On the Putative Presence of *Eupsophus* (Anura: Cycloramphidae) In Central Patagonia During the Oligocene

ON THE PUTATIVE PRESENCE OF *EUPSOPHUS* (ANURA: CYCLORAMPHIDAE) IN CENTRAL PATAGONIA DURING THE OLIGOCENE

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ABSTRACT: Fossil anuran remains from an outcropping of Oligocene sediments in central Patagonia have been attributed to the extant genus *Eupsophus* based on their putative similarity to the skeleton of living members of this genus. These remains would represent the only and oldest evidence of the existence not only of *Eupsophus,* but also of any cycloramphid anuran in Patagonia during the past. Given the scarcity of the anuran fossil record, these fossils have been long considered as significant evidence in the discussion of the evolutionary history of the South American batrachofauna. However, re-examination of these specimens reveals that some skeletal structures were misinterpreted and that these anurans clearly differ from living *Eupsophus*. Although osteological synapomorphies of this genus are still unknown, there is no evidence to link these fossil remains with the presence of *Eupsophus* in the Oligocene batrachofauna of Patagonia.

Key words: Chubut, Deseadan; *Eupsophus*; Fossil anurans; Oligocene; Patagonia; Scarritt Pocket

FOSSILS provide two levels of information about evolutionary history. They evidence past diversity and sometimes are exemplars of extinct taxa having unique combinations of characters that are absent in extant species. At the same time, however, a fossil specimen also possesses temporal information derived from its stratigraphic record that provides an age interval for the first recognized appearance of a taxon. Therefore, fossils have long been used in the field of evolutionary biology as temporal evidence to infer patterns and processes of evolution and distribution of living species. There has been an increased focus on fossils recently, owing to their use as calibration tools in molecular dating analyses. This application, however, must be supported by robust systematic hypotheses, which is not always the case (e.g., Lee, 1999; Dyke, 2001; Conti et al., 2004; van Tuinen and Hedges, 2004).

During the 1930s, researchers from the American Museum of Natural History undertook a series of expeditions in Patagonia that provided a rich fossil vertebrate collection, including anurans (Simpson, 1934a; Chafee, 1952; Marshall et al., 1986). Among these, several specimens from an outcropping of Oligocene sediments in the Scarritt Pocket locality, in central Patagonia, were attributed

to the extant genus *Eupsophus* (Schaeffer, 1949). This is a highly endemic and relatively diverse genus (10 species fide; Frost, 2011) that inhabits the temperate Andean *Nothofagus* forests of southern Chile and Argentina. *Eupsophus* is considered a member of the South American neobatrachian clade Cycloramphidae (Frost et al., 2006). Its presence in the Oligocene sediments of Scarritt Pocket would represent the only and the oldest evidence of the existence not only of *Eupsophus,* but also of Cycloramphidae in Patagonia in the past. Despite the enormous diversity of extant anurans in South America, their fossil record is notably sparse and diversity is low. Most Cretaceous and Paleogene frog remains are representatives of pipids or *Callyptocephallela* (Báez, 2000; Báez et al., 2000, 2006; Cione and Báez, 2007; Muzzopappa and Báez, 2009; Gómez et al., 2011), relatively basal clades of anurans that have comparatively restricted distributions on the continent today. The taxonomic affinities of the few other remains that may represent neobatrachian from sediments of the Cretaceous and Paleogene are uncertain (Báez and Perí, 1989; Báez, 1991; Báez and Fernicola, 1999; Báez and Nicoli, 2004; Báez et al., 2009). Given this context, the reported presence of *Eupsophus* in the Oligocene of Patagonia becomes particularly relevant. In fact, these remains have long been employed as

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evidence of that presence in discussions of the evolution of the South American batracho-fauna (Cei, 1962a,b; Hecht, 1963; Gallardo, 1965; Cei, 1968; Cei and Roig, 1968; Vuilleu-mier, 1968; Cei, 1969; Gallardo, 1972; Estes and Reig, 1973; Báez and Gasparini, 1977; Duellman and Veloso, 1977; Báez and Gas-parini, 1979; Díaz and Veloso, 1979; Penna and Veloso, 1990; Formas et al., 1991; Formas and Brieva, 1992, 1994; Correa et al., 2006; Nuñez et al., 2011). Moreover, they have been used as a calibration point in phylogenetic time-calibrated analyses (Marjanović and Laurin, 2007). Lynch studied the osteology of the extant species of *Eupsophus* exhaus-tively and repeatedly questioned the generic assignment of these fossils (Lynch, 1971, 1972, 1978), but subsequent authors did not act on his opinion. The goal of this article is to test this 60-yr-old paleontological systematic hypothesis by re-examining the fossil speci-mens involved, reconstructing the skeletal anatomy of the taxon, and re-evaluating its taxonomic placement.

Materials and Methods

The fossil material was collected by G.G. Simpson in 1934, during the Second Scarritt Expedition of the American Museum of Natural History (AMNH) in Patagonia, and housed in the collection of Vertebrate Paleontology of this institution (AMNH 3407, 3415, 3420, 3422, 3424–26, 3430). The fossils are preserved in several slabs, some of which represent part and counterpart of the same specimen. The preser-vation is poor; most of the bones are broken and their parts are preserved in different slabs. Thus, it is difficult to reconstruct the different elements in their entirety. In addition, the colors of the bones and sediment are similar. Their locality of provenance, Scarritt Pocket (SP), is located in the center of the Chubut Province, Argentina (Fig. 1). The sediments in the pocket are included in the Sarmiento Formation and would have accumulated in a small, shallow, ephemeral lake that may have been located in the crater of an extinct volcano (Simpson, 1934b; Chafee, 1952; Marshall et al., 1986). Marshall et al. (1986) estimated the age of the Scarritt Pocket sediments to be 23.4–21.0 million years, according to the K–Ar datings of several basalts and tuffs that bound the pocket.
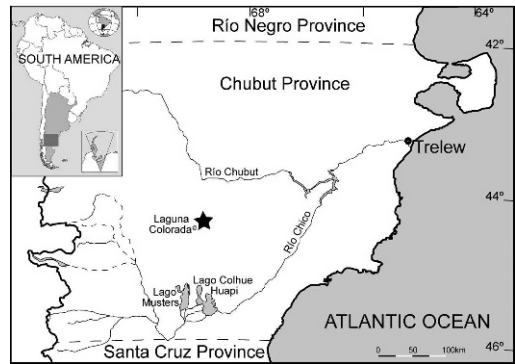

Fig. 1.—Location map showing the paleontological locality of Scarritt Pocket (black star) in Chubut Province, Argentina.

However, Flynn and Swisher (1995) stated that Swisher had obtained new ^{40}Ar–^{39}Ar dates from aliquots of the same samples dated by Marshall et al. (1986) ranging between 27 and 29 million years (middle Oligocene).

To date, phylogenetic analyses of *Eupsophus* (Veloso et al., 2005; Correa et al., 2006) have not included skeletal data and osteological synapomorphies are unknown for the genus. Lynch described the osteology of *Eupsophus* and discussed the possible relationships of the genus (Lynch, 1971, 1972, 1978), but he did not provide osteological characters that could be used to diagnose the genus. I analyzed the character states present in *Eupsophus* and its close relatives in the context of current phylogenetic hypotheses (Correa et al., 2006; Frost et al., 2006; Grant et al., 2006) and identified a series of nonexclusive, putative osteological synapomorphies for the genus as follows: (1) presence of a long pars palatina and (2) a pterygoid process on the maxilla; and (3) contact between the median ramus of ptery-goid and the parasphenoid. Because these cranial regions are not preserved in the fossils, I could not evaluate these character states. However, Schaeffer (1949) considered this fossil frog "…not separable from *Eupsophus* on the basis of available specimens." The single available specimen that he mentioned was AMNH 22104, from Corral, Chile, originally identified as *Eupsophus grayi*, a junior syno-nym of *E. roseus* (Grandison, 1961) and illustrated by Lynch (1971). Consequently, fossils attributed to *Eupsophus* were re-exam-ined and compared with extant species of the
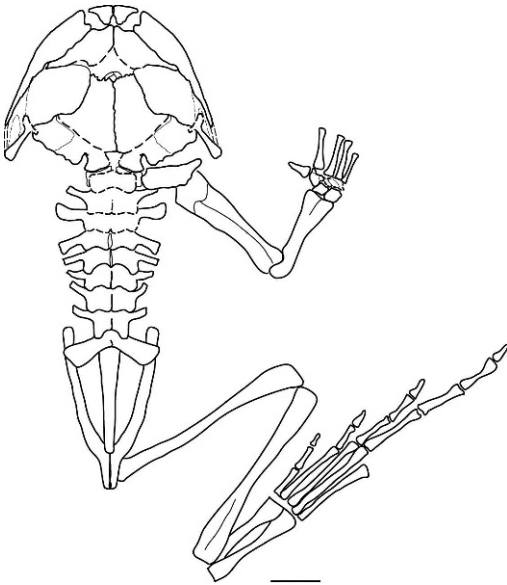
FIG. 2.—Reconstruction of the fossil anuran from Scarritt Pocket assigned by Schaeffer (1949) to *Eupsophus* sp. (bar = 3 mm). Reconstruction based on AMNH 3422.

RESULTS

The fossil frog represented by the SP material is a small anuran (snout–vent length approximately 30 mm) with a large head that is wider than long. The relatively well ossified skull possesses notably expanded antorbital and interorbital regions (Figs. 2 and 3). No dermal ornamentation is visible. The medial skull length is approximately equal to, or slightly shorter than, the length of the presacral vertebral column. The latter is composed by eight discrete, procoelous vertebrae. The sacral diapophyses are moderately dilated, and slanted posteriorly; their width is wider than the width of the presacral column at the level of the posterior presacrals and about the same as that of Presacral III. The urostyle is remarkably short, its length being approximately equivalent to that of five presacral vertebrae (Fig. 2). The pectoral girdle has robust clavicles, moderate-sized scapulae, and well-developed cleithra (Fig. 4). The pelvic girdle has relatively short ilial shafts, each of which seems to have a low, dorsal, ridge-like crest along its length. The hind limbs are long relative to the forelimbs and longer than the snout–vent length of the frog. The terminal phalanges are knobbed.

Schaeffer (1949) placed these fossil specimens in *Eupsophus* based on the presence of a series of generalized characters—that is, shallow, dentate maxillaries; relatively large nasals, possibly in contact; presence of frontoparietal fontanelle (sensu Trueb, 1973); nine procoelous vertebrae; bicondylar sacro-urostylar articulation; moderately expanded sacral diapophyses; and elongated hind limbs. The nasals, however, are broadly separated in all extant species of *Eupsophus* (Fig. 3B), and for this reason, Lynch (1971) argued that these fossils are not members of *Eupsophus*.

genus, particularly *E. roseus*, but also other species (Examined material: *E. calcaratus*: Dep. Chusamén, Parque Nacional Lago Puelo, Chubut, Argentina: MLP 4011, cleared and stained [C&S]. *E. roseus*: Lago Curruhué Grande, Neuquén, Argentina: MACN 37981 [C&S]. *E. vertebralis*: Valdivia, Chile: MACN 43704 [dry skeleton]). In addition to the exhaustive osteological descriptions of several species of *Eupsophus* provided by Lynch (1971, 1972), there are additional osteological observations available in other articles (e.g., Grandison, 1961; Lynch, 1978; Nuin and do Val, 2005; Grant et al., 2006; Lavilla et al., 2010). Institutional codes follow those of Leviton et al. (1985).
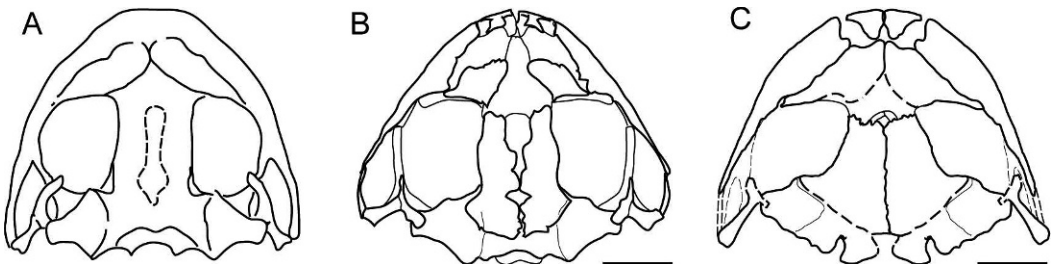

FIG. 3.—Dorsal view of skulls (bar = 3 mm) of (A) the fossil anuran from Scarritt Pocket reconstructed by Schaeffer 1949 (redrawing); (B) *Eupsophus roseus* (MACN 37981); (C) the fossil anuran from Scarritt Pocket, new reconstruction.
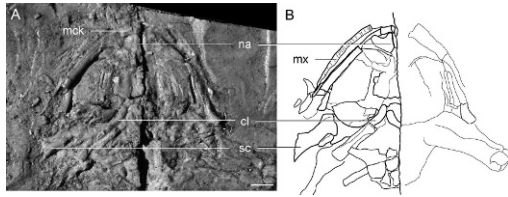
FIG. 4.—Specimen (AMNH 3407a) of the fossil anuran from Scarritt Pocket poorly preserved in ventral view (bar = 3 mm). (A) Photograph, (B) interpretative drawing. Abbreviations: cl, clavicle; mck, mentomeckelian bone; mx, maxilla; na, nasal; sc, scapula.

On the other hand, re-examination of this material reveals the presence of large, extensive nasals and frontoparietals that are in medial contact with one another. As Schaeffer (1949) noted, a well-ossified preorbital region, with an exposed sphenethmoid and large, extensive nasals is evident in the fossil specimens with skulls preserved in dorsal view. Although the size and edges of the nasals cannot be discerned in the dorsal view owing to unclear preservation, the anterior portions of these bones is visible in ventral view in AMNH 3407a (Plate 18.2 in Schaeffer, 1949; Fig. 4). In this specimen, the nasals can be seen to extend anteriorly nearly to the level of the maxillary arcade and to articulate with one another, at least in their anterior portions (Fig. 4).

In the notably broad interorbital region of the skulls preserved in dorsal view, a cavity that is framed by bone represents the anterior end of the broad frontoparietal fontanelle of the neurocranium (Fig. 5). Schaeffer characterized the fontanelle as being widely exposed, with the frontoparietals bordering it, although he acknowledged that the medial margins of these bones could not be determined (Figs. 3A, 5A). Examination of the specimens reveals that fragments of flat bones, with evidence of median longitudinal sutures in some regions, are preserved within the fontantelle in AMNH 3422 (Figs. 5B,C). This suggests the presence of large frontoparietals in medial contact with one another over the fontanelle; the delicate bones were subject to postmortem crushing within the neurocranial fontanelle. This interpretation is also supported by the analysis of AMNH 3425 (Fig. 6), a specimen preserved in two slabs. AMNH 3425a bears imprints of dorsal surfaces of the bones of the skull table, as well as bones preserved in ventral view. Similarly, AMNH 3425b possesses imprints in ventral view and bones of the skull table in dorsal view. Consequently, I have concluded that AMNH 3425a bears the dorsal portion of the specimen, whereas AMNH 3425b bears the ventral portion (Fig. 6). AMNH 3425a (dorsal portion) possesses an elevated area in the interorbital region, the shape of which matches the gap in the frontoparietal region of AMNH 3425b. Presumably, this area represents the sediment that filled the postmortem the neurocranial space (Fig. 6C). Medially sutured
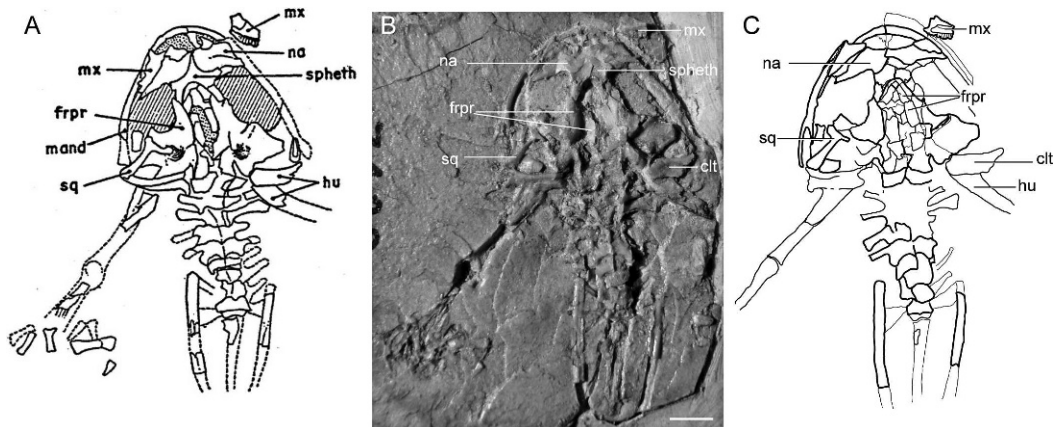

FIG. 5.—Specimen (AMNH 3422) of the fossil anuran from Scarritt Pocket preserved in dorsal view (bar = 3 mm). (A) Reproduction of the interpretative drawing produced by Schaeffer (1949) from this specimen, (B) photograph, (C) new interpretative drawing. Abbreviations: clt, cleithrum; frpr, frontoparietal; hu, humerus; mand, mandible; mx, maxilla; na, nasal; spheth, sphenethmoid; sq, squamosal.
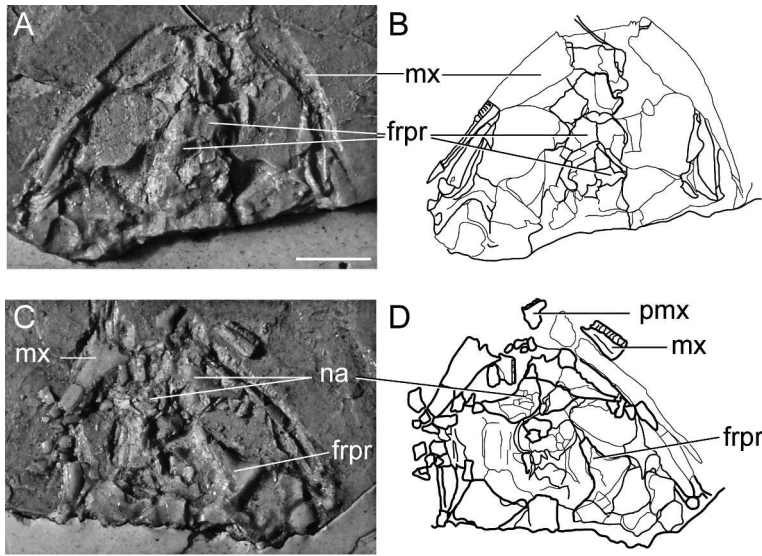
F<small>IG.</small> 6.—Specimen of the fossil anuran from Scarritt Pocket preserved in part and counterpart slabs (bar = 3 mm). (A) Photograph and (B) interpretative drawing of the slab that possesses the more dorsal portion of the specimen (AMNH 3425a). (C) Photograph and (D) interpretative drawing of the slab that possesses the more ventral portion of the specimen (AMNH 3425b). Abbreviations: frpr, frontoparietal; mx, maxilla; na, nasal; pmx, premaxilla.

fragments of flat bones are preserved over the entire surface of this elevated area. These are thought to be pieces of the frontoparietals that in life roofed the fontanelle and that postmortem, were broken by the overlaying sediment, and collapsed into the neurocranial cavity (Fig. 6). The lateral borders of frontoparietals diverge posterolaterally in all the specimens in which the bones are preserved (Figs. 4, 5). Schaeffer (1949) reported this morphology (Fig. 5A), but it is not depicted in his reconstruction of the SP frog (Fig. 3A). The uniformity and symmetry of this morphology in all the specimens in which the frontoparietals are preserved strongly indicates that this is the original configuration of the bones and not a postmortem effect. In summary, all evidence supports the presence of large, nonornamented frontoparietals in medial contact throughout their lengths and having posterolaterally oriented lateral borders (Fig. 3C). In contrast, all living species of *Eupsophus* possess comparatively narrow frontoparietals with incomplete medial contact and lateral borders that are more or less parallel to one another and not posterolaterally divergent (Fig. 3B).

The SP frog also differs from living *Eupsophus* in other aspects. In the fossil, the presacral column has relatively broad, imbricate neural arches, in contrast to the narrower, nonimbricate presacral neural arches of *Eupsophus* (Fig. 7). The length of the urostyle in *Eupsophus* always exceeds that of the eight presacrals plus the sacrum, whereas the length of the urostyle in the fossil species only equals the length of five presacrals (Fig. 7).

The morphology of squamosals is uncertain. The bone is only evident in AMNH 3422. In the photograph and drawing of this specimen (Fig. 5A; Schaeffer, 1949: Plate 18.1), the otic ramus is notably long, nearly half the length of the ventral ramus. However, I observed the otic ramus to be considerably shorter than shown in the photograph (Fig. 5B,C), suggesting that it may have been broken after its original description. My reconstruction of the zygomatic ramus differs from that of Schaeffer (Fig. 2); the 1949 photograph of AMNH 3422 is unclear and disparities may simply be differences in interpretation. The zygomatic and otic rami of the squamosal of *Eupsophus* do not resemble any of the interpretations of the morphology of these rami in the fossil, but given the uncertain preservation of the bone, I did not include the squamosal morphology as evidence of generic placement of the fossils.
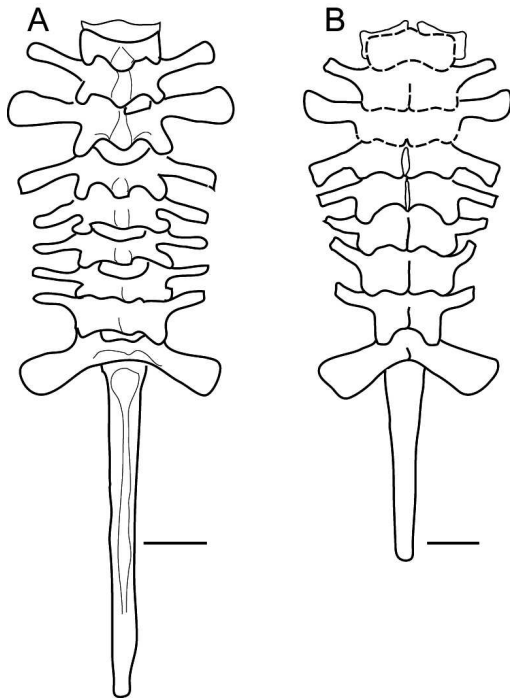
FIG. 7.—Vertebral column in dorsal view (bar = 2 mm) of (A) *Eupsophus roseus* (MACN 37981) and (B) the fossil anuran from Scarritt Pocket.

DISCUSSION

The re-examination of the specimens attributed by Schaeffer (1949) to *Eupsophus* sp. indicates that several features were misinterpreted. The revised skeletal anatomy of the SP fossil frog clearly differs from that of the extant *Eupsophus*. However, no exclusive osteological synapomorphies have been identified for *Eupsophus* and the putative nonexclusive osteological synapomorphies involve skeletal regions that are not preserved in the fossils. Thus, it is impossible to exclude the SP fossils from *Eupsophus* on the basis of absence of recognized synapomorphies. On the other hand, there is no evidence whatsoever that supports the inclusion of the fossils in this genus. Consequently, there is no reason to conclude that *Eupsophus* was present in central Patagonia during the Oligocene.

It is impossible to determine the taxonomic placement of the fossil remains at this time. Our understanding of the systematic relationships of anurans has changed dramatically in the last decade owing to molecular studies (e.g., Frost et al., 2006; Grant et al., 2006; Roelants et al., 2007). Most of the proposed new clades lack osteological data; thus, it is difficult to determine the placement of fossils in the phylogenetic framework. Moreover, a recent expedition to SP has provided several new anuran fossils that resemble the species originally attributed to *Eupsophus*; these remains are still under preparation. If they prove to be the same as the fossils described here, then we can anticipate learning more about the skeletal anatomy, and perhaps relationships, of this taxon. The consequences of Shaeffer's placement of the SP material in *Eupsophus* attest to its significance, as well as the necessity of robust systematic hypotheses from paleontology. Given the depauperate nature of the anuran fossil record, it is especially relevant to assess the relationships of the SP fossil with living taxa as we seek to understand the evolution of the South American batrachofauna and apply these data as a calibration point in phylogenetic time-calibrated analyses.

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