

REAPPRAISAL OF A CERATOPHRYID FROG FROM THE OLIGOCENE OF PATAGONIA: ASSIGNATION TO *CERATOPHRYS* AND NEW INSIGHT ABOUT ITS PROVENANCE



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Abstract. Fragmentary anuran remains in the Ameghino Collection in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" were recently considered as belonging in Ceratophryidae (the clade of the South American horned frogs) and coming from middle-late Oligocene sediments exposed south of Lake Colhue Huapi, Chubut, Argentina. However, both the taxonomic placement and the geographic and stratigraphic origin attributed to this material are problematic. A new study of these remains show they possess several features that allow their attribution to the extant genus *Ceratophrys* Wied-Neuwied. The available information on the collection locality of this material is dubious –namely Gran Barranca, where rocks range from the middle Eocene to early Miocene in age. Additionally, details of the history of this collection and the specimen itself suggest that its provenance should better be considered unknown.

Key words. Gran Barranca. Chubut. *Ceratophrys*. Anura. Neobatrachia.

Resumen. REVALUACIÓN DE UNA RANA CERATOPHRYIDAE DEL OLIGOCENO DE PATAGONIA: ASIGNACIÓN A *CERATOPHRYS* Y NUEVA CONCEPCIÓN DE SU PROCEDENCIA. Restos fragmentarios de anuros en la Colección Ameghino del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" fueron recientemente incluidos en Ceratophryidae (el clado de los escuerzos sudamericanos) y considerados como provenientes de sedimentos del Oligoceno medio-tardío del sur del Lago Colhue Huapi, Chubut, Argentina. Sin embargo, tanto la asignación taxonómica como el origen geográfico y estratigráfico atribuidos a este material son problemáticos. El reestudio de estos restos indica que poseen varios caracteres que permiten su atribución al género viviente *Ceratophrys* Wied-Neuwied. La información disponible acerca de la localidad de origen de este material es dudosa. Esta fue referida como Gran Barranca, donde las rocas expuestas tienen una edad comprendida entre el Eoceno medio y el Mioceno temprano. Además, ciertos detalles de la historia de la colección y el espécimen en sí sugieren que su proveniencia debería ser considerada desconocida.

Palabras clave. Gran Barranca. Chubut. *Ceratophrys*. Anura. Neobatrachia.

CERATOPHRYIDAE is the well-supported clade of the extant South American horned frogs (Haas, 2003; Darst and Cannatella, 2004; Correa *et al.*, 2006; Fabrezi, 2006; Frost *et al.*, 2006; Grant *et al.*, 2006; Evans *et al.*, 2008, 2014; Fabrezi and Quinzio, 2008; Pyron and Wiens, 2011). It includes eighteen extant and fossil species in three genera (*Ceratophrys* Wied-Neuwied, 1824, *Chacophrys* Reig and Limeses, 1963, and *Lepidobatrachus* Budgett, 1899) and three monotypic fossil genera (Casamiquela, 1963; Báez and Perí, 1989, 1990; Evans *et al.*, 2008, 2014).

Fossil anurans assigned to Ceratophryidae have been recorded since the late 19th century (*e.g.*, Ameghino, 1899; Rovereto, 1914; Rusconi, 1932; Casamiquela, 1963; Marshall and Patterson, 1981; Báez and Perí, 1989, 1990; Rinderknecht, 1998; Contreras and Acosta, 1998; Fernicola, 2001; Agnolín, 2005; Evans *et al.*, 2008, 2014; Tomassini *et al.*, 2011). The earliest referred remains are from Late Creta-

ceous sediments: *Beelzebubo ampinga*, from Madagascar (Evans *et al.*, 2008, 2014) and *Baurubatrachus pricei* from Brazil (Báez and Perí, 1989).

The putative immediately younger record of the group are fragmentary remains assigned to Ceratophryidae and referred to middle-late Oligocene sediments south of Lake Colhue Huapi, Chubut Province, Argentina (Agnolín, 2005). The potential importance of this evidence lies not only in the context of the evolutionary history of Ceratophryidae but in that of anurans. The anuran fossil record is scarce and few remains have been attributed to extant taxa, providing very few calibration points for molecular clocks. Thus, any fossil discovery attributed to an extant taxon represents valuable evidence with a considerable impact. In this context, the reported presence of Ceratophryidae in the Oligocene of Patagonia is reassessed, considering its identification, provenance and horizon.

MATERIALS AND METHODS

Fossil and extant skeletal material was examined using a Nikon SMZ 800 stereoscope. Photographs of extant specimens were taken with a Micrometrics digital camera attached to this stereoscope. Fossil specimens were photographed with a Sony DSC-XZ200 digital camera. Images were processed with Adobe Photoshop CS5. The sediment adhered to the anuran remains was mechanically removed and exposed to hydrochloric acid in order to establish its chemical composition.

The specimen included in Ceratophryidae by Agnolín (2005), *i.e.*, MACN-A 10434, consists of two disarticulated, black bones, a premaxilla and a radioulna. It belongs to the Ameghino Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, which houses part of the material collected and studied by the brothers Florentino (1854–1911; see below) and Carlos (1865–1936) Ameghino. MACN-A 10434 is stored in a round wooden shaving box (typically made and used by the Ameghino brothers). This box includes a piece of cotton and a handwritten label, presumably by Florentino Ameghino, which says “ColHuapi”. The number MACN-A 10434 is written (by another writer) on the side of the box. No other information is associated to the specimen.

Several skeletal specimens of Ceratophryidae, as well as from putatively related taxa, were examined (Appendix, Supplementary Information Online) and additional information was obtained from the literature (*e.g.*, Grandison, 1961; Reig and Limeses, 1963; Lynch, 1971, 1972, 1978, 1982; Reig, 1972; Pires Gayer, 1984; Laurent and Lavilla, 1986; Lavilla and Lobo, 1992; Wild, 1997, 1999; Lavilla and Ergueta Sandoval, 1999; Izecksohn *et al.*, 2005; Da Silva Vieira *et al.*, 2006; Fabrezi, 2006; Rosset *et al.*, 2007; Prado and Pombal Jr., 2008; Rosset, 2008). Institutional codes follow those of Leviton *et al.* (1985), with the addition of **MMH**: Museo de Ciencias Naturales “Vicente Di Martino”, Monte Hermoso, Argentina.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE OF THE REMAINS

Agnolín (2005) considered the anuran remains MACN-A 10434 “*provenientes del sur del lago Colhue Huapi (provincia de Santa Cruz, Patagonia, Argentina) y colectados en la Formación Sarmiento (Oligoceno medio-tardío)*” [from south of

Lake Colhue Huapi (Santa Cruz Province, Patagonia, Argentina) and collected in the Sarmiento Formation (middle-late Oligocene)], presumably on the basis of the label attached to the material. However, Ameghino has used the designation “ColHuapi” (indicated on that label) to refer to material collected along the cliff south of the Lake Colhue Huapi, the fossiliferous locality known to paleontologists as Gran Barranca, Chubut Province, Argentina, without specification of age or stratigraphic level (Simpson, 1967; Ciancio and Carlini, 2008). Carlos Ameghino explored Gran Barranca between 1895 and 1901 (Simpson, 1967; Madden and Scarano, 2010). He exploited at least four of the seven fossil-beds now recognized at Gran Barranca: the current “Barrancan”, “De-seadan”, “La Cancha”, and “Colhuehapien” faunas (*sensu* Simpson, 1967; Ré *et al.*, 2010; Bond and Deschamps, 2010). The sequence that contains these levels, included in the Sarmiento Formation, has recently been attributed to a period from the middle Eocene to the early Miocene (Madden and Scarano, 2010; Ré *et al.*, 2010). Thus, even considering that the information associated with the specimen is correct, MACN-A 10434 could have come anyway from any of these stratigraphic levels.

The origin of this specimen, however, should be approached with caution. On one hand, the Ameghino Collection has a complex history, only partially documented. For many years the Ameghino brothers conducted paleontological exploration and research independently from an official institution (Simpson, 1948; Bond, 2000; Podgorny, 2000; Fernicola, 2011). At least between 1889 and 1903, Carlos led approximately thirteen expeditions to Patagonia and collected thousands of fossils (Bond, 2000). In this way, as for many amateur collectors and researchers in the late eighteenth and early nineteenth century, the Ameghinos assembled an extensive private collection (Bond, 2000; Fernicola, 2011). The owners of these private collections decided their commercial value and which portions could be set apart for exchange or sale (Podgorny, 2000; Podgorny and Lopes, 2008). The sale and gift of these collections was a common practice and Florentino and his colleagues exchanged several specimens (Podgorny and Lopes, 2008). Thus, the Ameghino Collection received not only the material collected by Carlos, but also contained material donated by other contributors, exchange material, casts, etc. (Podgorny, 2000; A. Kramarz, pers. com.). In 1902, Florentino was appointed Director of the Museo Nacional de Histo-

ria Natural (currently MACN) and, the following year, Carlos was appointed “*naturalista viajero*” (traveling naturalist) of this Institution (Simpson, 1948; Bond, 2000; de Asúa, 2012). As traveling naturalist between 1903 and 1912, Carlos made several expeditions to Patagonia and several short expeditions to fossil localities of Buenos Aires and Catamarca (Bond, 2000). The material collected during those expeditions was housed at the MACN (in the MACN-PV Collection; A. Kramarz, pers. com.; Podgorny, 2000; de Asúa, 2012). The Ameghino Collection, however, continued growing from donations and exchanges of casts and materials (Podgorny, 2000). Finally, in 1928, most of the Ameghino private collection was purchased from Carlos (Florentino had died in 1911) by the Argentinean government and housed in the MACN, where it remained as a separate collection from the institutional collection of paleovertebrates (currently as MACN-A; A. Kramarz pers. com.; Bond, 2000; Ciancio and Carlini, 2008).

Ameghino never published collection numbers of the specimens that he described and only numbered a portion of his collection (Simpson, 1948; Ciancio and Carlini, 2008). This numeration was recorded in his notebooks and culminated in the number 10316 (Ciancio and Carlini, 2008). The specimens with higher collection numbers were added to the collection at some later time(s) during the following century at the institution (A. Kramarz, pers. com.). The only information for all those specimens that were not originally numbered is the associated handwritten labels on small slips of paper (Simpson, 1967). In addition, misplacement of labels and loss of material have been reported for this collection (*e.g.*, Simpson, 1948; Prevosti and Pardiñas, 2001; de La Fuente, 2005; González and Scilatto-Yané, 2008; Tejedor and Rosemberg, 2008; Carlini *et al.*, 2010; Scheinsohn *et al.*, 2011; Pérez and Vucetich, 2012). Despite efforts by the current curatorial staff to solve these problems, the identification or origin of the materials with only associated information on the handwritten labels (like MACN-A 10434) should be taken with caution, and this has been the prevailing approach by most recent researchers and the recommendation of the curators of the MACN.

MACN-A 10434 seems to be in its original box. However, the Ameghino brothers did not use cotton in their boxes (M. Bond, A. Kramarz, pers. com.). Thus, MACN-A 10434 must have been fitted later by curatorial personnel who in-

cluded cotton in the box and probably added the specimen to the collection. Both the collection card and the side of the box of this specimen have the handwriting of Mr. A. Ramos, a collection assistant that worked in the MACN Collection during the decade of 1990 (A. Kramarz, pers. com.). The collection card of MACN-A 10434 says “*cf. Ceratophrys, Colhuapi*”, but Ramos could not have personally arrived at this taxonomic identification (M. Bond, A. Kramarz, pers. com.). This specimen may have had associated additional information that has been lost or perhaps the original label might have been misplaced.

On the other hand, Ameghino never reported the presence of Ceratophryidae in Gran Barranca, even when he knew and described other ceratophryids earlier (Ameghino, 1899) and surely could have recognized the relevance of this discovery. Subsequent to Ameghino’s expeditions to Gran Barranca, the same locality was exhaustively explored during the past century (Madden and Scarano, 2010). This resulted in thousands of fossils, mostly mammal remains (Madden *et al.*, 2010). Among these numerous remains, small-sized specimens were identified, such as isolated teeth, cingulate osteoderms, and also fragmentary material (*e.g.*, Schaeffer, 1949; Báez, 1977; Carlini *et al.*, 2010; Gelfo, 2010; Goin *et al.*, 2010). All this small material is light in color whereas the bones of MACN-A 10434 attributed to Ceratophryidae are black. Black bones of mammals are known from different levels of the Gran Barranca locality, including megafauna remains from the Vera and Upper Puesto Almendra members (*sensu* Bellosi, 2010a; M. Bond, pers. com.). The fossils from the Vera Member have been attributed to the Tinguirirican South American Land Mammal Age (SALMA) and have a characteristic crust or patina of manganese oxide (Ré *et al.*, 2010). In the Puesto Almendra Member, black fossils are from the middle portion of the section and typical of the Deseadan SALMA. No small fossils have been recovered in these levels. In addition, none of the numerous (mostly unstudied) fragmentary anuran remains from Gran Barranca (lots MACN-A 11656, MLP 92-X-20-25) are attributable to Ceratophryidae (A.M. Báez, pers. com.; pers. obs.). Some of these have been assigned to *Calyptocephalella* (Schaeffer, 1949; Báez, 1977) and the remaining, unpublished material seems also to represent this genus (A.M. Báez, pers. com.; pers. obs.).

Ameghino (1899) mentioned the presence in the (now known) Pliocene of Monte Hermoso of a fossil species of

Ceratophrys, which he named *C. prisca*. He considered this species extremely similar to the extant species *C. ornata*, from which it differs in the smaller size, shorter skull and kind of sculpture of the dermal bones. The corresponding material was not illustrated nor described in more detail, and no reference was made to which specific bones were preserved. The whereabouts of this material remains unknown (Fernicola, 2001). All additional fossils from the Monte Hermoso Formation (Early Pliocene Age) attributed to Ceratophryidae, some of which are also housed in the MACN Collection, are black (e.g., MACN-Pv 14317-19, 14324) and morphologically indistinguishable from MACN-A 10434.

Both the Sarmiento Formation (exposed at Gran Barranca) and the Monte Hermoso Formation (named generally as “sedimentos pampeanos”) include sediments derived from volcanic sources and are mostly reworked (Zavala and Navarro, 1993; Belloso, 2010b). Thus, these sediments have a dominant silt fraction. Coincidentally, the sediment adhered to MACN-A 10434 revealed a siliceous composition non-reactive to hydrochloric acid. This evidence does not shed light on the origin of the fossil material.

In conclusion, there is no evidence supporting the age assigned to MACN-A 10434 by Agnolín (2005), even when considering that the locality information associated with the specimen is correct. It might have originated from middle Eocene to early Miocene sediments at Gran Barranca. However, considering the available information, the problematic history of the Ameghino Collection, and the absence of any other external evidence supporting the putative collecting locality of MACN-A 10434, its origin should better be considered unknown.

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813

NEOBATRACHIA Reig, 1958

CERATOPHRYIDAE Tschudi, 1838

Ceratophrys Wied-Neuwied, 1824

Type species. *Ceratophrys varius* Wied-Neuwied, 1824 [currently *C. aurita* (Raddi, 1823)]. Extant taxon, neotropical distribution.

***Ceratophrys* sp.**

Figures 1.1, 1.4, 2.1

Referred specimen. MACN-A 10434, left premaxilla (Figs. 1.1, 1.4) and right radioulna (Fig. 2.1).

Locality and age. Unknown. See above.

Description. The premaxilla is large and robust, showing a conspicuous but restricted oval patch of ornamentation that follows the morphology of the dorsal margin of the bone (Fig. 1.1). The alary process is well developed and considerably high; although its distal portion seems to be broken, it is nearly as high as the pars dentalis. In frontal view, the alary process is flat and broad-based, with the long axis parallel to the midline and with a laminar lateral margin (Fig. 1.1). The pars palatina and palatine processes are not differentiated. The pars dentalis seems to be completely preserved because the labial surface of its lateral border exhibits the notch that articulates with pars dentalis of the maxilla (Fig. 1.4). All dental positions are occupied by teeth, ten in total. Because all teeth are broken distally, it is not possible to determine the curvature of the teeth or if they are pedicellate. A maxillary process is well developed, though broken distally. The preserved portion of this process is long, having the length of four dental positions, and its robustness suggests that the processes were originally longer (Fig. 1.4).

The radioulna is a robust bone with a well-developed olecranon process (Fig. 2.1). Its total length represents less than three times the width of the base of the olecranon. The dual origin of the bone is evident in the distal half.

COMPARISONS AND DISCUSSION

Ceratophryidae includes twelve extant species in three genera: *Ceratophrys*, *Chacophrys*, and *Lepidobatrachus*. Several phylogenetic analyses including ceratophryids have been performed on the basis of different character systems (Haas, 2003; Darst and Cannatella, 2004; Correa *et al.*, 2006; Fabrezi, 2006; Frost *et al.*, 2006; Grant *et al.*, 2006; Evans *et al.*, 2008, 2014; Fabrezi and Quinzio, 2008; Pyron and Wiens, 2011). All of them included a reduced sampling of the Ceratophryidae and yielded incongruent results. In this way, both the relationships among the species of Ceratophryidae and those of Ceratophryidae with other anurans remain unresolved or poorly supported.

Some phylogenetic studies including ceratophryids have incorporated osteological information, resulting in a series of osteological synapomorphies for the clade (Fabrezi, 2006; Fabrezi and Quinzio, 2008). One of these, the absence of a discrete pars palatine of the premaxilla, is found in MACN-A 10434. This character state so far is an exclusive synapomor-

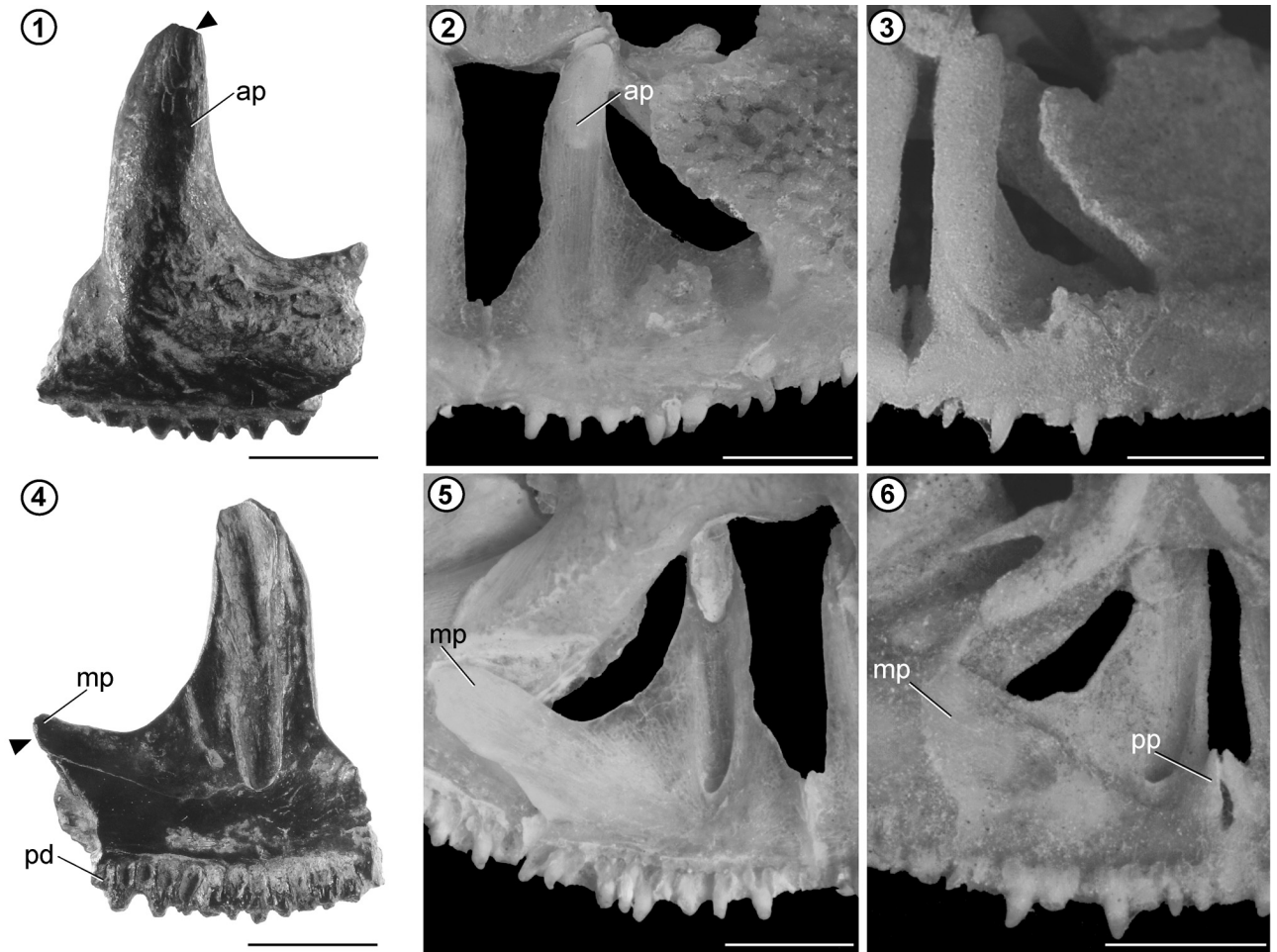


Figure 1. Premaxilla, comparison of the studied specimen with extant Ceratophryidae. **1, 4, *Ceratophrys* sp.**, MACN-A 10434; **1**, frontal view; **4**, posterior view. **2, 5, *Ceratophrys cranwelli***, FML 5475; **2**, frontal view; **5**, posterior view. **3, 6, *Lepidobatrachus llanensis***, FML 5221; **3**, frontal view; **6**, posterior view. Abbreviations: **ap**, alary process; **mp**, maxillary process; **pd**, pars dentalis; **pp**, palatine process. The black triangles indicate incomplete edges. Scale bar= 5 mm.

phy of Ceratophryidae. Except for the scarcely distinguishable palatine process present in *Lepidobatrachus* and *Chacophrys*, no evidence of the remaining shelf of the pars palatina is visible in the lingual surface of the premaxilla (Fig. 1.5–6). A reduced pars palatina has been reported in other taxa [e.g., *Pelodytes* (Sanchiz *et al.*, 2002); *Espadarana callistomma* (Guayasmin and Trueb, 2007); *Osteocephalus* (Trueb and Duellman, 1971)] but a palatal shelf is always still evident. Fabrezi (2006) considered absent the premaxillary pars palatina in the pipid *Hymenochirus boettgeri* and in the bufonid *Rhinella major* (as *Bufo granulatus*) in her data matrix. *Hymenochirus*, as others pipids, has a reduced pars facialis and a pars dentalis that cannot be distinguished from the well-developed pars palatina (Paterson, 1946; Trueb and Cannatella, 1982; Cannatella and Trueb, 1988). In *Rhinella major*, as in other bufonids of the *Rhinella granulosa* group (Pramuk, 2000), the maxillary pars facialis

projects forward, partially covering the premaxillae. A gap persists between the anterior margin of the pars facialis of both maxillae and it is filled with a mass of connective tissue. Thus, the premaxillary pars facialis is not evident externally. Anyway, a well-developed premaxillary pars palatine is evident in ventral view. The premaxilla of MACN-A 10434 lacks a discrete pars palatine (Fig. 1.4).

Several particular characters of the premaxilla of Ceratophryidae, not included in phylogenetic analyses, are also present in MACN-A 10434. Given the unresolved relationships of Ceratophryidae with other anurans the significance of these characters is equivocal. In Ceratophryidae as well as MACN-A 10434, the premaxillary pars palatina projects laterally in a process that articulates with maxilla (the maxillary process; Fig. 1.4–6). I noted that this process is absent in taxa suggested as close relatives of the Ceratophryidae by both



Figure 2. Radioulna, comparison of the studied specimen with extant anurans. **1**, *Ceratophrys* sp., MACN-A 10434, ventral view. **2**, *Ceratophrys cranwelli*, FML 5475, ventral view. **3**, *Telmatobius marmoratus*, KU 164080, ventral view. Scale bar = 3 mm.

Frost *et al.* (2006) and Pyron and Wiens (2011), including *Alsodes*, *Atelognathus*, *Batrachyla*, *Eupsophus*, *Hylorina*, *Limnomedusa*, *Proceratophrys*, and *Telmatobius*. In addition, the Ceratophryidae and MACN-A 10434 have premaxillae with long alary processes, which are always equal or longer than the pars dentalis of the same bone (Fig. 1.1–3). The analysis of the material available for comparison evidences that none of the taxa that may be close relatives of the Ceratophryidae exhibits alary processes as long as the pars dentalis.

Among the Ceratophryidae, the osteological synapomorphies that have been proposed for some genera correspond to bones that are not preserved in MACN-A 10434 (Fabrezi, 2006; Fabrezi and Quinzio, 2008). The premaxilla of *Ceratophrys*, however, possesses several synapomorphic character states that are present in MACN-A 10434. Lynch (1971) noted that the premaxilla of *Ceratophrys* is unique in lacking a discrete palatine process that is distinguishable from the alary process, while these are discrete and distinguishable in *Lepidobatrachus*. Fabrezi and Quinzio (2008) included this variation in their phylogenetic analysis (ch. 70), but they considered *Lepidobatrachus llanensis*, *L. laevis* and *Chacophrys* to lack a palatine process (70:2). My observations indicate, like those by Lynch (1971), that *Lepidobatrachus* possesses a discrete premaxillary palatine process (Fig. 1.6). A discrete palatine process is also observed in the premaxillae of *Chacophrys* (FML 1019, 9012). Like *Ceratophrys*, MACN-A 10434 lacks a

discrete palatine process (Fig. 1.4).

The alary processes of *Ceratophrys* are flat and with laminar lateral margins (Fig. 1.2), whereas those of *Lepidobatrachus* and *Chacophrys* show rounded surfaces and thick and projecting lateral margins (Fig. 1.3). The alary process of MACN-A 10434 has the same morphology as that of *Ceratophrys* (Fig. 1.1).

Some variation was observed in the maxillary process within the Ceratophryidae. While in all observed *Lepidobatrachus* and *Chacophrys* this process is short, reaching the level of the first one or two maxillary teeth, in *Ceratophrys* it is long, reaching at least the level of the fourth maxillary tooth (Fig. 1.5–6). Although the maxillary process of MACN-A 10434 is broken, the preserved portion is as long as four teeth (Fig. 1.4).

No differences have been observed among the premaxillae of the extant or fossil species of *Ceratophrys*. Only a few fossil specimens from the Monte Hermoso Formation that are attributable to *Ceratophrys* have preserved premaxillae (*C. ameghinorum* MACN 19731-14325; MMH 84-1-15). These specimens are indistinguishable from MACN-A 10434 (Fig. 3).

The radioulna is a bone with little variation among anurans. The robustness of the radioulna of MACN-A 10434 is consistent with that observed in Ceratophryidae (Fig. 3). In all the studied species of the Ceratophryidae, the total length represents less than three times the width in the base of the olecranon. That length is always more than three times the width in the base of the olecranon in other taxa that may be closely related (Fig. 2; Appendix, Supp. Inf. Online). However, others robust frogs (*e.g. Calyptocephalella*) that are not closely related exhibit the same radioulnar proportions as that observed in the Ceratophryidae.

In conclusion, there is evidence to consider MACN-A 10434 as an unidentified species of the extant genus *Ceratophrys*. However, its provenance should better be considered unknown; while it could have been collected in middle Eocene to early Miocene sediments of central Patagonia, it could as well have been collected in the Monte Hermoso Formation (Pliocene).

Several fossil anurans were assigned to *Ceratophrys*, but only two records, besides *C. prisca*, are from late Neogene times (Table 1). One of them is the fossil species *C. ameghinorum*, from outcrops of the Monte Hermoso Formation (Pliocene) in the Atlantic coast of the Buenos Aires Province,

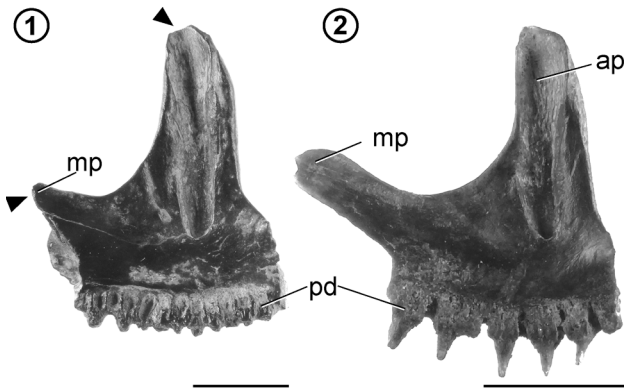


Figure 3. Premaxilla, comparison of the studied specimen with fossil *Ceratophrys*. **1**, *Ceratophrys* sp., MACN-A 10434, posterior view. **2**, *C. ameghinorum*, MACN 19731, posterior view. Abbreviations: **ap**, alary process; **mp**, maxillary process; **pd**, pars dentalis. The black triangles indicate incomplete edges. Scale bar= 5 mm.

Argentina (Fericola, 2001; Tomassini *et al.*, 2013). The other is a putative incomplete skull of *Ceratophrys* sp. mentioned in

a list of the fossil content of the Corral Quemado Formation (late Miocene–Pliocene), Catamarca Province, Argentina (Marshall and Patterson, 1981; Butler *et al.*, 1984). This remain was not described or illustrated and is currently lost [W. F. Simpson (Collections Manager of Fossil Vertebrates, Department of Geology, Field Museum of Natural History) pers. com.]. All other supposed *Ceratophrys* remains were collected in several Quaternary fossil-bearing sites of middle latitudes in South America (Table 1). Nowadays, extant *Ceratophrys* has a broad tropical distribution in this continent, north of the Patagonian region (Frost, 2014). Thus, if the Paleogene or Early Neogene Patagonian origin of MACN-A 10434 is confirmed, it would be the oldest and southernmost occurrence of *Ceratophrys*. The uncertainties regarding its collecting locality and horizon, however, are reason enough to be cautious and preclude using this fossil as evidence in the discussion of Ceratophryidae evolution or including it as a calibration point in molecular clock estimations.

TABLE 1 - Fossil record of Ceratophrys

Taxonomy	Provenance	Referred Material	Reference
Ceratophrys sp.	Corral Corrado Fm. (Miocene–Pliocene) Catamarca, Argentina	FMNH P 14402 (lost, see text). Listed	Marshall and Patterson, 1981
C. prisca (species inquirenda)	Monte Hermoso Fm. (Pliocene) Buenos Aires, Argentina	Unnumbered holotype lost. Briefly described	Ameghino, 1899 (Fericola, 2001)
C. ameghinorum	Monte Hermoso Fm. (Pliocene) ?Miramar Fm. (Pleistocene) Buenos Aires, Argentina	MACN Pv 14317-9, 14324-5, 19731 MLP 52-IX-27-11, 88-VII-20-1–2 MMH 84-1-15, 85-2-11. Described, illustrated	Fericola, 2001
C. ensenadensis	Ensenadense SALMA (Pleistocene) Buenos Aires, Argentina	Institutional collection number of material unreported (ICNU) Briefly described	Rusconi, 1932
C. rusconii	Miramar Fm. (Pleistocene) Buenos Aires, Argentina	MACN Pv 19744. Described, illustrated	Agnólin, 2005
Ceratophrys sp.	Pleistocene Colonia, Uruguay	MNHN 1560. Described, illustrated	Rinderknecht, 1998
Ceratophrys sp.	Tarija Fm. (Pleistocene) Tarija, Bolivia	ICNU (Museum National d’Histoire Naturelle- France). Described, illustrated	Vergnaud-Grazzini, 1968
Ceratophrys cornuta	Lagoa Santa (Pleistocene) Mina Gerais, Brazil	ICNU (British Museum of Natural History). Described, illustrated	Günther, 1859
Ceratophrys cf. ornata	Ñuapua Fm. (Pleistocene- Holocene) Chuquisaca, Bolivia	ICNU (Museum National d’Histoire Naturelle- France). Described, illustrated	Vergnaud-Grazzini, 1968
Ceratophrys sp.	La Postrera Fm. (Holocene) Buenos Aires, Argentina	MLP 86-VIII-1-1; 6. Described, illustrated	Perí, 1993
Ceratophrys cf. ornata	La Postrera Fm. (Holocene) Buenos Aires, Argentina	MLP 86-VIII-1-5. Described, illustrated	Perí, 1993
Ceratophrys sp.	Arqueological locality San Antonio (Holocene) Buenos Aires, Argentina	ICNU. Illustrated	Stoessel <i>et al.</i> , 2008

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