A NEW PIPOID ANURAN FROM THE LATE CRETACEOUS OF SOUTH AFRICA

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ABSTRACT—Numerous fossil pipoid frogs recovered from Late Cretaceous deposits of a closed crater-lake of Late Cretaceous age in the Marydale District of South Africa are described and referred to a new genus and species of pipoid anuran. The fossils include larvae and adult frogs that are thought to have been killed en masse following breakdown of the thermal stratification or possibly by CO2 degassing from the underlying magma. A cladistic analysis of fossil and extant pipoid frogs based on 49 osteological characters reveals the new taxon to be a member of the pipinomorph clade, which includes the Late Cretaceous *Exoxenopoides reunigi* also from South Africa, fossil and Recent hynemochirines from Africa, and living *Pipa* from South America. The new taxon is larger than the above taxa and differs from this contemporaneous taxon in having an antorbital process on the maxilla and seven presacral vertebrae, with the presacral being formed by fusion of Presacrals I and II. The curved shape of the ventral part of the braincase distinguishes this frog from hynemochirines, *Palaeoabatrachus*, and *Exoxenopoides*. The new anuran is distinguished from the Israeli fossil *Thoraciliacus* of about the same age by the possession of a conch-shaped tympanosquamosal bone, a short jaw, and fusion of the sacrum and urostyle.

INTRODUCTION

Relative to that of other anurans, the fossil record of pipoid frogs is exceedingly rich (Báez, 1996, 2000). Good material representing numerous genera is known from the Late Jurassic of western North America (Henrici, 1998), the Early Cretaceous of Israel (Nevo, 1968; Trueb 1999), and the Cretaceous and early Tertiary of South America (e.g., Báez, 1981; Báez and Pugener, 1998, 2003; Báez et al., 2000) and Africa (e.g., Estes, 1977; Báez and Rage, 1998; Báez, 1999).

Herein, a new genus and species of pipoid anuran from the Late Cretaceous of South Africa is described. The first examples of these fossils were discovered in the late 1970’s by diamond prospectors who excavated test pits into a kimberlite pipe on the Stompoor Farm in the Marydale District of the northwest Cape (Fig. 1). Photographs of two of the first fossils found (and currently sequestered in one or more private collections) were made available to D. E. van Dyjk, along with additional specimens from the original excavation; van Dyjk (1985) prepared a brief report on these fossils. Although van Dyjk (1985) remarked that *Exoxenopoides*, a fossil pipoid of similar age, had been found in cratere-lake deposits of the nearby locality of Banke (Fig. 1), he restricted his brief comparisons of the Marydale specimens to the Israeli Cretaceous pipoid *Thoraciliacus*. Although this seems curious now, perhaps it was the natural consequence of Enviaiar Nevo’s having examined the Marydale fossils during a visit to South Africa and having shared his observations with van Dyjk. The latter author reported that the taxa resemble one another in having long ilia, pectoral girdles thought to be arciferal, free ribs on Presacrals II–IV, and large hands. Van Dyjk (1985) distinguished the Marydale frogs from *Thoraciliacus* by the possession of a postsacral vertebra, eight presacral vertebrae, and only slightly dilated sacral diapophyses in the Marydale fossils.

A year later, Smith (1986, 1988) illustrated some new frog specimens along with fishes, bivalves, gastropods, ostracods, insect wings, and a possible bird bone that he recovered from a wide-diameter drill core sunk by De Beers Consolidated Mines Ltd. into the center of the Stompoor diatreme. His analysis of the sedimentary sequences in the core led him to conclude that the fossils were preserved within a closed crater-lake that existed immediately after cessation of volcanism, during the Late Cretaceous. The palynomorph assemblage from the core was dated as mid-Senonian (Campanian) in age (Scholtz 1985, 1987). In June of 1999, a team from the State University of New York at Stony Brook and the South African Museum Cape Town visited Stompoor Farm in the Marydale District (Fig. 1) and relocated the pits where the van Dyjk specimens had been found. They then sank a shaft (Fig. 2) into the deposit and recovered more than 200 primarily adult frog specimens, as well as a fragment of a dinosaurian vertebral column. All of the adult specimens share the skeletal anatomy described below, and are thought to represent a single taxon.

GEOLOGICAL SETTING

The Stompoor fossil frogs occur in an “epiclastic kimberlite” sequence, which is a succession of sediments that is confined to the top of a kimberlantic diatreme and wholly or partly derived from a kimberlítica source (Hawthorne 1975; Fig. 3). The Stompoor epiclastics comprise two superimposed sedimentary packages—a lower pyroclastic suite, deposited during the final phase of active volcanism, and an upper, post-eruption succession that accumulated on the floor of a crater-lake. The former is composed mainly of lapilli tuffs and breccias, whereas the latter is made up of locally derived, matrix-supported conglomerate, massive sandstone, and thinly bedded to finely laminated mudrock (Smith, 1986). Both sedimentary packages have a pronounced dip of 25°–45° toward the center of the crater. This oversteepening of the bedding is a characteristic feature of epiclastic deposits and is caused by continued movement of circular pressure fructures that originally formed the maat-type crater. These craters are normally wide, shallow depressions with steep sides and flat bottoms, and commonly are surrounded by a rim of volcanic ash.

The Stompoor diatreme intruded vertically along an angular unconformity between quartizes and shales of the Carboniferous Dwyka Group and Precambrian granites of the Namaqua...
Suite (Figs. 2, 3). It has an irregular oval shape in plan view and has dimensions of about 600 × 500 m. In the center of the diatreme, the crater-lake facies are covered by 42 m of coarse red sands and gravels of the Cenozoic Kalahari Sand Formation; drilling has shown them to extend to 168 m below the surface. Toward the margins, the crater facies are encountered beneath only 1 m of overburden. The first prospecting pits that yielded the frog specimens described by van Dijk (1985) were sunk along the margins of the diatreme. The latest shaft that yielded the specimens described here was positioned closer to the center, so as to avoid a zone of leaching along the contact with the country rocks, which, in some pits, has completely dissolved the fossilized bone.

Sedimentology and Paleonvironmental Interpretation

The Stompoor shaft entered the crater facies 3 m below the surface and penetrated to 11.1 m through a sequence dominated by debris-flow conglomerates (Fig. 3). These represent subaerial landslides that originated from slope failures in the surrounding tuff cone and slid downslope into the lake, ending up spread out over the lakebed. During this short period of subaqueous movement, the debris flow had the ability to entrain organic debris such as fish and frog cadavers and bivalve and ostracod shells that lay on the lakebed.

Between the conglomerate beds, much thinner, discontinuous beds of laminated siltstones with granule layers and claystone drapes yielded abundant, fully articulated frog skeletons, including several larval stages, a few woody plant stems, an araucarian cone, and a string of seven articulated caudal vertebrae of an ornithopod dinosaur (Ralph Molnaar, pers. comm.). The laminated beds are interpreted as storm-driven turbidites that were deposited during downpours when cool, sediment-laden runoff water entered the stratified lake and traveled as density underflows along the lakebed.

Thin layers of microlaminated mudrocks also were encountered in the pit. This facies consists of sub-millimeter-scale light/dark alternations imparted by carbonate-rich and carbonate-poor mudstone. These are interpreted as the normal background settling of a rain of suspended fines from the thermocline of a thermally stratified, closed-lake system with anoxic bottom conditions. The carbonate laminae possibly represent seasonal fluctuations in acidity resulting from algal blooms. Some of the frog specimens are preserved in this facies; however, the lack of well-defined partings makes them difficult to find and prepare.

Some slabs (ca. 22 × 28 cm) display three or four frog specimens with their longitudinal axes randomly oriented, although the frogs commonly lie on their bellies (i.e., dorsum-up) and in almost identical “spread-eagled” poses that are typical of aquatic pipoid anurans. These occurrences are strongly indicative of mass-mortality events that were reported for the fishes that inhabited the offshore parts of the lake (Smith, 1988; Anderson, 1998). The small, but significant, range of taphonomic variance among the frog skeletons mainly involves the degree of flexure of the limbs. There seems to be a continuum, from frogs with straightened legs and arms parallel to body, to frogs with slightly flexed legs with arms slightly raised away from the body, to frogs with fully flexed legs with toes pointing posteriorly and arms raised anteriorly, to frogs with extremely flexed, crossed-over legs and arms stretched anteriorly such that they nearly meet in front of the head. It is concluded that the frogs and fishes were killed en mass following breakdown of the thermal stratification or possibly by CO₂ degassing from the underlying magma, followed by a short period of postmortem desiccation prior to burial. The lakeshore is the most likely site for the cadavers to have dried out; thus, it is probable that mass-mortality episodes led to numerous carcasses being washed up onto the shore. During thunderstorms, sediment-laden sheet-flow running down the steep inner wall of the tuff cone may have washed the desiccated frog carcasses into the lake and buried them beneath a thin drape of silt. Anoxic conditions on the lakebed reduced bacterial decomposition to a minimum as layer upon layer of sediment stopped further decay.
layer of silt accumulated to protect the carcasses from compression.

Fossilization of the bones proceeded inside a cavity along a bedding plane. The bones were replaced with microcrystalline silica that has been stained with a variety of accessory minerals, including dark red hematite and black manganese dioxide, with the latter often surrounding the extremities of the fossil as delicate filamentous dendrites. Comparison of frog specimens from deep core and shallow, peripheral pits suggests that the secondary mineralization is related to post-fossilization weathering, rather than paleoenvironmental factors.

MATERIAL AND METHODS

A total of 250 articulated frog skeletons, including numerous tadpoles in various stages of development, was recovered mainly from coarsely laminated turbidite beds in the lower part of the Stompoor shaft. The dimensions of the shaft were 3.2 × 4 m and it was dug using a compressed-air-powered rock hammer and shovels; materials were raised to the surface with a simple, motor-driven crane. Excavated slabs of the laminated siltstones were dried in sunlight for approximately 12 hr before they were systematically opened along the bedding planes in search of fossils.

Part and counterpart of each fossil were carefully coated with a very thin (1% solution) of the acrylic consolidant "Paraloid B72" dissolved in acetone. Part and counterpart were given the same field number with a prefix ST1 (Stompoor Pit 1). Many of the specimens parted down the middle of the skeleton leaving bones on both part and counterpart. Some specimens were mechanically prepared in the laboratory using a needle. This proved to be extremely difficult because the long bones are brittle and hollow, and weaker than the surrounding matrix. Radiographs of unexhumed specimens proved to be an effective way to confirm the topology of skull-roof surfaces.

A preliminary cladistic analysis based on 49 osteological characters was performed to determine the phylogenetic position of the taxon described here in Pipidae. The characters scored were taken from Baez and Pugener (2003) and references cited in this work; the reader is referred to the latter paper and papers cited in it for descriptions and illustrations of the characters listed in Appendix 1. Building on the work of Baez and Trueb (1997), and Baez and Pugener (1998, 2003), we included the following taxa in the analysis (extinct taxa indicated by †: Discoglossus, Rhinophrynus, Chelomophyrynus bayi, Cordicepsalatus, Eoxenopoides reuningi, Palaeobatrachus, Shelania laurenti, S. pascuali, "Xenopus roumani", and Llankibatrachus. In addition, we included the Early Cretaceous pipoid Thoracilicus, which was redescribed by Trueb (1999). The character list and data matrix are presented in Appendices 2 and 3, respectively. The phylogenetic analysis was performed with PAUP 4.0b10 for Macintosh (Swofford, 2002). All multi-state characters were treated as unordered and evolution of character states on the most parsimonious trees was traced using the accelerated transformation option (ACCTRAN). Trees were rooted using Discoglossus and Rhinophrynidae. TreeRot (Sorenson, 1999) was used to calculate the Bremer Decay Index (Bremer, 1994) as an estimate of the strength of each node in the tree.

Genus *VULCANOBATRACHUS*, gen. nov.

**Type Species**—*Vulcanobatrachus mandelai* sp. nov.

**Etymology**—The generic name is derived from the Latin Vulcans, the god of fire, from which the word volcano is derived, and the Greek batrachos, meaning frog, in reference to the volcanic crater-lake in which these animals resided.

**Diagnosis**—As for the type and only known species.

*VULCANOBATRACHUS MANDELAI*, sp. nov.

*(Figs. 4–12)*

**Holotype**—SAM-PK-K9614 (Field No. ST1/108), complete skeleton (Figs. 4, 5).

**Paratypes**—SAM-PK-K9613; SAM PK-K9535a,b, 9596, 9599a,b, 9642, 9644a,b, 9654a,b, 9664, 9686; SAM 6451a,b.

**Referred Specimens**—SAM-PK-K9571a,b, 9596, 9599a,b, 9683 (larvae), 9684, 9734 (larvae), 9994.

**Horizon and Type Locality**—Undesignated kimberlite epiclastics, Prieska District, Marydale (Stompoor: 21°52’0” E; 29°47’59” S), Cape Province, South Africa.

**Distribution**—Late Cretaceous (mid-Senonian) of South Africa.

**Diagnosis**—Moderate-sized pipinomorph frog (sensu Báez and Pugener, 2003) that differs from *Eoxenopoides reuningi* by the larger size of *Vulcanobatrachus mandelai* (x = 31.9 mm SVL, n = 53 versus x = 23.9 mm SVL, n = 18 in *Eoxenopoides*), the absence of ossification or mineralization in the antorbital region of the skull (present in *Eoxenopoides*), the presence of an antorbital process (absent in *Eoxenopoides*) on the maxilla in *Vulcanobatrachus*, and the presence of seven, rather than six (*Eoxenopoides*), separate presacral vertebrae in *Vulcanobatrachus*. The ventrolateral regions of the braincase in *Vulcanobatrachus* are curved, rather than distinctly angled as in *Eoxenopoides*, hymenochirines, and *Palaeobatrachus*.

*Vulcanobatrachus* differs from both *Cordicephalus* and *Thoraciliacus* in possessing a conch-shaped tympanosquamosal bone and a much shorter jaw, in contrast to the Cretaceous Israeli taxa that have a T-shaped squamosal and longer jaws. *Vulcanobatrachus* has longer transverse processes on Presacrals III and IV than does *Thoraciliacus*, and straighter processes on these vertebrae than does *Cordicephalus*. It differs from *Xenopus arabensis* (upper Oligocene, Yemen) in having antorbital processes on the maxillae and clavicles that are slender and acuminate medi ally. *Vulcanobatrachus* is easily distinguished from *Singidella latecostata* (Eocene, Tanzania) by the number of free presacrals.
(7 versus 6), the slender versus expanded transverse processes on the anterior presacrals, the large versus modest-sized otic capsules, and the slender versus medially expanded coracoids in Singidella. Vulcanobatrachus differs from the hymenochirine Pachybatrachus (Upper Cretaceous, Niger) in lacking its hyperossified skull. It can be distinguished from the various species of Palaeobatrachus (Paleocene–Pliocene, Europe), Shelania (Paleogene, Argentina) and Saltenia ibanezi (Upper Cretaceous, Argentina) by suites of cranial and postcranial features too numerous to detail here.

Etymology—The specific epithet honors Nelson Mandela, the first popularly elected leader of the Republic of South Africa.

DESCRIPTION

General Habitus

Vulcanobatrachus mandelai is a moderate-sized frog. The average snout–vent length of 53 specimens is 31.9 mm, with a range of 24.0–42.0 mm; the latter suggests that the sample either represents a mix of juvenile and adult individuals or that there may have been marked sexual dimorphism in size. The head is large and slightly broader than it is long (Figs. 4–7). The medial skull length is approximately equal to, or slightly shorter than, the length of the presacral vertebral column (i.e., exclusive of the sacrum and urostyle), and the length of the presacral portion of the column is slightly subequal to that of the fused sacrum and urostyle (Fig. 8). The sacral region is markedly narrow, with the width of the sacral diapophyses being less than, or about the same as, that of the width of the presacral column at the level of Presacrals III and IV. The presacral vertebrae lack free ribs in the adult; the transverse processes of the anterior three presacrals are long and slender in contrast to the stocky, curved, and relatively short transverse processes on the posterior four presacrals. The pelvic girdle is robust and bears especially long ilial shafts. The hind limbs are long relative to the forelimbs and longer than the snout–vent length of the frog. The pectoral girdle had robust clavicles, rather slender coracoids, and a well-developed suprascapula. The preservation of the hands and feet precludes description of most of the carpal and tarsal elements, as well as description of the phalanges. The lengths of the metacarpals and metatarsals preserved indicate that the hand and foot digits probably were long. No remains were found of a hyoid, sternum, or an epipubis.

Cranium

The overall proportions of the skull are shown best in SAM-PK-K9599a, 9609b, 9644a, 9686, and 6451a,b (dorsal exposures), and SAM-PK-K9613, 9614, and 9664 (ventral exposures). The skull is wider than long, with its greatest width being at the level of the squamosals at the anterolateral corners of the otic capsules (Fig. 9). The otic capsules are exceptionally large; the width of each capsule accounts for nearly 40% of the total width of the skull and the length accounts for about half the median skull length. The capsules are more quadrangular than oval in shape and protrude significantly posterior to the levels of the occipital condyles; accordingly, the skull has a distinct cordiform shape. The jaw articulation is located forward of the fenestra ovalis at the anterolateral corner of the otic capsule. The azygous frontoparietal is shallowly convex, smooth, and bears a parietal fora-
men. Paired nasals cover the rostrum. The maxilla extends to the posterior portion of the orbit, and the maxillary arcade is incomplete. The braincase is broad and shallow and underlain by a long, slender parasphenoid that lacks lateral alae. There is no evidence of neopalatines (= palatines of some authors) or vomers. The mandible lacks mentomeckelians. Neither the septomaxillae nor the hyoid apparatus is known.

**Sphenethmoid**—Dorsal (SAM-PK-K9994, 6451a, 9571a, 9654b, 9686) and ventral (SAM-PK-K9596, 9613, 9614, 9664) exposures of the anterior and orbital region of the braincase reveal the sphenethmoid to be a well-ossified, shallow, and exceptionally broad element (Figs. 5, 7, 9). In SAM-PK-K9994, 6451a, and 9571a, the margins of the sphenethmoid underlying the frontoparietal are exposed. The dorsolateral margins of the bone are straight, seemingly lacking a taenia tecti marginalis; likewise, a dorsal ethmoid plate (or tectum) seems to be absent anteriorly. The presence of a frontoparietal fontanelle is logically impossible because the marginal elements of the ethmoidal cartilage that ossify as the dorsal part of the sphenethmoid and define the edges of the frontoparietal fontanelle are absent.

At its anterior terminus, the width of the sphenethmoid is more than half that of the entire skull at the level of the planum antorbitale (Figs. 7, 9), whereas in most anurans, this metric would be a quarter and occasionally perhaps a third of the skull width at this level. Owing to the width of the ossified sphenethmoid and its position near the end of the snout, the planum antorbitale region is narrow. Although the nasal, together with the antorbital process of the maxilla, might have provided reinforcement or dorsal protection for this region, the short planum must have been cartilaginous.

No indications of orbitonasal foramina were observed. It is possible that the orbitonasal foramina lay at the anterolateral margins of the sphenethmoid and were not completely formed in bone. Possibly a pair of optic foramina were present in the midorbital region. There is a pair of holes on either side of the braincase in SAM-PK-K9654b that might be optic foramina. However, in SAM-PK-K9613, in which the sides of the neurocranium are fragmented but in situ, no foramina are apparent. A pair of immense openings seems to separate the posterior end of the sphenethmoid from the prootics of the otic capsules. Possibly these fenestrae accommodated the trochlear, optic, oculomotor, trigeminal, and facial nerves, the foramina of which were separated from one another in cartilage or connective tissue.

![FIGURE 8. Vulcanobatrachus mandelai, gen. et sp. nov. Restoration of skeleton in dorsal view. Hyoid apparatus, right suprascapula, and left limbs not shown. Dashed lines represent restorations.](image)

![FIGURE 9. Vulcanobatrachus mandelai, gen. et sp. nov. Restoration of skull in dorsal (left) and ventral (right) views. Gray area represents unossified area of palate. Dashed lines are restorations.](image)
Prootic and Exoccipital—Although fragmented, the integrity of the shape of the otic capsules and their relationships to other parts of the cranium is preserved in several specimens in dorsal and ventral exposures (e.g., SAM-PK-K6451a, 9599a, 9609b, 9613, 9614, 9644a, 9664, and 9686). The large capsules seem to have been well ossified, with a complete synostotic union of the exoccipital and prootic. [The fused prootic and exoccipital = the otocipital of Estes (1977).] The otic capsules are exceptionally large, with the greatest width of each comprising about 40% of the greatest width of the skull and the length about 50% of the median skull length. They seem to lack, or to have narrow, cartilaginous cristae paroticae because the squamosals lie closely adjacent to the anterolateral corners of the ossified capsules. Overall, the capsules are quadrangular, with the posterior corners protruding prominently posterior to the levels of the foramen magnum and occipital condyles (Fig. 9).

In the dorsal exposure of SAM-PK-K9599a, the endochondral exoccipitals are fused medially to form a complete dorsal margin for the foramen magnum. The positions and orientations of the occipital condyles are evident in SAM-PK-K9599a, 9609b, 9644a, and 9686. They are widely separated from each other, shallowly stalked, and the articular surface of each lies in a posterior mediolateral plane. It is impossible to determine whether the exoccipitals are fused to each other ventromedially.

The configuration of the posterior part of the neurocranium, apparent in several specimens (e.g., SAM-PK-K9571a, 9613, 9994), suggests that although the massive, endochondral prootics were fused to the exoccipitals, the prootics remained separate from each other. Dorsally, the epiotic eminences are distinct and massive. Ventrally, the central part of each prootic seems to have a depression that represents the Eustachian canal (e.g., SAM-PK-K9613, 9614). The position of the fenestra ovalis in the posterior lateral corner of the prootic is evident in SAM-PK-K9609b. The presence of a basal process could not be confirmed, but a pterygoid knob is absent.

Plectral Apparatus—Part of the stapes is preserved in at least five specimens: SAM-PK-K9614, 9599a, 9609a, 9644a, and 9686. The endochondral bone (pars media plecttri) is robust, long, and curved (Figs. 5.9). It extends from the fenestra ovalis along the lateral margin of the otic capsule to the squamosal. In one specimen (SAM-PK-K9614), it is possible to view the stapes and squamosal in lateral aspect. The parts interna and externa plectri could not be identified and may have been cartilaginous; likewise, an operculum is not evident.

Frontoparietal—Pieces of this large, fragile, dermal bone are evident in nearly every specimen in which at least part of the cranium is preserved. The dorsal configuration is best shown in SAM-PK-K9599a, 9609b, 9642, 9644a, and 9654a,b, whereas the ventral aspect is best exposed in SAM-PK-K9614, 9644b; Fig. 5). The terminal position of the nasals suggests that the external nares were terminal and directed anterolaterally.

Parasphenoid—This dermal bone underlies the median braincase (Fig. 9) and is not well preserved in the sample. In some dorsal exposures (e.g., SAM-PK-K9599a, 9686), the slender, lanceolate anterior end of the parasphenoid is exposed in front of the rostrum; the cultriform process either has been broken or the entire bone has shifted forward with respect to the skull table. In ventral exposures (e.g., SAM-PK-K9614, 9664; Fig. 5), the anterior end of the cultriform process can be seen to extend beyond the sphenethmoid and terminate just posterior to the maxillary arcade. The relationship of the cultriform process to the underlying sphenethmoid is unclear. In some specimens, the shape of the cultriform process cannot be distinguished from the sphenethmoid, whereas in others (e.g., SAM-PK-K9614), there seem to be faint, intermittent indications of the margins of the long, slender process. This suggests that the parasphenoid was partially or wholly fused with the adjacent sphenethmoid. In one specimen (SAM-PK-K9596), the parasphenoid can be identified as a long, narrow, median bone. The frog is small and the cranium poorly developed, suggesting that it metamorphosed recently. If we are correct in our assumption, then the parasphenoid is incompletely developed and not yet fused to the braincase in this specimen. Only one specimen (SAM-PK-K9613) gives any indication of the possible configuration of the posterior parasphenoid corpus. In this frog, a median bone that may be the parasphenoid forms the ventral margin of the prootic foramen. Posterior to this level the lateral margin seems to be curved to conform to the adjacent otic capsule. The condition of the posterior end is undetermined.

Vomers—There are three possibilities for vomerine arrangements in pipoids. Vomers might be independent, paired elements anterior to the sphenethmoid and flanking the cultriform process of the sphenethmoid. Alternatively, the bones might be fused to each other and the parasphenoid-sphenethmoid complex, or the vomers might be absent. Since neither independent vomers nor indication of incorporation of the vomers into the braincase, we consider these elements to be absent.

Septomaxillae—No bony remains could be identified as these dermal bones, which are located within the olfactory capsules.

Neopalatine—This dermal bone usually is associated with the ventral surface of the planum antorbitalis between the maxilla and the sphenethmoid at the anterior margin of the orbit. This area is exceedingly narrow in Vulcanobatrachus mandelai and there is neither indication of dermal nor endochondral ossification or mineralization. Thus, it seems likely that a neopalatine is absent.
**Maxillary Arcade**—In anurans, the maxillary arcade of the upper jaw is composed of as many as three pairs of dermal elements—viz., premaxillae anteriorly, maxillae, and quadratojugal series posteriorly. *Vulcanobatrachus mandelai* lacks quadratojugal series; thus, the maxillary arcade is incomplete and the maxillae are not connected to the ventral rami of the squamosals.

We found only two specimens in which part of the premaxilla might be exposed—SAM-PK-K9571a and 9614. In the latter specimen, in which the rostrum is exposed both dorsally and ventrally, there is a pair of relatively flat bones lying in front of the nasals. We assume that these are the premaxillae, which are only partly visible from the dorsal surface and therefore not depicted in the photographs of the ventral exposure of the holotype (Figs. 4, 5). The left premaxilla articulates with the maxilla. There is no evidence of dentition. Owing to the poor preservation, it is not possible to describe the partes dorsalis or palatina of the premaxilla.

Fragments of the maxillae are preserved in several specimens, with the best examples being SAM-PK-K6451a, 9571a, 9599a, 9609a,b, 9613, 9614, and 9664. The maxilla is an edentate, moderately robust bone that bears a slender antorbital process (SAM 6451a; Figs. 7, 9). The part of the bone preserved most consistently is the lateral face, the pars facialis. We could not identify the pars palatina; however, we assume that a relatively narrow palatal shelf must have been present. In two specimens (SAM-PK-K9613, 9664), the length of the maxilla is evident. The maxilla had a robust articulation with the anterior ramus of the pterygoid in the posterior region of the orbit and seems to have terminated slightly anterior to the squamosal and otic capsule (Fig. 9).

**Pterygoid**—Several specimens (e.g., SAM-PK-K9609a,b, 9686, 9994) preserve crushed remnants of the anterior ramus of the pterygoid, and in some, these are associated with fragments of the maxilla. The best examples of the pterygoid in situ are found in the ventral exposures of SAM-PK-K9613, 9614, and 9664 (Fig. 5). Normally, the pterygoid is described as triradiate, but in *Vulcanobatrachus mandelai* the rami are so short and stout that the bone is better described as triangular (Fig. 9). The anterior ramus is the longest; it articulates with the medial surface of the maxilla just anterior to the otic capsule in the posterior part of the orbit. The posterior ramus is short, owing to the anterior position of the jaw articulation. There is no distinct elaboration of a posterior versus a medial ramus; the margin of the bone is slightly concave and diagonally oriented across the anterolateral part of the otic capsule. The medial ramus seems to have abutted the basal process along the anterocentral margin of the otic capsule. The vertebral column is composed of seven presacral vertebrae, with Presacrals I and II being fused (e.g., SAM-PK-K9599a, 9609b, 9994); the compound vertebra is only slightly longer than the more posterior vertebrae (Figs. 8, 10). The width of the neural arch of Presacral I + II is about twice as wide as the midline length of the arch, whereas the widths of the remaining presacrals are about three times their midline lengths (e.g., SAM-PK-K9599a). None of the presacrals is imbricate (SAM-PK-K9599a, 9609b) and in all specimens examined, the contralateral halves of the neural arches seem incompletely fused at the midline. In a few specimens (SAM-PK-K9599a, 9994a,b), some postzygapophyses are visible; these are simple, flat processes.

The vertebrae are reasonably well preserved in two specimens in ventral exposure (SAM-PK-K9613, 9614). However, owing to the preparation and preservation of these individuals, it is im-
possible to determine with certainty the nature of the articulations of the centra. Whereas the proximity between adjacent presacrals make it seem unlikely that the vertebral column was notochordal, we cannot distinguish whether the articulations in these specimens are procoelous, opisthocoelous, or bearing intervertebral discs.

Transverse processes are well developed in *Vulcanobatrachus mandelai*. Those of Presacral I-II are stout, about half the width of the neural arch, and owing to the shallowness of the vertebra, the transverse processes lie posteriorly adjacent to the otic capsules of the cranium (e.g., SAM-PK-K 9609b, 9994a). The transverse processes of Presacrals III and IV are longer, their lengths being approximately equal to the width of the vertebra. Those of Presacral IV are slightly longer than those of Presacral III, and the width of the entire Vertebra IV (tip of transverse process to tip of transverse process) is equal to or greater than the greatest width of the pelvic girdle. In juvenile specimens (SAM-PK-K9734), radiographs reveal that there are free ribs on Presacrals II-IV (Fig. 11); obviously, these fuse to the vertebrae to form the so-called transverse processes of the adults. The transverse processes of Presacrals V-VIII are short, broad-based elements that have acuminate tips. Those of Presacral V are directed approximately laterally, whereas those of the Presacrals VI-VIII are oriented anterolaterally (e.g., SAM-PK-K9599a, 9614; Fig. 4).

The sacrum is composed of a single vertebra that is fused to the urostyle posteriorly. The sacral diapophyses are oriented laterally and moderately expanded, with the lateral margin of the blade being about four times larger than the base of the diapophysis (e.g., SAM-PK-K9609b; Fig. 10). The diapophyses seem to be moderately symmetrical, with the anterior and posterior parts being about equally developed. The overall width of the sacrum is less than that of Presacral III and less than or equal to that of Presacral IV. The length of the sacrum and the urostyle is approximately equal to, or slightly less than, that of the presacral portion of the axial column. There is no indication of the presence of postsacral vertebrae in adults. Owing to the preservation, there is little that can be said about the urostyle other than it seems to have a relatively uniform width throughout its length.

**Appendicular Skeleton**

**Pectoral Girdle and Forelimb**—The best preservation of the ventral aspect of the pectoral girdle is found in SAM-PK-K9539a, b, 9613, 9614, and 9664 (Fig. 4). The clavicles are robust, strongly curved bones that were not fused to the scapulae. In SAM-PK-K9613 and 9614, it is evident that the clavicles are about uniform in width throughout their length, with tapered medial ends. There are fragments of coracoids in several specimens, but these bones are best preserved in SAM-PK-K9539a,b. In this specimen, it is possible to see that the coracoid is a stout element that is expanded at both ends; the expansion of the sternal end of the bone is approximately twice that of the glenoid end, and the glenoid end is approximately twice the width of the midshaft of the coracoid (Fig. 12). The internal angle between the clavicle and coracoid is about 80°. It is likely that the pectoral girdle was arciferal, although it is possible that the epicoracoid cartilages might have been fused in the midline to produce a "pseudofirmisternal" condition resembling that of living pipids (Cannatella and Trueb, 1988).

Scapulae are not well represented. Fragments of these bones seem to be present in SAM-PK-K9609b and 9642. The left scapula was identified in SAM-PK-K9664, in which it seems evident that the bone is short, stocky, and weakly bicapitate. Suprascapulae are preserved in several specimens (e.g., SAM-PK-K9571a, 9609a, 9644a, 9686 and 9994). The flat, bladelike bone is moderately expanded distally with its posterior margin being longer than the anterior margin.
The humerus is commonly preserved (e.g., SAM-PK-K9614, 9596, 9609b, and 9644a, and 9664), but the radoulna is less common, and hands are fragmentary in those specimens in which they occur (e.g., SAM-PK-K6451a, Fig. 6). The radioulna is present in SAM-PK-K9596, 9609b, 9644a, and 9664, and hands are best preserved in SAM-PK-K9642, and 9644a. The head of the humerus (caput humeralis) is robust and seems distinctly larger than the distal end of the bone. Because the humeral shaft is straight, it seems unlikely that either a crista medialis or a deltoïd crest was especially well developed. The radioulna is a moderately robust, symmetrical bone with a well-developed olecranon process. The radius is completely fused to the ulna; a faint sulcus intermedius is evident and indicates that the head of the radius is slightly broader than that of the ulna but not distinctly longer. A moderate-sized ulnare was identified, along with the bases of the metacarpals and fragments of phalangeal elements. However, the phalangeal elements are too poorly preserved to discern the phalangeal formula or the relative lengths of the digits.

**Pelvic Girdle and Hind Limb**—The pelvic girdle is represented in several specimens and is well preserved in four individuals (SAM-PK-K6451a, 9613, 9664, and 9686). The overall shape is revealed by SAM-PK-K 9593a, 9596, and 9614, in which the internal margins of the ilia describe a V-shape in which the base is rounded, rather than angular. The ilial shafts are narrow basally in the postascalar region, but bear a broad dorsolateral crest in their anterior halves. The ilial shafts are extraordinarily long, with their anterior ends located at the level of the transverse processes of Presacral VI (Fig. 8). The ischia and posterior ilia seem to be fused medially. In the best ventral exposures of the pelvic girdle (SAM-PK-K6451, 9614, 9664), the pubes are small and either cartilaginous or perhaps composed of cartilage that was partially mineralized—a common phenomenon in extant taxa. The ventral configuration of the ilium reveals that a preacetabular ilium was absent. Because the pelvic girdle was preserved only in dorsal and ventral aspects, we could not determine the shape of the acetabulum, which apparently had a margin formed mostly in bone of the ilium and ischium. The hind limb is long with a weakly sigmoid femur and a straight tibiofibula that are equal in length (e.g., SAM-PK-K6451a, 9596, 9664, 9644a; Fig. 8). The head of the femur (caput femorale) is slightly larger than the distal end. The ends of the tibiofibula are about equal in size. The condition of the tibiale [= astragalus of some authors] and fibulare [= calcaneum of some authors] is difficult to discern. In SAM-PK-K9896 (a small individual), the bones seem unfused; however, in the larger SAM-PK-K9644a, the tibiale and fibulare seem to be fused proximally. Thus, we would judge synostosis between these elements to be minimal and perhaps incomplete distally. Some proximal tarsal elements are present, along with the bases of some metatarsal bones, but the preservation is too poor to describe the tarsal elements or the phalangeal formula and relative lengths of the digits.

**COMPARISONS AND RELATIONSHIPS**

The monophyly of Pipidae has been demonstrated by multiple studies of fossil and Recent taxa (e.g., Cannatella and Trueb, 1988; Báez and Trueb, 1997; Henrici, 1998; Báez and Pugener, 1998, 2003). Further, based on these studies, Pipidae is diagnosed by the following suite of synapomorphies: (1) optic foramina bound in sphenethmoidal ossification; (2) large, flat, arcuate septomaxillae; (3) parasphenoid forming part of neurocranial floor; (4) conch-shaped tympanosquamosal bone; (5) pterygoid bearing otic plate formed by expansion of medial and posterior rami; (6) prootics deeply excavated to form bony canals for Eustachian tubes; (7) maxilla not bearing distinct parts palatina, facialis, and dentalis in orbital region; (8) vertebral centra with opisthocoelous articulations; and (9) sacrum and urostyle fused.

*Vulcanobatrachus mandelai* possesses some pipid synapomorphies—viz., the conch-shaped tympanosquamosal bone, pterygoid with otic plate, parasphenoid incorporated into braincase floor, and fused sacrum and urostyle. Owing to the poor preservation of the specimens of *Vulcanobatrachus*, we cannot be certain of the condition of the optic foramina or the nature of the vertebral centra, and the septomaxillae are unknown. *Vulcanobatrachus* lacks the pipid synapomorphies involving the modifications of the prootics and maxillae.

The parsimony analysis conducted to elucidate the phylogenetic placement of *Vulcanobatrachus mandelai* produced two equally most-parsimonious trees of 99 steps (consistency index = 0.6263; rescaled consistency index = 0.4748). The trees differ only in the arrangement of *Llankibatrachus* to *Shelania laurenti* and “*Xenopus* romeri”, a conflict that has no direct bearing on the placement of *Vulcanobatrachus*. The results of this analysis corroborate the monophyly of Pipidae with reasonable Bremer and bootstrap support (Fig. 13).

Within Pipidae, there are two clades—Xenopodinomorpha and Pipinomorpha of B. Trueb and Trueb, 1988, 1992. Further, based on these studies, Pipidae comprises the Cretaceous South African *Llankibatrachus*, a conflict that has no direct bearing on the placement of Pipidae.
Six autopomorphies (none unique) diagnose *Vulcanobatrachus*. The Eustachian canal is present in a shallow anterior depression of the prootic bone (Character 7), as it is in palaeobatrachids, *Thoraciliacus*, and *Cordicephalus*. In the remaining pipids, the prootic bears a deep furrow for the Eustachian canal. Thus, the state of this character in *Vulcanobatrachus* is explained most easily as a reversal. The presence of an antorbital process on the maxilla (Character 18) in *Vulcanobatrachus* distinguishes this taxon from the other pipinomorphs, as discussed above. *Vulcanobatrachus* is the only pipid that retains a maxilla that has distinct parts: facialis, dentalis, and palatina in the orbital region (Character 19). In this feature, it resembles *Thoraciliacus*, *Cordicephalus*, palaeobatrachids, and *Rhinophrynus*. Similarly, the abutment of the anterior ramus of the pterygoid against the maxilla (Character 22) is the same arrangement that is found in *Cordicephalus* and *Rhinophrynus*. Another feature of the pterygoid—the presence of an indentation in the medial ramus—is found in *Vulcanobatrachus* and in all xenopodinomorphs (unknown in *Shelania laurenti* and “*Xenopus*” *romeri*) except *Saltenia*. In having a short, stocky scapula (Character 41), *Vulcanobatrachus* differs from the other pipinomorphs and *Thoraciliacus* and resembles *Cordicephalus* and most of the xenopodinomorphs (except *Saltenia*).

**DISCUSSION**

Careful comparison of the specimens described here with the photographs provided by van Dijk (1985:fig. 1a,b) in his note of a new fossil frog from “near Marydale” in South Africa provides reasonably compelling evidence that they represent the same taxon, viz., *Vulcanobatrachus mandelai*. Van Dijk did not have a precise locality for the specimens that he examined from a private collection, but the vicinity of Marydale could be considered coincident with the farm locality known as Stompoor. Van Dijk concentrated on comparisons of this anuran with the Late Cretaceous Israeli frog *Thoraciliacus*, described by Nevo (1968) and redescribed by Trueb (1999). These anurans are geographically and temporally disparate, but their sizes and preservation are similar. Morphologically, they share several plesiomorphic pipid traits, including fusion of the first two presacral vertebrae, long ilia that are narrowly separated, short, stocky scapulae and a general pectoral architecture that is similar, an incomplete mandibular arcade, long pterygoid process, large anteroventral portion of the otic plate, short rostrum, and presence of antorbital processes on the maxilla. Nevertheless, *Vulcanobatrachus* possesses several derived features that are absent in *Thoraciliacus*. The maxillary arcade is shorter in *Vulcanobatrachus*, with the angle of the jaw being located forward of its position in *Thoraciliacus*. The squamosal of *Thoraciliacus* is T-shaped, whereas in *Vulcanobatrachus*, there is a conch-shaped tympanosquamosal bone, a longer jaw articulation, and proportionally larger otic capsules. The cultriform process of the parasphenoid is incorporated into the floor of the neurocranium in *Vulcanobatrachus*, whereas it is not synostotically united with the sphenethmoid in *Thoraciliacus*.

Perhaps a more obvious comparison is with *Eoxenopoides reiningi*, which is the sister taxon to *Vulcanobatrachus* + *Pipa* and the hymenochirines in the analysis performed here, and also geographically and temporarily, is a species more closely related to *Vulcanobatrachus*. *Eoxenopoides* is about the same size as *Vulcanobatrachus* and was collected from similar sediments filling a volcanic pipe at Banke, located about 300 km west of Stompoor/Marydale (Fig. 1). This taxon was described originally by Haughton (1931) and later reexamined in detail by Estes (1977). *Eoxenopoides* is distinctly smaller than *Vulcanobatrachus*; the estimated average snout-vent length of 18 *Eoxenopoides* is 23.9 mm, in contrast to 31.9 mm in *Vulcanobatrachus*. Further, it has a much shorter axial column composed of only six presacral vertebrae and a notably short urostyle. The presacral vertebrae are...
imbricate, whereas they are nonimbricate in *Vulcanobatrachus*. Both taxa have conch-shaped squamosals and long, curved stapes. *Eoxenopoides* has an independent parasphenoid in contrast to the fused parasphenoid of *Vulcanobatrachus*, and has an azygus vomer, whereas *Vulcanobatrachus* seems to lack vomers. In *Eoxenopoides*, the planum antorbitalis is ossified or mineralized and the maxilla lacks an antorbital process, whereas in *Vulcanobatrachus*, an antorbital process is present and the planum antorbitalis apparently was cartilaginous. The nasals of *Eoxenopoides* are crescent-shaped, with concave anterior margins that do not overlap the maxilla and premaxilla. The nasals of *Vulcanobatrachus*, in contrast, have slightly convex anterior margins that overlap the maxillary arcade.

**Biogeography**

As our understanding of the relationships of fossil and Recent pipoid frogs has expanded with the descriptions and analyses of new taxa, an intriguing biogeographic picture of an apparently ancient group of anurans is emerging (Fig. 13). The pipoid clade is represented by living and extinct taxa in North America (Rhinophrynidae; Late Jurassic and Recent) and Europe (Palaebatrachidae; Upper Cretaceous and Paleogene), but reaches its greatest taxonomic and historical diversity in South America and Africa, where fossils date from the Cretaceous and modern representatives live today—*Pipa* in South America and *Xenopus*, *Silurana*, and hynenochirines in Africa. *Rhadinostus parvus*, a rhinophrynid from the Late Jurassic of North America (Morrisson Formation, Utah), is the oldest pipoid fossil known (Henrici, 1998). *Thoracicus* and *Cordicephalus* are younger, dating from the Late Cretaceous of Israel about 118 million years ago (Nevo, 1968; Gvirtzman et al., 1996). They originate from the Arabian Peninsula, which is part of the African Plate and was located near the Tethyan shoreline in a tropical environment (Partrish et al., 1982).

Thus, it would appear, as suggested by Savage (1973), that pipoids are an ancient group (Old Tropical Assemblage) that must have thrived on the supercontinent Pangea in the Upper Triassic when warm, temperate conditions are thought to have prevailed (Scotese, 2002). The breakup of Pangea in the Early Jurassic to form two continents was the vicariance event that is suggested to have caused the clad to be separated. After the split, the South American lineages seem to have enjoyed only modest success in the austral regions before disappearing in the mid-Paleogene, perhaps 40 million years ago. In contrast, African xenopodinomorphs were immensely more successful as judged from their geological history, modern taxonomic diversity, and broad distribution throughout sub-Saharan Africa today. The pipinomorph clade seems to have diversified mainly in Africa. The minor radiation of *Pipa* in northern South America suggests that an ancestral stock, clad to the hynenochirines, invaded northern South America before the continent was completely separated from western Africa and subsequently diversified into the micro- and macro-*Pipa* assemblages recognized today. As other fossils are found and become available to study, we will be able to evaluate this hypothesis more effectively.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


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APPENDIX 1

Specimens examined.

Exooneloides reungsi: SAM-PK-K4596, K4601, K4602, K4604, K4605, K4614, K4625, K4626c, K4627b. SAM-PK-K9548, K9553, K9561, K9601, K9604, K9618, near Bank (30°22′S, 18°26′E) in the Gamoep area near Platbakkies, Namaqualand, Republic of South Africa.

Vulcanobatrachus mandelai: SAM-PK-K6451a, b, K9507–K9509, K9514, K9515, K9517, K9533, K9535a,b, K9540, K9549, K9550, K9552, K9553, K9557–K9559, K9564, K9566, K9568, K9571a,b, K9581, K9582, K9585, K9588, K9589, K9591, K9592, K9593, K9596a,b, K9599a,b, K9602, K9605, K9607, K9609a,b, K9610, K9613, K9614, K9616, K9617, K9619, K9622, K9624, K9625, K9633, K9635, K9638, K9641, K9642, K9644a,b, K9653, K9654a,b, K9658, K9660, K9664–K9667, K9672, K9676, K9681, K9683, K9684, K9686, K9734, K9994; Prieska District, Marydale (Stompoe: 21°52′0″E, 29°47′59″S), Cape Province, Republic of South Africa.

APPENDIX 2

List of characters used. See Baez and Pugener (2003) and Baez and Trube (1997) for descriptions.

Cranial Characters

1. Skull shape in lateral profile: 0, rounded; 1, wedge-shaped.

2. Anterior margin of frонтoparietal fenestra: 0, sphenethmoidal ossification surrounding frontoparietal fenestra anteriorly; 1, sphenethmoidal ossification not surrounding fenestra anteriorly.

3. Olfactory foramen: 0, bound completely or partially in bone; 1, bound in cartilage.

4. Olfactory foramen: 0, present, partially or completely cartilaginous; 1, ossified up to the maxillary arcade.

5. Floor of braincase in orbital region: 0, rounded; 1, distinctly angled.

6. Optic foramen: 0, not completely bound in sphenethmoidal ossification; 1, bound in sphenethmoidal ossification.

7. Eustachian canal: 0, absent; 1, present, prootic with deep furrow; 2, present, prootic with shallow anterior depression.

8. Inferior perilymphatic foramen: 0, present, not ventral to jugular foramen; 1, present, ventral to jugular foramen; 2, absent.

9. Superior perilymphatic foramen: 0, present; 1, absent.

10. Relative position of lower-jaw articulation: 0, lateral to otic capsule; 1, at anterolateral corner of otic capsule.

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3. Olfactory foramen: 0, bound completely or partially in bone; 1, bound in cartilage.

4. Antorbital bone of skull: 0, partially or completely cartilaginous; 1, ossified up to the maxillary arcade.

5. Floor of braincase in orbital region: 0, rounded; 1, distinctly angled.

6. Optic foramen: 0, not completely bound in sphenethmoidal ossification; 1, bound in sphenethmoidal ossification.

7. Eustachian canal: 0, absent; 1, present, prootic with deep furrow; 2, present, prootic with shallow anterior depression.

8. Inferior perilymphatic foramen: 0, present, not ventral to jugular foramen; 1, present, ventral to jugular foramen; 2, absent.

9. Superior perilymphatic foramen: 0, present; 1, absent.

10. Relative position of lower-jaw articulation: 0, lateral to otic capsule; 1, at anterolateral corner of otic capsule.
11. Frontoparietal: 0, paired; 1, azygous.
12. Frontoparietal(s) and nasal(s): 0, frontoparietal(s) not overlapping nasal(s); 1, frontoparietal(s) overlapping posterior margin(s) of nasal(s).
13. Nasal region: 0, one-third (or more) skull length; 1, one-fourth (or less) skull length.
14. Nasals: 0, paired; 1, fused.
15. Septomaxillae: 0, small and complex; 1, large and arcuate.
16. Vomers: 0, medial to choanae; 1, posterior to choanae; 2, absent.
17. Anterior end of maxilla: 0, lacking pointed process that overlaps premaxilla; 1, having pointed process that overlaps premaxilla.
18. Antorbital process of maxilla: 0, absent; 1, present.
19. Parts of the maxilla in orbital region: 0, distinct; 1, not distinct.
20. Maxillary arcade: 0, complete; 1, incomplete.
21. Pterygoid knob: 0, absent; 1, present.
22. Position of anterior ramus of pterygoid: 0, medially adjacent to maxilla; 1, abutting maxilla; 2, dorsal to maxilla; 3, absent.
23. Medial ramus of pterygoid: 0, present, lacking indentation; 1, present, with indentation; 2, absent.
24. Configuration of pterygoid in otic region: 0, not expanded; 1, expanded to form otic plate.
25. Parasphenoid and braincase: 0, not fused; 1, partially or completely fused.
26. Anterior extent of parasphenoid: 0, not reaching maxillary arcade; 1, reaching maxillary arcade.
27. Parasphenoid alae: 0, present; 1, absent.
28. Postero medial extent of parasphenoid: 0, terminus near ventral margin of foramen magnum; 1, terminus distinctly anterior to ventral margin of foramen magnum.
29. Squamosal shape: 0, T-shaped without stapedial processes; 1, T-shaped with stapedial processes; 2, conch-shaped.
30. Zygomatic ramus of squamosal: 0, well developed; 1, reduced or absent.
31. Coronoid process of angulosplenial: 0, poorly developed; 1, blade-like.

**Postcranial Characters**

32. Shape of vertebral centra: 0, cylindrical; 1, depressed.
33. Articular facets of vertebral centra: 0, notochordal; 1, opisthocoelous; 2, procoelous.
34. Articulation of facets of postzygapophyses: 0, flat; 1, with grooves and ridges; 2, curved ventrally.
35. Neural spines of presacral vertebrae: 0, sagittal; 1, parasagittal.
36. Presacral vertebrae I and II: 0, separate, weak or no imbrication; 1, separate, broad imbrication; 2, fused.
37. Ribs: 0, free ribs present in larvae and adults; 1, free ribs present in larvae and fused to transverse processes in adults; 2, ribs absent in larvae and adults.
38. Sacrum and urostyle: 0, not fused; 1, fused.
39. Relationship of lateral end of clavicle to scapula: 0, articulating with medial edge of pars acromialis; 1, overlapping anterior edge of scapula; 2, fused to scapula.
40. Medial end of clavicle: 0, not expanded; 1, expanded.
41. Proportions of scapula: 0, glenoid area one-third total length of scapula; 1, glenoid area more than one-third total length of scapula.
42. Cleithrum: 0, not covering posterior edge of suprascapular cartilage; 1, covering part of the posterior edge of suprascapular cartilage.
43. Sternal expansion of coracoid relative to its length: 0, expansion less than half length of coracoid; 1, nearly half length of coracoid; 2, nearly equal to length of coracoid.
44. Ilial supra-acetabular expansion: 0, present; 1, absent.
45. Ilial preacetabular expansion: 0, present; 1, absent.
46. Pubis: 0, cartilaginous; 1, ossified.
47. Length of postero medial process of hyoid: 0, less than half antero-posterior length of lower jaw; 1, more than half anteroposterior length of lower jaw.
48. Anterior end of postero medial process of hyoid: 0, wider than posterior end; 1, narrower than posterior end.
49. Parahyoid bone: 0, present; 1, absent.
APPENDIX 3. Data matrix of 49 osteological characters for 18 anuran taxa

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<td>&quot;Xenopus&quot; romeri</td>
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<td>Thomychilus</td>
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<tr>
<td>Vulcanaobatrachus</td>
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<td>1 1 1 1 1 1 1 1 1</td>
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<tr>
<td>Cordicephalus</td>
<td>0 0 1 0 0 1 2 2 2</td>
<td>1 1 1 1 1 1 1 1 1</td>
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<tr>
<td>Llankibatrachus</td>
<td>0 0 0 0 0 0 0 0 0</td>
<td>0 0 0 0 0 0 0 0 0</td>
</tr>
</tbody>
</table>

Character states are designated as 0, 1, 2. '?' denotes condition unknown because appropriate anatomical part either is not preserved or its condition is unclear.