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ANATOMY AND PHYLOGENETIC RELATIONSHIPS OF *CALAMOPS PALUDOSUS* (TEMNOSPONDYLI, STEREOSPONDYLI) FROM THE TRIASSIC OF THE NEWARK BASIN, PENNSYLVANIA

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ABSTRACT—The holotype of the large temnospondyl *Calamops paludosus* is the oldest known tetrapod fossil from the Triassic of the Newark basin in Pennsylvania. Although it is usually placed in Metoposauridae, its affinities have remained unknown since its original description because the unique specimen had never been prepared. Preparation and casting of the specimen, which comprises three pieces of a left mandibular ramus, now permits detailed anatomical description of the jaw and assessment of its affinities. *Calamops paludosus* is a valid taxon of trematosauroid temnospondyls that can be diagnosed by several autapomorphies. It represents one of the geologically youngest known records of long-snouted trematosauroids and the first record of these temnospondyls from the Late Triassic of North America.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Despite extensive exposures of fluvio-lacustrine strata of mostly Late Triassic age in eastern North America, temnospondyl tetrapods have a surprisingly poor fossil record from that region. Fluvial deposits of the lower Wolfville Formation near Lower Economy, Nova Scotia (Canada), have yielded fragmentary cranial and jaw remains referable to Trematosauridae (Lonchorhynchinae; Welles, 1993) and to Capitosauroidea. Huber et al. (1993) considered the lower Wolfville Formation probably early Middle Triassic (Anisian) in age based on assumptions concerning the affinities of some of the tetrapod fossils to Anisian-age taxa elsewhere. However, most of these comparisons are not based on apomorphies, and the age of the lower Wolfville has yet to be constrained. To date, the Late Triassic record of temnospondyls from eastern North America for the most part comprises occurrences of Metoposauridae, a distinctive clade of stereospondyls. Metoposaurs are known from Europe, North Africa, eastern North America, and possibly Madagascar (Colbert and Imbrie, 1956; Dutuit, 1976; Hunt, 1993; Schoch and Milner, 2000; Milner and Schoch, 2004; Sulej, 2007). They have large, flat skulls with anterolaterally placed and widely separated small orbits. Their postcranial skeleton is well ossified and the limbs are small. In eastern North America, skeletal remains of metoposaurs have been reported to date from the middle Wolfville Formation of Nova Scotia, the upper Stockton Formation of New Jersey, the Lockatong Formation of Chester County and the New Oxford Formation of York County, Pennsylvania, and the Cummock Formation of North Carolina (Leidy, 1856; Cope, 1866, 1868; Colbert and Imbrie, 1956; Baird, 1986; Hunt, 1993; Schoch and Milner, 2000). In addition to these metoposaurid fossils, there is a singular record of a large temnospondyl from the basal portion of the Stockton Formation in Bucks County, Pennsylvania, which has been virtually ignored

since its initial announcement by Sinclair (1917). All Triassic tetrapod remains from eastern North America come from strata of the Newark Supergroup, and we will briefly review the overall geological context before returning to Sinclair's discovery.

The breakup of Pangaea commenced along the junction between present-day North America and Africa, from Greenland to Mexico, during the Triassic (Olsen, 1997). Strong crustal extension along the rift axis led to the formation of a chain of rift basins. Most of the basins are half-grabens that are asymmetrically bounded by large border faults. The rift basins were filled by continental sedimentary strata, which were capped by or interbedded with extensive basalts and often intruded by diabase dikes or sills. Collectively, these infills are known as the Newark Supergroup (Fig. 1A). The Newark basin is the largest completely exposed rift basin, covering an area of approximately 7770 km² and extending for some 220 km along its long axis from New York State across New Jersey to Pennsylvania (Olsen and Rainforth, 2003; Fig. 1B). It contains the most extensive fill of any exposed Newark Supergroup basin and records a considerable span of geologic time. For this reason, the Newark basin has long played a key role in geological studies of the Newark Supergroup.

The sedimentary and igneous rock content of the Newark basin is divided into nine formally designated and lithostratigraphically distinguishable formations. These are (in ascending order from oldest to youngest; Olsen and Rainforth, 2003): (1) Stockton Formation, comprising mainly fluvial, tan and red sandstones and conglomerates as well as red mudstones, with less common intervals of gray sandstone and black and gray mudstone (maximum thickness of more than 2000 m); (2) Lockatong Formation, predominantly made up of cyclical gray and black mudstone, with less common red mudstones and sandstones of various colors (maximum thickness of more than 1100 m); (3) Passaic Formation, comprising cyclical, predominantly red but also gray and black mudstones, sandstones, and conglomerates (maximum thickness of more than 5000 m); (4) Orange Mountain Basalt (maximum thickness of more than 300 m);

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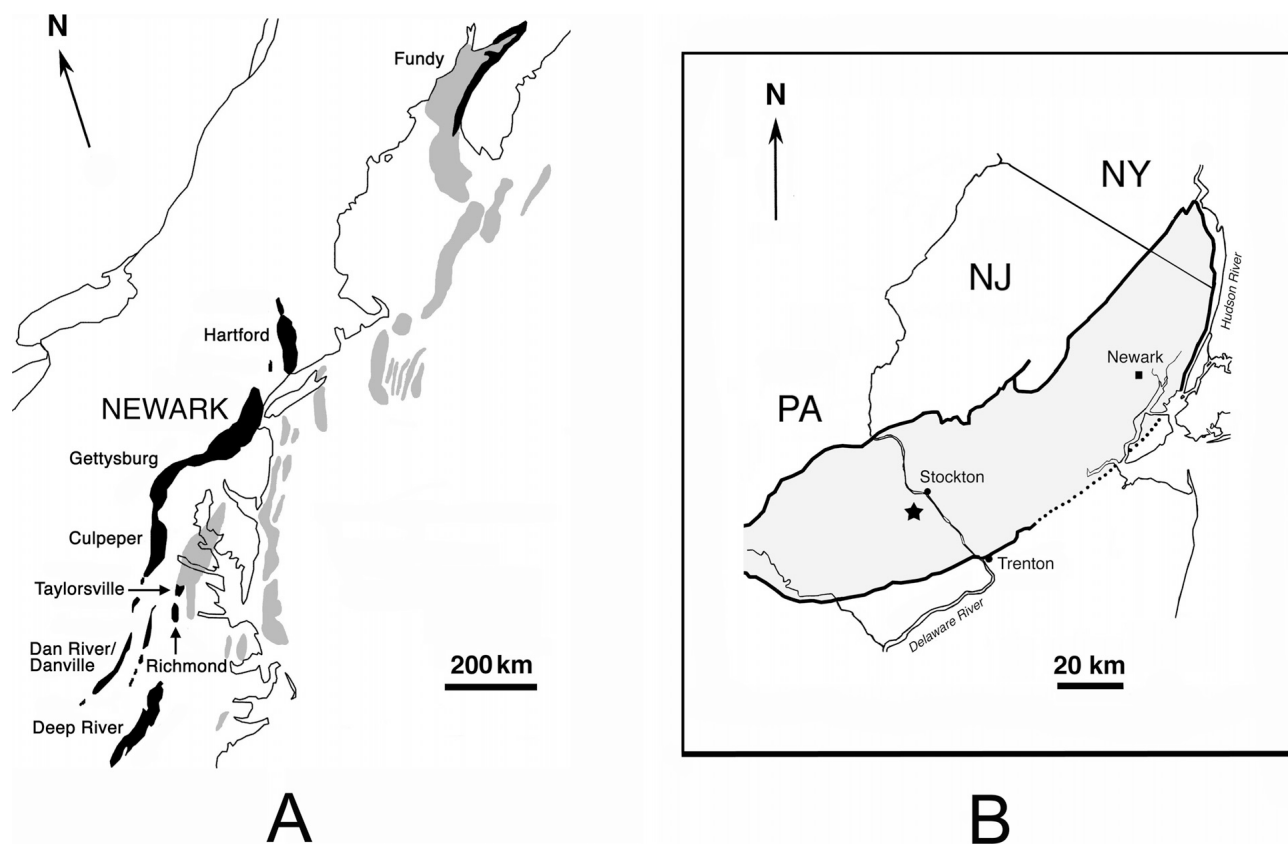


FIGURE 1. Map showing the rift basins of the Newark Supergroup in eastern North America. Exposed strata of the Newark Supergroup are shown in black and subsurface strata are shown in gray. Inset map shows outline of the Newark basin with position (indicated by a star) of the type locality of *Calamops paludosus*. Modified from Olsen (1997) and Olsen and Rainforth (2003), respectively.

(5) Feltville Formation, a sequence with two cycles of black, gray, and red limestone at its base, followed by vaguely cyclical, mostly red mudstone, sandstone, and minor conglomerate; (6) Preakness Basalt (maximum thickness of more than 300 m), with minor interbedded red sedimentary deposits; (7) Towaco Formation, comprising cyclical red, gray, and black mudstone, sandstone, and conglomerate (maximum thickness of more than 375 m); (8) Hook Mountain Basalt (maximum thickness of more than 150 m); and (9) Boonton Formation (maximum thickness of more than 500 m), which closely resembles the Towaco Formation lithologically but differs from it in the greater frequency of thin gray layers as well as lesser frequency of microlaminated black mudstones. Olsen and Rainforth (2003) noted that the boundaries between the Stockton, Lockatong, and Passaic formations vary in age along the axis of the basin.

The Stockton Formation, which has yielded the temnospondyl fossil discussed in this paper, has been divided into four members based on lithological attributes (in ascending order from oldest to youngest): Solebury, Prallsville, Cutaloosa, and Raven Rock (Olsen and Rainforth, 2003; Fig. 2). Olsen and Rainforth (2003) interpreted the Solebury and Prallsville members as belonging to Olsen's (1997) Tectonostratigraphic Sequence (TS) II, which comprises the early synrift sedimentary sequences of the Newark Supergroup. Based on lithological and magnetostratigraphic correlations between the upper part of the Stockton Formation and the Newfound Formation in the Taylorsville basin of the Newark Supergroup in Virginia, Olsen and Rainforth (2003) postulated the existence of a depositional hiatus at the base of the Cutaloosa Member, which they regarded as representing the

unconformity separating TS II and TS III elsewhere in the Newark Supergroup.

The Solebury Member consists of buff and gray sandstones with conglomerate and gray, black, and red mudstones. It is overlain by the Prallsville Member, which comprises mostly buff and pink arkoses with minor conglomerate and bioturbated red mudstone. According to Olsen and Rainforth (2003), both members appear to be primarily fluvial in origin, although thin gray and black mudstones in the former suggest intervals of lacustrine or paludal deposition. Based on the correlation scheme by Olsen et al. (2011), the Solebury and Prallsville members of the Stockton Formation are no younger than Carnian and possibly older. Olsen and Rainforth (2003) interpreted the overlying Cutaloosa Member as a basal coarse-grained sequence of TS III. The uppermost member of the Stockton Formation, the Raven Rock Member, comprises thick cycles of gray and tan sandstones with less common black and gray mudstones, overlain principally by red mudstones and tan sandstones. Many of these sequences appear to be lacustrine or deltaic in origin. Magnetostratigraphic correlation to the more southern basins of the Newark Supergroup indicates the well-developed cyclical lacustrine strata of the lower member of the Cow Branch Formation, the lower part of the Port Royal Formation, and the Cummock Formation are equivalent in stratigraphic age to the lower part of the Raven Rock Member (Olsen and Rainforth, 2003). Olsen et al. (2011) considered all of the aforementioned units Norian in age.

Unlike those in other basins of the Newark Supergroup, strata representing Tectonostratigraphic Sequence II in the Newark basin have not been extensively prospected for fossils to date.

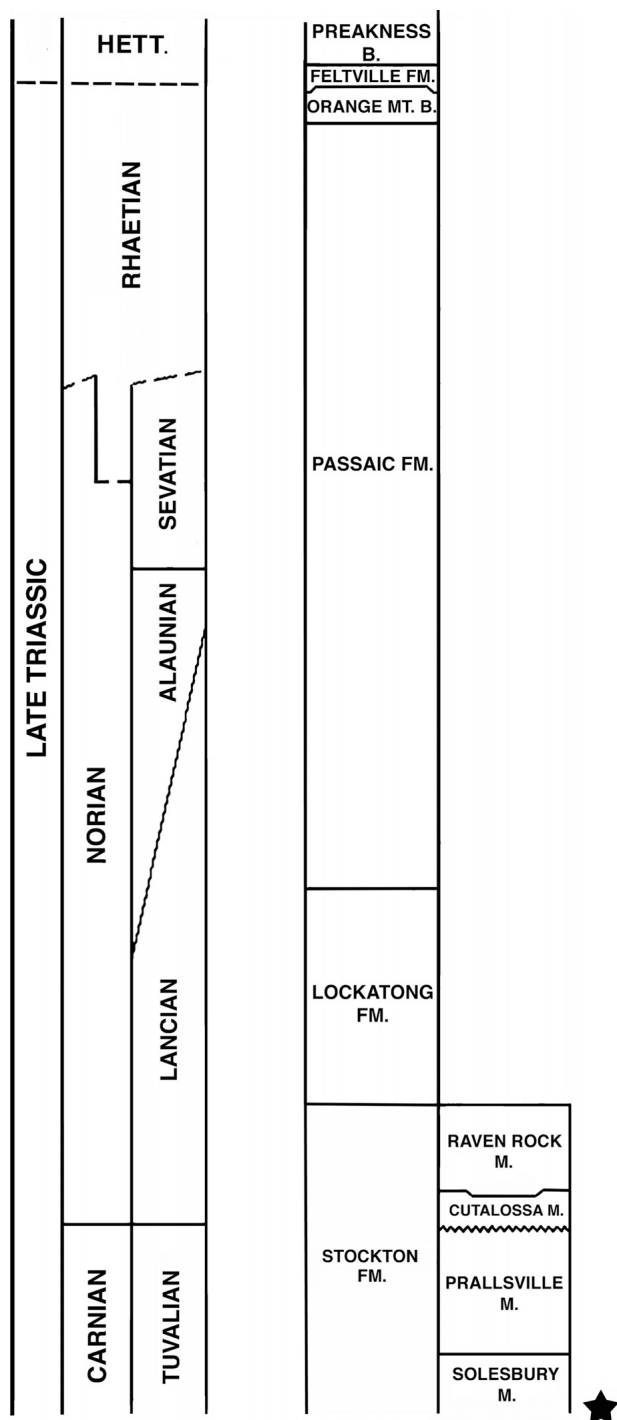


FIGURE 2. Succession of Late Triassic strata in the Newark basin of the Newark Supergroup. A star indicates the stratigraphic position of the occurrence of *Calamops paludosus*. Modified from Olsen et al. (2011).

With the exception of the singular temnospondyl specimen that forms the subject of this paper, the known fossil record from the lower part of the Stockton Formation comprises root traces, compression fossils of cycadeoids, and silicified conifer wood, along with abundant arthropod burrows referable to the ichnogenus *Scoyenia* (Olsen and Rainforth, 2003).

In 1905, Gilbert Van Ingen of Princeton University and his colleague William J. Sinclair collected associated fragments of a

lower jaw from the base of the Solebury Member at Holicong in Bucks County, Pennsylvania (Fig. 1B). Sinclair correctly recognized the find as representing an unusually large 'labyrinthodont' and published a note on it (Sinclair, 1917). The jaw (YPM VPPU 12302) was preserved in close association with numerous impressions of equisetalean (horsetail) stems, which led Sinclair to propose the generic name *Calamops* (Greek for 'reed face').

Sinclair (1917:319) noted that the bones, which he characterized as "quite soft and spongy," were encased in hard, tightly adhering siltstone, which in places attained a thickness of "up to half an inch [1.27 cm] or so." Teeth and bone were exposed only in a few places. The preservation of the fossil prevented preparation at the time, and thus Sinclair literally described the specimen "sight unseen."

Although the holotype of *Calamops paludosus* is the oldest known tetrapod fossil from the Newark basin, it has been virtually ignored since Sinclair's original account. Without discussion, Colbert and Imbrie (1956) and later authors referred *Calamops paludosus* along with all other then-known temnospondyls from the Newark Supergroup to the Metoposauridae.

The late Donald Baird, long-time curator of the Princeton University Museum of Natural History, first initiated a proper investigation of the holotype of *Calamops paludosus*. At his request, Arnold Lewis (then at the Museum of Comparative Zoology, Harvard University) split the rock encasing the fossil lengthwise using a diamond saw, employed airbrasive to remove all remaining bone, and cast the resulting mold in black polysulfide rubber. This effort revealed, for the first time, the actual structure of the lower jaw of *Calamops paludosus*. Subsequently, R. William Selden (Rutgers University) studied these casts and interpreted *Calamops paludosus* as a large capitosaur. Olsen (1980) and Olsen and Rainforth (2003) cited Selden's conclusion in major overviews of the geology of the Newark basin, and, in turn, Schoch and Milner (2000) cited Olsen (1980) in their synoptic review of Stereospondyli. Selden never published the results of his investigation, and thus we cannot evaluate the basis for his classification. Baird subsequently offered the casts of the holotype of *Calamops paludosus* for examination to H.-D.S.

We present here the first anatomical description of the holotype and only known specimen of *Calamops paludosus* and assess the phylogenetic position of this intriguing taxon.

Institutional Abbreviations—SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; YPM VPPU, former Princeton University vertebrate paleontology collection, now housed in the Peabody Museum of Natural History at Yale University, New Haven, Connecticut, U.S.A.

Anatomical Abbreviations—aco, anterior coronoid; an, angular; ar, articular; co, coronoid; d, dentary; f.c.t, foramen for chorda tympani; gl, glenoid fossa for craniomandibular joint; h.p, hamate process; ico, intercoronoid; m.f, Meckelian fenestra; pa, prearticular; pg.g, postglenoid groove; ps.f, postsymphyseal foramen; psp, postsplenial; s.d, sulcus dentalis; s.p, pits on anterolateral surface of dentary; sa, surangular; sp, splenial; sy.t, alveolus for symphyseal tusk.

SYSTEMATIC PALEONTOLOGY

TEMNOSPONDYLI Zittel, 1888

STEREOSPONDYLI Zittel, 1888

TREMATOSAUROIDEA Säu-Söderbergh, 1935, sensu Yates and Warren, 2000

CALAMOPS PALUDOSUS Sinclair, 1917
(Figs. 3, 4)

Holotype—YPM VPPU 12302, partial left mandibular ramus (Figs. 3, 4). Sinclair (1917:319) noted that the specimen comprises the "front part of the left half of the lower jaw" and "two

large pieces, evidently belonging to the back of the jaw, [which] do not make contact with the tooth-bearing portion of the ramus." The latter pieces comprise much of the posterior portion of the mandibular ramus but they cannot be fitted to each other. Olsen and Rainforth (2003:fig. 6C) illustrated an outline of the mandibular ramus (in lateral view) with photographs of the casts of the tooth-bearing portion and a large piece comprising the posterior end of the dentary and parts of the angular and surangular, but they did not include the piece comprising the posterior end of the mandibular ramus. Based on first-hand comparisons with lower jaws of various temnospondyls, we have established that the cast of the latter piece comprises part of the prearticular and the articular in medial view.

Type Locality—On the farm of John S. Ash, Holicong, Bucks County, Pennsylvania, U.S.A. Collected by G. Van Ingen and W. J. Sinclair (Princeton University) on October 7, 1905.

Type Horizon—Sinclair (1917:319) gave the type horizon as "locally basal beds of Norristown Shale." Lyman (1895) first proposed this stratigraphic designation, but Kümmel (1897) and later authors included the Norristown Shale in the Stockton Formation. According to Olsen and Rainforth (2003), the holotype of *Calamops paludosus* came from the base of the Solebury Member. The age of this member is not well constrained but is no younger than Carnian and possibly older.

Diagnosis—Distinguished by the possession of the following autapomorphies: (1) dentary with deep pits arranged in several rows on anterolateral surface of symphyseal region; (2) dorsal margin of dentary rising markedly towards tall preglenoid process; (3) postglenoid area short and with shallow dorsal depression; and (4) foramen for chorda tympani in large depression on medial surface of prearticular.

DESCRIPTION

The preserved segment of the tooth-bearing portion of the mandibular ramus (Fig. 3) has a greatest length of 44.6 cm. Neither of the other two jaw fragments can be fitted to this piece nor to each other, but we estimate an overall length of the mandibular ramus of 80–90 cm based on the proportions of the lower jaws in related stereospondyls. The pronounced ornamentation of the lateral (labial) surface of the ramus (Fig. 3A, B) indicates that the jaw belonged to a mature individual. The mandibular ramus was preserved with relatively little damage due to postmortem crushing, although the symphysis was apparently rotated into a slightly steeper angle relative to the long axis of the mandibular ramus. Sutures are clearly evident on the casts and readily distinguished from breaks. The dorsal outline of the mandibular ramus (Fig. 4A) indicates a long, triangular snout.

In contrast to many other known stereospondyls, the mandibular ramus as a whole is markedly deeper dorsoventrally at mid-length and has a deep preglenoid process. The uncertainty about the length of the missing parts leaves open the question how abruptly the preglenoid process rose from the tooth-bearing portion of the dentary.

The long tooth-bearing portion of the mandibular ramus is narrow mediolaterally. Its dorsal and ventral margins converge slightly anteriorly toward the symphysis, and this part of the jaw is fairly straight except for a short segment that curves medially at the symphyseal end. In side view, the splenial portion of the mandibular symphysis is ventrally flat and low, forming a short, chin-like projection, a common feature among trematosauroids (Schoch, 2006, 2011), although it is less pronounced in *Calamops paludosus*. The dentary and splenial form the symphysis. On the medial (lingual) surface, a long fissure (postsymphyseal foramen) separates these two bones. The symphyseal facet is more or less crescent-shaped and extends posteroventrally. The splenial facet is longer than the dentary one, extending over the entire

length of the symphysis. There is no trace of any mentomeckelian ossification.

The lateral surfaces of the dentary, angular, splenials, and surangular bear pronounced sculpturing (Figs. 3, 4). (The lateral portion of the glenoid and postglenoid regions is not preserved.) The sculpturing comprises widely spaced and well-defined ridges that are relatively high. Ventrally, they merge into a longitudinal ridge that borders the medial side of the jaw. Strong ridges radiate from a point near the ventral margin of the posterior part of the angular. The surangular, the splenials, and the more ventral portion of the dentary bear long, raised, and anteroposteriorly extending ridges, which are separated by deep grooves. The ridges become more undulating near the ventral margin of the jaw further anteriorly. On the lateral surface of the dentary, the anteroposteriorly extending sulcus dentalis of the lateral-line system (Bystrov and Efremov, 1940) separates the heavily sculptured ventral portion from the less sculptured dorsal part of the bone. A distinctive feature is the presence of a number of conspicuous, deep pits, some of which are aligned in short rows, close to the anterolateral end of the symphyseal portion of the dentary. The ventral row of pits forms the anterior continuation of the sulcus dentalis. Because some of the pits are located in the sulcus, it is conceivable that they represent sensory pits.

The dentary is by far the largest mandibular element. On the lateral surface of the jaw, it contacts the splenials and the angular ventrally and the surangular posteriorly. The sutural contact with the surangular appears rather blunt, but based on the striated lateral surface of the latter element, it may have been more tapered. On the medial surface of the mandibular ramus, the dentary meets the splenial and coronoids ventrally and at least part of the anterior margin of the adductor fossa. The teeth have pleurodont implantation. All preserved tooth crowns bear numerous fine, vertical ridges, which reflect the labyrinthine infolding of the enamel. Few details of the apical regions of most crowns are evident on the cast. Sinclair (1917) noted that some crowns are apically flattened with acute mesial and distal edges (carinae). Such carinae are known on the tooth crowns in various trematosauroids (Schoch and Milner, 2000; Schoch, 2011). The preserved portion of the tooth-bearing ramus has 33 closely spaced tooth positions, of which 23 have tooth crowns or parts of crowns. The anterior tooth crowns are less tall than the more posterior ones. As in most stereospondyls, the bases of the tooth crowns are wide mediolaterally and oval in transverse section. Most of the tooth crowns are gently curved medially in mesial or distal view. A large alveolus for a symphyseal tusk or fang is situated just posterior to the symphyseal facet and medial to the anterior marginal teeth. It is possible that there was a second tusk anteromedial to this tooth, as in most temnospondyls, but details in the critical region are not clear on the cast and it is possible that there was some damage to the symphysis on the specimen. In contrast to the condition in some capitosauroids and *Metoposaurus*, there are no additional small teeth posterior to the tusk (postsymphyseal teeth) nor is there a distinct ossified surface medial to the alveolus. The symphyseal portion of the dentary around the tusk is not thickened as it is in *Mastodonsaurus*, and the base of the preserved tusk is also not as large as in the latter.

The splenial (presplenial) and postsplenial are well developed (Fig. 3C, D). The medial surface of the splenial bears a small, elliptical foramen about 20 mm behind the symphyseal facet. The postsplenial forms the anterior margin of the long and low Meckelian fenestra (posterior Meckelian fenestra; Nilsson, 1943). The ventral margin of that opening can be traced for about 70 mm, but the remainder of the margin cannot be as clearly delineated.

The coronoid elements all lack teeth, denticles, or ornamentation and are sutured to the dentary laterally (Fig. 3C, D). Together with the dentary they form a broad, shelf-like area medial to the marginal tooth row. The anterior end of the anterior coronoid (precoronoid) tapers toward the symphysis, terminating

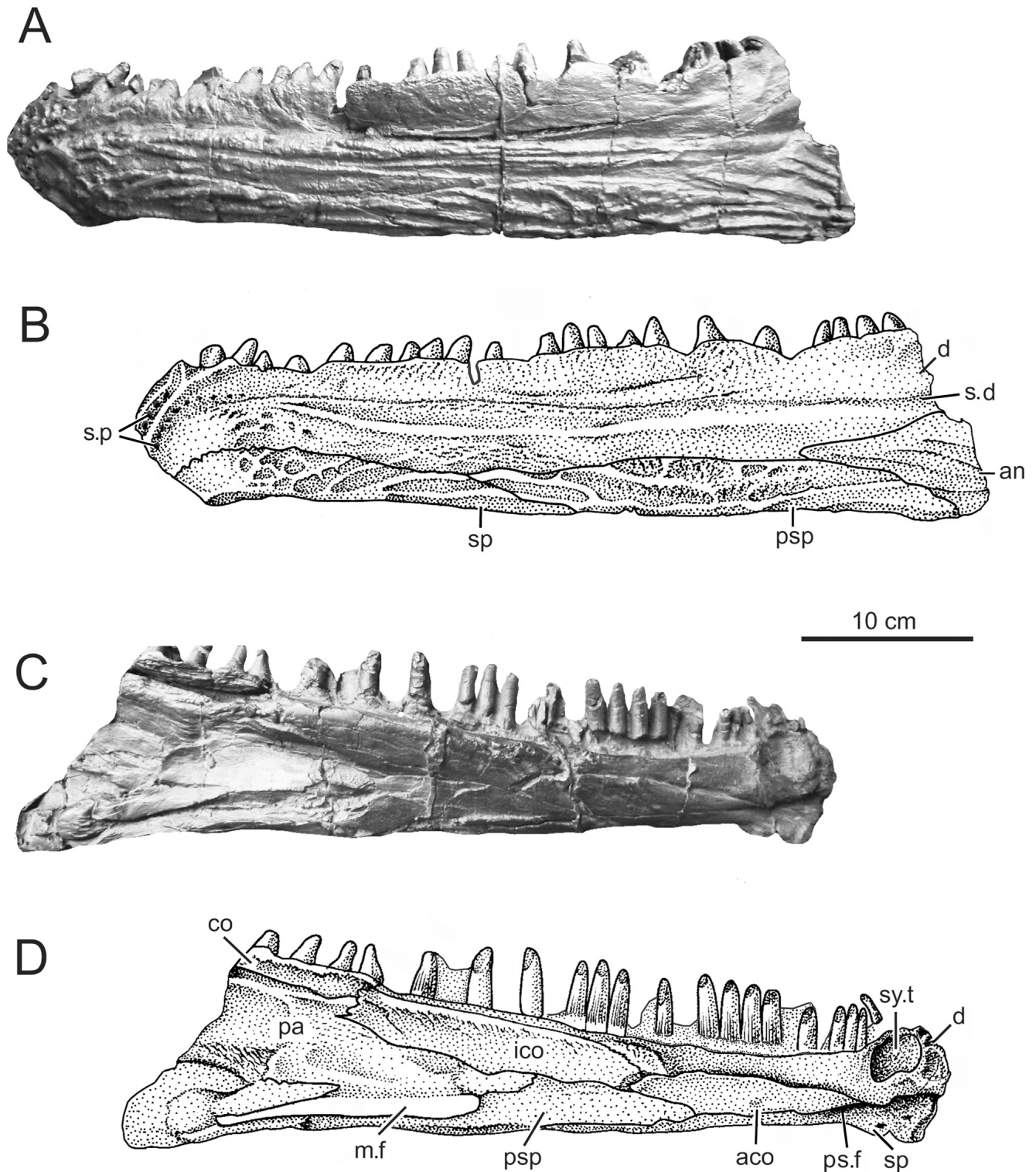


FIGURE 3. Left mandibular ramus of *Calamops paludosus* (YPM VPPU 12302, holotype, cast). **A, B**, tooth-bearing portion of mandibular ramus in lateral view (photograph and interpretative drawing). **C, D**, tooth-bearing portion of mandibular ramus in medial view (photograph and interpretative drawing). Breaks have been omitted from the drawings. Scale bar equals 10 cm.

below the alveolus for the tusk, and its posterior end is wedged between the postsplenial and the long middle coronoid (intercoronoid). Little of the posterior coronoid (coronoid) is preserved.

The surangular is only partially preserved (Fig. 4E, F). It forms much of the posterodorsal portion of the lateral surface of the mandibular ramus. The contribution of the surangular to the postglenoid region cannot be ascertained on the casts. The dorsal

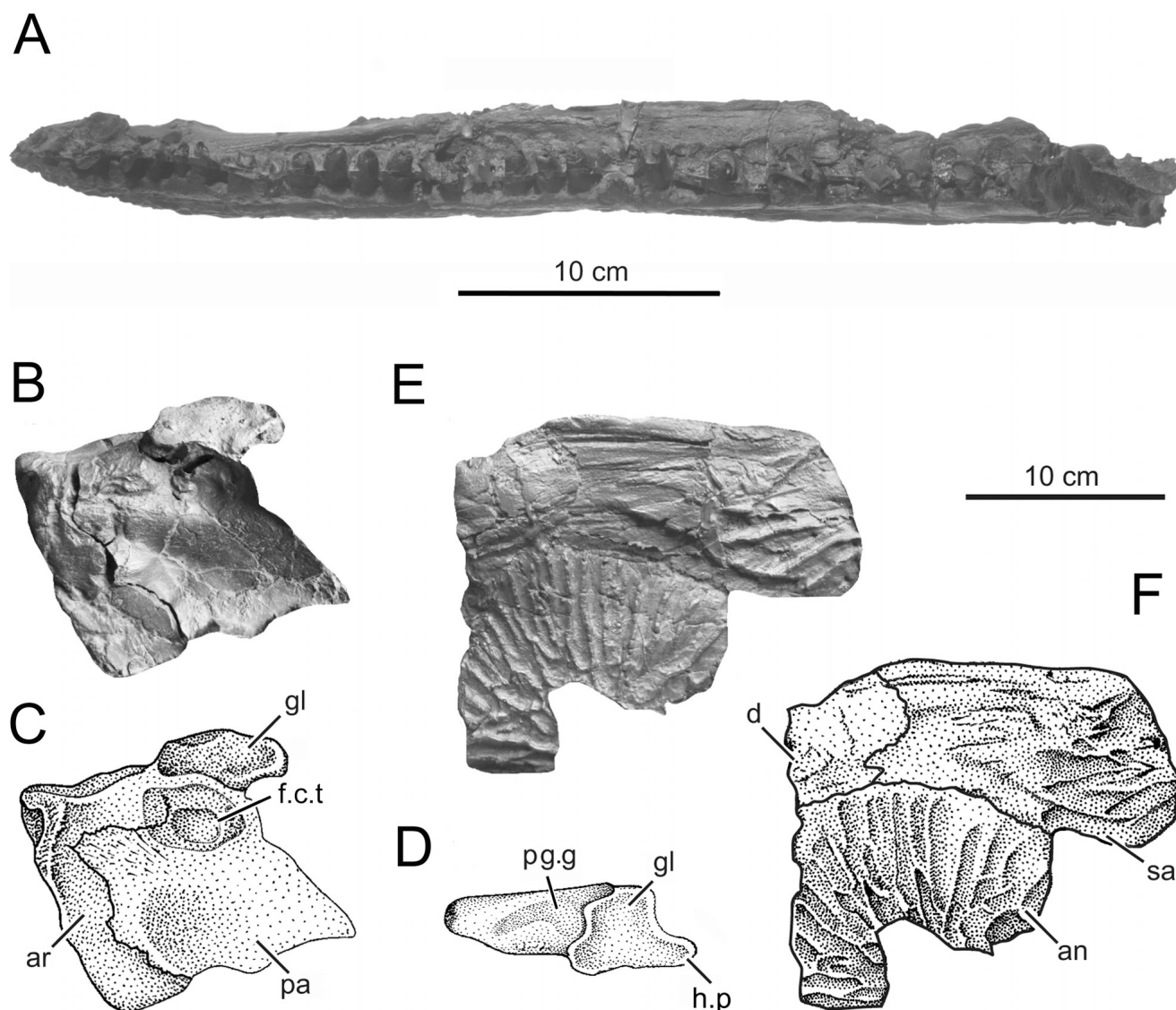


FIGURE 4. Left mandibular ramus of *Calamops paludosus* (YPM VPPU 12302, holotype, casts). **A**, tooth-bearing portion of mandibular ramus in dorsal view. **B**, **C**, posterior end of mandibular ramus in medial view (photograph and interpretative drawing). **D**, glenoid and postglenoid region of mandibular ramus in dorsal view. **E**, **F**, portion of mandibular ramus comprising posterior end of dentary and parts of the surangular and angular in lateral view (photograph and interpretative drawing). Breaks have been omitted from the drawings. Scale bars equal 10 cm.

margin of the surangular anterior to the glenoid region forms a thick, transversely broad ridge (torus arcuatus; Bystrov and Efremov, 1940), which medially overhangs the lateral wall of the adductor fossa.

Only part of the central region of the angular is preserved (Fig. 4E, F). It formed the more ventral portion of the lateral wall of the adductor fossa. It attains its greatest thickness near the ventral margin of the jaw.

The glenoid fossa was rather shallow (although this may be partially due to infilling by matrix) and appears to be delimited by low ridges anteriorly and posteriorly (Fig. 4D). Only the anteroposteriorly expanded medial portion of this facet and the median ridge between its lateral and medial portion are visible. Although there appears to be some damage in this region, the hamate process is clearly visible. It was much smaller and lower than in any known capitosauroid and more similar to those in trematosauroids and lydekkerinids (Schoch and

Milner, 2000). The postglenoid region generally resembles those of *Benthosuchus* (Bystrov and Efremov, 1940) and especially an unnamed trematosauroid from the Middle Triassic of Jordan (Schoch, 2011; hereafter referred to as 'the Jordan taxon'). As in many stereospondyls, the articular extends along the posterior part of the postglenoid region on the lateral side. The prearticular contributes a small portion to the postglenoid region, corresponding to Jupp and Warren's (1986) type 2, although this feature is not clearly defined and rather variable across stereospondyls. A large foramen for the chorda tympani is situated in a distinct depression on the medial surface of the glenoid region (Fig. 4B, C). Similar concavities are present in the Jordan taxon (Schoch, 2011), *Benthosuchus korobkovi* (SMNS 80063), and *Metoposaurus* (Sulej, 2007). A feature shared by *Calamops* (Fig. 4D) and *Inflectosaurus* (Shishkin, 1960) is a longitudinal groove on the dorsal side of the postglenoid region, apparently for attachment of the depressor mandibulae muscle. Although

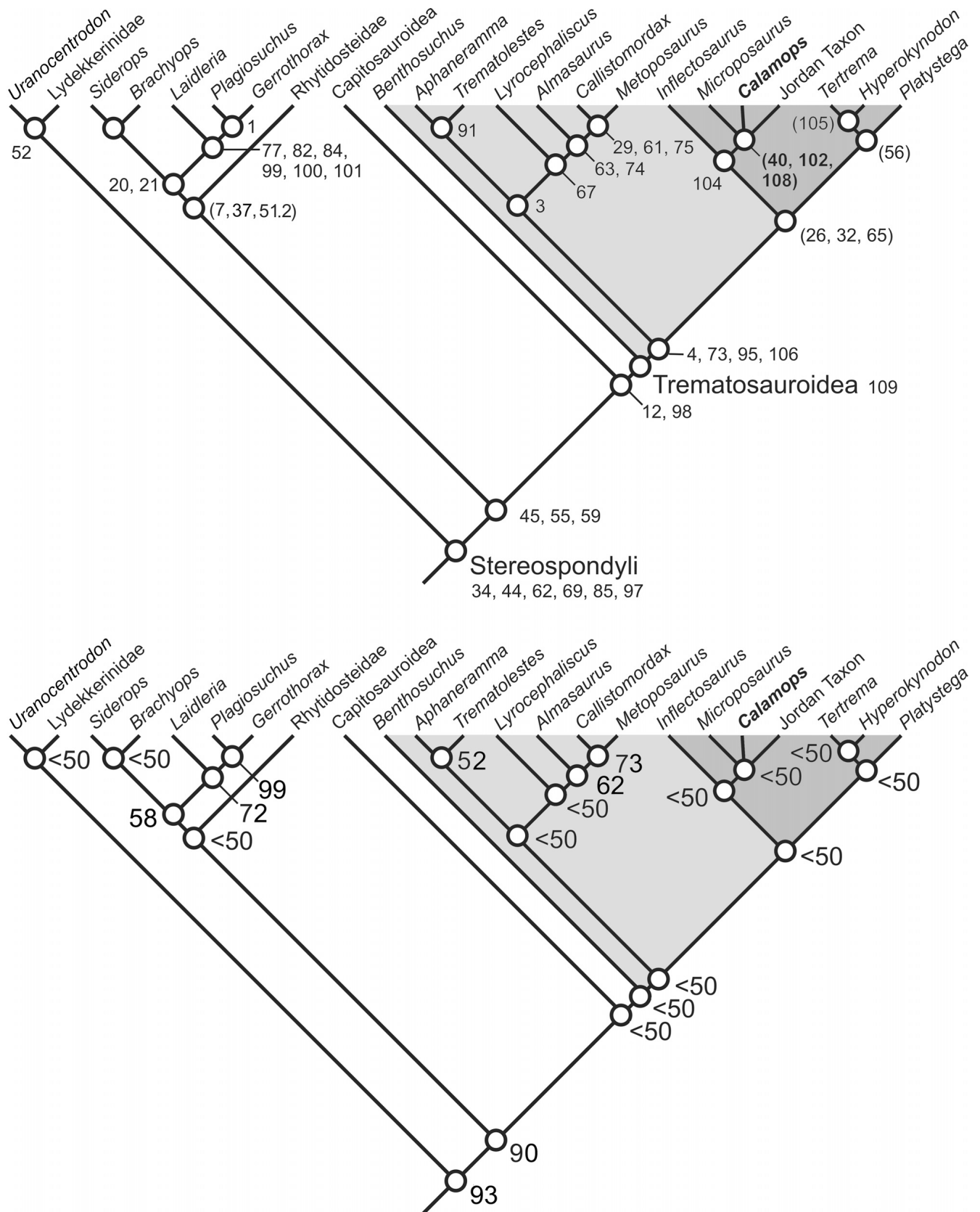


FIGURE 5. Strict consensus of three most parsimonious trees showing the phylogenetic position of *Calamops paludosus* among Stereospondyli. (The outgroup taxa were omitted from the illustration for layout purposes.) **A, top**, distribution of character states mapped onto the cladogram. Ambiguous synapomorphies are shown in parentheses for those nodes that are not supported by unambiguous synapomorphies. **B, bottom**, bootstrap values for each node.

present in some large capitosauroids (e.g., *Mastodonsaurus*; Schoch and Milner, 2000) and the trematosaurid *Trematolestes* (Schoch, 2006), such grooves are absent in other trematosauroids. In contrast to the condition in the other cited taxa, the groove is aligned posterolaterally in *Calamops*. The posterior end of the surangular is not visible on the cast.

PHYLOGENETIC RELATIONSHIPS OF *CALAMOPS PALUDOSUS*

In order to assess the phylogenetic position of *Calamops paludosus*, we conducted a parsimony analysis using the character-taxon matrix compiled by Schoch (2008, 2011), which focused on trematosauroid relationships. We have added nine characters to Schoch's (2008) original data matrix (see Appendix 1) as well as seven additional trematosauroid taxa (see Appendix 2). The data file with the character-taxon matrix is available in Supplementary Data. The character-taxon matrix was compiled in MacClade 3.0 (Maddison and Maddison, 1992), and the parsimony analysis was undertaken with PAUP 4.0b10 (PPC) (Swofford, 2003). All characters were treated as unordered. The heuristic search option was implemented, and the analysis was run under ACCTRAN optimization. *Dendrerpeton*, *Sclerocephalus*, and *Trimerorhachis* served as outgroup taxa. *Microposaurus* was scored based on the well-documented type species *M. casei* (redescribed by Damiani, 2004) rather than the incompletely known *M. averyi* (Warren, 2012). *Calamops* could only be scored for 15 out of the 109 characters (13.76%). The analysis generated three most parsimonious trees, each with a length (TL) of 238 steps (consistency index: 0.4916, retention index: 0.7206; rescaled consistency index: 0.3542) (Fig. 5). Bootstrap analysis using the fast-heuristic search option (1000 replicates) revealed only weak support for many of the nodes.

We obtained results generally comparable to those of Schoch (2011). In this topology, Stereospondyli resolves into three clades: (1) a basal group composed of Rhinesuchidae and Lydekkerinidae; (2) a larger clade of short-snouted taxa (Rhytidosteidae, Brachyopidae, Chigutisauridae, *Laidleria*, and Plagiosauridae); and (3) a large group comprising Capitosauroida and Trematosauroida. This topology is similar to one of the two alternative trees found by Schoch (2008). Within Trematosauroida, *Benthosuchus* forms the most basal taxon, followed crownward by two large clades: (1) a trematosaurid-metoposauroid group and (2) a *Microposaurus-Tertrema* group. The first one falls into the Trematosauridae sensu stricto (here represented by *Aphaneramma* and *Trematolestes*) and the grade leading to the Metoposauridae (*Lyrocephalus*, *Almasaurus*, and *Callistomordax*). Individual taxa within the trematosaurid-metoposauroid clade are relatively completely known and well studied (Steyer, 2002; Schoch, 2006, 2008; Sulej, 2007), whereas the material from the *Microposaurus-Tertrema* group is for the most part incomplete.

Calamops paludosus clearly is a stereospondyl because the bases of the marginal teeth of its dentary extend at a right angle to the long axis of the tooth row, which is a character state diagnostic for all stereospondyls more derived than Rhinesuchidae (Schoch and Milner, 2000). Based on the low and flat symphysis and the possession of large, medially curved, and bicarinate tooth crowns, it most likely represents a trematosauroid. However, large, medially curved tooth crowns are also present in Brachyopidae and Chigutisauridae. The occurrence of mesial and distal carinae on some crowns is shared by other trematosauroid taxa (Schoch, 2011). These observations are consistent with the results of our cladistic analysis, which found *Calamops* deeply nested within Trematosauroida. It is noteworthy that it does not fall into the same grouping as the possibly more or less coeval long-snouted trematosaur *Hyperokynodon keuperinus*, from which it differs in the dentition and outline of the snout

(see below). Long-snouted trematosauroids are a widely distributed group of temnospondyls of predominantly Early and early Middle Triassic age (Schoch and Milner, 2000). Some forms (Lonchorhynchinae) have greatly elongated snouts that extend anteriorly well beyond the external nares (Welles, 1993).

Calamops falls within a grouping of Trematosauroida that also includes *Inflectosaurus*, *Microposaurus*, and the Jordan taxon (Schoch, 2011). A grouping of the latter two and *Calamops* is supported only by three ambiguous synapomorphies and its internal relationships remain unresolved. The sister group of this unresolved group is composed of *Tertrema*, *Hyperokynodon*, and *Platystega*, in which the former two are placed together.

We found no evidence in support of capitosauroid affinities for *Calamops paludosus*. It is possible that Selden's suggestion was based at least in part on the unusually large size of the jaw, which already reminded Sinclair (1917) of that of the giant capitosauroid *Mastodonsaurus*. The rather large size of most individual teeth, the absence of a prominent hamate process on the prearticular, and the dorsoventrally low symphysis of *Calamops* all militate against capitosauroid affinities (Schoch, 2011).

CONCLUSIONS

Calamops paludosus represents the first record of large stereospondyls other than metoposaurs from the Upper Triassic of North America. It is most similar to long-snouted trematosauroids from South Africa (*Microposaurus casei*; Damiani, 2004), Australia (*Microposaurus averyi*; Warren, 2012), Russia (*Inflectosaurus amplus*; Shishkin, 1960), and Jordan (unnamed taxon; Schoch, 2011). These temnospondyls are predominantly Early and Middle Triassic in age and had a wide geographic distribution (see Schoch and Milner, 2000). The occurrence of *Calamops paludosus* in presumably Carnian-age fluvial deposits parallels that of *Hyperokynodon keuperinus* (with an estimated skull length of 80 cm) in the fluviodeltaic sandstones of the Schilfsandstein (Stuttgart Formation; Carnian) in northern Baden-Württemberg, Germany (Hellrung, 1987; Schoch et al., 2002). Although there is no anatomical overlap between the known skeletal remains of *Calamops* and *Hyperokynodon* (which is known only from cranial fragments of two individuals; Schoch et al., 2002), the former appears to have been more robustly built and its dentary teeth are much larger than the premaxillary and maxillary teeth of *Hyperokynodon*. Furthermore, the slender skull outline of *Hyperokynodon* differs from the apparently more broadly triangular outline inferred for *Calamops*. The outline of the skull of *Calamops* would have more closely resembled those of *Microposaurus* (Damiani, 2004) and the Jordan taxon, whereas the outline of the skull of *Hyperokynodon* is more similar to those of *Tertrema* and *Platystega* (Säve-Söderbergh, 1936; Hellrung, 1987). Large (3–4 m long) long-snouted trematosauroids appear to have been a shared faunal element in early Late Triassic rivers of eastern North America and Central Europe. (The overall length of these temnospondyls is estimated based on the skeletal proportions of the Ladinian-age trematosaurid *Trematolestes hagdorni* [Schoch, 2006].) They further testify the wide geographic distribution of *Microposaurus*-like trematosauroids. The presence of *Calamops paludosus* demonstrates that metoposaurs were not the only Late Triassic temnospondyls in eastern North America. Capitosauroids and plagiosaurs, two other important groups of temnospondyls from Central Europe and East Greenland, have as yet no Late Triassic fossil record from North America.

Schoch et al. (2002) suggested that the superficially crocodile-like phytosaurs might have replaced long-snouted trematosauroids in the ecological role of large, slender-snouted predators in fluvial settings during the Late Triassic. In eastern North America, phytosaurs are first documented by skeletal remains from the upper part of the Stockton Formation and the lower portion of the Lockatong Formation (Olsen, 1980). By contrast,

Hyperokynodon keuperinus comes from the same formation as (but from a different locality than) the long-snouted archosauriform “*Zanclodon*” *arenaceus* (Hungerbühler, 2001); however, no undisputed phytosaurs are known from this unit. Further work is needed to explore the possible ecological replacement of long-snouted temnospondyls by phytosaurs during the early Late Triassic.

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Gerrothorax

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Plagiosuchus

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Capitosauroida

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Benthosuchus

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Aphaneramma

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Trematolestes

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Lyrocephaliscus

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Almasaurus

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Metoposaurus

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Callistomordax

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Inflectosaurus

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Microposaurus

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Jordan taxon

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Calamops

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Tertrema

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Hyperokynodon

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Platystega

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