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THE EARLIEST KNOWN PIPOID FROG FROM SOUTH AMERICA: A NEW GENUS FROM THE MIDDLE CRETACEOUS OF ARGENTINA

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ABSTRACT—Vertebrate remains from the Late Albian–Early Cenomanian Candeleros Formation of northwestern Patagonia include those of a pipoid frog, which is described herein. The fossils consist of partially articulated and disarticulated elements, some of them badly broken, that are mostly exposed in ventral aspect. The description is based on one incomplete skeleton that presumably belongs to a single individual; this specimen possesses a combination of character states not present in other known non-palaeobatrachid pipimorph taxa and is identified here as a new genus and species, *Avitabatrachus uliana*. The species is moderately small (estimated snout-vent length ca. 35 mm) and shares with Pipidae conch-like squamosals, deeply excavated prootics to form channels for the Eustachian tubes, articulations for the lower jaws at the anterolateral corners of otic capsules, and fused sacrum and urostyle. *Avitabatrachus* possesses at least eight presacral vertebrae, the first two of which are fused, with flat, opisthocelous centra. Unique features of this taxon are the presence of parasagittal flanges along the posterior halves of the otic capsules and the wide transverse processes of the posterior presacral vertebrae, which are only slightly anteriorly directed. Preliminary comparisons with other fossil pipoid taxa in the context of recent parsimony analyses suggest that it is the sister taxon of Pipidae. However, this phylogenetic placement of the new taxon should be corroborated in a future rigorous analysis that should include some putative stem pipid taxa that currently are being restudied.

INTRODUCTION

Apart from the basal frogs *Vieraella herbstii* and *Notobatrachus degiustoi* of Jurassic age, hitherto known Mesozoic records of anurans in South America are primarily from the Upper Cretaceous. Furthermore, most of these remains are from beds in the Campanian–Maastrichtian range. These data document that pipid and neobatrachian frogs had a long history in this continent, and that significant diversification had taken place before the end of the Cretaceous. However, this extensive gap in the South American record to date has failed to furnish evidence on the early evolution and historical biogeography of these amphibian taxa. This is particularly unfortunate because substantial modification of intercontinental relationships, as well as drastic physiographic and climatic changes related to Gondwana breakup and opening of the Atlantic Ocean, occurred during this span of time. The role that those events may have played on the evolution of continental vertebrate faunas in general has been discussed extensively, and the relevance of new finds that fill this gap in the fossil record to test phylogenetic and paleobiogeographic hypotheses is obvious.

Herein we describe the remains of a pipoid frog discovered as a result of the systematic paleontological search conducted recently by members of the Museo de Paleontología, Universidad Nacional del Comahue, in mid-Cretaceous continental beds of northwestern Patagonia (Báez and Calvo, 1990). In addition to the frog remains, the frequently articulated bones of other tetrapods, some still undescribed, as well as footprints, were collected in outcrops of the Candeleros Formation surrounding the Ezequiel Ramos Mexía water reservoir (Fig. 1). The anuran bones are from a locality known locally as El Gigante, on the eastern margin of the artificial lake, Río Negro Province.

This record extends the known presence of pipoids in South America back by about 20 million years. Previously, the oldest remains of this anuran group were those of the Campanian *Saltenia ibanezi*, a taxon represented mainly by impressions from

the Las Curtiembres Formation in northwestern Argentina (Báez, 1981). Fragmentary remains of a pipoid bearing a resemblance to the living African pipid *Xenopus* were described from the Los Alamos Formation considered to be late Campanian–Maastrichtian in age (Báez, 1987), whereas all other reported records in South America are from Cenozoic deposits (Báez, 1996).

Living pipoids comprise two groups: the fossorial Rhinophrynidae and the highly aquatic Pipidae. Pipoidae also includes Palaeobatrachidae, an extinct clade of Holarctic frogs with an aquatic mode of life; recent cladistic analyses (Cannatella and De Sá, 1993; Báez and Trueb, 1997; Báez and Pügener, 1998; Henrici, 1998) support the sister group-relationship of palaeobatrachids and pipids. The oldest record of pipoids is from the Upper Jurassic of North America (Henrici, 1998); thus, this record places a minimum age to the divergence of this group from pelobatoids according to our present understanding of anuran and pipoid phylogeny (Ford and Cannatella, 1993; Báez and Trueb, 1997; Maglia, 1998). Furthermore, if the rhinophrynid affinity of the Kimmeridgian *Rhadinosteus* (Henrici, 1998) from the Morrison Formation is confirmed, rhinophrynids and stem-pipids were already differentiated by the end of the Jurassic. Known records of palaeobatrachids and fossil rhinophrynids are restricted to the Northern Hemisphere, whereas the only living species of the latter group survives in southern North America and northern Central America. In contrast, all pipid fossil records hitherto known, as well as extant representatives, are from areas that were part of western Gondwana.

Institutional Abbreviations. BMNH, Department of Palaeontology, The Natural History Museum, London, U.K.; KU, The University of Kansas Natural History Museum, Division of Herpetology, U.S.A.; KUVp, The University of Kansas Natural History Museum, Division of Vertebrate Paleontology, U.S.A.; MB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; MUCPv, Museo de Geología y Paleontología

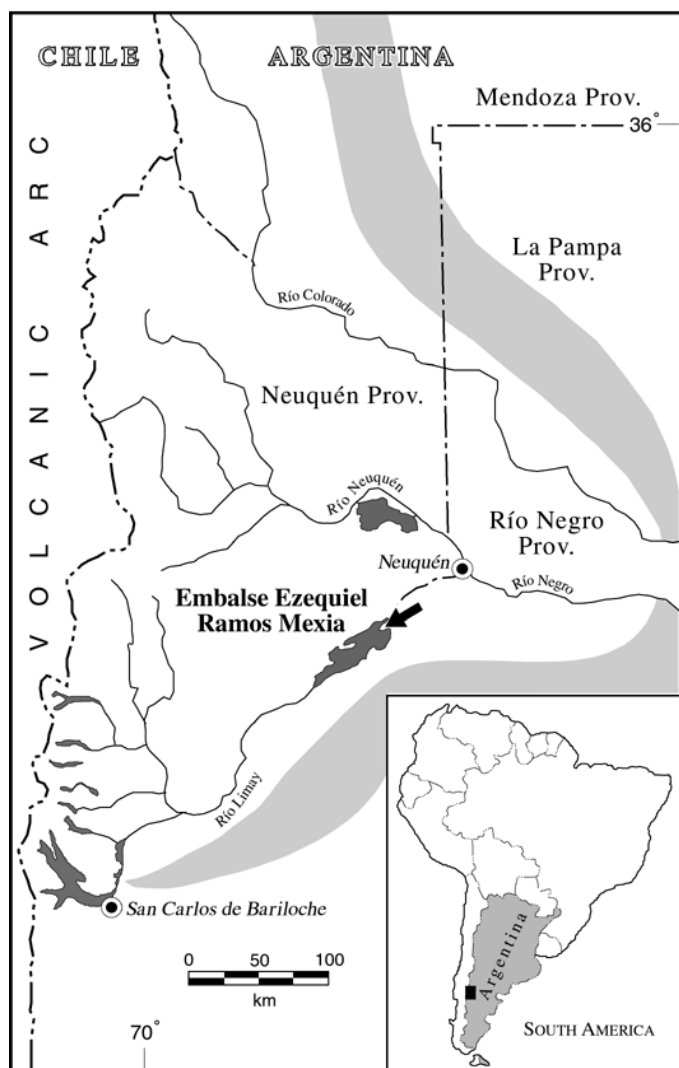


FIGURE 1. Map of west-central Argentina showing locations of the Neuquén Basin and fossil site. Stippled areas on the right indicate eastern boundaries of the basin: the Sierra Pintada, to the north, and the North Patagonian Massif, to the south.

de la Universidad Nacional del Comahue, Sección Paleontología de Vertebrados, Neuquén, Argentina.

GEOLOGICAL SETTING

The anuran remains from El Gigante are contained in an over 1000-m thick red-bed series, the Neuquén Group, that crops out extensively away from the Andean foothills in west-central Argentina (Mendoza, Neuquén, and Río Negro provinces). This continental sequence accumulated in the Neuquén Basin, a back-arc depocentre behind the Pacific margin of South America (Legarreta and Gulisano, 1989; Legarreta and Uliana, 1991; Fig. 1), as a result of renewed tectonic activity in the earliest Cenomanian (Orchuela and Ploszkiewicz, 1984; Vergani et al., 1995) or in the late Early Cretaceous. The Neuquén Group is dominated by fluvial-alluvial and locally lacustrine facies (Cazau and Uliana, 1973; Uliana and Dellapé, 1981; Legarreta and Gulisano, 1989). It comprises, from top to bottom, the Río Colorado, Río Neuquén, and Río Limay subgroups that formerly were given formation rank (Leanza and Hugo, 1997). The frog remains were collected from basal strata of the lower unit of

the Río Limay Subgroup, the Candeleros Formation, which outcrops in the northern and eastern margins of the Ezequiel Ramos Mexia Reservoir (Fig. 1). The depositional environment of the Candeleros sequence, which has a general fining-upward trend, has been interpreted as a meandering fluvial system (Gazzera and Spalletti, 1990). The frog-bearing horizon is 40 cm thick and consists of a reddish-brown, fine-grained sandstone containing lenses of medium sandstone. In places this bed is extensively bioturbated and desiccation cracks occur at the top. Desiccation cracks occur at the top of the underlying finely stratified siltstone also; this suggests intermittent flooding and subaerial exposure.

Over the last decade, geological and paleontological fieldwork in the area led to the discovery of a taxonomically diverse collection of vertebrate remains in the Candeleros Formation. These remains include those of unidentified chelid turtles (de Lapparent-de Broin et al., 1997), an araripesuchid crocodile (Ortega et al., 2000), and sauropod and theropod dinosaurs (Calvo and Bonaparte, 1988, 1991; Calvo and Salgado, 1995). Ornithischian and saurischian dinosaur footprints also were described from the Candeleros Formation (Calvo, 1991). Fossils found so far are poor biochronologic indicators but, because of the presence of trackways identified as those of iguanodontids, the dinosaur-bearing unit was tentatively bracketed in the Albian-Cenomanian (Calvo, 1991). Recently, an older, possibly Albian, age was suggested for this stratigraphic unit (Calvo and Salgado, 1996) based on the general similarity of the fossil vertebrate fauna with those recorded in the mid-Cretaceous of northeastern Brazil and Africa. Because it is from near the base of the red-bed series, the frog from El Gigante tentatively is considered to be about 100 Ma, at a time when continental separation had proceeded enough to allow a fully developed, but still exceedingly narrow, Atlantic Ocean (Nürnberg and Müller, 1991; Janssen et al., 1995).

MATERIAL AND METHODS

The material is preserved as an assemblage of disarticulated and partially articulated bones (Figs. 2A, 3) in three blocks glued together. The bones represent at least two individuals. However, the relative sizes and arrangement of some of the bones, as well as a distinctive macroscopic appearance, permitted association of a set of elements that correspond to an individual. The description below is based on one incomplete skeleton that presumably belongs to a single individual and that has been designated as the holotype. Most of the bones are exposed in ventral aspect; those of the skull, the braincase in particular, are superimposed and badly broken (Figs. 2B, 3). The carpus and the majority of the distal bones of the hands are missing, whereas most bones of both hind limbs are incompletely or not preserved; thus, the relative proportions between some structural units of the skeleton remain unknown. The snout-vent length is estimated to have been about 35 mm. In spite of its relatively small size, the high degree of ossification in the cranium, vertebral column, and epiphysial portions of the preserved limb bones indicates that this individual unquestionably completed metamorphosis.

The sediment that partially or completely covered the bones was removed mechanically with fine needles under a binocular microscope. A weak solution of lacquer gum in thinner was used to strengthen the bones. Drawings were executed under a Nikon M8 stereomicroscope, with a camera-lucida attachment. The general proportions of this frog are shown in Figure 4, which depicts a tentative partial restoration of the skeleton in ventral aspect.

In addition to the fossil material described herein and information from pertinent literature, specimens of fossil and extant

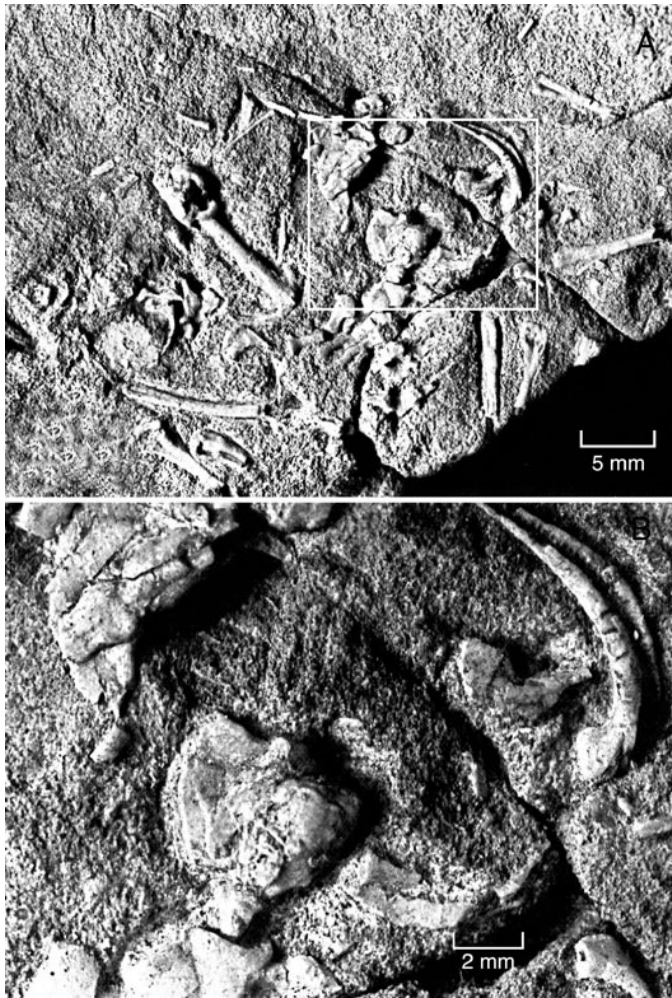


FIGURE 2. A, *Avitabatrachus uliana* (MUCPv 123). General view of scattered remains. White box indicates area of enlargement shown below. Refer to Figure 3 for identification of elements; B, enlargement of part of remains showing the braincase on the upper left corner and the left otic capsule below and to the right of braincase; the left angulosphenial and maxilla are located on the right. All elements are exposed in ventral aspect.

taxa were examined for comparisons; these specimens are listed in Appendix 1.

SYSTEMATIC PALEONTOLOGY

AMPHIBIA Linnaeus, 1758

ANURA Rafinesque, 1815

PIPOIDEA Fitzinger, 1843

PIPI MORPHA Ford and Cannatella, 1993

Genus *AVITABATRACHUS* gen. nov.

Type Species—*Avitabatrachus uliana* sp. nov.

Etymology—From the Greek *avita*, meaning ancient, primitive, in reference to this being an older record of pipoids in South America than those previously known, and *batrachos*, meaning frog.

Diagnosis—As for type and only known species.

AVITABATRACHUS ULIANA sp. nov.

Figs. 2–8

Holotype—MUCPv 123

Etymology—The specific epithet honors the late Miguel An-

gel Uliana, for his important contribution to the knowledge of the stratigraphy and evolution of the Neuquén Basin.

Horizon and Type Locality—Basal part of the Candeleros Formation, Río Limay Subgroup of the Neuquén Group; Albian or earliest Cenomanian. El Gigante, eastern margin of the artificial lake Embalse Ezequiel Ramos Mexia, Río Negro Province, Argentina.

Diagnosis—Moderately small pipimorph frog (sensu Ford and Cannatella, 1993) that shares with Pipidae conch-like squamosals, deeply excavated prootics to form channels for the Eustachian tubes, articulations for the lower jaws at the anterolateral corners of otic capsules and fused sacrum and urostyle; it differs from all pipimorph taxa in having distinct flanges along the posterior halves of the prootics medial to the inner ear region and four posterior presacral vertebrae bearing wide transverse processes that are not strongly directed anteriorly. Differs further from *Saltenia* and *Shelania* in the presence of toothed maxillae and rectangular pterygoid otic plates, and from *Saltenia* also in the fusion of the first two vertebrae. The narrow cultriform process of parasphenoid additionally distinguishes it from pipine genera.

DESCRIPTION

Cranium

The skull is about as long as wide, with prominent otic capsules, each lacking an obvious ossified crista parotica (Figs. 2B, 4). The articulation for the lower jaw is located in the anterior area of the otic capsule. The anteroposterior length of the skull, including the occipital condyles, represents about one third of the estimated snout-vent length (ca. 35 mm).

Frontoparietal—Portions of this bone are visible beneath the sphenethmoid and parasphenoid (Figs. 2B, 3, 5A), whereas a distinct impression of rounded margin clearly corresponds to the dorsal imprint of the posterior part of this element. The integrity of the margin indicates that the frontoparietal was a broad, azygous plate. The frontoparietal has an exceedingly shallow contour with a low crest along its margin. Partial disassociation of the frontoparietal from the braincase, and reorientation of the long axis of the bone with respect to that of the sphenethmoid strongly suggests that the frontoparietal was not fused with the underlying endochondral elements. Incomplete preservation prevents detailed reconstruction of the shape of the anterior and lateral margins, and determination of the presence of a pineal foramen.

Nasals—A pair of laminar bones preserved on a piece of rock adjacent to the anterior end of the sphenethmoid is tentatively identified as the nasals (Fig. 5A). The overall shape suggests that the nasals were in contact with each other along their medial margins. Each nasal probably roofed the olfactory capsule completely, and lacked a distinct rostral process. The posterior margins of these bones are shallowly convex posteriorly and, apparently, they were slightly overlapped by the anterior part of the frontoparietal.

Maxillae—A nearly complete left maxilla, exposed in ventral aspect, is preserved alongside the lower jaw (Figs. 2, 3, 5B). It bears about 30 tooth sockets, but teeth are not preserved; the dentition extended nearly to the rounded posterior terminus of this bone. There is no evidence that the maxilla was in articulation with a quadratojugal; the latter bone probably was absent. Although the anterior end is broken, the part of the maxilla preserved is large, indicating that the bone was relatively long, subtending at least two thirds of the orbit. The extremely fragile condition of this bone prevented removal of the sediment to expose its dorsal aspect; thus, the presence of a preorbital process could not be assessed.

Prootics and Exoccipitals—These endochondral elements are indistinguishably fused to form the proportionally large otic

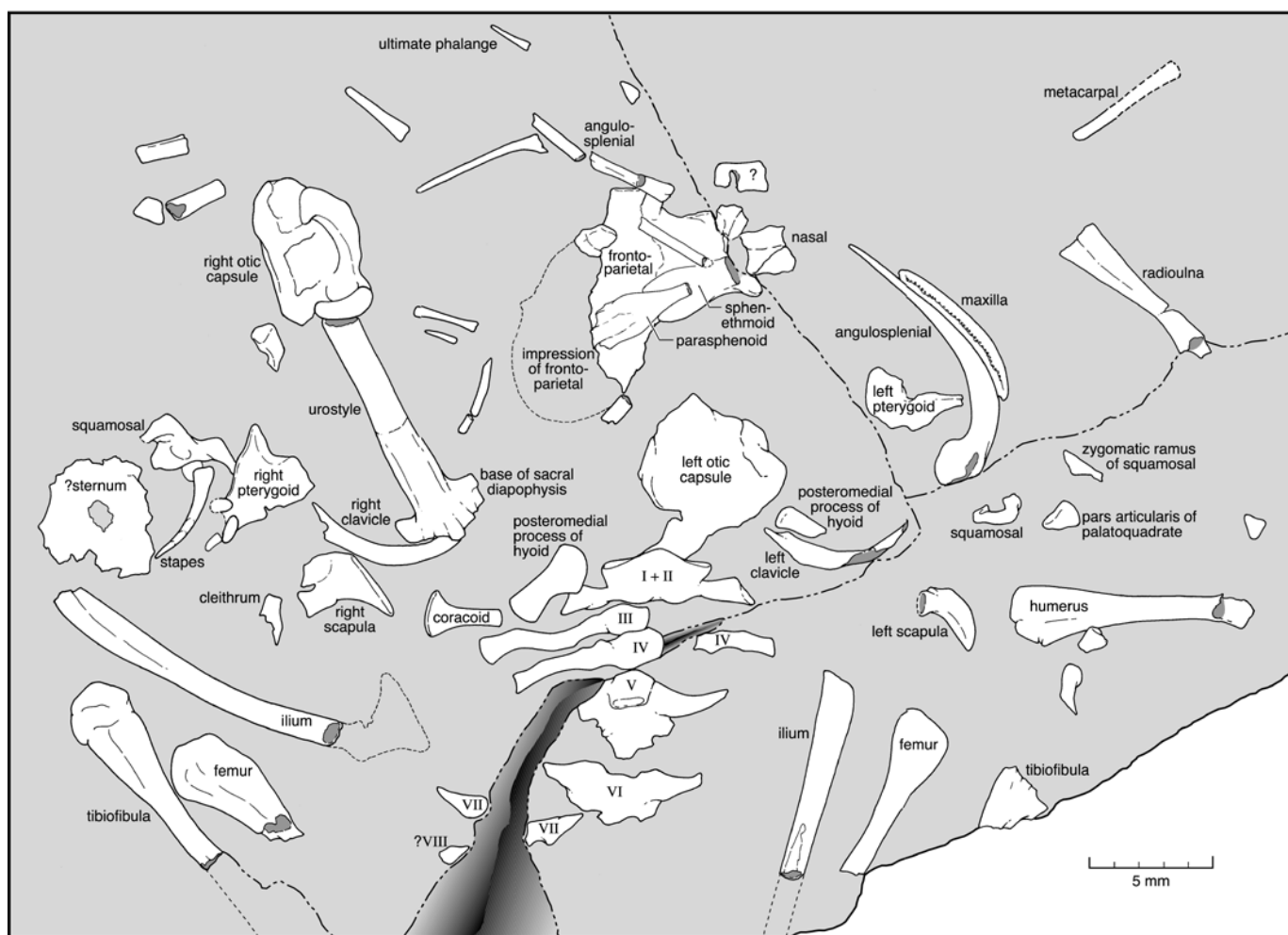


FIGURE 3. *Avitabatrachus uliana*. Diagram showing position and identification of remains of holotype (MUCPv 123). Gray background indicates sediment; broken line indicates impression; and dashed lines show fractures in rock.

capsules (Figs. 2A, 2B, 3, 4). Separation of left and right capsules indicates that the prootics were not synostotically united medially and that the exoccipitals were not completely fused to each other; thus, the margin of the foramen magnum was not entirely bound in bone. Each otic capsule is quadrangular, lacking a well-developed crista parotica. The dorsal surface of the otic capsule is smooth (Fig. 6A), lacking crests or a prominent epiotic eminence. Ventrally, the inner ear region is relatively bulbous. Anterior to the latter region, a transverse concave area served to accommodate the medial portion of the middle ear cavity, or Eustachian tube, in life (Fig. 6B). The anteroventral ledge bears a small process that may correspond to the basal process. A narrow, but distinct longitudinal flange is located along the medial margin of the ventral surface of the otic capsule; the flange is approximately one-third the length of the capsule. The lateral wall of the otic capsule bears a large fenestra ovalis. The occipital condyles are large and kidney-shaped; lateral to each of the latter structures there is a considerably deep condyloid fossa at the end of which a wide jugular foramen opens. No other openings are evident.

Plectral Apparatus—An isolated bone associated with the squamosal is identified as the stapes (Figs. 3, 7A). This elongate bone extended anterolaterally around the side of the otic capsule. The proximal portion of the pars media plectri is wider than the distal end. The stylus narrows at the point of flexion

around the otic capsule. No accessory processes articulating with the squamosal are present. Proximally, the stapes bears a distinct expanded pars interna plectri, or footplate, that partially filled the fenestra ovalis.

Squamosals—Each of these bones is highly modified into a funnel-shaped structure that surrounds the associated stapes (Figs. 3, 7A). Although the detailed morphology can not be discerned owing to the poor preservation, the overall shape of this element suggests that the tympanic annulus participated in the formation of a complex tympanosquamosal bone. A moderately long zygomatic process that did not articulate with the maxilla is present.

Parasphe-noid—This bone is not fused to the braincase and lacks posterolateral alae underlying the otic capsules (Figs. 2B, 4). The cultriform process is narrow; however, it is broken into several pieces. The process seems to have extended slightly anterior to the level of the plana antorbitalae at the anterior margins of the orbits, but apparently did not reach the premaxilla. The corpus is slightly expanded laterally at the level of the anterior margin of the otic capsules and slightly constricted posteriorly. It bears a narrow ridge along the midline of the corpus. The most posterior portion of this bone is not preserved.

Vomers—There are no remains that could be identified as vomers. It is also noteworthy that no scars that might have marked an area of contact of vomers are visible on the ventral

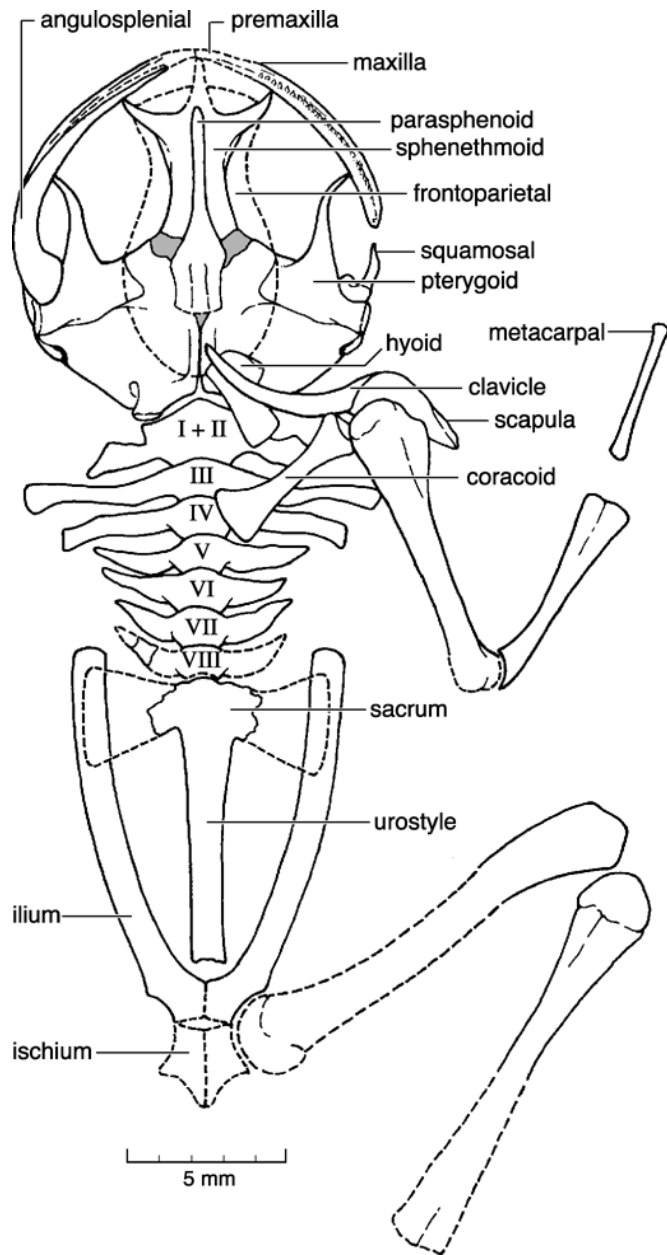


FIGURE 4. Partial restoration of the skeleton of *Avitabatrachus uliana* in ventral aspect. Lower jaw removed on left side.

surface of the sphenethmoid or parasphenoid cultriform process. Although negative, this evidence suggests that these bones either were absent or were located in the palate floor anterior to the level of the antorbital plane and not preserved.

Sphenethmoid—The sphenethmoid is single and extensively ossified, especially in the olfactory region (Fig. 5A). In the orbitotemporal region, it forms the relatively narrow braincase that extends posteriorly nearly to the anterior walls of the otic capsules. Its convex ventral surface is invested by the cultriform process of the parasphenoid; in the orbital region, the sides of the sphenethmoid are sloped dorsolaterally toward the roof of the cranium, but the width of the sphenethmoid is much less than that of the overlying frontoparietal. On either side of the parasphenoid, there is a notch in the posteroventral margin of the sphenethmoid; these notches might correspond to the anterior margins of the optic foramina or of common foramina

for the optic and prootic nerves. The dorsal aspect of the sphenethmoid is unknown, because the bone is exposed in ventral aspect; the shape and size of the frontoparietal and presumed nasal fragments suggest that in its natural position, the sphenethmoid was completely obscured dorsally by these dermal bones. Anteriorly, the sphenethmoidal ossification extends laterally on both sides to form complete vertical osseous walls between the nasal capsules and the orbits; therefore, the plana antorbitale were ossified (Fig. 5A). The orbitonasal foramina are enclosed in bone. The left and right olfactory capsules are separated by a bony partition formed by the septum nasi.

Neopalatines—We were unable to identify a scar that might be attributed to the area of contact between these bones and the bony sphenethmoid. Thus, it is presumed that these palatal bones were absent owing to the extensive ossification of the postnasal walls.

Pterygoids—The anterior ramus of this triradial bone was directed anterolaterally to articulate with the maxilla in the mid-orbital region. A small temporal flange is present along the posterior part of this ramus. The medial and posterior rami are laminar, and form a rectangular plate (Figs. 5B, 7A); this otic plate seems to have floored the most lateral part of the Eustachian canal. The short posterior ramus extends posterolaterally to articulate with the squamosal and invests the ventromedial aspect of the ossified pars articularis of the palatoquadrate cartilage.

Mandibles—A nearly complete left angulosplenia is preserved (Figs. 2, 3, 5B). This well-ossified bone lacks ridges and odontoids; it is relatively long and probably extended to the mandibular symphysis. Posteriorly, the angulosplenia bears a poorly developed coronoid flange. The Meckelian canal seems to be closed. No bone fragment could be positively identified as a dentary; however, based on the shape and proportions of the angulosplenia, we think that the dentary must have been a slender, rather short component of the mandible. There is no evidence of mentomeckelian bones.

Hyolaryngeal Skeleton—The only preserved components of this structure are the ossified portions of the posteromedial processes. These are robust bones; although both of their ends are expanded, the anterior termini are more broadly expanded than the posterior ends (Figs. 3, 7B).

Postcranial Skeleton

Presacral Vertebrae—The vertebral column is composed of at least seven discrete presacral vertebrae, which are partially articulated and exposed in ventral aspect (Fig. 7B). Only fragmentary remains represent the posterior presacrals. The opisthocoeleous condition is obvious in the three available disarticulated presacral centra, and, in addition, an anterior condyle is present on the centrum of the sacral vertebra; thus, all trunk vertebrae are assumed to have been structurally opisthocoeleous. The vertebral centra are dorsoventrally flattened (Fig. 8), and, thus, probably had an epichordal mode of development. The first presacral vertebra or the atlas, bears short transverse processes that are slightly expanded distally. A foramen is located just in front of each transverse process; this suggests that this vertebra is a compound of Presacrals I and II. The atlantal centrum is relatively short; anteriorly, the cervical cotyles are narrowly separated, and their articular surfaces extend medially onto the convex anteroventral margin of the atlas. No intercotylar notch is present. Presacral Vertebrae III and IV have short centra and bear unusually long, slender, and slightly undulated transverse processes; discrete ribs are absent. The transverse processes of Presacral III are the longest and directed almost horizontally; the overall width of this vertebra seems to have exceeded that of the sacrum. The transverse processes of Presacral IV are directed slightly posteriorly and are about twice as long as the

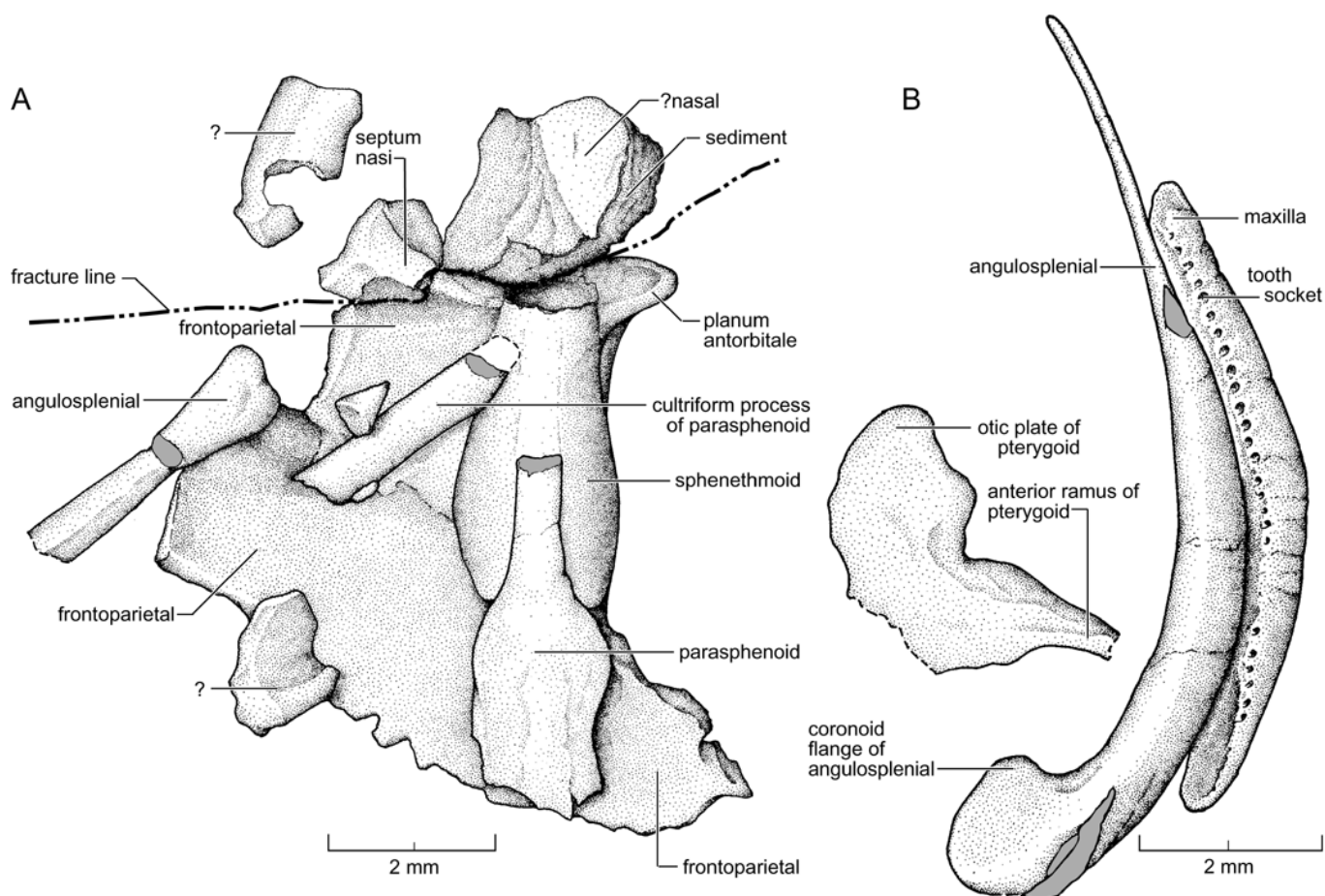


FIGURE 5. *Avitabatrachus uliana* (MUCPv 123). **A**, braincase and associated elements in ventral aspect; **B**, left maxilla, angulosplenic and pterygoid in ventral aspect. Fracture planes of bones are shown in cross hatching.

atlantal transverse processes. All posterior presacral vertebrae bear short transverse processes that are exceedingly wide basally and tapered distally. The transverse processes of Presacrals V and VI are almost perpendicular to the longitudinal axis of the column, whereas those of Presacral VII, and possibly those of Presacral VIII, are directed slightly anteriorly. The neural arches of Presacrals V and VI are preserved in ventral view; they are well ossified and extend posteriorly well beyond the level of the postzygapophyses. This posterior development of the neural arches indicates that at least the posterior presacrals were completely imbricate. The postzygapophyses have transversely elongated, flat articular surfaces that lack sulci and ridges (Fig. 8).

Sacrum—The sacrum is formed by one vertebra and is fused to the urostyle (Figs. 3, 7A). The sacral diapophyses are constricted medially but this basal part is distinctly broad. Although the distal portions of both diapophyses are missing, the morphology of the parts that are preserved indicates that they were distally dilated in an anteroposterior direction, with the distal expansion no more than twice the width at the base. No nerve foramina are visible.

Urostyle—This bone is relatively short, its length being approximately equivalent to that of the first six presacral centra. It is relatively wide also, but there is no evidence of the presence of postsacral vertebrae (Figs. 2A, 3, 7A).

Pectoral Girdle—Based on the morphology, and the relative positions of the clavicles and coracoids, the pectoral girdle is thought to have been structurally arciferal. The scapula is ro-

bust, with its length being about one and half times greater than its medial width (Fig. 7A). Medially, the partes acromialis and glenoidalis are separated by a well-defined cleft. The anterior margin is slightly convex; the lateral end of the clavicle, which was not fused to the scapula, overlay most of it. The shaft is relatively poorly developed, as the transverse diameter of the glenoid fossa represents more than half of the total length of the scapula. The posterolateral corner of the shaft is elaborated into a distinct projection. The lateral margin bears a groove for the suprascapular cartilage.

The clavicle is anteriorly concave and relatively wide in an anterior-posterior dimension (Fig. 7A). It seems to have extended an equal distance over the dorsum and the venter of the procoracoid cartilage. Its medial end is acuminate, whereas its tapered lateral end broadly overlapped the anterior margin of the scapula, but was not synostotically fused to the latter bone. The lateral (i.e., glenoid) half of the right coracoid is preserved; its medial (i.e., sternal) half is represented by a distinct impression. The lateral end of this bone is slightly expanded to bear a subcircular articular facet. There also is a distinct anterior process extending from the anterolateral margin of the coracoid toward the clavicle. The sternal end is broadly expanded, particularly anterior to its longitudinal axis. A thin, subcircular plate of bone with the central part missing may represent an ossified part of the sternum.

Forelimbs—The left humerus is nearly complete, but poorly preserved in lateral view (Fig. 2A, 3). It is a straight and rather slender bone with a distinctly dilated proximal end. The deltoid

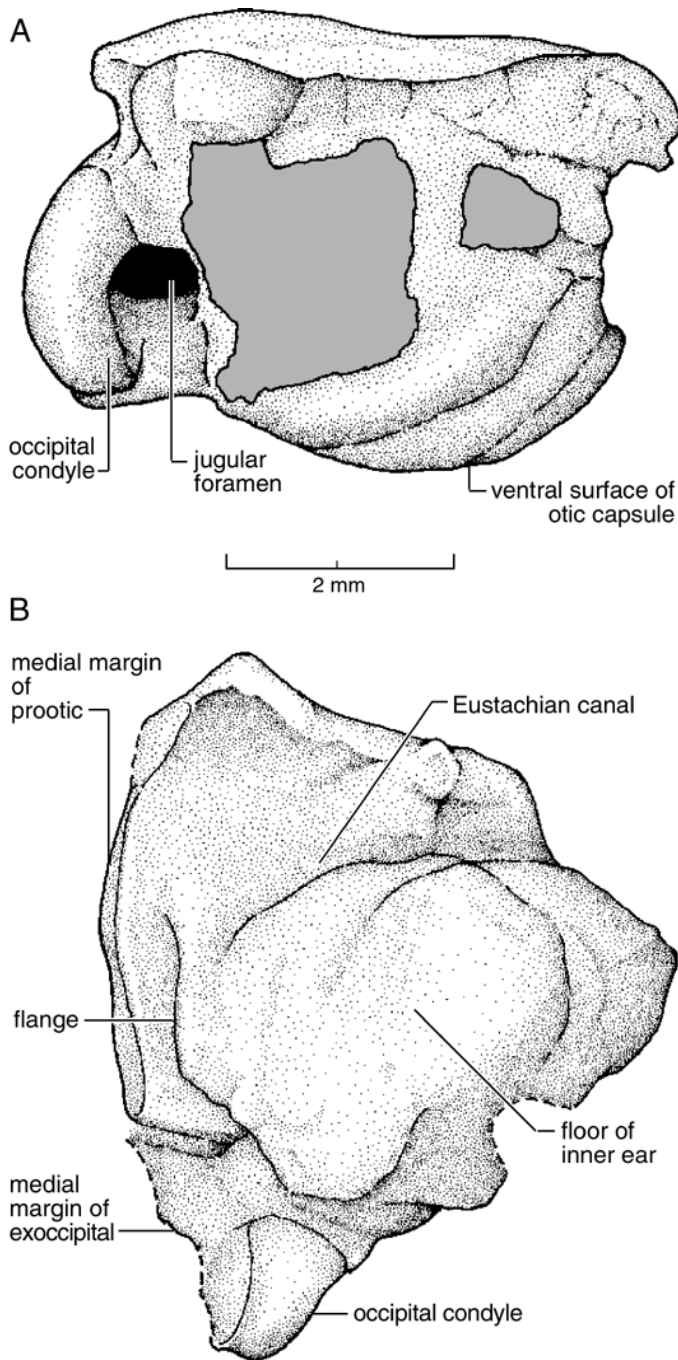


FIGURE 6. *Avitabatrachus uliana* (MUCPv 123). **A**, right otic capsule in lateral aspect; **B**, left otic capsule in ventral aspect. Gray areas are broken portions of the otic capsule filled with sediment.

crest is conspicuous and extends over one third of the bone length. The outline of the distal part of the bone indicates the ventral ball was relatively small, not protruding much beyond the small lateral epicondyle.

Based on the preserved left radioulna, the length of each component of this compound bone represents about three-quarters that of the humerus. The proximal end has a distinct olecranon process, whereas the distal end is expanded. A longitudinal groove along the distal third of the shaft corresponds to the zone of fusion between radius and ulna.

The components of the distal segments of the forelimb are not preserved in situ; thus, it is difficult to identify these elements confidently, even if present. An isolated metacarpal seems to belong to the holotype. It is an elongated bone, the length of which is approximately three quarters that of the radioulna. Disarticulated, scattered, small triangular bones are probably distal phalanges of the hand.

Pelvic Girdle—The complete right ilium is preserved, although its posterior part was lost during preparation. Nevertheless, description of the lost section is based on a photograph and the impression in the sediment left by the missing part. The anterior half of the left ilial shaft also is preserved. The most anterior portion of the shaft is dorsoventrally flattened and bears a longitudinal sulcus, whereas the remaining part is rod-like and lacks crests and ridges. The posterior, or acetabular, part of this bone is approximately triangular. Anterodorsal to the elongated acetabular fossa, there is a low, rounded dorsal prominence. The supra-acetabular region is well developed and has only a modest dorsal projection; it is less expanded than the subacetabular region. The pubes and ischia are unknown.

Hind Limbs—The hind limbs are represented by meager portions of the distal ends of both femurs and the proximal ends of each tibiofibula. The shape of the distal segment of the right femur suggests that this bone was slightly sigmoid.

DISCUSSION

The anuran from the Candeleros Formation is a member of Pipoidae based on its possession of a parasphenoid lacking subotic alae and an azygous frontoparietal, both features are considered pipoid synapomorphies (Ford and Cannatella, 1993; Báez and Trueb, 1997; Henrici, 1998). Pipoidae is the node-based name applied to the clade that includes the most recent common ancestor of living pipids and rhinophrynids and all of its descendants. Pipoid taxa that are more closely related to living Pipidae than to living rhinophrynids comprise Pipimorpha (Ford and Cannatella, 1993).

Phylogenetic placement of the new taxon within Pipoidae can be examined in the context of recent parsimony analyses of pipoid frogs (Báez and Trueb, 1997; Báez and Púgener, 1998; Henrici, 1998). In addition, it seems relevant to make preliminary comparisons with the Early Cretaceous pipoids *Thoraciliacus rostriceps* and *Cordicephalus* spp. (Nevo, 1968; Trueb, 1999; pers. obs) from the Hatira Sandstone or equivalent strata in southern Israel (Estes et al., 1978; Mateer et al., 1992), even though the restudy of these taxa is in progress and their cladistic relationships need to be appraised. Moreover, several features of *Thoraciliacus* and *Cordicephalus* merit reinterpretation and should be described; thus, a rigorous cladistic analysis of the interrelationships of pipoids, including *Avitabatrachus*, as well as the putative stem pipids *Cordicephalus* and *Thoraciliacus*, is necessary and is in preparation.

Several synapomorphies unite palaeobatrachids and pipids into a clade (Báez and Trueb, 1997; Báez and Púgener, 1998). These are: (1) anterior pointed process of the maxilla that reaches the alary process of the premaxilla; (2) incomplete maxillary arcade; (3) prootic with knob-like process; (4) medial and posterior rami of pterygoid expanded to floor the Eustachian tube at least partially; (5) parasphenoid reaching the maxillary arcade; (6) squamosal surrounding the stapes; (7) depressed vertebral centra; (8) glenoid area of scapula about half, or less, of scapular width; (9) ilia with wide interilial expansion in ventral region; and (10) ossified pubis. Henrici (1998) mentioned other putative synapomorphies that can be added to this list: (11) teeth conical, (12) elongate metapodials, and (13) ribs present. Some of conditions listed above, such as 1, 10, 11 and 13, can not be assessed in the available material of *Avitabatrachus*, whereas character states 2, 3, 4, 6, 7, 8, 9, and 12 are present,



FIGURE 7. *Avitabatrachus uliana* (MUCPv 123). A, right pterygoid and squamosal with associated stapes above; right scapula and clavicle below; B, vertebral column.

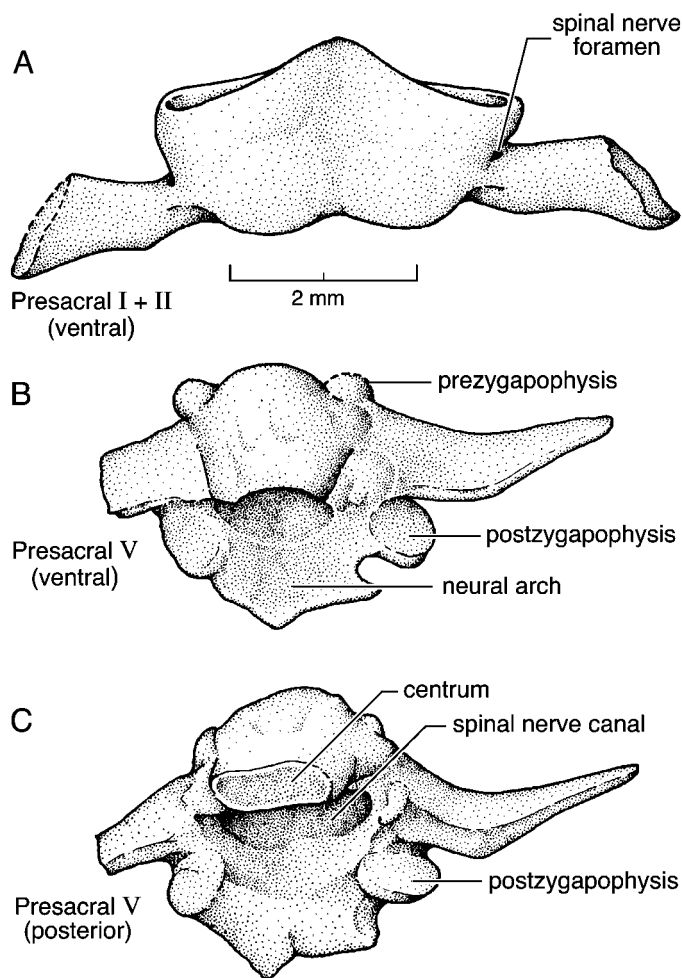


FIGURE 8. *Avitabatrachus uliana* (MUCPv 123). Presacral vertebrae. A, fused Vertebrae I and II in ventral aspect; B, Vertebra V in ventral aspect; C, Vertebra V tilted to show the dorsoventrally flattened centrum.

thus indicating that, minimally, the new taxon is a member of Pipimorpha. With respect to character state 5, in *Avitabatrachus*, the parasphenoid seems not to have extended anteriorly beyond the level of the antorbital plane, a reversal that occurs in Hymenochirini within Pipidae; however, this bone is broken into several fragments in the fossil from El Gigante and some of the pieces might be missing.

Character state 7 merits some comments. Traditionally, the shape of the vertebral centra has been considered to reflect distinctive morphogenetic patterns (Griffiths, 1963); thus, extremely flat centra, as those of pipids, result from their epichordal (sensu Kluge and Farris, 1969) mode of development. The vertebral centra of *Avitabatrachus* are shallow, as are the centra of palaeobatrachids and *Cordicephalus* (e.g., KUVV 127525); thus, the vertebral columns in these taxa are presumed to have had a developmental pattern similar to that in living pipids. In contrast, the centra of *Thoraciliacus* have been described as ectochordal (Nevo, 1968; Trueb, 1999), a condition that also occurs in rhinophrynids and a closely related fossil taxon (Henrici, 1998). At present, the phylogenetic significance of the pattern of vertebral development in anurans is unclear, owing to the intrafamilial and intrageneric variation and the occurrence of intermediate states, as discussed by Kluge and Farris (1969). Moreover, depth of centra varies along the individual column (pers. obs.) and some vertebral centra of taxa reported as having epichordal vertebrae may have an almost circular cross section (Báez and Trueb, 1997: fig. 17), thus making it difficult to infer the morphogenetic pattern from the shape of the adult centra alone. A critical, comparative study of the developmental mode of the vertebral centra based on a sound assessment of the phylogenetic relationships will elucidate the history of this character change in anurans.

The teeth are not preserved in the studied specimen; thus, it is not possible to assess the presence of conical teeth (synapomorphy 11 of the list above). However, it should be noted that, among pipoids, *Rhadinosteus* (Henrici, 1998), *Thoraciliacus* (Trueb, 1999) and *Cordicephalus* (e.g., KUVV 127543) have pedicellate bicuspid teeth; unambiguous resolution of the phylogenetic placement of these taxa is necessary to corroborate that monocuspid teeth is a synapomorphy that supports common ancestry of palaeobatrachids and pipids, and not a convergent condition in these clades.

The metacarpals are elongate in *Avitabatrachus*, as in palaeobatrachids and pipids in general. However, the relative proportions of these bones and radioulnae vary among fossil and living taxa, but the evolutionary and functional implications of these differences have not been examined. In *Avitabatrachus* the length of the metacarpus represents about two-thirds the length of the radioulna, whereas in *Palaeobatrachus*, the metacarpals are about as long as the radioulna (e.g., MB 108.03; BMNH 35811); the proportions of these bones in *Thoraciliacus* and *Cordicephalus* are almost intermediate, according to the measurements given by Nevo (1968).

The fossil from El Gigante shares with pipids several derived character states that indicate that it is more closely related to the crown group Pipidae than to palaeobatrachids, as discussed below. Unlike *Thoraciliacus*, *Cordicephalus*, and palaeobatrachids, which have an essentially T-shaped squamosal, the squamosal of *Avitabatrachus* is a conch-like structure (Fig. 7A); this suggests that the tympanic annulus may be synototically fused with this bone as in pipids. In *Avitabatrachus*, the undersides of the prootics are deeply excavated to form channels for the Eustachian tubes. Although elongated Eustachian tubes may have been present in *Cordicephalus* and *Palaeobatrachus*, deep canals on the ventral surface of the auditory capsules are not evident in the material of these taxa examined. In addition, the length and orientation of the posterior rami of the squamosals in the new taxon indicate that the articulation for the lower jaw lies at the anterolateral corner of the otic capsule. The articulation is more posterior in *Thoraciliacus* (e.g., Trueb, 1999) and *Cordicephalus* (e.g., KUVV 127543, 127544), and distinctly ventrolateral to the otic capsules in palaeobatrachids (e.g., *Palaeobatrachus luedeki* MB. Am. 875; *P. grandipes* KUVV 124943; *P. diluvianus* KUVV124955). The maxillae lack distinct partes dentales; such structures occur in the maxillae of palaeobatrachids (*Palaeobatrachus*, Špinar, 1972; *Pliobatrachus*, Vergnaud Grazzini and Mlynarski, 1969), *Thoraciliacus*, and *Cordicephalus*. In *Avitabatrachus* the sacrum is fused to the urostyle as it is in pipids. In contrast, the sacrum and urostyle are unfused in palaeobatrachids (bicondylar sacrum-urostyle articulation), *Thoraciliacus* (monocondylar sacrum-urostyle articulation), and, probably, *Cordicephalus* (possibly monocondylar sacrum-urostyle articulation).

Some of the synapomorphies that support the monophyly of Pipidae (Báez and Trueb, 1997; Báez and Pügener, 1998) occur in the plesiomorphic state in *Avitabatrachus uliana*. This suggests that this species might be placed outside the node that unites the most recent common ancestor of the living pipids and all of its descendants. Unlike pipids, the margins of the optic foramina are not completely enclosed in the sphenethmoidal ossification. This plesiomorphic condition is present in palaeobatrachids (Špinar, 1972; e.g., KUVV 124935, 124971); the configuration of the braincase in the posterior orbital region in *Thoraciliacus* and *Cordicephalus* is difficult to ascertain owing to the crushed condition of this area in the specimens examined. As in *Thoraciliacus*, *Cordicephalus*, and palaeobatrachids, the parasphenoid is not incorporated into the braincase in *Avitabatrachus*, whereas it is partially fused with the overlying endochondral bones in adult pipids. The angulosplenials bear poorly developed coronoid processes in the new taxon; the processes are not expanded into a flange, a derived condition of pipids (Cannatella and Trueb, 1988). In palaeobatrachids the coronoid processes are tubercle-like, a configuration that also characterizes *Thoraciliacus* and *Cordicephalus*.

Avitabatrachus might have shared with pipines, a subclade of Pipidae represented today by the South American *Pipa* and African *Hymenochirus* and *Pseudhymenochirus*, one of the four unique synapomorphies that support that clade: the anterior position of the posterior margin of the parasphenoid (Báez and Trueb, 1997). Although the posterior part of the parasphenoid

is missing in *Avitabatrachus*, the presence of distinct flanges medial to the inner ear region along the posterior halves of the prootics suggests that the parasphenoid did not extend posteriorly to near the foramen magnum in this taxon. These flanges are a distinctive feature of *Avitabatrachus*; flanges on the underside of the otic capsules anterad to the foramen magnum do not occur in other pipoid taxa, except in living hymenochirines in which they are associated with the posteromedial margins of the Eustachian canals and the extensive otic plates elaborated by the pterygoids. In *Avitabatrachus*, these flanges may have served for the insertion of the soft tissues that floored the median Eustachian tube before opening into the pharynx. Other pipine synapomorphies are either in their plesiomorphic state or the state in *Avitabatrachus* is unknown.

The poor preservation of the available material of *Avitabatrachus* precludes assessment of other features of comparative interest that might help to resolve its phylogenetic placement unambiguously. The vomers are reduced or absent in pipids, a derived condition that contrasts with the large extent of these palatal bones in most frogs. They are conspicuous in rhinophrynids, palaeobatrachids (Špinar, 1976) and *Cordicephalus* (e.g., KUVV 127543, 127544), but no evidence of these elements was found in the type specimen of *Avitabatrachus uliana*. Also, because of the fragility of the preserved maxilla and the difficulty in preparing it, it is not possible to ascertain the presence of conspicuous antorbital processes on the maxillae, a feature that occurs in several fossil pipid taxa from South America (Báez, 1996; Báez and Pügener, 1998), and was discovered in *Thoraciliacus* (Trueb, 1999) and *Cordicephalus* (e.g., KUVV 1275443). The septomaxillae are large and arcuate in pipids, a derived condition that contrasts with the small, complex septomaxillae of other anurans; these elements, however, were not identified in *Avitabatrachus*.

Other features of *Avitabatrachus*, the evolutionary significance of which are still equivocal, should be commented on. The nasal capsules are well ossified in *Avitabatrachus*; in particular, the postnasal wall is extensively ossified as it is in *Cordicephalus* (e.g., KUVV 127544), the Cretaceous–Paleogene pipid *Eoxenopoides* (Estes, 1977) and hymenochirines. The nasals, if correctly identified, lack distinct rostral processes and probably roofed the nasal capsules completely. These dermal elements formed the extensive dorsal covering of the nasal capsules in *Cordicephalus*, *Thoraciliacus*, and pipines. The extremely shallow nasals of palaeobatrachids and *Xenopus* probably are derived conditions that evolved independently in these taxa.

The parasphenoid, although incompletely preserved, resembles those of the rhinophrynids *Chelomophrynus* (Henrici, 1991) and *Rhinophrynus* (Trueb and Cannatella, 1982), and *Thoraciliacus* (e.g., KUVV 127555, 127556, 127558) in the presence of a clear distinction between a subotic, relatively wide corpus and an anterior, narrow cultriform process. This bone has an overall lanceolate outline in palaeobatrachids (Špinar, 1976) and *Cordicephalus* (e.g., KUVV 127543, 127544). As in some palaeobatrachids (Špinar, 1976) and unlike most pipimorph taxa, the parasphenoid bears a distinct longitudinal ridge on its ventral surface; in *Avitabatrachus* this is restricted to the posterior corpus of the bone.

One of the paired bony posteromedial processes of the hyoid, or thyrohyals, is preserved in the holotype of *Avitabatrachus*. It is remarkable in being robust, dorsoventrally flattened, and expanded at both ends, particularly at the anterior end; thus, it clearly resembles the same bones in the extant *Rhinophrynus* (Trueb and Cannatella, 1982) and the Eocene *Chelomophrynus* (Henrici, 1991). In the latter two taxa, the expanded surfaces of these bones might reflect the hypertrophy of the hyoglossus muscle in connection to the specialized mechanism of tongue protrusion for underground feeding described by Trueb and

Gans (1983). In some palaeobatrachids weakly ossified elements were identified as thyrohyals (Špinar, 1976), whereas in *Cordicephalus* (e.g., KUVV 127545) the bony posteromedial processes are slim and short. In extant pipids, which lack a tongue, the long, slender thyrohyals support the highly derived laryngeal apparatuses of these frogs (Trueb, 1996). In other fossil pipid taxa in which these bones are known, such as in *Shelania* and *Saltenia*, they are extremely long and expanded at their posterior ends only.

The first two presacral vertebrae are fused in *Avitabatrachus*; this fusion is common in pipimorph taxa and characterizes palaeobatrachids, *Cordicephalus* (e.g., KUVV 127543–45), *Thoraciliacus* (Trueb, 1999), and pipines within Pipidae. This condition varies intragenerically in xenopodines and closely related taxa. However, the vertebral column of the new taxon can be distinguished from those of other pipimorphs in many respects. Apart from the procoelous condition of the vertebral centra, the palaeobatrachids are characterized by the long transverse processes of Vertebrae III to VI and the incorporation of Vertebrae VII and VIII into the sacrum. In *Thoraciliacus* and *Cordicephalus* only Vertebrae III and IV bear long transverse processes, and the four most posterior presacrals have shorter processes. In the latter two taxa, the transverse processes of Vertebrae VI–VIII are markedly anteriorly oriented, as they are in pipids, whereas in *Avitabatrachus* these structures are only slightly so. In addition, in *Avitabatrachus* the transverse processes of the posterior presacral vertebrae are peculiar in the relatively wide basal portion, a configuration reminiscent that in *Thoraciliacus*.

The scapulae of *Avitabatrachus* resemble those of *Thoraciliacus* and *Cordicephalus* in the overall proportions and in the presence of a medial notch that separates the pars glenoidalis from the pars acromialis. The medial notch is absent and the scapular shaft is relatively larger in palaeobatrachids (Špinar, 1972; Manourová, 1976). Rhinophrynids (Henrici, 1991), palaeobatrachids, *Cordicephalus*, and *Thoraciliacus* lack synostotic fusion of the scapula and clavicle, as well as the extensive scapular process of the medial end of the clavicle. In addition, the scapulae are not fused to the clavicles in some fossil and living pipid taxa (Báez and Trueb, 1997); this evidence suggests that fusion of these two bones in xenopodines and hymenochirines within Pipidae is homoplastic.

CONCLUSIONS

From the above comparisons, it is clear that the frog material described herein represents a new pipoid taxon. Moreover, several derived conditions, such as the incomplete maxillary arcade, the reduced scapula, and long metapodials, indicate that this taxon is more closely related to Pipidae than to Rhinophrynidae; thus, it is a member of the stem-based Pipimorpha as defined by Ford and Cannatella (1993). In addition, the presence of presacral vertebrae with flat and opisthocelous centra, the synostotic fusion of sacrum and urostyle, the development of deep Eustachian canals anterior to the inner ear region on the prootics, and the conch-shaped squamosals support a closer relationship with pipids than with palaeobatrachids. Further resolution of the phylogenetic relationships of *Avitabatrachus* is obscured by the incomplete preservation of the available material and the still equivocal placement of the Early Cretaceous taxa from Israel. With regard to the latter, their incorporation into an analysis of fossil and extant pipoid taxa is critical in understanding character evolution among pipoids and the distinction between characters that are shared because of common ancestry and those that are shared because of a common way of life.

The specimen from the Caneleros Formation possesses a combination of character states not present in other known non-

palaeobatrachid pipimorph taxa and is here identified as a new genus and species: *Avitabatrachus uliana*. It is more derived than *Thoraciliacus* and *Cordicephalus* in the presence of a conch-like squamosal and deep excavations for the Eustachian tubes on the ventral surface of the prootics; unlike *Thoraciliacus* (Trueb, 1999), the vertebral centra are stegochordal and the sacrum is fused to the urostyle. The short posteromedial processes of the hyoid, which are expanded at both ends, the flanges along the medial portion of the posterior half of the otic capsules, the wide and slightly anteriorly directed transverse processes of the posterior presacral vertebrae differentiate the new taxon from other pipimorph taxa, including the extinct South American *Saltenia* and *Shelania* (Báez and Trueb, 1997; Báez and Pügener, 1998). Unlike these two latter taxa, *A. uliana* has toothed maxillae and a parasphenoid with a wide posterior corpus. The new taxon can be further distinguished from *Saltenia* in the fusion of first two vertebrae and the distinctly expanded transverse process of the resulting compound element, and from *Shelania* in the relatively delicate anterior rami of the pterygoids and the rectangular shape of the otic plate.

In summary, the foregoing comparisons suggest that *Avitabatrachus* is the sister taxon of Pipidae, although it seems to possess some pipine synapomorphies. The placement of the new taxon might be resolved in a complete phylogenetic analysis which should also include other known fossil pipimorph taxa that might be closer to the common ancestor of pipids than to palaeobatrachids and that, because of their combination of character states, are likely to change our understanding of character evolution among pipoid frogs. However, it is noteworthy that the available material of *Avitabatrachus* precludes assessment of the state of several significant characters and, thus, discovery of additional and better preserved remains appears essential to clarify its phylogenetic relationships.

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APPENDIX 1. List of comparative material used.

Recent Material—*Discoglossus pictus* KU 148617, Baixo Alentijo, Portugal; *Discoglossus sardus* KU 129239, Var, Ihle de Port Gros, near Hyeres, France; *Pelobates fuscus* MCZ 1012-3 (dry) Milan, Italy; *Pelobates varaldii* MCZ 31970 (dry) Mamora, Maroc; *Rhinophrynus dorsalis* KU 84886, Caculutla, Guerrero, Mexico.

Fossil Material—*Palaeobatrachus* spp., Bechlejovice, near Bratislava, Bohemia, Czech Republic, KUVF 12497A, B, 124972 A, 124975 A, B, 124976 A, B; *Palaeobatrachus luedeckei*, Markvartice, Bohemia, Czech Republic, MB Am 875; *Palaeobatrachus luedeckei*, Kostálova, Bohemia, Czech Republic, BMPD 37233, 35811, 35812, 35814; *Cordicephalus* spp. Maktesh Ramon, southern Negev, Israel, KUVF 127543–47; *Thoraciliacus rostriceps*, Maktesh Ramon, southern Negev, Israel, KUVF 127548, 127551–7, 127559–61, 127564–65, 127568–70.