ANNALS OF CARNEGIE MUSEUM

VOL. 81, NUMBER 4, PP. 295–309 30 SEPTEMBER 2013

AERUGOAMNIS PAULUS, NEW GENUS AND NEW SPECIES (ANURA: ANOMOCOELA): FIRST REPORTED ANURAN FROM THE EARLY EOCENE (WASATCHIAN) FOSSIL BUTTE MEMBER OF THE GREEN RIVER FORMATION, WYOMING

AMY C. HENRICI
Collection Manager, Section of Vertebrate Paleontology,
Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213
henricia@carnegiemnh.org

ANA M. BÁEZ
Departamento de Geología, Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires, Ciudad Universitaria, 1428 Buenos Aires, Argentina,
baez@gl.fcen.uba.ar

LANCE GRANDE
Division of Science and Education, The Field Museum,
1400 South Lake Shore, Drive, Chicago, Illinois 60605
lgrande@fieldmuseum.org

ABSTRACT

Five anurans have been previously reported from the Eocene Green River Formation, of which only two, a nearly complete skeleton and a tadpole, have been described. The skeleton has been identified as either *Eopelobates* Parker, 1929, or a pelobatid close to *Eopelobates* and *Pelobates* Wagler, 1830, but the tadpole is indeterminate. Another specimen has been figured but not described, another is a skin impression that is probably indeterminate, and the other is presumably lost. A sixth specimen is reported here. It represents a **new genus and species, *Aerugoamnis paulus*,** which is the first anuran to be reported from the Wasatchian (early Eocene) Fossil Butte Member of the Green River Formation. It consists of a single specimen that is dorsoventrally flattened and exposed primarily in dorsal view on one slab of rock, with a poor impression of the skull and a few bone fragments representing the counterpart. The specimen is nearly complete and the bones are preserved in articulation or in close association. The presence of a spiral groove of the iliac shaft suggests affinity with Anomocoela, a hypothesis that was tested through a phylogenetic analysis including representatives of the major clades of Costata, Xenoanura, Neobatrachia, and Anomocoela. The analyzed data set consists of 66 osteological characters scored for six fossil and 20 extant taxa. Results of the analysis place *Aerugoamnis* as a member of the stem of Pelodytidae. This placement is based on possession of two synapomorphies: presence of a distinct otic ramus of the squamosal and the crista parotica is poorly developed. Unlike extant pelodytids, *Aerugoamnis* has nasals that are separated by a narrow gap, a ventral flange on the pterygoid, and unfused tibiale and fibulare. Prior to the discovery of *Aerugoamnis*, fragmentary remains from the middle Eocene of Europe, the earliest of which are Lutetian (MP 13), have been questionably referred to the family. *Aerugoamnis* now is the earliest known occurrence of the anomocoelan lineage represented today by Pelodytidae.

KEY WORDS: Acosmanura, Amphibia, Green River Formation, North America, Pelodytidae, Pelodytomorpha

INTRODUCTION

The Green River Formation is famous for the abundant and exquisitely preserved fossils that it has produced, including a variety of vertebrate fossils. The formation was deposited primarily in three lakes, Lake Gosiute, Lake Uinta, and Fossil Lake during the Eocene. Among vertebrate fossils, fishes are the most common, followed by birds and turtles, with remains of crocodilians, amphibians, and mammals being somewhat rare (Grande 1984). To date, only five occurrences of fossil frogs have been reported from the Green River Formation. Cope (1884) mentioned the presence of a partial skull and vertebral column of a possibly immature anuran collected by Hayden. Grande (1984) has suggested that it most likely is from Hayden's "Petrified Fish Cut," which is in the lower 10 meters of the Laney Member of Lake Gosiute near Green River, Wyoming. The repository of this specimen is currently unknown. Grande (1984) reported on the presence of two additional, complete anurans, one from the G-4 locality in the Laney Member of Lake Gosiute and the other from the U-2 locality in the upper Parachute Creek Member of Lake Uinta, near Douglass Pass, Colorado. The G-4 specimen is a nearly complete anuran preserved as an impression of the dorsal surface of the skeleton, which Grande (1984) identified as a probable new species of the pelobatid genus *Eopelobates* Parker, 1929. Roček and Rage (2000) later corroborated its identity as a pelobatid (*Eopelobates* + *Pelobates* Wagler, 1830). The U-2 specimen consists of the skin impression of an anuran that Grande (1984) attributed to *Eopelobates* and Roček and Rage (2000) regarded as indeterminate. Another specimen from the Parachute Creek Member of Lake Uinta is a metamorphosed frog from Rio Blanco County, Colorado, that was figured, but not described, by Johnson and Stucky (1995; Gardner, 1999). An anuran tadpole, preserved as a skin impression, from the Evacuation Creek Member of Lake Uinta, near the ghost town of Watson, Uintah County, Utah, was described by Gardner (1999), but he was unable to identify it due to the lack of diagnostic characters.

This paper reports an additional anuran that was collected from the Fossil Butte Member deposits of Fossil

TABLE 1. Skeletal measurements of *Aerugoamnis paulus*. Measurements are in millimeters.

	Length	Width
SVL (snout-vent-length)	19.3	
Skull	6.6	7.8
Posteromedial process of hyoid apparatus, left	1.5	
Posteromedial process anterior end		1.4
Posteromedial process posterior end		1.6
Vertebral column	6.7	
Urostyle	4.5	
Cleithrum, left	2.2	
Scapula, left	1.9	
Humerus, left	4.0	
Radioulna, left	2.9	
Metacarpal III, right	1.1	
Femur, right	8.1	
Tibiofibula, right	8.3	
Tibiale, right	3.7	
Fibulare, right	3.9	
Metatarsal IV, right	~2.9	
Forelimb	8.0	
Hind limb	23.2	

Lake, near Kemmerer, Wyoming, which is identified here as a new genus and species of a stem pelodytid. The fossil was obtained from a whitish, laminated calcimicrite that was dated at about 52 Ma (Smith et al. 2010), which places it in the Wasatchian North American Land Mammal age. It represents the first anuran to be recovered from the Fossil Butte Member of the Green River Formation and adds greatly to our knowledge of anuran evolution, diversity, and paleobiogeography.

ABBREVIATIONS

Anatomical.—as, angulosplenial; **c,** columella; **d,** dentary; **eo-po,** fused exoccipital-prootic; **fp,** frontoparietal; **il,** ilium; **is,** ischium; **m,** maxilla; **mk,** mentomeckelian; **n,** nasal; **pm,** premaxilla; **p,** parasphenoid; **pp,** posteromedial process of hyoid apparatus; **pt,** pterygoid; **qj,** quadratojugal; **sg,** spiral groove; **sp,** sphenethmoid; **sq,** squamosal; **sv,** sacral vertebra; **svl,** snout-vent length; **u,** urostyle.

Institutional.—AMNH, American Museum of Natural History, New York; **CM,** Carnegie Museum of Natural History, Pittsburgh; **DMNH,** Denver Museum of Natural History; **FCEN,** Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires; **FMNH,** The Field Museum, Chicago; **KU,** University of Kansas, Lawrence; **MACN,** Museo Argentino de Ciencias Naturales, Buenos Aires; **MCNS,** Museo de Ciencias Naturales, Salta; **MCZ,** Museum of Comparative Zoology, Cambridge; **MNCN,** Museo Nacional Ciencias Naturales, Madrid; **MSU,** Michigan State University, East Lansing; **USNM,** United States National Museum, Washington, D.C.; **UTA,** University of Texas at Austin.

SYSTEMATIC PALEONTOLOGY

Amphibia Linnaeus, 1758
Anura Fischer von Waldheim, 1813
Anomocoela Nicholls, 1916

Aerugoamnis, new genus

Type Species.—*Aerugoamnis paulus*, new species

Diagnosis.—A member of Anomocoela based on the presence of a spiral groove on the iliac shaft. Within Anomocoela two characters indicate pelodytid affinities: otic ramus of squamosal forms distinct process and the crista parotica reduced. *Aerugoamnis* differs from extant *Pelodytes* Bonaparte, 1838, in that the nasals are separated medially by a narrow gap and the pterygoid bears a ventral flange. It differs from *Pelodytes* and *Miopelodytes* Taylor, 1941, in lack of fusion of the tibiale and fibulare to form a single element.

Etymology.—A combination of *aerugo*, Latin, for green and *amnis*, Latin, for river, in reference to the Green River Formation.

Aerugoamnis paulus, new species

Holotype.—FMNH PR2384: (Fig. 1) a nearly complete, articulated skeleton preserved as part on a slab of limestone. The unnumbered counterpart to this specimen, which consists of a poor skull impression and very little bone, is held in a private collection and thus is not a component of the holotype.

Locality and horizon.—Thompson Ranch Locality #1

(sensu Grande 2013) near Kemmerer, Wyoming, in the sandwich horizon of the Fossil Butte Member of the Green River Formation; lower Eocene, Wasatchian.

Diagnosis.—As for genus (currently monotypic).

Etymology.—*paulus*, Latin, for little.

Description

General.—The only known specimen is exposed as part, FMNH PR2384 (holotype: Fig. 1), and counterpart, which is unnumbered and held in a private collection but available to us for study. The majority of the skeleton is preserved on the part, whereas the counterpart contains only a few pieces of original bone and poor impression of the skull. Both the rock and some of the bone has been restored in FMNH PR2384. Here, a broad crack extends across the slab, passing through the sacral vertebra and left manus. The left tibiofibula is crossed by two broad cracks, one just distal of its midlength and another at its distal end. The latter crack also passes through the proximal ends of the tibiale and fibulare. These cracks have been filled with a material that closely resembles the surrounding matrix. Where the broad cracks cross the fossil skeleton, the missing bone has been restored. The specimen is coated with a thick layer of glue that forms a yellowish halo around the specimen and obscures detail in parts of the skeleton.

The specimen is nearly complete, and the bones are preserved in articulation or are closely associated. Strong dorsoventral compression has flattened the skeleton to a horizontal plane. The skull and vertebral column are preserved in dorsal aspect, with the limbs being fully extended and splayed from the trunk. Most of the elements of the skeleton are represented by bone, though the superficial bone is missing in some, and a minor number of bones or portions of bone are represented by impressions.

The specimen is small, with a snout-vent length (measured from tip of snout to end of pelvic girdle) of 19.3 mm (Table 1). The presence of an ossified columella indicates that the frog is a postmetamorphic individual. In most anurans in which the ossification sequence is known a columella, when present, always ossifies after metamorphosis is completed (e.g., Wiens 1989; Rodríguez Talavera 1990; Hall and Larsen 1998; Maglia 2003). Some carpal bones are ossified, but none of the tarsal bones are. Carpal and tarsal bones are usually the last to ossify in anurans (Wiens 1989; Maglia 2003), and this may occur well after the end of metamorphosis.

Skull.—(Figs. 1C, D). Sculpturing does not occur on any of the dermal skull bones. The premaxilla has a tooth-bearing pars dentalis and a long alary process that is laterally deflected at its distal end. Fifteen tooth positions are evenly distributed along the pars dentalis with 12 and ten teeth preserved in the left and right premaxillae, respectively. The long, slender, distally tapering maxilla extends posteriorly beyond the midlength of the orbit, but it does not reach the level of the posterior end of the orbit. The preorbital portion of the pars facialis of the maxilla is relatively high and of constant height up to the level of the anterior margin of the orbit, where it forms a distinct, acute, medially directed process. Because the skull is flattened, it cannot be determined if this is a preorbital process, which in an articulated specimen would be directed towards and/or articulate with the maxillary process of the nasal, or a palatine process. In the orbital region, the maxillary pars facialis is shallow, lacking a zygomatic process for articulation with the squamosal posteriorly. About 48 tooth positions are present along the pars dentalis of the maxilla. The small size of the teeth, coupled with poor exposure of some of them, make an accurate count difficult. As in the premaxilla, the teeth are pedicellate and, presumably, bicuspid. The anteriormost end of the maxilla is edentulous and in an articulated specimen would have overlapped a small portion of the lateral end of the premaxilla dorsal of the tooth row, where the premaxilla is beveled for reception of the maxilla. Posteriorly, the maxilla ends in an acuminate, edentulous posterior process that most likely articulated with the quadratojugal. The right quadratojugal is present in the counterpart, and a sliver of the left quadratojugal is present in FMNH PR2384.

As preserved, the bone comprising the nasals is very thin and somewhat translucent, especially the distal periphery of the bone, resulting in the underlying paired vomers being partially visible through the nasals. The nasals are sickle-shaped with a concave anterior margin that embraces posteriorly the fenestra exonarina. They are separated medially by a narrow gap and diverge from one another at their posterior ends. The distally tapering maxillary process extends laterally to form the anterior margin of the orbit and may have contacted the maxilla in an articulated specimen. Posteriorly, the nasals contact the anterior margin of the sphenethmoid.

Dorsoventral compression has caused the medial edges of the frontoparietals to be ventrally declined. As a result the medial edges of the frontoparietals, just posterior of the midlength of this element, contact the dorsal surface of the cultriform process of the parasphenoid, which is partially exposed between the frontoparietals. The anteriormost ends of the frontoparietals are not in contact, allowing the underlying sphenethmoid to be visible. From here to about the midlength, the medial edges of the frontoparietals are difficult to discern due to a covering of glue and matrix. Some bone in this region may be missing, which could have occurred when the specimen was collected. The frontoparietals are not in contact posteriorly. Because of uncertainty about the completeness of the medial edges of the frontoparietal, it cannot be determined if the right and left halves of the frontoparietal were medially separate from one another throughout their length. The lateral edges of the frontoparietals are straight and roughly parallel to one another, with no development of supraorbital flanges.

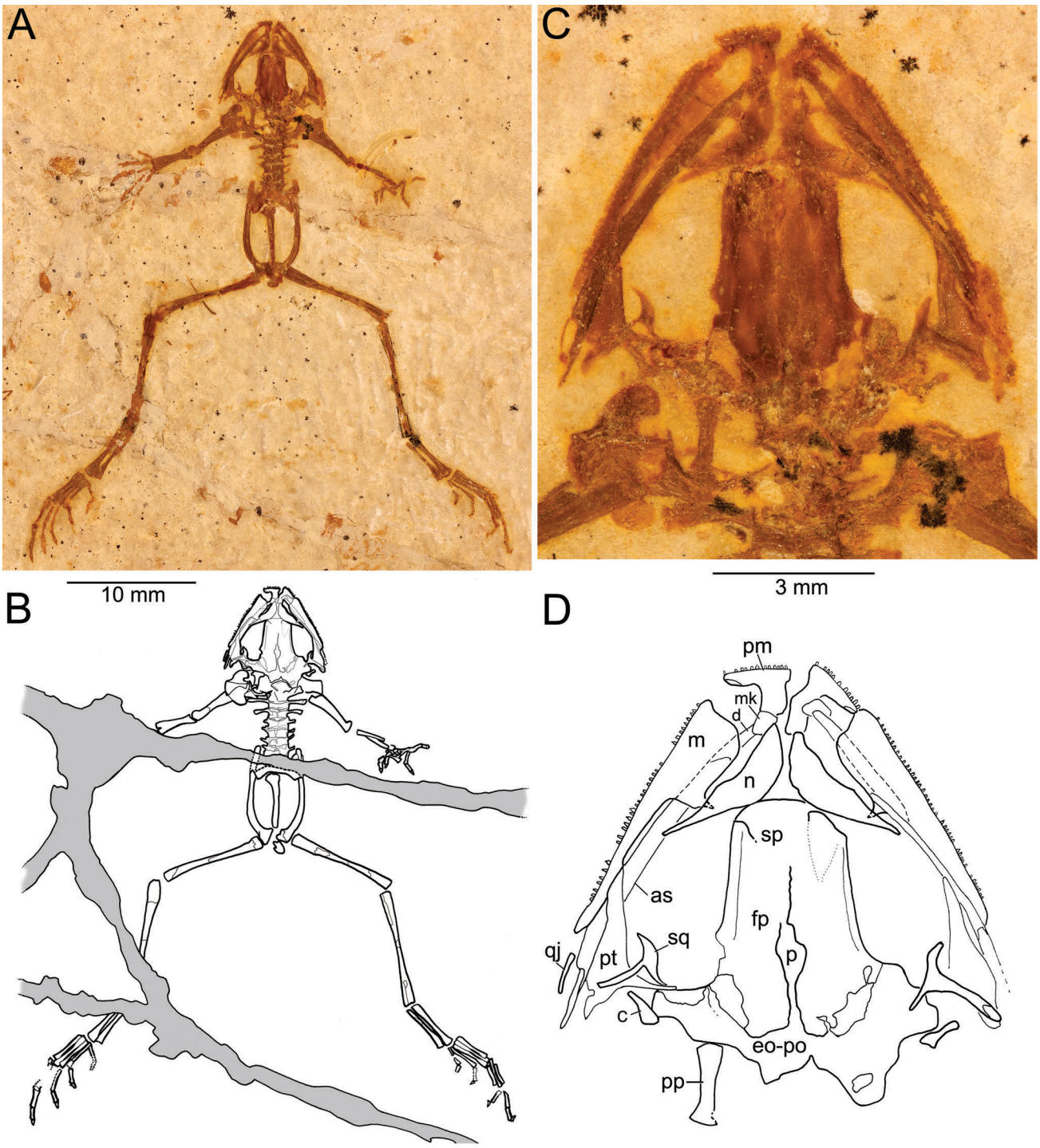

Fig. 1.— *Aerugoamnis paulus*, new genus and new species, FMNH PR2384. **A,** photograph of specimen in dorsal view; **B,** outline drawing of skeleton that excludes inaccurate skeletal recontruction of left manus and digit V of left pes; **C,** photograph of skull, posteromedial process of hyoid apparatus, and shoulder girdle in dorsal view; **D,** outline drawing of skull and posteromedial process of hyoid apparatus in dorsal view. Areas shaded gray represent reconstructed matrix. See abbreviations in text.

It cannot be determined if posterolateral processes were present due to damage in this region. The posterior margins of both frontoparietals appear to be incomplete.

The anterior end of the roof of the sphenethmoid is exposed between the nasals and frontoparietal. The sphenethmoidal ossification does not extend much anterolaterally, so it is assumed that the antorbital planes were entirely cartilaginous.

The squamosal bears distinct and nearly equally developed zygomatic and otic rami, as well as a longer ventral ramus. The otic ramus is very thin and dorsally convex, more so in the left than in the right. A well-developed otic plate for articulation with the crista parotica is absent. The gracile zygomatic ramus tapers distally and has a convex dorsal border and a concave ventral border. The relatively short length of the zygomatic ramus, together with the lack of a zygomatic process on the maxilla, indicates that the squamosal and maxilla were not in articulation. The ventral ramus is the longest of the three rami.

Most of both pterygoids are visible in dorsal aspect and are triradiate. The anterior ramus is straight, lacking a distal curvature, and is preserved in articulation with the maxilla. This articulation occurs at the anterior one-third of the orbital length, resulting in a wide separation between the anterior ramus of the pterygoid and the planum antorbitale. The right posterior ramus is better preserved than the left and is considerably shorter than the anterior ramus, terminating distally in a rounded margin. The medial ramus of the left pterygoid is exposed, and it is less than twice the length of the anterior ramus. It cannot be determined if the medial ramus articulated with the corresponding parasphenoid ala because of overlying bones on both sides of the skull. An arcuate ventral flange is present on the lateral edge of the pterygoid, and it extends from the medial portion of the anterior ramus to the medial portion of the posterior ramus.

The exoccipitals and prootics are fused to form the otic capsules, which are incompletely and poorly preserved. This region has been strongly dorsoventrally compressed and a considerable amount of bone from the dorsal surface is missing. The ventrolateral edges of the foramen magnum from the level of the occipital condyles converge towards one another and meet at the skull midline, giving the foramen magnum a triangular outline. The occipital condyles are narrowly separated and are not stalked. The cristae paroticae do not extend greatly laterally. Both right and left columellae are preserved adjacent to their respective otic capsules. The medial end of the columella is expanded to form the footplate, and the slender lateral end forms the stylus.

The mandibles are visible in openings of the skull or through thin overlying skull bones. The nearly complete left mandible is exposed in medial aspect. It is missing only the distal end of the angulosplenial, and the left mentomeckelian and left premaxilla covers the anterior end of the dentary. The right angulosplenial is dorsomedially exposed, and its distal end is represented by an impression. A mentomeckelian bone is present at the anterior end of the left dentary, which is exposed in medial aspect. The lower jaw articulation is located slightly anterior to the level of the occiput.

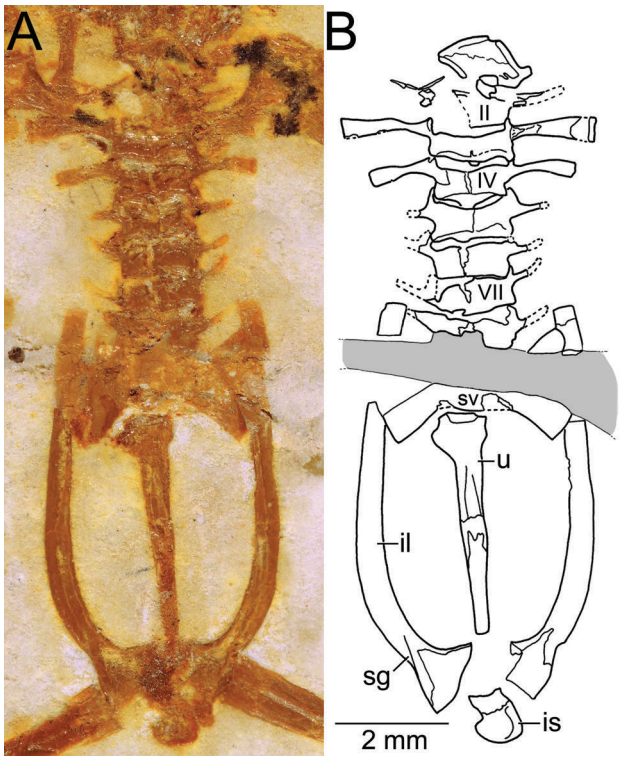

Fig. 2.— *Aerugoamnis paulus*, new genus and new species, FMNH PR2384. **A,** photograph of vertebral column and pelvis; **B,** outline drawing of same. Roman numerals indicate selected presacacral vertebrae. Gray shading represents reconstructed matrix.

Hyoid apparatus.—The only preserved bone of the hyoid apparatus is the left posteromedial process, which is exposed between the left otic capsule and left clavicle (Figs. 1C, D). A long, broad shaft separates the transversely expanded proximal and distal ends. The distal end has a greater width than the proximal end (Table 1).

Vertebral column.—The vertebral column (Fig. 2) consists of eight presacral and one sacral vertebrae and the urostyle. Most of the neural arches have cracks or matrix-filled gaps that extend from the anterior to posterior edges of the arches. Because most of these cracks do not occur along the vertebral midline, they are thought to be the result of dorsoventral compression rather than reflecting incomplete ossification. Presacrals one, two, seven, and eight are incomplete, and all of their transverse processes, with the exception of those on presacral four, are represented by a combination of bone and impressions. The atlantal neural arch is mainly represented by an impression of its ventral surface, with a portion of its lateral edges and posterior end preserved as bone. The dorsal

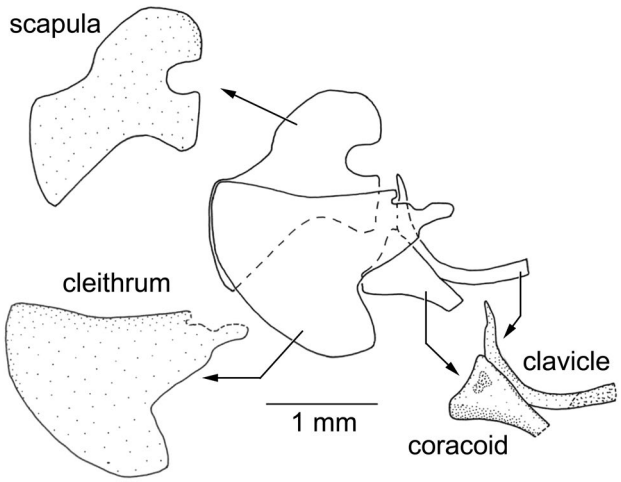

Fig. 3.— *Aerugoamnis paulus*, new genus and new species, FMNH PR2384. Drawing of left shoulder girdle. The center drawing depicts the shoulder girdle as preserved, and it is surrounded by drawings of the individual elements. Note that the translucency of the shoulder girdle bones allow those preserved underneath others to be seen.

edge of the atlantal cotyles is preserved as bone, however, and the cotyles are narrowly separated by a shallow intercotylar notch that conforms in shape to type II of Lynch (1971). The neural arches of presacrals two through seven (that of the eighth is too incomplete to determine its complete form) are wider than long, lack a neural spine, have a relatively straight posterior margin, and are nonimbricate. Anteroposterior length of the neural arches varies along the vertebral column. The atlantal neural arch is too poorly preserved to interpret its shape. The second presacral is also damaged and difficult to interpret, but the posterior portion of the right half of the neural arch is preserved and indicates that it is short and nonimbricate. The third presacral has the shortest neural arch of the presacral column, the fourth is slightly longer, and presacrals five through seven are of subequal length and slightly longer than the fourth. In presacral eight the left half of the neural arch is incomplete posteriorly, but enough of the right half is preserved to determine that it is slightly longer than the neural arch of presacral seven. Transverse processes of differing lengths occur on presacrals two through eight and free ribs are absent. In the second presacral the transverse processes are not fully exposed or preserved, but they appear to be thin and anteriorly directed. Transverse processes of the third and fourth broaden distally and are slightly arched posteriorly, with those of the third being longer and broader. Those of presacrals five through eight are of subequal length and thickness, being considerably shorter than the preceding ones. In presacral five the transverse processes are inclined slightly anteriorly, and they become successively more anteriorly inclined in presacrals six and seven, with those of presacral eight resembling those of presacral seven.

A broad, infilled crack extends transversely across the sacral vertebra, and the only remaining bony portions are the left posterolateral and the right anterolateral and posterolateral corners of the diapophyses and the posterior margin of the dorsal surface of the sacrum. The degree of expansion of the sacral diapophyses thus cannot be determined, because the reconstructed gap between the anterior and posterior portions of the sacral vertebra may not be accurate. Enough of the sacral diapophyses are preserved, however, to indicate that the lateral edges are convex and that the diapophyses are dorsoventrally flat, rather than rounded. The sacral condyle is not visible, but the urostyle bears a single cotyle at its anterior end, which indicates that the sacrum articulated to the urostyle via a single condyle. The urostyle bears laterally projecting transverse processes at the anterior end that are unequally developed. The left process is triangular and large, whereas the right process is smaller and rounded. This is possibly the result of inaccurate reconstruction of the left process, which appears to have some paint on it. Posterior of the transverse processes, the urostyle gradually tapers in width. A midline dorsal crest extends from the level of the posterior end of the left transverse process to approximately the midlength of the element, at which point the dorsal surface of the bone is missing.

Shoulder girdle and forelimb.—Bones of the shoulder girdle (Figs. 1C, 3) are preserved in articulation or are loosely articulated, but most of them are not completely exposed. Both cleithra overlie most of the scapulae and portions of the clavicles and coracoids. The anterior and lateral edges of the cleithra are well ossified, but the bone becomes considerably thinner, and in the better preserved left cleithrum, it appears as either a thin lamina overlying other bones of the shoulder girdle or as an impression with distinct edges and of a different color than the surrounding matrix. The outline shape of the right cleithrum is not as obvious, due to some black staining on portions of it and surrounding bones, and thus, description of this bone is based on the left element. The translucent nature of the cleithrum allows the shapes of underlying bones to be determined. The mediolateral length of the cleithrum is greater than that of the scapula. It has a narrow proximal end and broadens distally, lending the bone an overall fan shape. The distal end is bifurcate, and the anterior and posterior processes diverge from one another. The scapulae are short, in that their length is less than that of the preserved length of the clavicles, and bicapitate with well-developed pars acromialis and glendoidalis that are separated by a broad, U-shaped notch. An anterior tubercle is absent. Distal to the proximal head, the scapula abruptly narrows to form a short shaft that lacks an anterior lamina. Medial ends of the clavicles and coracoids are covered by the vertebral column, but enough of the clavicles are exposed to show that they are strongly arched, indicating an arciferal shoulder girdle. The shape of the proximal ends of the clavicle and pars acromialis of the scapula indicates

that the clavicle could not have overlapped the scapula anteriorly, but rather articulated with the proximal end of the pars acromialis of the scapula. The lateral ends of the coracoids are expanded, and the exposed portions of their shafts are slender.

Right and left humeri are exposed in lateral aspect; the proximal ends of both bones are partially covered by the corresponding scapula and cleithrum, and in both the lateral surface bone of the distal end is missing. The humeral shaft is curved so that the apex projects ventrally. The crista ventralis is deepest at the proximal end of the humerus and gradually diminishes in height distally, extending beyond the midpoint of the shaft. Projecting at a right angle from the shaft is the round humeral ball. The left radioulna is well preserved, whereas the right is damaged and incomplete, so the description is based on the left. Only the distal end of the radioulna is not completely fused together. It is shorter than the humerus and bears a well-developed olecranon process.

The left manus has been entirely and incorrectly reconstructed. It lies mainly on a broad, infilled crack and was inaccurately reconstructed as bearing five digits and will not be considered herein. Four digits are preserved as bone or impressions in the right manus (Fig. 4A), in which bones of each digit are preserved in articulation, but the digits are not preserved in articulation with the carpus. At least three carpal bones are present, but because they are not in articulation with each other or the metacarpals, their identities cannot be determined. In the first digit part of the proximal half of the first metacarpal is missing, but the rest of the digit is represented by bone. The second digit is nearly complete, with only the distal end of the metacarpal and the proximal end of the first phalanx missing. In digit three portions of the metacarpal and the first phalanx are represented by impressions and the remainder is bone. Except for its proximalmost end, the metacarpal of the fourth digit is preserved as an impression. The proximal end of the first phalanx is preserved as an impression, and the distal end of the terminal phalanx is missing. Relative lengths of the digits are as follows: I<II<IV<III. The phalangeal formula is: 2-2-3-3.

Pelvic girdle and hind limb.—The ilia (Fig. 2) are preserved near their natural position, though flattening of the specimen has caused them to be splayed and exposed in medial aspect. The shaft is arched, lacks an obvious dorsal crest, and a strongly developed spiral groove is present where the shaft joins the acetabular region. The dorsal acetabular expansion is preserved in the left ilium and is missing in the right. It is not greatly expanded, and a dorsal prominence is not present on its dorsal margin. All that can be said about the ventral acetabular expansion is that it is moderately developed and joins the shaft at an obtuse angle.

A small left ischium (Fig. 2) is exposed in lateral aspect and is missing its portion of the acetabulum. It is anteroposteriorly long, and the distal end is not convex. An ossified pubis is not preserved and was most likely absent.

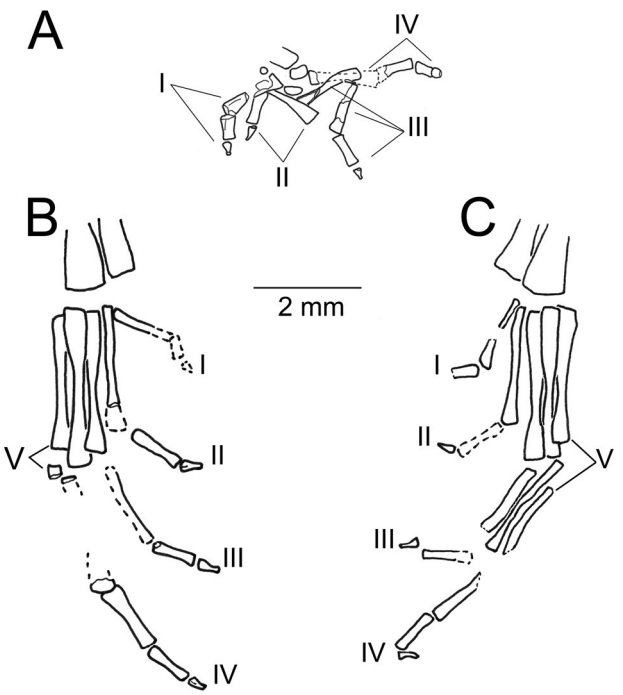

Fig. 4.— *Aerugoamnis paulus*, new genus and new species, FMNH PR2384. **A,** outline drawing of right hand; **B,** outline drawing of left foot that excludes inaccurate reconstruction of digit V; **C,** outline drawing of right foot. Dashed lines indicate outlines of bone impressions.

The right femur, tibiofibula, and tibiale and fibulare are better preserved than the left, so the description will be based on them, whereas the hind foot description is based on both the right and left. The elongate hind limb bones are 2.9 times longer than the forelimbs (Table 1). The femur and tibiofibula are of subequal length (Table 1), and the femur has a slight sigmoidal curve. Crests on the shaft of the femur are not visible. Proximal and distal ends of the tibiofibula are not greatly expanded, and the shaft is slender. The tibiale and fibulare are separate bones throughout their length and longer than the fourth metatarsal, the longest metatarsal of the series. Like the tibiofibula, the proximal and distal ends of the tibiale and fibulare are not greatly expanded and their shafts are slender. Bones of the distal tarsal series are not preserved and may not yet have been ossified.

There are five digits in the hind foot. The left hind foot has been incorrectly restored, giving the illusion that the fifth digit consists of four phalanges and is longer than the fourth, which is atypical for anurans. Figures 4B, C show our interpretation of the actual preserved bones and bone impressions of both hind feet. The relative lengths of the metatarsals are as follows: MI < MII < MV < MIII ≤ MIV. Digits I–IV increase in length serially, but the length of Digit V cannot be determined because it is incomplete in both feet. The phalangeal formula is 2-2-3-4-?.

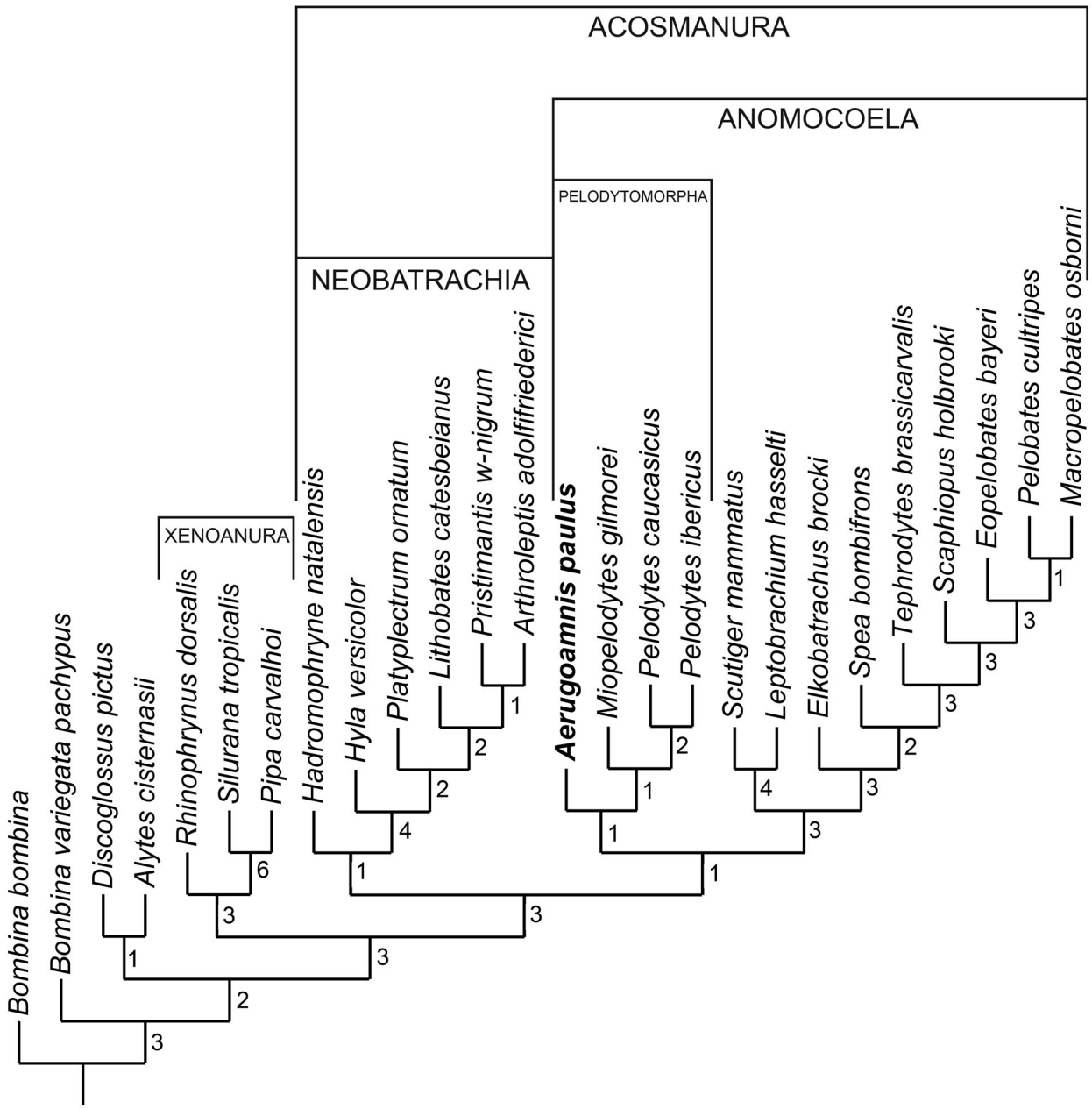

Fig. 5.—Single most parsimonius tree of 231 steps showing hypothesis of phylogenetic relationship of *Aerugoamnis paulus* as a basal member of Pelodytomorpha. Bremer support values are included in the tree.

RELATIONSHIPS

Of the five other frogs previously reported from the Green River Formation (Cope 1884; Grande 1984; Gardner 1999), only one can be compared to *Aerugoamnis*. This specimen from the Laney Member is three million years younger than *Aerugoamnis* and consists of an impression of a nearly complete skeleton. It was initially identified as a probable new species of *Eopelobates* (Grande 1984), but Roček and Rage (2000), who provided a preliminary description of it, identified it as a paedomorphic adult close to *Eopelobates* and *Pelobates*. The other specimens cannot be compared for different reasons. The specimen reported by Cope (1884) cannot be located and is presumably lost. Another specimen consists of a skin impression that Grande (1984) referred to *Eopelobates* and Roček and Rage (2000) considered as indeterminate. The fourth specimen has not been described and is on exhibit at DMNH (Johnson and Stucky 1995; Gardner 1999), and the fifth is a skin impression of a tadpole (Gardner 1999). The specimen described herein clearly represents a taxon different from the Laney Member frog because, among other characters, its frontoparietal is paired rather than being comprised of three or more ossifications.

A phylogenetic analysis was undertaken in order to investigate the relationships of *Aerugoamnis*. This analysis incorporated extant representatives of the major lineages of costatans, xenoanurans, anomocoelans, and neobatrachians, with emphasis placed on extinct and extant anomocoelan taxa, because the presence of a spiral groove of the ilium in *Aerugoamnis* suggests an affinity with this group. A spiral groove ("oblique groove" of some authors) of the ilium occurs primarily in anomocoelans (Evans and Milner 1993), although it has been documented in some indeterminate isolated ilia from the Late Cretaceous of Utah (Roček et al. 2010, 2012) and the costatan *Bombina* Oken, 1816. Roček has theorized that it also occurs in *Prosalirus bitis* Shubin and Jenkins, 1995, the earliest known anuran, although this was inferred from the occurrence of a deep depression on the dorsal margin of the shaft just anterior of the acetabular area. Extinct anomocoelans included in the analysis are *Eopelobates bayeri* Špinar, 1952, from the early Oligocene–middle Miocene of central Europe, *Macropelobates osborni* Noble, 1924, from the Oligocene of Mongolia, *Elkobatrachus brocki* Henrici and Haynes, 2006, from the middle Eocene of Nevada, *Tephrodytes brassicarvalis* Henrici, 1994, from the late Oligocene of Montana, and *Miopelodytes gilmorei* Taylor, 1941, from the middle Eocene of Nevada. The analyzed data set consists of 66 osteological characters (Appendix 1) scored for six fossil and 20 extant taxa. Characters included in this phylogenetic analysis have been taken from previous phylogenetic analyses (Henrici 1994, 2009; Henrici and Haynes 2006; Báez et al. 2009, 2012; Báez 2012; and literature cited therein), although some of them were modified to better describe morphological variation in the included taxa. The matrix was constructed using Mesquite (Maddison and Maddison 2011) and is presented in Appendix 2. A list of specimens examined is presented in Appendix 3. The characters were equally weighted and multistate characters were treated non-additively (unordered). Parsimony analysis of the data was conducted using TNT version 1.1 (Goloboff et al. 2008), in which a heuristic search was performed building 500 replicates of Wagner trees followed by tree bisection reconnection (TBR) branch swapping, with a hold of ten trees by replicate. This analysis resulted in one most parsimonious tree of 231 steps (CI=.394, RI=.632) found in 459 out of 500 replicates in which the major monophyletic clades (terminology of Frost et al. 2006) of Xenoanura, Acosmanura, Anomocoela, and Neobatrachia were retrieved (Fig. 5). *Aerugoamnis* is placed as a member of Anomocoela, whose monophyly is supported by five characters, of which only one is preserved in *Aerugoamnis*. This character is the presence of a spiral groove of the ilium (character 60, state 1), which outside of Anomocoela occurs only in *Bombina*. Other characters supporting Anomocoela are as follows: presence of an incomplete hyale (character 35, state1), which is the only character supporting this clade that does not exhibit homoplasy; palatine process of pars facialis present (character 10, state 1); parasphenoid posteromedial process distally rounded (character 20, state 1); and sternum ossified (character 56, state 1). *Aerugoamnis* is placed as the sister taxon of a clade that includes *Miopelodytes gilmorei*, *Pelodytes ibericus* Sánchez-Herráiz, Barbadillo, Marchordom and Sanchiz, 2000, and *Pelodytes caucasicus* Boulenger, 1896, based on two characters: the presence of a distinct otic ramus of the squamosal (character 23, state 1), which also occurs in the neobatrachian clade of *Platyplectrum* Günter, 1863 (*Lithobates* Fitzinger, 1843 (*Pristimantis* Jiménez de la Espada + *Arthroleptis* Smith, 1849)) and the Anomocoelan clade of *Scaphiopus* Holbrook, 1836 (*Eopelobates* (*Pelobates* + *Macropelobates* Noble, 1924)), as well as the costatan *Discoglossus* Otth, 1837; and crista parotica poorly developed (character 25, state 0); which also occurs in *Bombina*, *Hadromophryne* Van Dijk, 2008, and *Arthroleptis*. *Miopelodytes* shares with the clade formed by *P. caucasicus* and *P. ibericus* the presence of tibiale and fibulare fused throughout their length (character 65, state 1), which occurs convergently in *Tephrodytes* Henrici, 1994. In turn, the two species of *Pelodytes* are united by three characters that exhibit a high degree of homoplasy and are: sacral diapophyses are widely expanded (character 46, state 0); sacral diapophyses have straight lateral margins (character 47, state 0), and tibiofibula is longer than the femur (character 64, state 2). It should be noted that we restrict the term Pelodytidae to the crown group, whereas we apply the stem-based term Pelodytomorpha to the clade consisting of crown pelodytids and all taxa sharing a more recent common ancestor with them than with other living anomocoelan taxa (Fig. 5). *Aerugoamnis* differs from *Pelodytes* in the nasals being medially separated by only a slight gap (character 2, state 1) and possession of a ventral flange of the pterygoid (character 29, state 0). Neither character can be scored in *Miopelodytes*.

Although the results of the phylogenetic analysis place *Aerugoamnis* as a basal member of the stem of the pelodytid clade, this position seemingly is not strongly supported because it has a Bremer support of only one (Fig. 5). In four of the six suboptimal trees one step longer than the most parsimonious tree, *Aerugoamnis* is the sister taxon of the clade formed by *Miopelodytes* and the extant *Pelodytes*, thus holding the same position as in the most parsimonious tree. In the fifth tree *Aerugoamnis* forms a clade with *Miopelodytes* that is, in turn, sister to the clade of *Pelodytes ibericus* and *P. caucasicus*, whereas in the remaining sixth tree *Aerugoamnis* is placed as the sister taxon to Acosmanura.

DISCUSSION

Today Pelodytidae is restricted to Eurasia, but putative fossil relatives occur in the Eocene of North America. *Aerugoamnis* is currently the oldest member of the pelodytid lineage; another stem pelodytid from North America, *Miopelodytes gilmorei*, is based on a single specimen from the Elko Formation, near Elko, Nevada (Taylor 1941). This

formation was once regarded as Miocene in age (Taylor 1941) but is now considered to be middle Eocene (Haynes 2003; Henrici and Haynes 2006). The locality information for *Miopelodytes* is not precise, so refinement of its geologic age cannot be made. Based on the results of the phylogenetic analysis presented herein, *Tephrodytes brassicarvalis*, from the late Oligocene Cabbage Patch Formation of Montana, can no longer be regarded as a member of the pelodytid lineage. This is not totally unexpected, because in the original description of *Tephrodytes*, it was observed that it possessed several derived characters that also occur in pelobatids (including Scaphiopodidae) (Henrici 1994). Isolated bones identified as cf. *Pelodytes* have been reported from middle to late Eocene (MP 16–MP 19) French localities (Crochet et al. 1981; Rage 1988, 2006). A fragmentary ilium from the middle Eocene (Lutetian, MP 13), however, may represent the oldest occurrence of the family in Europe (Rage and Roček 2003). An extinct species of *Pelodytes*, *P. arevacus* Sanchiz, 1978, is known from the middle Miocene (Serravallian, MN 7–8) of Spain (Sanchiz 1978, 1998). Sanchiz (1998) considered *P. arevacus* to resemble *P. ibericus* and *P. punctatus* Daudin, 1802, more closely than it does *P. caucasicus*.

Aerugoamnis, unlike all other described members of the pelodytid lineage, lacks a completely fused tibiale and fibulare, which was considered to be diagnostic of the pelodytid lineage (Taylor 1941; Duellman and Trueb 1986; Ford and Cannatella 1993; Henrici 1994). A fused tibiale and fibulare occurs in the extant species of the Eurasian *Pelodytes*, *P. caucasicus*, *P. ibericus* and *P. punctatus*, as well as the extinct *P. arevacus*. This character, however, has yet to be reported among the fragmentary remains described from middle to late Eocene western European localities and referred to as cf. *Pelodytes* (Crochet et al. 1981; Rage 1988; Böhme and Ilg 2003) and as a questionable pelodytid (Duffaud and Rage 1997). The presence of a fused tibiale and fibulare in the extinct *Miopelodytes gilmorei*, which is placed outside the node uniting the extant pelodytids in our analysis, corroborates that this feature characterizes a more inclusive clade than crown Pelodytidae. A completely fused tibiale and fibulare is known elsewhere only in Centrolenidae (Taylor 1951), in which the degree of fusion has been shown to be variable, and the character is now considered to be diagnostic at only the generic level (Sanchiz and de la Riva 1993).

The occurrences of North American pelodytomorphs (early–middle Eocene) and the earliest records of European pelodytids (middle Eocene) coincide with a time when the climate was considerably warmer and more equable than today (Zachos et al. 2001; Scotese 2003). Indeed, *Aerugoamnis* was present during the Early Eocene Climatic Optimum, which was the warmest period of the Cenozoic (Zachos et al. 2001). At this time, the Fossil Lake basin was a lowland with a warm, wet, subtropical environment that was surrounded by highlands and mountains containing pine and other more temperate highland flora (Grande 2013). The first records of pelodytids in the middle Eocene of Europe occurred when that region was isolated from other continents (Rage and Roček 2003). Pelodytids have been reported from numerous localities throughout the remainder of the Cenozoic of Europe (Sanchiz 1998; Böhme and Ilg 2003; Roček and Rage 2000; Rage and Roček 2003; Rage 2012), when the climate underwent a long term cooling trend that culminated in the Pleistocene (Zachos et al. 2001; Scotese 2003). Additional fossils, however, are needed to provide a more comprehensive understanding of the origin, evolution, and paleogeographic history of this poorly known group of anurans.

ACKNOWLEDGMENTS

The authors are grateful to the following people and institutions for loans of specimens: Marissa Fabrezi, MCNS; Julian Faivovich, MACN; Steve Rogers, CM; Alan Resetar, FMNH; José Rosado, MCZ; Borja Sanchiz, MNCN; Linda Trueb, KU; and Jim Tynsky of Kemmerer, Wyoming. One of the authors (AB) thanks the Consejo de Investigaciones and the Agencia Nacional para la Promocion Cientifica de Argentina (PICT 1895) for financial support. The senior author is grateful to Pauline Coster (CM) and Michelle Spaulding (CM) who provided her with advice and assistance with using TNT. David Cannatella (UTA) and David Berman (CM) are thanked for helpful discussion on amphibian anatomy. Richard Palmer skillfully shot the photographs that appear in Figures 1 and 2. Mark Klingler is acknowledged for skillfully rendering Figure 1B and providing advice and assistance with other figures. Gene Cooper of Four Chambers Studio LLC, California and John Rawlins (CM) are acknowledged for shooting and collating, respectively, a GigaPan image of the frog, which enhanced study of the specimen. This paper benefitted from the reviews by James Gardner and an anonymous reviewer.

LITERATURE CITED

BÁEZ, A.M. 2012. Anurans from the Early Cretaceous Laggerstätte of Hoyas, Spain: new evidence on the Mesozoic diversification of crown-clade Anura. Cretaceous Research, dx.doi.org/10.1016/j.cretres.2012.11002

BÁEZ, A.M., R.O. GÓMEZ, AND M. TAGLIORETTI. 2012. The archaic ilial morphology of an enigmatic pipid frog from the Upper Pleistocene of the South American Pampas. Journal of Vertebrate Paleontology, 32:304–314.

BÁEZ, A.M., G.J.B. MOURA, AND R.O. GÓMEZ. 2009. Anurans from the Lower Cretaceous Crato Formation of northeastern Brazil: implications for the early divergence of neobatrachians. Cretaceous Research, 30:829–846.

BÖHME, M., AND A. ILG. 2003. fosFARbase. Available from www.wahre-staerke.com.

COPE, E.D. 1884. The Vertebrata of the Tertiary formations of the West. United States Geological and Geographic Survey of the Territories, 3:1–1009.

CROCHET, J.Y., J.L. HARTENBERGER, J.C. RAGE, J.A. REMY, B. SIGE, J. SUDRE, AND M. VIANEY-LIAUD. 1981. Les nouvelles faunes de Vertébrés antérieures à la "Grand Coupure" découvertes dans les Phosphorites du Quercy. Bulletin Muséum National Histoire Naturelle, Section C, 3:245–266.

DUELLMAN, W.E., AND L. TRUEB. 1986. Biology of Amphibia. McGraw-Hill Book Company, New York. 670 pp.

DUFFAUD, S., AND J.C. RAGE. 1997. Les remplissages karstiques polyphasés (Eocène, Oligocène, Pliocène) de Saint Maximin (Phosphorites du Gard) et leur apport à la connaissance des faunes européenes, notamment pour l'Eocène moyen (MP13). Amphibiens et reptiles.

EVANS, S.E., AND A.R. MILNER. 1993. Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. Journal of Vertebrate Paleontology, 13:24–30.

FORD, L.S., AND D.C. CANNATELLA. 1993. The major clades of frogs. Herpetological Monographs, 7:94–117.

FROST, D.R., T. GRANT, J. FAIVOVICH, R.H. BAIN, A. HAAS, C.F.B. HADDAD, R.O. DE SÁ, A. CHANNING, M. WILKINSON, S.C. DONNELLAN, C.J. RAXWORTHY, J.A. CAMPBELL, B.L. BLOTTO, P. MOLAR, R.C. DREWES, R.A. NUSSBAUM, J.D. LYNCH, D.M. GREEN, AND W.C. WHEELER. 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History, 297:1–370.

GARDNER, J.D. 1999. Comments on amphibians from the Green River Formation, with a descripton of a fossil tadpole. In Vertebrate Paleontology in Utah (D.D. Gillette, ed). Miscellaneous Publication Utah Geological Survey, 99-1:455-461.

GOLOBOFF, P., J. FARRIS, AND K. NIXON. 2008. T.N.T.: Tree Analysis Using New Technology. Program and documentation available from the authors, and at www.zmuc.dk/public/phyolgeny.

GRANDE, L. 1984. Paleontology of the Green River Formation, with a review of the fish fauna. Geological Survey of Wyoming Bulletin, 63:1–333.

———. 2013. The Lost World of Fossil Lake: Snapshots from Deep Time. University of Chicago Press, Chicago. 440 pp.

HALL, J.A., AND J.H. LARSEN, JR. 1998. Postembryonic ontogeny of the spadefoot toad, *Scaphiopus intermontanus* (Anura: Pelobatidae): skeletal morphology. Journal of Morphology, 238:179–244.

HAYNES, S.R. 2003. Development of the Eocene Elko Formation, northeastern Nevada: implications for paleogeography and regional tectonism. Unpublished Masters of Science thesis, University of British Columbia, Vancouver. 159 pp.

HENRICI, A.C. 1994. *Tephrodytes brassicarvalis*, new genus and species (Anura: Pelodytidae), from the Arikareean Cabbage Patch beds of Montana, USA, and pelodytid-pelobatid relationships. Annals of Carnegie Museum, 63(2):155–183.

———. 2009. Reassessment of *Scaphiopus neuter* Kluge, 1966 (Anura: Pelobatoidea: Pelobatidae), based on new material from Anceney, Montana (early Barstovian). Annals of Carnegie Museum, 78(3):273–287.

HENRICI, A.C., AND S.R. HAYNES. 2006. *Elkobatrachus brocki*, a new pelobatid (Amphibia: Anura) from the Eocene Elko Formation of Nevada. Annals of Carnegie Museum, 76(1):11–35.

JOHNSON, K.J., AND R.K. STUCKY. 1995. Prehistoric Journey: A History of Life on Earth. Robert Rhinehart Publishers, Boulder.

LYNCH, J.D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. University of Kansas Miscellaneous Publications, 53:1–238.

MADDISON, W.P., AND D.R. MADDISON. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. Available from http://www.mesquiteproject.org.

MAGLIA, A.M. 2003. Skeletal development of *Pelobates cultripes* and a comparison of the osteogenesis of pelobatoid frogs (Anura: Pelobatidae). Scientific Papers Natural History Museum of the University of Kansas, 30:1–13.

RAGE, J.-C. 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Gardonne, France) et sa faune de vertébrés de l'Eocène supérieur. I. Amphibiens et Reptiles. Palaeontographica Abteilung A, 205:3–27.

———. 2006. The lower vertebrates from the Eocene and Oligocene of the Phosphorites du Quercy (France): an overview. Strata, 13:161–173.

———. 2012. Amphibians and squamates in the Eocene of Europe: what do they tell us? Palaeodiversity and Palaeoenvironments, 92:445–457.

RAGE, J.-C., AND Z. ROČEK. 2003. Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. Amphibia-Reptilia, 24:133–167.

ROČEK, Z., J.D. GARDNER, J.G. EATON, AND T. PŘIKRYL. 2010. Evolution of anuran assemblages in the Late Cretaceous of Utah, USA. Palaeobiodiversity and Palaeoenvironments, 90:341–393.

———. 2012. Similarities and differences in the ilia of Late Cretaceous anurans and urodeles. Bulletin de la Société géologique de France, 183:529–535.

ROČEK, Z., AND J.-C. RAGE. 2000. Tertiary Anura of Africa, Asia, Europe, North America, and Australia. Pp. 1334–1389, *in* Amphibian Biology, 4 (H. Heatwole and R.L. Carroll, eds.). Surrey Beatty & Sons, Chipping Norton.

RODRÍGUEZ TALAVERA, M.-R. 1990. Evolución de pelobátidos y pelodítidos (Amphibia, Anura): morfología y desarrollo del sistema esquéletico. Unpublished PhD dissertation, Universidad Complutense de Madrid, Madrid.

SANCHIZ, B. 1998. Salientia. Handbuch der Paleäoherpetologie Pars 4. Dr. F. Pfeil, Munich. 275 pp.

SANCHIZ, B., AND I. DE LA RIVA. 1993. Remarks on the tarsus of centrolenid frogs (Amphibia, Anura). Graellsia, 49:115–117.

SANCHIZ, B., M. TEJEDO, AND M. J. SÁNCHEZ-HERRÁIZ, 2002. Osteological differentiation among Iberian *Pelodytes* (Anura, Pelodytidae). Graellsia, 58 (2): 35–68.

SANCHIZ, F.B. 1978. Nuevos restos fósiles de la familia Pelodytidae (Amphibia, Anura). Estudios Geológicos, 34:9–27.

SCOTESE, C.R. 2003. Paleomap project. Available from http://www.Scotese.com.

SMITH, M.E., K.R. CHAMBERLAIN, B.S. SINGER, AND A.R. CARROLL. 2010. Eocene clocks agree: coeval 40Ar/39Ar, U-Pb, and astronomical ages from the Green River Formation. Geology, 38(6):527–530.

TAYLOR, E.H. 1941. A new anuran from the middle Miocene of Nevada. University of Kansas Science Bulletin, 27(4):61–69.

———. 1951. Two new genera and a new family of tropical American frogs. Proceedings of the Biological Society of Washington, 64:33–40.

WIENS, J.J. 1989. Ontogeny of the skeleton of *Spea bombifrons* (Anura: Pelobatidae). Journal of Morphology, 202:29–51.

ZACHOS, J., M. PAGANI, L. SLOAN, E. THOMAS, AND K. BILLUPS. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 292:686–693.

APPENDIX 1.

Description of characters used in the phylogenetic analysis. The characters were primarily taken from Henrici (1994, 2009), Henrici and Haynes (2006), Báez et al. (2009, 2012), and Báez (2012). Some of the characters were modified for this study to better describe variation in the included taxa.

1. Dermal sculpture: (0) absent; (1) present.
2. Nasals, medial contact: (0) well separated; (1) in contact or very narrowly separated.
3. Frontoparietal, relationship with nasal: (0) not in contact; (1) in contact.
4. Frontoparietals, relationship to one another: (0) separate throughout length; (1) in partial contact; (2) sutured together throughout length and/or partially fused; (3) fused with no trace of suture.
5. Frontoparietal, supraorbital flange: (0) absent; (1) present.
6. Planum antorbitale, ossification: (0) completely cartilaginous or ossified/mineralized less than one-half; (1) ossified/mineralized more than one-half.
7. Perilymphatic foramina, position: (0) superior perilymphatic foramen anterior to jugular foramen, inferior perilymphatic foramen posterior to jugular foramen; (1) both superior and inferior perilymphatic foramina posterior to jugular foramen.
8. Maxilla-premaxilla relationship: (0) slight or no overlap; (1) pointed process of pars facialis of maxilla that reaches alary process of premaxilla.
9. Maxilla, preorbital process: (0) absent or weakly developed; (1) present and well developed.
10. Maxilla, palatine process of pars facialis: (0) absent; (1) present.
11. Maxilla, length: (0) does not extend beyond midlength of orbit; (1) extends beyond midlength of orbit.
12. Quadratojugal: (0) present; (1) absent.
13. Vomer: (0) present; (1) absent.
14. Vomer, contact with inner surface of pars facialis of maxilla: (0) absent; (1) present.
15. Vomer, postchoanal process: (0) short; (1) elongate and articulates with pars facialis of pars palatina of maxilla; (2) absent.
16. Palatine: (0) absent; (1) present.
17. Parasphenoid, anterior extent of cultriform process: (0) does not reach antorbital plane; (1) reaches antorbital plane but not maxillary arcade; (2) reaches maxillary arcade.
18. Parasphenoid, lateral alae: (0) present; (1) absent.
19. Parasphenoid, posteromedial process: (0) absent; (1) present.
20. Parasphenoid, posteromedial process shape: (0) posteriorly directed apex; (1) distally rounded; (2) distally rectangular; (3) distally concave.
21. Squamosal shape: (0) generally triradiate; (1) funnel shaped.
22. Squamosal, zygomatic ramus, contact with maxilla: (0) absent; (1) present.
23. Squamosal, otic ramus: (0) greatly reduced to absent; (1) present, forming distinct process.
24. Squamosal, otic plate: (0) reduced to absent; (1) well developed.
25. Crista parotica: (0) poorly developed; (1) well developed.
26. Occipital artery: (0) dorsal to skull roof; (1) in closed canal that exits laterally; (2) in closed canal that exits dorsally.
27. Pterygoid, anterior ramus length: (0) short, less than twice the length of medial ramus; (1) elongate, greater than twice the length of medial ramus.
28. Pterygoid, medial ramus contact with parasphenoid lateral ala: (0) contact; (1) no contact.
29. Pterygoid, ventral flange: (0) present; (1) absent.
30. Angulosplenial, coronoid process: (0) poorly developed; (1) present and blade-like; (2) present and knob-like (thumb-like).
31. Jaw articulation, position: (0) lateral to otic capsule; (1) posterior to otic capsule; (2) at anterior margin of otic capsule.
32. Hyoid apparatus, posteromedial process, anterior end width: (0) wider than posterior end; (1) narrower than or equal to posterior end.
33. Hyoid apparatus, parahyoid bone: (0) present; (1) absent.
34. Hyoid apparatus, parahyoid bone shape: (0) single; (1) paired.
35. Hyoid apparatus, hyale general configuration: (0) complete; (1) incomplete.
36. Atlas, cotyles configuration: (0) closely juxtaposed or forming single articular surface; (1) widely separated.
37. Vertebral centra, formation: (0) perichordal; (1) epichordal.
38. Vertebral centra, articular facet of last presacral vertebra: (0) opisthocoelous; (1) procoelous; (2) amphicoelous.
39. Presacral vertebrae VI and VII, posterior margin of the neural arch: (0) slightly concave to straight or with a minute spine; (1) projecting in a well-developed spine; (2) deeply notched.
40. Presacral vertebrae I and II, relationship of neural arches: (0) not fused, weak or no imbrication; (1) not fused, broad imbrication medially only; (2) not fused, imbrication involving all of neural lamina; (3) synostotically fused to form long, combined element.
41. Presacral vertebrae IV and V, transverse process relative length: (0) transverse process length of presacral IV less than that of presacral V; (1) transverse process length of presacral IV is greater than that of presacral V; (2) transverse process length of presacral IV is subequal to that of presacral V.

APPENDIX 1. *(continued from previous page)*

42. Presacral vertebra VI, orientation of the posterior margin of the transverse processes relative to the axial axis: (0) nearly perpendicular; (1) moderately anteriorly; (2) strongly anteriorly; (3) moderately posteriorly.
43. Ribs: (0) free ribs present in adults; (1) free ribs absent in adults.
44. Sacrum and urostyle articulation: (0) monocondylar; (1) bicondylar; (2) fused; (3) strap-like.
45. Sacrum, diapophyses, distal cross section: (0) flattened; (1) subcircular.
46. Sacrum, diapophyses expansion: (0) broadly expanded, length greater than or equal to combined process width; (1) expanded, length greater than half process width but less than combined process width; (2) not expanded, length less than half process width.
47. Sacrum, diapophyses lateral margins: (0) straight; (1) convex.
48. Clavicle, lateral end relationship to scapula: (0) contacts medial edge of pars acromialis; (1) overlaps anterior edge of pars acromialis; (2) fused to scapula.
49. Scapula, proportions: (0) dorsoventral length of glenoid area one-third or less dorsoventral length of scapula; (1) dorsoventral length of glenoid area greater than one-third dorsoventral length of scapula.
50. Scapula-clavicle, proportions: (0) scapula shorter than clavicle; (1) scapula longer than clavicle; scapula of subequal length to clavicle (2).
51. Scapula, anterior tubercle: (0) absent; (1) present.
52. Scapula, anterior lamina: (0) present; (1) absent.
53. Cleithrum, distal margin: (0) bifurcate; (1) not bifurcate.
54. Coracoid, sternal expansion relative to coracoid length: (0) sternal expansion less than half the length of coracoid; (1) sternal expansion greater than half the length of coracoid.
55. Omosternum, presence: (0) present; (1) absent.
56. Sternum, condition: (0) cartilaginous; (1) ossified.
57. Sternum, shape: (0) linear; (1) triradiate.
58. Postaxial carpals (ulnare and distals 3, 4, and 5), configuration: (0) all free; (1) ulnare and 3 free, 4 and 5 fused; (2) ulnare free, 3, 4, and 5 fused; (3) ulnare fused to 5, 4 free
59. Carpal torsion: (0) absent; (1) present.
60. Iliac shaft, spiral groove: (0) absent; (1) present.
61. Iliac shaft, dorsal crest: (0) absent; (1) present as low ridge; (2) present as well-developed flange.
62. Dorsal crest, position on iliac shaft: (0) restricted to distal half of shaft; (1) restricted to proximal portion of shaft; (2) extends along nearly entire length of shaft.
63. Ischium, shape in lateral aspect: (0) long with subrectangular outline; (1) short with convex distal margin and semi-circular outline.
64. Tibiofibula, length: (0) shorter than femur; (1) of subequal length with femur; (2) longer than femur.
65. Tibiale-fibulare relationship: (0) not fused or fused only at proximal and distal ends; (1) fused throughout length to form single bone.
66. Prehallux, distal bone: (0) not modified into spade; (1) modified into spade.

APPENDIX 2.

Taxon-character matrix used for phylogenetic anaylsis presented in this paper. 0, 1, 2, and 3 refer to different character states. Abbreviations: A, 1&2; B, 1&2&3; -, inapplicable character; ?, character state unknown.

	1	2	3	4
	123456789	0123456789	0123456789	0123456789	0123456789
Aerugoamnis paulus	010?00?0?	?100?0????	?00100?1?0	?01???0??0	?11100?101
Alytes cisternasii	010100000	0100000100	-000010111	10?0100100	1200101111
Arthroleptis adolfifriederici	000000?00	0100021101	1001?0?111	?011-01010	0231112?00
Bombina bombina	010000000	0100000001	0000000110	?010000100	?010000111
Bombina variegata pachypus	010000000	0100000001	2000000011?	1010000100	1010000111
Discoglossus pictus	01A100000	1100000A00	?011010100	1000100101	1000101111
Elkobatrachus brocki	0??10???0	1????????01	3??????2???	?????????0	111100111?
Eopelobates bayeri	110211??0	110?????01	301111??00	?????????1?	1121200001
Hadromophryne natalensis	000000?01	0100001100	-000000111	1001-00010	2201101101
Hyla versicolor	00000010A	0100001001	0000010111	2011-01?10	0201102100
Leptobrachium hasselti	000200000	1100000001	2000112001	0111-10012	1111001000
Lithobates catesbeianus	011200101	0100001101	0001110011	11???00021	1231112A01
Macropelobates osborni	1??21?0??	??????????	?011?11???	???????0?11	112?000001
Miopelodytes gilmorei	1??00???0	?10????????	??1100????	??????????	?121?011??
Pelobates cultripes	111311000	1100100101	1011111000	0001-10111	2121000001
Pelodytes caucasicus	000200?00	1?00000?01	10011000?1	????1?0?10	01110000?1
Pelodytes ibericus	000000000	1100000101	1001000111	1010111110	0121B000A1
Pipa carvalhoi	001310-10	0011--021-	010001?0-0	1211-??102	3??120?010
Platyplectrum ornatum	000000101	0100001101	0001012001	1011-00010	3211102100
Pristimantis w-nigrum	010200101	?100001101	000101001?	?0?1-01110	0231112?20
Rhinophrynus dorsalis	011311000	000000011-	-000010--1	02000?0?21	2131002111
Scaphiopus holbrooki	111211000	1110110101	1011111000	0011-10111	1101201100
Scutiger mammatus	000200000	1010000001	2000112001	01?1-10012	1111001101
Spea bombifrons	000101000	1010110101	10001120A1	0011-10011	1111201101
Silurana tropicalis	001300-10	0?11--021-	-10001?0-0	1211-??100	3??120?021
Tephrodytes brassicarvalis	11110???0	110?????0?	?0101121??	??????0?1?	1121B001?1

	5	6
	0123456789	0123456
Aerugoamnis paulus	0?10??????	10-0100
Alytes cisternasii	0000010000	00-1100
Arthroleptis adolfifriederici	1?11000121	0221200
Bombina bombina	0000010000	10-1100
Bombina variegata pachypus	0000010000	10-1000
Discoglossus pictus	0000000000	0221200
Elkobatrachus brocki	?01???11??	10-1001
Eopelobates bayeri	100?1?11??	????200
Hadromophryne natalensis	0?00000101	?0-?200
Hyla versicolor	101000?121	0100000
Leptobrachium hasselti	1010101 1?1	10-0100
Lithobates catesbeianus	101110??21	0220100
Macropelobates osborni	100?1?????	?230001
Miopelodytes gilmorei	0?????????	??0?110
Pelobates cultripes	1000101101	10-1001
Pelodytes caucasicus	??1?0?111?	10-0210
Pelodytes ibericus	0100001111	10-0210
Pipa carvalhoi	000001013?	02??100
Platyplectrum ornatum	1?11000111	0130101
Pristimantis w-nigrum	2?10000121	0221200
Rhinophrynus dorsalis	001111--0?	00-1001
Scaphiopus holbrooki	1010000101	10-1001
Scutiger mammatus	1110001101	10-0100
Spea bombifrons	1010000101	10-1001
Silurana tropicalis	???001010?	010?200
Tephrodytes brassicarvalis	011???????	10-?21?

APPENDIX 3.

Specimens examined for comparison and phylogenetic analysis. Abbreviations other than institutional acronyms: cs, cleared and stained; ds, dried skeleton; fs, fossil skeleton; ld, data taken from literature with the citation following in parentheses.

Costata

Alytidae.—*Alytes cisternasii* Bosća, 1879: FCEN UN, ds; *Discoglossus pictus* Otth, 1837: CM 34977, 34977a, cs, CM 54753, ds, FCEN UN, ds.

Bombinatoridae.— *Bombina bombina* (Linnaeus, 1761): private, uncataloged collection, ds; *Bombina variegata pachypus* (Linnaeus, 1758) FCEN 401, ds.

Xenoanura

Rhinophrynidae.—*Rhinophrynus dorsalis* Duméril and Bibron, 1841: MACN, 42616, cs, 42617, ds; MSU 2256, 2269, 2274–2276, 2278, 2295, ds.

Pipidae: *Pipa carvalhoi* Miranda-Ribeiro, 1937: MACN 42606–42608, ds, 42609–42610, cs; *Silurana tropicalis* Gray, 1864: MACN 42625, CS, 42633, ds.

Anomocoela

Megophryidae.—*Leptobrachium hasselti* Tschudi, 1838: FMNH 131998, ds; *Scutiger mammatus* (Gunter, 1896): FMNH 15157, 22286, 22287, ds.

Elkobatrachus brocki Henrici and Haynes, 2006: CM 70370–70376, fs.

Pelobatidae (crown group).—*Macropelobates osborni* Noble, 1924: AMNH 6252, 6630, fs; *Pelobates cultripes* (Cuvier, 1829): CM 54755, 55769, ds, MACN 42618, cs; *Scaphiopus holbrooki* (Harlan, 1835): CM 18719, 32299, 32300, 37440, 70609, 92261, 118968, ds; *Spea bombifrons* (Cope, 1863): CM 48928–48932, ds; *Tephrodytes brassicarvalis* Henrici, 1994: ld (Henrici 1994).

Pelodytomorpha.— *Miopelodytes gilmorei* Taylor, 1941: USNM 12356, fs, ld (Taylor 1941).

Pelodytidae.—*Pelodytes ibericus* Sánchez-Herráiz, Barbadillo, Marchordom, and Sanchiz, 2000: CM 55771, ds; CM 54318d-I, cs. *Pelodytes caucasicus* Boulenger, 1896, ld (Sanchiz et al. 2002).

Neobatrachia

Arthroleptidae.—*Arthroleptis adolfifriederici* Nieden, 1911: MCN 822, cs.

Craugastoridae.—*Pristimantis w-nigrum* (Boettger, 1892): KU 170094, ds.

Heliophrynidae.—*Hadromophryne natalensis* (Hewitt, 1913): KU 195926, cs, ld (Lynch, 1971).

Hylidae.—*Hyla versicolor* LeConte, 1825: CM 144791, 33948a, 33948b, ds.

Limnodynastidae.—*Platyplectrum ornatum* (Gray, 1842): MACN 42620, ds, MCZ 73129, 73130, ds.

Ranidae.—*Lithobates catesbeianus* (Shaw, 1802): CM 4051, ds.