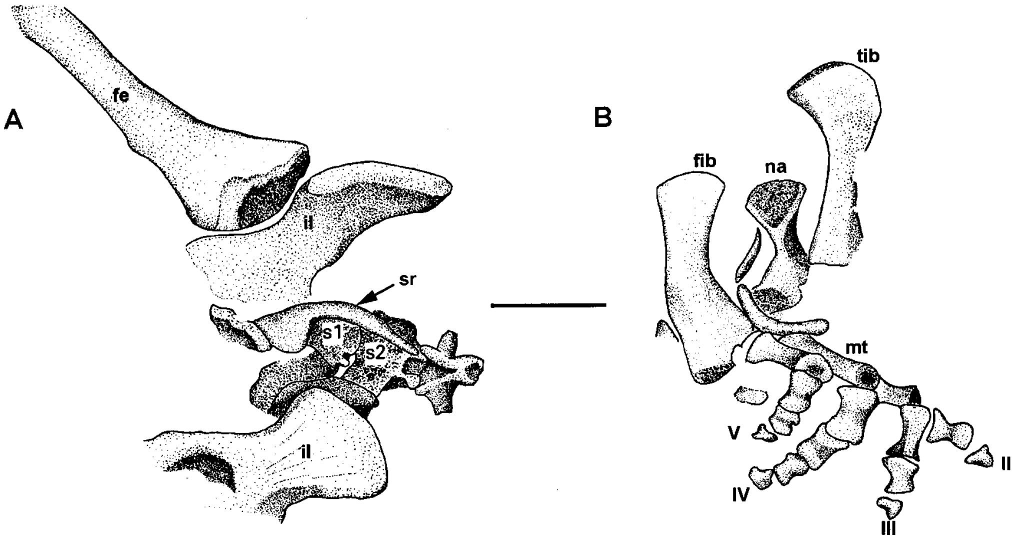
What may be an isolated neural arch and rib are closely associated with the right hindlimb (Text-fig. 9B).

Appendicular skeleton. All that remains of the pectoral girdle is the right clavicle preserved in a position covering the posterior ventral margin of the braincase (Text-figs 6–7). The clavicle consists of a relatively broad, triangular ventral plate that is approximately as long as it is wide. It is continued with a narrow, dorsal stem that tapers distally, but, due to dorsoventral crushing, the two components occupy the same plane with their external surfaces exposed. The medial margin of the ventral plate is incomplete, and the remainder of its external surface exhibits a sculpturing pattern of transversely oriented, irregular ridges and grooves. The non-sculptured stem joins the ventral plate in a smooth arc.

A partial right humerus is preserved (Text-fig. 8A), but, unfortunately, most of the information about this element is derived from an impression, leaving little or no account of its detailed structure. The length of the humerus can be estimated to be at least 26 mm. The proximal head is broadly flared, and the presence of a well-developed deltopectoral tuberosity is indicated by a deep depression adjacent to the anterior margin of the head. The shaft is distinctly differentiated from the proximal head and is oval in cross section, with the long axis lying in the same plane as the head; the oval cross section may have been exaggerated by post-mortem crushing. The proximal and distal heads are not twisted about the shaft and thus lie in the same plane. However, this probably does not reflect the life position and is possibly also due to crushing. Although most trematopids exhibit a well developed supinator process, *Tambachia* is not preserved well enough to allow confident determination of its presence or absence.

The radius, ulna, and manus of both forelimbs are preserved (Text-fig. 8). The radius is 13 mm long, with the right one more accurately portraying the outline shape of the element. The proximal and distal ends taper, more strongly so on the lateral margin, to a short, narrow shaft that is sub-circular in cross section. There is no evidence of a laterally directed shelf of the shaft as in *Phonerpeton* (Dilkes 1990). The ulna is approximately 16 mm long. Its shaft is strongly waisted, more so on the medial margin, and mediolaterally is oval in cross section. Although there is no obvious development of an ossified olecranon process or semilunar notch, there is a pronounced extension of the lateral margin of the proximal head; the olecranon process is apparently one of the last appendicular skeletal structures to ossify fully (Berman *et al.* 1985).

No carpal elements are preserved. Each manus (Text-fig. 8) consists of four metacarpals and the digits that they support. The metacarpals and phalanges are short and stout; those of the left manus, however, are represented primarily as impressions. As a complete manus is unknown in trematopids, it cannot be assumed



TEXT-FIG. 9. *Tambachia trogallas* gen. et sp. nov.; MNG 7722. A, portion of pelvic-sacral region and right femur in mainly dorsal view. B, partial right hindlimb and pes. Second metatarsal is not visible in this view. Scale bar represents 10 mm.

that a fifth metacarpal and digit were not present. A manus consisting only of the carpus was described (Williston 1909; Olson 1941) in *Acheloma* (as *Trematops*) as having five distal carpals. If true, then it might be expected that five digits were also present. On the other hand, the primitive, Late Pennsylvanian dissorophoids *Amphibamus* and *Eoscopus* both possess four metacarpals with digits (Carroll 1964; Daly 1994). The metacarpals in *Tambachia* increase in size through to the third, whereas the fourth is intermediate in size between the first and second. On the basis of both left and right manus, the preserved phalangeal formula is 2,2,2,3; the second and third digits obviously each lack at least the distal phalanx.

All that is visible of the pelvic girdles are the dorsal blades of the ilia (Text-fig. 9A), the right in medial and the left in lateral view. The blades are low and slightly waisted, lack indications of a posterior extension or process, and thicken slightly toward the crest. Their smoothly finished surfaces exhibit no scars for muscular or ligamentous attachments.

Of the hindlimb and pes only elements from the right side are represented. The femur (Text-fig. 9A) is preserved in association with the pelvis and separated by a short distance from the rest of the limb and pes (Text-fig. 9B), which include the tibia, fibula, and four metatarsals and digits preserved in articulation, or in nearly their correct association. The absence of the tarsals is almost certainly due to non-ossification and reflects immaturity. All that remains of the femur is the proximal head, exposed in dorsal or anterodorsal view, and most of the shaft preserved as an impression. As preserved, the femur measures 26 mm long, but the total length was probably about 30 mm. Its expanded head bears no distinct processes and quickly tapers to a long, narrow shaft. The partially exposed articular surface is of unfinished bone. The strongly compressed tibia and fibula are essentially complete and measure *c.* 18 mm long. The articular margin of the greatly expanded proximal head of the tibia is strongly convex in dorsal view, but much less so along its more expanded lateral portion. The medial and lateral margins of the bone are deeply concave; more so along the lateral margin because of the greater lateral expansion of the proximal head. The shaft is narrowest at the midlength of the bone, where it is sub-circular in cross section. The distal head is modestly expanded and symmetrical, and, although not complete, appears to end in a transverse articular margin that is oval in end view. Neither the proximal nor the distal articular surface of the fibula is completely preserved or visible. The proximal head is only modestly expanded, with the articular margin being slightly convex in dorsal view. In end view the articular surface is weakly crescentic in outline, with the convex margin being dorsad. The distal head is more expanded than the proximal head, and its articular margin is very slightly convex in dorsal view. A dorsal thickening of the lateral half of the distal head produces a low, broad ridge that becomes slightly more pronounced as it extends to the articular margin. Only the lateral half of the distal articular surface is visible and is clearly sub-elliptical in outline, with the medial end gradually tapering to a much thinner surface. The shaft, which is narrowest at the midlength of the bone, has a straight or very slightly convex lateral margin and a strongly convex medial margin, giving the bone a bowed appearance.

It is assumed that the pes originally possessed five metatarsals and digits. Of the four preserved metatarsals, the two central ones are the longest and are subequal in length. Four digits are associated with the metatarsals and are complete, as indicated by their terminal phalanges ending in a narrow, pointed core support for a claw. Because the third preserved digit possesses the greatest number of phalanges and is the longest, it undoubtedly represents the fourth digit. Therefore, it is assumed that the preserved metatarsals and associated digits represent two through to five and that the first metatarsal and digit are absent. On this basis the phalangeal formula for the pes would be ?–2–3–4–3. There is evidence to accept this partial formula, and the first digit probably possessed two phalanges. Daly (1994) described the phalangeal formula of the pes in the Late Pennsylvanian amphibamid dissorophoid *Eoscopus* as 2–2–3–4–3. Further, she reinterpreted the 2–3–4–4–2 pes formula given by DeMar (1968) for *Dissorophus* as more probably 2–2–3–4–3, concluding that this is a more common formula among temnospondyls.

ASSIGNMENT AND RELATIONSHIPS OF *TAMBACHIA*

Tambachia *as a trematopid*

Significant work has been done on the structure and relationships of dissorophoids by Boy (1972); however, the two most recent phylogenetic schemes of intrarelationships of this group, both based on cladistic methodology, have been presented by Dilkes (1990) and Daly (1994). These can be utilized to determine the phylogenetic position of *Tambachia* within the superfamily. In Daly's (1994) analysis, the more comprehensive of the two, three major families of the Dissorophoidea are recognized: Amphibamidae, consisting of the aquatic genera *Amphibamus*, *Eoscopus*, *Doleserpeton* and *Tersomius*, was determined to be an early derivative of the Dissorophoidea, whereas the terrestrial families Trematopidae and Dissorophidae were considered more closely related to one another than either is to Amphibamidae. Boy (1972) has also argued for the removal of *Amphibamus* from Dissorophidae and placement in its own family. In considering the aberrant dissorophoids *Platyhystrix*, *Astreptorhachis*, and *Ecolsonia*, viewed as dissorophids by most authors (Vaughn 1971; Berman *et al.* 1981; Berman *et al.* 1985), Daly united the first two in a new family, the Platyhystricidae, whereas the familial assignment of *Ecolsonia* was judged as unresolved and best left as *incertae sedis*. In Dilkes' (1990) analysis, Dissorophoidea was treated as if consisting only of the families Trematopidae and Dissorophidae. However, the problematical genera *Amphibamus* and *Tersomius*, traditionally considered as unarmoured members of the Dissorophidae (Carroll 1964; DeMar 1968; Bolt 1974*a*), were suspected by Dilkes to have probably shared a more distant relationship with the trematopids and other dissorophids. On the basis of this relationship, Dilkes used *Amphibamus* as the outgroup, although still considering it a dissorophoid, in his analysis of the intrarelationships of the Trematopidae. The validity of his choice of *Amphibamus* as an outgroup was, therefore, reaffirmed by the results of Daly's (1994) study. Here we utilize both *Amphibamus* and the more recently described *Eoscopus* for outgroup information.

In addition to *Tambachia*, only four other genera can be assigned to the Trematopidae: *Acheloma* Cope, 1882, *Actiobates* Eaton, 1973, *Anconastes* Berman, Reisz and Eberth, 1987 and *Phonerpeton* Dilkes, 1990. Familial assignment of two of these genera, however, has been questioned. Dilkes (1990) only tentatively assigned *Anconastes* to the Trematopidae, as available material permits recognition of only two of the five synapomorphies recognized by him as uniting it with other members of the family. On the other hand, three of the five characters used by Daly (1994) to define Trematopidae can be confirmed in *Anconastes*, and, as it exhibits no dissorophid features (Berman *et al.* 1987), there is little doubt that its original assignment was correct. In addition, *Anconastes* shares three derived characters with *Tambachia* (discussed below) that not only further support a trematopid assignment of the former, but indicates that the two genera are more closely related to one another than either is to any other trematopid. *Actiobates* was excluded by Dilkes (1990) from his analysis of the interrelationships of the trematopids on the assertion that it possessed a combination of trematopid and dissorophid characters. This view was also expressed in the original description of *Actiobates* by Eaton (1973), who believed it to be a dissorophid with a trematopid-like external naris. However, Berman *et al.* (1985) effectively argued that *Actiobates* is a trematopid and that the few dissorophid-like features it appears to exhibit most probably represent a juvenile, probably early postmetamorphic, stage of development. Daly (1994) apparently also viewed *Actiobates* as a trematopid, but excluded it from her cladistic analysis of the dissorophoids. Of the five characters she used to diagnose Trematopidae, the holotype and only known specimen of *Actiobates* allows examination of three, all of which confirm her assignment. This was further confirmed by Milner (1985), who, on reconsidering the familial status of *Actiobates*, provisionally placed it in Trematopidae. Finally, after re-examining the holotypes of *Acheloma cumminsi* Cope, 1882, and *Trematops milleri* Williston, 1909, Dilkes and Reisz (1987) declared the latter to be a subjective junior synonym of the former. Thus, as they asserted, the commonly applied name *Trematops* is invalid and must be replaced by *Acheloma*.

In view of the similarity of the assessments by Dilkes (1990) and Daly (1994) of the relationship of the Amphibamidae as the sister outgroup to the Trematopidae and Dissorophidae, it is not surprising that they presented nearly identical lists of characters to define Trematopidae. In the following list of synapomorphies uniting the trematopids, characters 1 through to 4 were used by both authors, whereas characters 5 (with modifications) and 6 were used only by Dilkes and Daly, respectively.

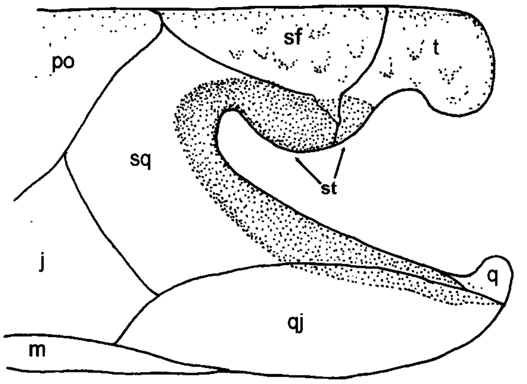
1. *Presence of an elongate external naris.* This character was expanded by Dilkes (1990, p. 238) to include the presence of 'a concave narial flange composed of separate sheets from the nasal, prefrontal, and lacrimal that meets the antorbital bar'. The use of the shorter, traditional version of this character was argued for by Daly (1994), because she noted the presence of a narial flange in the amphibamids *Eoscopus* and *Tersomius*. On the basis of this distribution, the presence of a narial flange was instead used by Daly to define Dissorophoidea. The presence of an elongated external naris in the dissorophid *Ecolsonia* must, therefore, be considered a homoplastic feature (Berman *et al.* 1985). An elongated external naris and a nasal flange are present in *Tambachia*, and both structures conform in detail to those in all other trematopids.

2. *Presence of a premaxillary caniniform tooth beneath the functional external naris and a pair of maxillary caniniform teeth below the posterior expansion of the external naris.* This character, originally noted by Olson (1941) as distinguishing the trematopids from dissorophids, was later used by Berman *et al.* (1987), as well as by Dilkes (1990) and Daly (1994); it is present in *Tambachia* and all other trematopids.

3. *Presence of a median vomerine septum.* This character was originally described as unique to the trematopids by Dilkes and Reisz (1990) and Dilkes (1990), and was accepted by Daly (1994) as defining the family. This structure appears to be present in *Tambachia*, and additional preparation has also revealed its presence in *Anconastes*. The area of the median vomerine septum was not described in the original description of *Actiobates* by Eaton (1973), and its presence or absence probably could not be demonstrated without partial destruction of the holotype.

4. *Inflection of the prearticular along the medial rim of the adductor fossa.* The use of this character to define Trematopidae was proposed by Dilkes (1990) and was subsequently accepted by Daly (1994). Dilkes (1990) was able to identify this character with certainty only in *Acheloma* and *Phonerpeton*; the area of the adductor fossa is unknown in *Actiobates* and *Anconastes*. According to Dilkes, the medial inflection of the prearticular in *Phonerpeton* doubles the width of the jaw at that level; although the inflection appears to be less developed in *Tambachia*, it is pronounced.

5. *Unsculptured supratympanic flange of the otic notch includes the squamosal, semilunar flange of the supratemporal, and a small area of the tabular which has a broad contact between the tabular and the*



TEXT-FIG. 10. Diagrammatic reconstruction of the otic notch and associated supratympanic flange of a trematopid amphibian in left lateral view.

squamosal beneath the semilunar flange of the supratemporal. This character was originally proposed by Dilkes (1990, p. 239) as the 'Absence of dermal sculpturing along the entire dorsal rim of the otic notch.' As presented by Dilkes, this character was rejected by Daly (1994), because she considered it to be present also in *Eoscopus*. Alternatively, she used this character to unite the Dissorophoidea, and considered (p. 50) the 'replacement of the supratympanic shelf with sculpturing that covers the lateral area above the otic notch and most of the tabular' as a character uniting the Dissorophidae, including platyhystricids and *Ecolsonia*. According to Daly (1994), *Eoscopus* possesses an unsculptured supratympanic flange that is accompanied by a supratympanic shelf, semilunar flange of the supratemporal, and semilunar flange of the squamosal (Bolt 1974*c*). However, there is still some reason to doubt whether the supratympanic flange in amphibamids is entirely like that in trematopids. In *Eoscopus* the tabular contribution to the supratympanic flange is relatively much smaller and does not extend anteriorly beneath the semilunar flange of the supratemporal. As a result, Daly (1994) was unable to determine whether the squamosal and tabular contact one another along the ventral margin of the supratympanic flange. The contribution of the tabular to the flange is also reduced posteriorly, as Daly notes, by a ventral curvature of its lateral margin, which also exhibits a light pitting. Bolt (1974*c*) described the supratympanic flange in the *Tersomius* specimens studied by him as representing an intermediate state between the primitive state of being absent and the advanced state exhibited by the trematopids as follows: 'the smooth supratympanic flange is weakly developed with a straight ventral margin that does not end posteriorly by rising up to the ventral surface of the tabular, and the squamosal-tabular contact is indeterminate.' A supratympanic flange does not appear to have been present in *Amphibamus* (Carroll 1964; Daly 1994) and is absent in *Doleserpeton* (Bolt 1974*c*). The structure of the supratympanic flange in the amphibamids is obviously quite variable and apparently expressed in its most derived state in *Eoscopus*. For this reason character 5 has been expanded to include the presence of a broad, squamosal-tabular contact beneath the semilunar flange of the supratemporal (Text-fig. 10). In addition, the definition of the supratympanic flange is restricted here to include only the unsculptured portion of the vertical, laterally facing shelf of bone that forms the dorsal margin of the otic notch. This definition of the supratympanic flange seems more appropriate than one which includes the entire vertical, dorsal margin of the otic notch, inasmuch as the probable dorsal limit of the attachment of the tympanum was the boundary between the smooth-surfaced and sculptured bone (Bolt and Lombard 1985).

The structure of the supratympanic flange is, unfortunately, not known in all trematopids. Although this area of the skull appears to be preserved in *Actiobates*, it was neither described nor illustrated sufficiently by Eaton (1973) to enable the detailed comparisons necessary here. In *Anconastes* (Berman *et al.* 1987) only enough of the supratympanic flange remains to demonstrate its presence. On the other hand, the otic notch regions in *Acheloma* and *Phonerpeton* are exceptionally well preserved and not only exhibit an unsculptured supratympanic flange that includes the squamosal, semilunar flange of the supratemporal, and the tabular, but a broad squamosal-tabular contact beneath the semilunar flange of the supratemporal.

Casual inspection of the otic notch of *Tambachia* would seem to suggest that its supratympanic flange does not conform to the trematopid pattern in one important feature: the smooth portion of the supratympanic flange extends along only the anterior two-thirds of the dorsal margin of the otic notch, with the posterior third being completed by a strongly sculptured contribution from the tabular. However, the supratympanic flange in *Tambachia* conforms exactly to that in other trematopids in its relative size and structure, and the relationships and proportions of the squamosal, tabular and supratemporal. Therefore, the posterior, sculptured portion of the dorsal margin of the otic notch is not a part of the original or true supratympanic flange. Rather, the supratympanic flange in *Tambachia* is considered unique among trematopids in having a sculptured, posterior extension formed by the tabular (discussed below). With the exception of *Ecolsonia*, in those instances where the dorsal margin of the otic notch in dissorophids is well documented (DeMar 1968; Bolt 1974*b*) it consists of the same three elements and exhibits the identical sutural pattern as in trematopids. Noticeably different, however, is that the smooth portion of the supratympanic flange in dissorophids does not include the semilunar flange of the supratemporal, and the tabular is limited to a relatively much smaller area adjacent to its contact with the squamosal. As a consequence, the dorsal border of the smooth supratympanic flange angles sharply downward and posteriorly in dissorophids, rather than being horizontal or slightly convex dorsally as in trematopids (Text-figs 4c, 10). Character 5, therefore, has been altered here to exclude the dissorophid features of the supratympanic flange described above. Among the nontrematopid dissorophoids, only in the aberrant *Ecolsonia* is the supratympanic flange like that in trematopids (Berman *et al.* 1985).

6. *Internal process of the pterygoid is hemicylindrical with the articular facet facing dorsally.* This character was proposed by Daly (1994). Its usefulness, however, is equivocal, because the structure of the internal process of the pterygoid and the nature of its union with the basipterygoid process of the braincase in dissorophoids are quite variable and often poorly known or vaguely described. The primitive state of this character, as described by Daly (1994) in the amphibamids *Eoscopus*, *Tersomius* and *Amphibamus*, is a cylindrical internal process that is slotted posteriorly for the reception of the basipterygoid process of the braincase. However, judging from Bolt's (1969) illustrations, in *Doleserpeton*, which was not accounted for by Daly, the internal process is also cylindrical, but has a transverse contact with the basipterygoid process.

Although the structure of the internal process of the pterygoid in *Tambachia* and *Anconastes* conforms largely to the derived state ascribed to trematopids by Daly (1994), those of other trematopids do not strictly agree. Eaton's (1973) illustration of *Actiobates* suggests that its internal process is cylindrical, but has a dorsally facing contact with the basipterygoid process. In *Phonerpeton*, judging from Dilkes' (1990) illustrations, the internal process is hemicylindrical, but has a transverse contact with the basipterygoid process. The palate and braincase are indistinguishably fused and appear to be joined by a rod-like structure in *Acheloma* (Olson 1941; Dilkes and Reisz 1987).

Daly's (1994) use of character 6 to unite the trematopids is also greatly weakened, as Daly admits, by fusion which obliterates the nature of the basicranial joint in most dissorophids. To this must be added that in some dissorophids, such as *Dissorophus* (DeMar 1964) and *Kamacops* (Gubin 1980), the pterygoid and braincase appear to be joined by a continuous, nearly cylindrical, thick, rod-like structure. In addition, although Daly (1994) views *Ecolsonia* as an aberrant dissorophoid whose family status is unresolved, she describes its internal process and basicranial articulation as duplicating exactly the primitive amphibamid condition.

Shared derived characters uniting Tambachia *and* Anconastes

7. *Absence of an internarial fenestra.* Believing that an internarial fenestra is absent in *Amphibamus* and *Anconastes*, Dilkes (1990) interpreted the presence of this structure as a synapomorphy of

Phonerpeton and *Acheloma*. An internarial fenestra, however, is present in all amphibamids, as well as in the trematopids *Actiobates*, *Phonerpeton* and *Acheloma*. Among the dissorophids, including *Ecolsonia*, only the poorly known *Conjunctio* appears to possess this structure (Carroll 1964). Therefore, we judge that the absence of an internarial fenestra is a shared derived character uniting *Tambachia* and *Anconastes* and which evolved in parallel in dissorophids.

8. *Suborbital process of the lacrimal is greatly reduced or absent and not accompanied by an exposure of the palatine on the lateral and/or dorsal surface of the ventral rim of the orbit.* Two primitive states of this character are randomly distributed in all other dissorophoids: (1) suborbital process of the lacrimal is very short or absent and is accompanied by an exposure of the palatine on the lateral and/or the dorsal surface of the ventral rim of the orbit; or (2) suborbital process of the lacrimal is long, but not accompanied by a lateral and/or dorsal exposure of the palatine along the ventral rim of the orbit.

In the amphibamids *Tersomius* and *Doleserpeton* the suborbital process of the lacrimal is greatly abbreviated and the palatine is not only exposed along the dorsal margin of the ventral rim of the orbit, but also has a sculptured exposure on the lateral margin (Bolt 1969, 1974*c*). Although the palatine is restricted to the dorsal surface of the ventral rim of the orbit in *Eoscopus* (Daly 1994), the suborbital bar of the lacrimal is greatly shortened. A lateral and/or dorsal exposure of the palatine accompanying the long suborbital process of the lacrimal has not been documented in *Amphibamus*, yet Daly (1994) has reported that a laterally exposed palatine may be present.

Among the trematopids, only *Phonerpeton* exhibits a short suborbital process of the lacrimal that is accompanied by a lateral exposure of the palatine (Dilkes 1990). *Actiobates* provides the only example of an alternative character-state. In Eaton's (1973) description and illustration of *Actiobates* there is no indication of an exposure of the palatine on either the dorsal or lateral surface of the ventral rim of the orbit. Instead, long suborbital processes of the lacrimal and jugal are narrowly separated by the maxilla. *Acheloma* is unique among the dissorophoids in the absence of the palatine, ectopterygoid, and maxilla from the ventral rim of the orbit. Here, the suborbital bar has become extraordinarily deep, and the great displacement of these bones from the ventral rim of the orbit is seemingly replaced by a very broad lacrimal-jugal contact. The long suborbital process of the lacrimal in *Acheloma* is interpreted as a character reversal. As far as can be determined, in those dissorophids in which the ventral margin of the orbit is well preserved and has been carefully examined, a laterally exposed palatine is present and the suborbital process of the lacrimal is either greatly reduced or absent (DeMar 1968; Bolt 1974*c*). When the first primitive state of this character is present, it is assumed that the suborbital process of the lacrimal has been reduced or lost by the encroachment of the palatine on the lateral and/or dorsal surface of the orbital rim.

9. *Maxilla contributes to both the dorsal and lateral surfaces of the ventral orbital rim in the absence of a contribution to either surface by the palatine.* Three primitive states of this character are randomly distributed in all other dissorophoids except the trematopid *Acheloma*: (1) the maxilla is excluded from both the dorsal and lateral surfaces of the orbital rim with the palatine contributing to both surfaces; (2) the maxilla contributes to the lateral surface, but is excluded from the dorsal surface of the orbital rim by the palatine; or (3) the maxilla and palatine contribute to the dorsal and lateral surfaces of the orbital rim.

Among the amphibamids, *Doleserpeton* (Bolt 1969, 1974*c*) exhibits primitive state 1, *Tersomius* (Carroll 1964; Bolt 1974*c*; Daly 1994) exhibits primitive states 1 and 2, and *Eoscopus* (Daly 1994) exhibits primitive state 2. The structure of the ventral orbital rim in *Amphibamus* is apparently not determinable in existing specimens (Bolt 1974*c*; Daly 1994).

In the trematopids, *Phonerpeton* exhibits primitive state 1, but there is also an exposure of the ectopterygoid on the dorsal and lateral surfaces of the ventral rim of the orbit (Dilkes 1990). *Acheloma*, on the other hand, is unique among all dissorophoids in the exclusion of the palatine, ectopterygoid, and maxilla from the orbital rim. Its extraordinarily deep suborbital bar has seemingly resulted in the wide displacement of these three elements from the orbital rim by a very broad contact between the lacrimal and jugal. It cannot be determined, however, from what ancestral state the unique structure of the suborbital bar in *Acheloma* was derived. Unfortunately, the structure of the suborbital bar in *Actiobates* is not clear from Eaton's (1973) description, which shows the lacrimal and jugal narrowly separated by the maxilla along the ventral rim of the orbit; the entrance of the maxilla into the very large orbit in *Actiobates* may reflect an early postlarval stage of development (Berman *et al.* 1985).

Unfortunately, the ventral rim of the orbit has been re-examined in only a few genera of dissorophids (DeMar 1968; Bolt 1974*c*; Berman *et al.* 1985) in light of the recent discoveries of the participation of the palatine in the formation of this structure in other dissorophoids. Most recent studies, however, suggest that the dissorophids, including *Ecolsonia* (Berman *et al.* 1985), exhibit primitive state 3.

This survey strongly suggests that the participation of the palatine in the structure of the ventral rim of the orbit is a primitive feature of dissorophoids and that, as far as is known, only *Tambachia* and *Anconastes* on the one hand, and *Acheloma* on the other, exhibit different derived states of this character.

Unique characters of Tambachia

10. *Subnarial process of the lacrimal is short.* With the possible exception of *Actiobates*, the lacrimal in *Tambachia* is unique among trematopids in having a very short subnarial process that does not appear to reach the midlength level of the posterior portion of the external naris. On the other hand, in all other trematopids the subnarial process of the lacrimal extends anteriorly to nearly the level of the subdivision of the external naris and, therefore, equals or slightly exceeds half the total length of the opening. This is interpreted as the primitive state, because in the amphibamids and typically in temnospondyls the lacrimal extends forward to the unexpanded external naris. A short subnarial process in *Actiobates* is unexpected considering its early occurrence (Upper Pennsylvanian) and the otherwise primitive anatomy of this genus (Eaton 1973). The short subnarial process of the lacrimal in this taxon may represent an early ontogenetic stage of development, as do many other features of its skull (Berman *et al.* 1985).

11. *Dorsal margin of the otic notch is extended posteriorly by a sculptured, downturned lateral expansion of the tabular.* In all dissorophids, including *Platyhystrix* (Berman *et al.* 1981) and *Ecolsonia* (Berman *et al.* 1985), the dorsal margin of the otic notch is also extended posteriorly by a sculptured, downturned lateral expansion of the tabular. However, since this feature does not appear to be present in either the amphibamids or any trematopid except *Tambachia*, it is judged to be a unique character of this genus that developed in parallel in the dissorophids. As a consequence of this character, in *Tambachia* and dissorophids the dorsal margin of the otic notch extends posteriorly to a level equal to the posteroventral corner of the skull roof.

It is difficult to confirm the absence of this feature in *Actiobates*, because of the inadequate description and illustrations given by Eaton (1973). However, the small, triangular exposure of the tabular on the skull table lies a short distance anterior to the level of the posteroventral corner of the skull roof. It is also possible that the moderately long posterior extent of the dorsal margin of the otic notch may reflect an early postlarval feature (Berman *et al.* 1985) or an illusion created by severe dorsoventral crushing of the holotype. In *Phonerpeton* (Dilkes 1990) the posterior extent of the dorsal margin of the otic notch lies far anterior to the level of the posteroventral corner of the skull roof. Although the dorsal margin of the otic notch is incomplete in *Anconastes* (Berman *et al.* 1987), enough of the tabular portions of the skull table remain to indicate that the posterior margin of the tabulars failed to reach the level of the posteroventral corners of the skull roof by a considerable degree. In *Acheloma*, the dorsal margin of the otic notch is of typical trematopid structure except for the presence of a greatly elongated tabular horn (Dilkes and Reis 1987). However, the tabular horn is basically a posterior extension of the skull table, rather than a downturned lateral expansion of the tabular.

12. *Occipital margin of the skull table lies at a level nearly equal to the posteroventral corner of the skull roof.* In all amphibamids and trematopids except *Tambachia* the midline occipital margin of the skull roof lies far anterior to the level of the posteroventral corner of the skull cheek. On the other hand, in *Tambachia* and all dissorophids (Carroll 1964; DeMar 1968), including *Platyhystrix* and *Ecolsonia* (Berman *et al.* 1981, 1985), the midline occipital margin of the skull roof lies at or just anterior to the level of the posteroventral corner of the skull roof. The distribution of these two character states suggests that the relatively farther posterior level of the midline occipital margin of the skull roof in *Tambachia* and dissorophids represents the derived state. The occurrence of the derived state only in *Tambachia* among the trematopids is judged here as a unique character of the genus that evolved in parallel with the condition in dissorophids.

13. *Deep channel on the ventral surface of the parasphenoid separates the basipterygoid process from the body of the braincase.* Among the dissorophoids, only in *Tambachia* is there a deep, well-defined channel on the ventral surface of the parasphenoid that separates the basipterygoid process from the body of the braincase. The only possible exception to this distribution is seen in *Actiobates*, where Eaton (1973, p. 5) reported that 'The basisphenoid is exposed on either side of the converging, ventralmost part of the parasphenoid; the bone bears grooves for the internal carotids. The medial edges of these grooves are bounded by the parasphenoid except in their anterior parts, where the basipterygoid processes project laterally.'

14. *Width of the basipterygoid process extremely broad and extends along almost the entire lateral margin of the parasphenoid and slightly exceeds the width of the internal process of the pterygoid.* This character is not duplicated in any dissorophoid in which this area of the braincase is known.

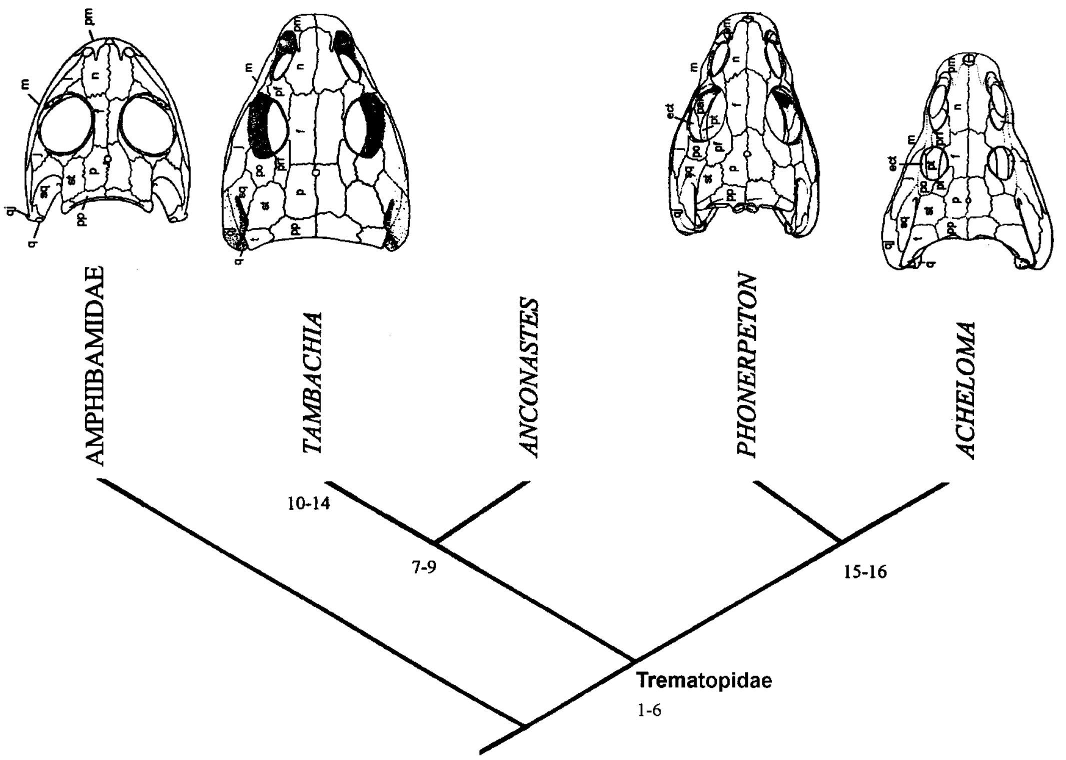
Shared derived characters uniting Phonerpeton *and* Acheloma

15. *Absence of parasphenoidal denticle field.* This synapomorphy of *Phonerpeton* and *Acheloma* was first recognized by Dilkes (1990). Among the amphibamids and trematopids, a parasphenoidal denticle field is absent only in *Phonerpeton* and *Acheloma*. With one exception, in the few specimens of dissorophids (*Broiliellus*, *Dissorophus*) in which this feature would probably be preserved if present, it is apparently absent; re-examination of the aberrant *Ecolsonia*, however, has indicated the presence of a small parasphenoidal denticle field.

16. *The length and width of the parasphenoidal plate of the braincase are subequal.* In *Phonerpeton* and *Acheloma* the body of the parasphenoidal plate of the braincase is approximately square, with the maximum width posterior to the basipterygoid processes being equal to or slightly less than the length of the parasphenoid, excluding the rostrum. In the amphibamids and the other trematopids the width of the parasphenoidal plate exceeds the length by as little as 30 to over 200 per cent., whereas in those dissorophids in which this measurement is available, the width exceeds the length from *c.* 10 to 60 per cent.

These hypotheses of interrelationships of the trematopids reaffirm those presented by Dilkes (1990), with the exception of the addition of *Tambachia*, and are shown here diagrammatically in Text-figure 11. The analysis presented supports the following conclusions.

1. Trematopidae is a monophyletic group (characters 1–6).
2. *Tambachia* is definitely a trematopid (characters 1–6). Assignment of *Anconastes* to the Trematopidae is considered very likely and is based on two sets of characters: first, although characters 3–5 are not observable in the holotype, and character 6 is too derived to determine its ancestral state, it exhibits trematopid characters 1 and 2; and second, three shared derived characters (7–9) unite it with *Tambachia*.
3. *Tambachia* and *Anconastes* share a more recent common ancestor than either does with any other



TEXT-FIG. 11. Cladogram indicating hypothesis of intrarelationships of Trematopidae (*Actiobates* excluded). Amphibamidae is represented by *Eoscopus* (Daley 1994). *Phonerepeton* and *Acheloma* are after Dilkes (1990) and Dilkes and Reisz (1987) respectively.

trematopid (characters 7–9), and *Phonerpeton* and *Acheloma* share a more recent common ancestor than either does with any other trematopid (characters 16 and 17).

4. *Tambachia* and *Anconastes*, on the one hand, and *Phonerpeton* and *Acheloma* on the other, form sister group clades.
5. *Actiobates* is probably a trematopid, as it exhibits characters 1, 2, and possibly 6. However, the absence of well-documented synapomorphies prevents confident determination of its relationships with other members of the family.

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