

BUFONID TOADS FROM THE LATE OLIGOCENE BEDS OF SALLA, BOLIVIA

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ABSTRACT—Isolated fragmentary anuran remains from several fossil-bearing levels of the continental succession exposed in the Salla-Luribay basin, Eastern Cordillera, are described herein. The anuran material consists of poorly preserved postcranial bones that are referable to toads of the nearly cosmopolitan genus *Bufo*, now widely distributed in South America. Moreover, these remains strikingly resemble skeletal elements of extant South American species of the *B. marinus* group, most of which inhabit humid to semiarid lowlands. Based on the ilial morphology, two species appear to be represented in the Salla Beds: one close to *B. arenarum* and another, possibly new, that attained large size. This study does not confirm an earlier suggestion that a taxon closely related to the living South American aquatic leptodactylid *Caudiverbera* is represented in the Salla succession. This record supports an Early Tertiary, or even older, major diversification of bufonids.

INTRODUCTION

In recent years, the search for fossil vertebrates, particularly mammals, in South America has led to the discovery of anuran remains. Because most of these fossil frogs are from Patagonia, discoveries outside this region are significant, not only for anuran phylogeny, but also for anuran biogeography, as they provide clues to understand former distributional patterns. In this paper we describe Paleogene anuran remains collected in western Bolivia by joint expeditions of the University of Florida, Natural History Museum of Los Angeles County, and Servicio Geológico de Bolivia, between 1981 and 1992.

The frog-bearing beds are part of a continental succession exposed in the Salla-Luribay basin, which is located in the Eastern Cordillera of the Andes of Bolivia (Fig. 1A). This succession, called Salla Beds, yields a rich vertebrate assemblage that also includes mammals, turtles, and birds, collected since 1952 (e.g., Hoffstetter, 1968; MacFadden et al., 1985; Marshall and Sempere, 1991). Moreover, this Tertiary site is famous because the oldest known South American primate, the ceboid *Branisella boliviana* (Hoffstetter, 1969), was discovered in these beds.

Based on the preliminary examination of early finds, Hoffstetter (1968) concluded that the mammalian fauna from Salla is synchronic with the Deseadan mammals from Patagonia, then considered of early Oligocene age. Subsequent studies confirmed the assignment of the mammalian remains to the Deseadan South American Land Mammal “age,” although there is still some disagreement over the relative age of the Salla fauna with respect to the Deseadan local faunas known from Argentina (Flynn and Swisher, 1995; Kay et al., 1998, and papers cited therein). These paleontological studies were complemented with detailed examination of the stratigraphical distribution of the fossils, as well as with magnetostratigraphic analyses and isotopic dating of tuffaceous levels intercalated in the sequence (MacFadden et al., 1985). Available evidence now suggests that the fossiliferous beds at Salla are Oligocene in age (Kay et al., 1998).

In 1968 Hoffstetter reported the presence of frogs in the Salla Beds. These fossils were referred to a large form close to *Caudiverbera* (“proche de *Calyptocephalella*”) by Vergnaud-Grazzini (in Hoffstetter, 1968), although they were never described or illustrated. Additional anuran remains were collected subsequently and housed at the Florida State Museum, University

of Florida, Gainesville (UF). This latter material consists of isolated incomplete postcranial bones that are the result of surface prospecting and is described herein. Comparisons with living representatives of several anuran groups indicate that these fossils are referable to the nearly cosmopolitan genus *Bufo*, now broadly distributed in South America. Moreover, some of these remains strikingly resemble extant species that are endemic to this continent, thus confirming earlier suggestions that major diversification of *Bufo* into several supraspecific groups is a relatively old event (Estes and Reig, 1973; Savage, 1973; Estes and Báez, 1985).

PROVENANCE AND AGE OF THE ANURAN REMAINS

The Salla Beds are about 540 m thick and consist mostly of reddish and gray claystones and siltstones with interbedded volcanic and bentonized tuffs. This succession appears to have been deposited principally in a fluvial environment (MacFadden et al., 1985). The Salla Beds conformably, or possibly mildly disconformably, overlie the early Tertiary Luribay Conglomerate and locally are covered by an unnamed unit of probable Pleistocene age (Hoffstetter, 1976; MacFadden et al., 1985).

Several fossiliferous levels are known within the Salla Beds (Fig. 1B); the most paleontologically rich of these levels are located in the middle one-third of this unit (MacFadden et al., 1985). The total fossiliferous interval at Salla spans the time between 29.4 and 25.5 Ma based on the magnetic polarity stratigraphy of the Salla Beds and some isotopic age determination (⁴⁰Ar/³⁹Ar) of tuffaceous levels (Kay et al., 1998). The earliest stratigraphically documented frogs come from the Red rodent zone that falls in the 25.99–26.55 Ma interval. Anuran remains occur also at the *Branisella* level, the age of which is estimated to be between 25.95 and 25.99 Ma, and at the Upper White Level, which represents the 25.82–25.89 Ma interval (Fig. 1B). Thus, the frog-bearing levels are late Oligocene in age according to the time scale by Berggren et al. (1995).

SYSTEMATIC PALEONTOLOGY

ANURA Rafinesque, 1815
NEOBATRACHIA Reig, 1958
BUFONIDAE Gray, 1825
Bufo Laurenti, 1768

Type Species—*Bufo viridis* Laurenti, 1768.
Age—Paleocene to Recent.

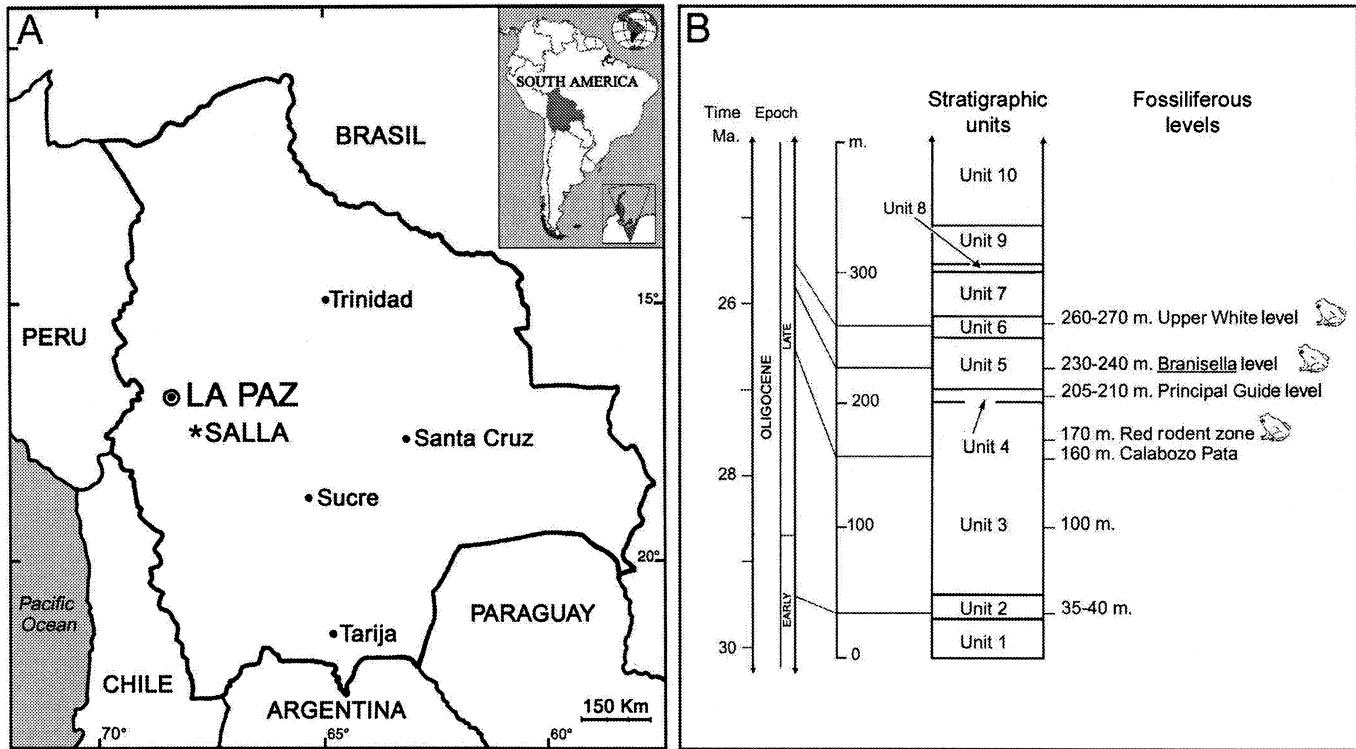


FIGURE 1. A, map of Bolivia, showing location of the fossiliferous area. B, stratigraphical distribution of the frog-bearing horizons (modified from Kay et al., 1998).

Discussion—Iliia are among the most frequently recovered anuran bones in fossil collections (see e.g., Sanchiz, 1998). Although some intraspecific variation does occur, the ilium is one of the more useful postcranial elements for identification to the familial or generic level. Referral of the material described herein to this genus is based on the following combination of characters: posterior portion of shaft lacking dorsal crest; dorsal acetabular expansion moderately or little developed; anterior margin of distinct dorsal prominence extended to position anterior to anterior margin of acetabulum; supra- and pre-acetabular fossae present; interiliac tuber absent; no dorsal groove between ilial shaft and dorsal acetabular expansion. However, some of these features, such as the supra-acetabular fossa, may be absent in some species of this genus (Sanchiz, 1977).

Bufo aff. *B. arenarum* Hensel, 1867

Fig. 2A, B

Referred Material—UF 92824, well-preserved, incomplete, basal portion of a left ilium.

Locality and Horizon—"Red rodent zone," Unit 3 of Kay et al. (1998), at Calabozo Pata, Departamento de La Paz, Bolivia.

Description—The posterior portion of the robust ilial shaft has a slightly laterally compressed cross-section and lacks a dorsal crest. The most posterior portion of the dorsal acetabular expansion (=pars ascendens) is missing in this specimen, whereas the preserved portion of the ventral acetabular expansion (=pars descendens) indicates that this region was well developed and formed an angle of about 90° with the ilial shaft. The pre-acetabular zone (sensu Lynch, 1971) is broad, with a deep pre-acetabular fossa. The ilial portion of the shallow acetabulum has a rounded shape. Most of the dorsal prominence is located at a level anterior to the acetabulum and is amply separated from the acetabular dorsal border. This prominence

is relatively low, its height being about 28% the length of its base. The anterior slope of the prominence is slightly steeper than the posterior one. The conspicuous dorsal protuberance (=tuber superius) has an internal valley that determines two, anterior and posterior, distinct lobes. The anterior lobe is round and presents a slight depression in the middle. The posterior lobe is smaller and more elongate than the anterior lobe. The prominence-protuberance complex is distinctly extero-laterally oriented. Posteriad to this complex there is a deep supra-acetabular fossa that is somewhat expanded posteriorly.

Discussion—Examination of ilia of various extant species of the genus *Bufo* demonstrated the frequent presence of division of the dorsal protuberance into several lobes, although this feature may vary within species (Sanchiz, 1977). This trait was also figured in several Cenozoic fossil species of *Bufo* (Tihen, 1962b). Conversely, we did not observe a multi-lobed dorsal protuberance on the ilia of representatives of other anuran groups available for examination of this trait. This evidence, thus, lends some additional support to our generic assignment.

Within the genus *Bufo*, numerous strictly phenetic species groups based largely on a few osteological, mainly cranial, and external morphological characters have been recognized (Tihen, 1962a; Martin, 1972; Duellman and Schulte, 1992). However, the monophyly and phylogenetic relationships of these groups and the species they contain are poorly understood (Maxson, 1984). Moreover, even the monophyly of *Bufo* has been questioned (Graybeal, 1997). Comparisons with skeletal materials of members of South American, as well as extra-continental, groups of species show a close resemblance of UF 92824 with extant species of the *B. marinus* group. The latter is one of the eight groups now inhabiting South America, the others being the *B. guttatus*, *B. typhonius*, *B. granulosus*, *B. crucifer*, *B. spinulosus*, *B. veraguensis*, and *B. valliceps* groups (Duellman and Schulte, 1992). *Bufo typhonius* and *B. haematiticus*, placed in

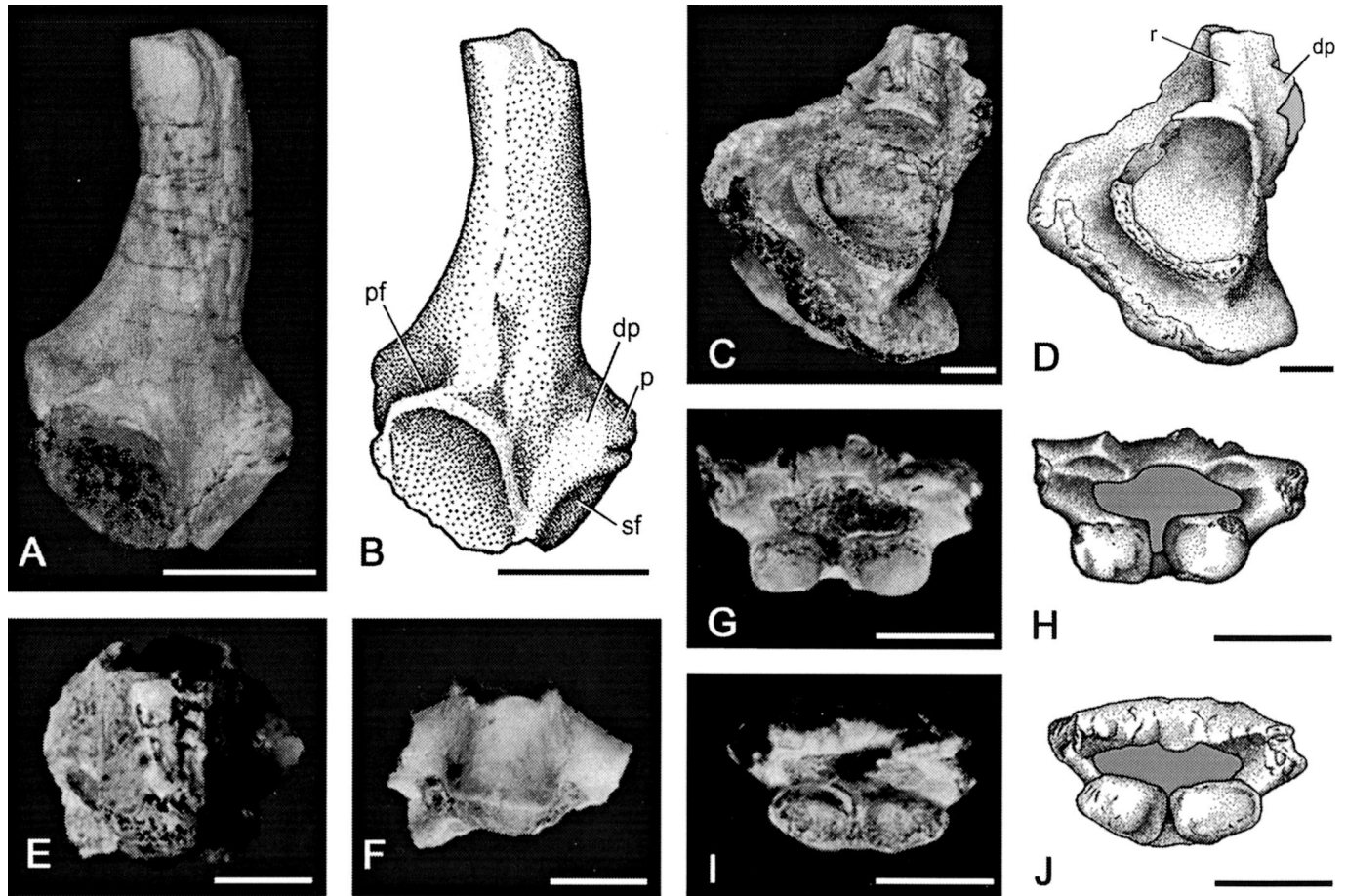


FIGURE 2. Remains referable to the genus *Bufo*. **A, B**, *Bufo* aff. *B. arenarum* (UF 92824), portion of left ilium in external (lateral) view; **A**, photograph, **B**, line drawing. **C, D**, *Bufo* sp. (UF 205709), incomplete, articulated pelvic girdle in external (lateral) view; **C**, photograph, **D**, line drawing. **E–F**, *Bufo* sp. (UF 204998, UF 173000.3), posterior presacral vertebrae in ventral view. **G–J**, *Bufo* sp., sacral vertebrae in posterior view; **G**, photograph of UF 204996.3; **H**, line drawing of same specimen; **I**, photograph of UF 204996.2; **J**, line drawing of same specimen. **Abbreviations:** **dp**, dorsal prominence; **p**, protuberance; **pf**, pre-acetabular fossa; **sf**, supra-acetabular fossa. Scale bar equals 5 mm.

the *B. typhonius* and *B. guttatus* groups respectively, have delicate and flattened ilia with relatively few muscle insertion scars. In both species the dorsal prominence is low and antero-posteriorly expanded, unlike the same structure on the ilium from Salla. The ilia of *Bufo granulatus*, a member of the *granulosus* group, differ from the fossil specimen in the more posterior location of the anterior margin of the prominence, which coincides with the anterior border of the acetabulum, and the distinctly flattened shafts. *Bufo spinulosus*, a typically Andean species representative of the *spinulosus* group, has ilia with less extended dorsal prominences than in UF 92824, lacking supra-acetabular fossae and dorsal acetabular expansions wholly developed in the acetabular plane. Unlike the ilium from Salla, the ilia of *Bufo crucifer* have a flattened overall aspect owing to the dorsal acetabular expansion developed in the acetabular plane and the laterally compressed ilial shaft. Examination of several species of the *B. marinus* group revealed some variation in the ilial morphology, in spite of the evident similarity of other parts of the skeleton (Tihen, 1962a; Martin, 1972). Amongst the species of this group available for comparisons, *Bufo marinus* and *B. ictericus* agree in having ilia with relatively flat basal parts of shafts, dorsal prominence-protuberance complexes parallel to the acetabular planes, and dorsal protuberances not well demarcated from the prominences. These features contrast with the ilia of *Bufo arenarum*, *B. paracnemis*,

and UF 92824, in which the shafts are robust, the dorsal prominence-protuberance complexes are distinctly laterally projected, and the dorsal protuberances are clearly delimited from the prominences. In addition, these extant species and the fossil specimen resemble one another in the presence of distinct supra-acetabular fossae and dorsal acetabular expansions slightly medially inclined with respect to the acetabulum. The fossil specimen resembles *B. arenarum* most closely in the well-developed and elongate supra-acetabular fossa and a dorsal protuberance divided into two unequal lobes by a groove. This latter feature, however, is not present in all examples of this extant species examined, whereas none of those of *B. paracnemis* has a protuberance subdivided into distinct lobes in agreement with observations of other authors (Vergnaud-Grazzini, 1968). In this regard, it is noteworthy that the groove present in UF 92824 is deeper than those observed in ilia of *B. arenarum*. Additionally, in this extant species the dorsal prominence is slightly lower than in the fossil specimen.

Bufo sp.
Fig. 2C, D

Referred Specimens—UF 204997, basal portion of a left ilium, "Red rodent zone," Unit 3 at Sici Lomo Cayo; UF 205000, 205709, distal portions of articulated pelvic girdles,

including ilia, ischia, and pubes, "Upper White Level," Unit 6 at west Tapijal Pampa, Departamento de La Paz, Bolivia.

Description—The similarity in the features preserved in all referred specimens strongly suggest that they represent a single species, which attained a large body size, comparable to *B. paracnemis*. A prominent rounded ridge extends along the lateral surface of the bone anterior to the acetabulum (Fig. 2C, D) in all three specimens, despite their disparate sizes. These specimens agree in having dorsal acetabular expansions notably narrow (Fig. 2C, D) and slightly medially oriented with respect to the acetabulum, and ventral acetabular expansions moderately developed. Also, in all of them the pre-acetabular zone is broad, with a deep pre-acetabular fossa, and the ilial portion of the acetabulum is subtriangular. The dorsal prominence is best preserved in UF 205709, in which it is possible to observe that its anterior margin extends to a position well anterior to the anterior margin of the acetabulum. The posterior half of this prominence lies adjacent to the acetabular dorsal margin, from which is separated by a depressed region. The apical portion of the dorsal prominence is not preserved in any of these specimens; thus, we were unable to describe the characteristics of the scar left by the insertion of the gluteus magnus muscle. However, it is evident that the prominence-protuberance complex was laterally projected.

In the largest specimens (UF 205000, 205709) the articulation of both ilia forms a strong symphysis that determines an acute angle between these bones ventrally, and a wider angle dorsally. Each ilium is fused to the corresponding ossified pubis; only traces of the former suture between these elements are evident. The right and left ischia are completely fused to each other, but each is only partially fused with the corresponding ilia and nearly so to the pubes.

Discussion—Referral to the genus *Bufo* is based on the combination of characters noted above, although poor preservation of all assigned specimens prevents us from asserting that a dorsal crest was absent on the ilial shaft. All specimens resemble the extant *B. arenarum* and *B. paracnemis*, in the robustness of the shaft, the lateral projection of the prominence-protuberance complex, the presence of pre- and supra-acetabular fossae, the orientation of the dorsal acetabular expansion, and the relative sizes of the dorsal and ventral acetabular expansions. However, the prominent lateral ridge anterior to the acetabulum and the dorsal prominence separated from the acetabular fossa by a depression are unlike the conditions in all examples of *Bufo* and other anuran taxa that we examined, thus suggesting that this poorly preserved material represents a new species.

Other Remains Referable to *Bufo* Without Specific Allocation

Several postcranial bones are referable to *Bufo*, although it is difficult to determine the proper association of these bones with each other and with the ilia and pelvic girdles described above. As with the ilia, the strongest resemblances between these elements and those of any extant group are with species of the *B. marinus* group, although we did not find any particular species in which all the characters of the fossil material are present.

All the presacral vertebrae (UF 92847, 204996.1, 24998, Red rodent zone; UF 13289.1, *Branisella* level; UF 173000.3-4, Upper White Level) are procoelous and have wide, short neural arches lacking well-developed spinous processes. Neural spines are lacking, although some of the vertebrae show a fine medial crest. Even though morphological variations along the vertebral column were considered, we were able to recognize two morphotypes that may indicate the presence of two species in the Salla beds (Fig. 2E, F). The two examined sacral vertebrae (UF 204996.2-3, Red rodent zone) agree in having an anteriorly

concave centrum and two posterior condyles. The sacral diapophyses are not sufficiently complete to permit an estimation of their distal expansion; their basal parts have a dorsoventrally flattened cross section and are slightly posteriorly directed. The neural canal is extremely reduced and the neural arches are thick, as they are in all examined presacral vertebrae from Salla. In spite of these general similarities, the two fossil sacrals differ in the shape and separation of the condyles, the condyles being rounded and separated from each other in UF 204996.3 (Fig. 2G, H) whereas they are grossly triangular and almost in contact in UF 204996.2 (Fig. 2I, J). We interpret these differences as indicative of the presence of two taxa coexisting in the same fossiliferous horizon. A well-preserved anterior urostylar fragment (UF 204995.1, Red rodent zone), the size of which suggests that the bone belongs to a large individual, lacks lateral processes. This urostyle differs from the same bone of all representatives of extant taxa examined in the presence of a distally thick dorsal crest, lacking all evidence of fusion of left and right halves in the preserved portion.

The single humeral fragment preserved in the sample (UF 13289.2, *Branisella* level) has a spherical and well-ossified eminentia capitata. The ventral fossa is not well defined and does not extend far anteriorly from the eminentia capitata.

THE PUTATIVE PRESENCE OF THE LEPTODACTYLID *CAUDIVERBERA* IN THE SALLA BEDS

The first report on the discovery of anuran remains in the Salla Beds was by Hoffstetter in 1968. In his preliminary account of the fossils from Salla, this author quoted the opinion of Vergnaud-Grazzini that numerous, but monotonous, anuran remains are referable to a large form close to *Calyptocephalella* (= *Caudiverbera*). Because of this tentative taxonomic assignment of anuran bones collected in the Salla Beds, we stressed the comparisons of the material available to us with specimens of the single living species of this South American genus obtained in the University of Buenos Aires Vertebrate Collection (FCEN-V). These comparisons made evident that neither this species nor a close relative is represented by our sample. The ilia of *C. caudiverbera* differ strikingly from those described herein in the presence of a shaft bearing a well-developed dorsal crest. Moreover, the dorsal prominence is confluent with this dorsal crest and the dorsal acetabular expansion has a marked dorsal vector and is as broad as or broader than the ventral acetabular expansion (Fig. 3A, B). The presacral and sacral vertebrae of *Caudiverbera* have wider neural canals and better developed neural spines than the same bones from Salla (Fig. 3C, D). As in UF 204995, the urostyle of *Caudiverbera* has a high dorsal spine but the apical terminus of this spine is not laterally expanded. The morphology of the humerus does not support a close relationship with *Caudiverbera* as the ulnar (lateral) and radial (medial) epicondyles are differently developed. This fossil produces a distinctly asymmetrical aspect to the distal end of the bone that is not obvious in the humeri of this extant genus (Fig. 3E, F).

The material collected by Hoffstetter is now housed in the Muséum National d'Histoire Naturelle in Paris (MNHN) and was incidentally examined by one of us (AMB) several years ago. The specimens come from the general Salla area and no specific locality data are known. These specimens consist of poorly preserved isolated or partially articulated postcranial bones, some of them large, that resemble the ones studied herein. The material includes series of two or three articulated anterior (MNHN Sal 273) and posterior (MNHN Sal 276) procoelous presacral vertebrae, one sacral vertebra (MNHN Sal 275), one distal fragment of a humerus, one distal portion of a large pelvis (MNHN Sal 274), and several tibiofibulae. The atlas and second vertebra bear blunt neural spines, whereas the

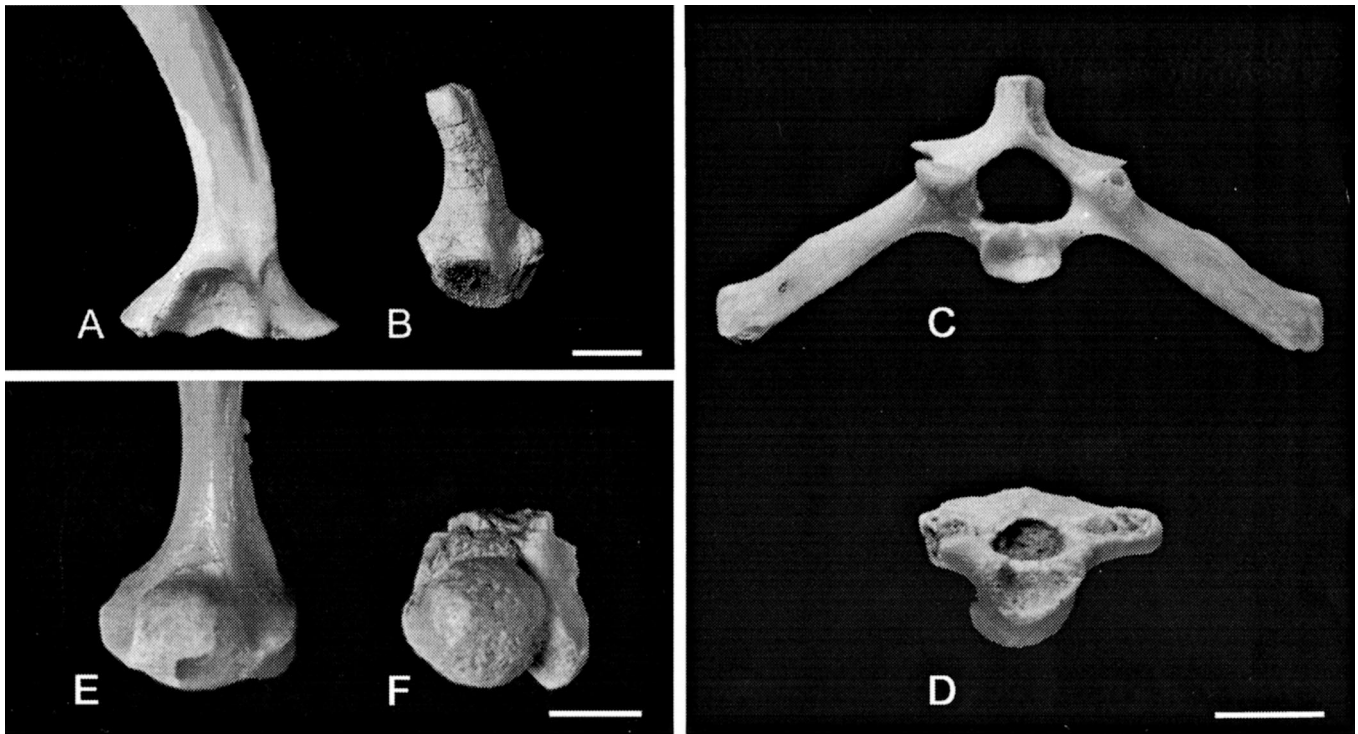


FIGURE 3. Elements from the Salla Beds and the same elements of *Caudiverbera caudiverbera* (FCEN-V-1052). Left ilium in external (lateral) view, **A**, *C. caudiverbera*, **B**, *Bufo* aff. *B. arenarum* (UF 92824). Presacral vertebra in anterior view, **C**, *C. caudiverbera*; **D**, *Bufo* sp. (UF 173000.3). Distal right humerus in ventral view, **E**, *C. caudiverbera*, **F**, *Bufo* sp. (UF 13289.2). Scale bar equals 5 mm.

posterior presacrals have neural arches ornamented with fine longitudinal “wrinkles” and lack prominent neural spines. The sacrum bears two closely set condyles; the neural canal is notably shallow. The distal parts of the sacral diapophyses are missing, but the flat cross-sections of the preserved portions indicate that the diapophyses were not round. The most conspicuous features of these bones allow us to conclude that this material does not represent *Caudiverbera* and likely pertains to the same taxa documented by the specimens described above.

DISCUSSION

The fossil remains described herein indicate that at least two anuran species that we refer to *Bufo* are represented in the Salla Beds, both presumably close to species currently placed in the *Bufo marinus* group. However, it should be noted that the interrelationships of the numerous species of this genus and non-*Bufo* bufonids are far from being resolved, and that postcranial osteological data, the only information on the anurans from Salla available to us, are rarely included in most taxonomic accounts on bufonids.

The *B. marinus* species group includes middle- to large-sized toads, most of them robust and well ossified, which are widespread in the Neotropical region. Extant species of this group occur in the Pacific lowlands from Mexico to northern Peru, and east of the Andes from northern South America to central Argentina (Duellman and Schulte, 1992). Relatively complete fossil remains from the middle Miocene Honda Group (Flynn et al., 1997) in the upper Magdalena Valley, Colombia, were referred to the living species *Bufo marinus* (Estes and Wassersug, 1963). This record indicates that this group was already differentiated by middle Tertiary times, a hypothesis endorsed by the resemblance between the material from Salla and the same elements of endemic South American species currently placed in the *B. marinus* group.

MacFadden et al. (1994) estimated that the elevation of Salla was 500 m or less at the time of deposition of these rocks, a situation that contrasts strikingly with the present altitude of about 3,600 m. The presence of relatives of the *Bufo marinus* group lends some support to this proposal, as most species in this group are characteristic of tropical and subtropical lowlands and do not occur at such high elevations today. However, *Bufo arenarum*, perhaps the most ecologically versatile species placed in this group, has been reported to occur occasionally in eastern slopes of the Andes at well over 1,000 m (Cei, 1980; De La Riva, 1990). Prior to Salla time, during the Eocene and early Oligocene, the paleo-Andes were located west of the Bolivian territory and a wide alluvial plain that probably resembled the Chaco-Beni lowlands occupied what is at present the Altiplano and most of the Eastern Cordillera of Bolivia (Marshall and Sempere, 1991). Thus, species of *Bufo* closely related to the *B. marinus* group might have been widespread in this region. Initial uplift of the eastern Andes of Bolivia started around 27 Ma; as a result of this major tectonic upheaval several intermontane basins, such as the Salla Luribay basin, developed in the Andean domain (Sempere et al., 1990; Marshall and Sempere, 1991). Subsequent elevational and climatic shifts, particularly since the late Miocene (see Gregory-Wodzicki et al., 1998), related to the central Andes tectonism, had significant biotic consequences. The Andes create a rain shadow, which blocks moisture from the Amazon basin; hence, present batrachofaunas of high montane habitats in this region of Bolivia are characterized by species resistant to extreme dryness and low temperatures, such as those of the *B. spinulosus* group (Morrison, 1992).

Pedogenic carbonate, or calcrete, nodules occur interbedded in the Salla sequence (MacFadden, 1990). Also, fossil mammals include many herbivorous taxa with high-crowned evergrowing teeth and with cursorial adaptations (MacFadden, 1990; Sán-

chez Villagra and Kay, 1997; Shockey, 1997, 1999). This evidence from sediments and associated fauna was interpreted as indicating a semi-arid open environment at Salla in the late Oligocene-early Miocene (MacFadden et al., 1994). These environmental conditions are consistent in general with the presence of *Bufo*, as most species of this genus are terrestrial or fossorial, and several species placed in the *Bufo marinus* group (e.g., *B. arenarum*, *B. paracnemis*) extend their distribution to semi-arid regions bordering savannas today.

Oldest unquestionable remains of *Bufo* in South America to date come from late Paleocene rocks (formerly middle Paleocene; see Marshall et al., 1997, for this new age assessment) at Itaborai, Brazil (Estes, 1970; Estes and Reig, 1973). These remains consist of isolated ilia notoriously different from the ones described herein (pers. obs.) that clearly represent other bufonid species and have been interpreted as relatives of extant South American taxa (Estes and Báez, 1985). All other *Bufo* remains hitherto known come from Miocene or younger horizons of Europe, North and South America, and represent taxa close to the extant species living in these same regions (Sanchiz, 1977; Bailon and Hossini, 1990; Báez, 1991, 2000; Roček and Rage, 2000). Hence, the fossil record indicates that the genus *Bufo* had already attained a considerable degree of diversification and main distributional patterns were established by mid Tertiary times.

ACKNOWLEDGMENTS

We gratefully acknowledge David Webb and Bruce MacFadden (University of Florida) for the loan of the material from Salla. Special thanks are extended to Jean-Claude Rage and Christian de Muizon (Muséum national d'Histoire Naturelle, Paris) for their help to locate the material collected by Hoffstetter and for providing photographs of these specimens. We are also indebted to Diana Echeverría (Universidad de Buenos Aires), Linda Trueb (University of Kansas), Esteban Lavilla, and Sonia Kretzschmar (Instituto Lillo) for the loan of comparative material under their care. Jorge Gonzalez collaborated in the preparation of the drawings. This research was financially supported by the University of Buenos Aires (Grant TX 01 to AMB)

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Received 26 April 2002; accepted 24 March 2003.