

THE OLDEST RECORD OF *CERATOPHRYS* (ANURA, CERATOPHRYIDAE) FROM THE LATE MIOCENE OF CENTRAL ARGENTINA

LAURA NICOLI,^{*1} RODRIGO L. TOMASSINI,² and CLAUDIA I. MONTALVO³; ¹División Herpetología, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Av. Angel Gallardo 470, C1405DJR, Ciudad Autónoma de Buenos Aires, Argentina, lnicoli@macn.gov.ar; ²INGEOSUR-CONICET, Departamento de Geología (UNS), San Juan 670, 8000, Bahía Blanca, Buenos Aires, Argentina, rodrigo.tomassini@yahoo.com.ar; ³Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Avenida Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina, cmontalvo@exactas.unlpam.edu.ar

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Ceratophrys is the most diverse and widely distributed genus of Ceratophryidae, the clade of South American horned frogs. It includes eight extant species, the relationships of most of which have been recently studied on the basis of molecular information (Faivovich et al., 2014). In addition, numerous remains from the Cenozoic of South America, including several fossil species, have been attributed to this genus (see Faivovich et al., 2014; Nicoli, 2014; Scanferla and Agnolín, 2015). Several of these assignments, however, are problematic (see Faivovich et al., 2014; Nicoli, 2014) and are being revisited by the authors. One of the questionable aspects of this record is that only in a few cases were the taxonomic assignments properly discussed (i.e., establishing the presence of synapomorphies or possible synapomorphies of *Ceratophrys* in the fossil remains). In addition, in most cases, the stratigraphic provenance of the fossils and the age estimates of the fossil-bearing rocks are not well known, preventing the use of fossils as calibration points in molecular clock analyses (Faivovich et al., 2014).

In this context, several cranial remains collected with strict stratigraphic control in the Miocene Arroyo Chasicó Formation were briefly described and assigned to *Ceratophrys* in a meeting abstract (Urrutia and Rosset, 2006), but a detailed study has not subsequently been published. This sedimentary sequence was later studied (Zárate et al., 2007), including radiometric dating of some levels, thereby providing age estimates for the anuran-bearing beds. Herein, we describe and discuss, with a broad comparative taxon sampling (Supplemental Data, Appendix) and in a phylogenetic context, the taxonomic placement of these remains. These would represent not only the oldest record of *Ceratophrys* to date but also that of Ceratophryidae, considering that the taxonomic position of the oldest putative representatives of this family has recently been questioned (Agnolín, 2012; Faivovich et al., 2014; Nicoli et al., 2016).

Institutional Abbreviations—**FML**, Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán Province, Argentina; **MD-CH**, Museo Municipal de Ciencias Naturales ‘Carlos Darwin,’ Arroyo Chasicó collection, Punta Alta, Buenos Aires Province, Argentina.

GEOGRAPHIC AND STRATIGRAPHIC PROVENANCE

The fossiliferous locality Arroyo Chasicó, which constitutes the type locality of the Arroyo Chasicó Formation (sensu Pascual, 1961), is located in southwestern Buenos Aires Province, Argentina (Fig. 1). It has provided an important collection of vertebrate remains, mostly mammals (see Bondesio et al., 1980; Cione and Tonni, 2005, and references therein). Zárate et al. (2007) carried out a detailed stratigraphic and sedimentological study of this formation and proposed a scheme that includes three lithofacies associations. Lithofacies Association 1, including lithofacies Sp, represents a channel-bar deposit consisting of three episodes of aggradation, probably originating as a braided to meandering fluvial system. Lithofacies Association 2, including lithofacies FSp and FSm, represents high-density flows accumulated in a marginal channel and/or floodplain environment. Lithofacies Association 3, including lithofacies FSh, Fm, and Fh, represents low-energy conditions of sedimentation in a swampy environment. Zárate et al. (2007) interpreted the succession as the result of episodic sedimentation in a fluvial environment of a mixed-load stream under progressively decreasing energy.

Based on a radiometric (⁴⁰Ar/³⁹Ar) age of 9.23 ± 0.09 Ma, obtained from impact glass (escoria) registered in lithofacies Sp, and high-resolution magnetostratigraphic profiles, Zárate et al. (2007) concluded that Lithofacies Associations 1 and 2 were accumulated between 9.43 and 9.07 Ma and Lithofacies Association 3 is younger than 9.02 Ma. However, the total duration of sedimentation remains unconstrained and could have extended to 8.7 Ma. The materials studied in the present contribution were recovered in lithofacies Fh (Lithofacies Association 3), associated with typical mammals of the Chasicocoan Stage/Age.

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.

*Corresponding author.



FIGURE 1. Map showing the location of the fossiliferous locality Arroyo Chasicó and the current distribution of the *Ceratophrys* species of the Chacoan Domain (sensu Cabrera, 1994). Distributions are represented by areas that include all the reported records for each species. Modified from Barrio (1980) following Lynch (1982), Langone (1995), and Maneyro and Langone (2001).

CERATOPHRYS sp.
(Figs. 2B, E; 3B, E)

Referred Specimen—MD-CH-06-165, skull fragments (incomplete interorbital region and left maxillary arcade).

Locality, Horizon, and Age—Arroyo Chasicó, Buenos Aires Province, Argentina. Arroyo Chasicó Formation (lithofacies Fh, sensu Zárata et al., 2007), Upper Miocene.

Description—Specimen MD-CH-06-165 consists of two skull fragments that belong to the same individual. Although they do not fit perfectly, their close spatial association in the fossil-bearing level and their shapes suggest that they were anatomically connected and that not too much material has been lost between them. They represent part of the interorbital region (Fig. 2B, E) and the left maxillary arcade (Fig. 3B, E) of a robust and well-ossified skull. All bones are synostotically fused. A conspicuous ornamentation is evident on the nasals, frontoparietals, and maxilla. The nasals are extensive bones that seem to roof all of the nasal region of the neurocranium (Fig. 2B). They had robust maxillary processes, which is mainly evident in the portion of right nasal fused to the pars facialis of the maxilla (Fig. 3B). This latter portion seems to represent almost the entire process, being uniformly wide. Laterally, the nasals and frontoparietals project beyond the neurocranium, forming a supraorbital shelf (Fig. 2E).

The neurocranium is completely ossified in the preserved regions, including solum, tectum and septum nasi, and planum antorbitale. Ventrally, two symmetrical anterior notches in the neurocranium seem to represent the scars of the unpreserved vomers. Robust neopalatines, medially close and bearing conspicuous odontoid ridges, are preserved in both skull fragments (Figs. 2E, 3E). The anterior end of the cultriform process of the parasphenoid reaches the level of the neopalatines (Fig. 2E).

Only the central portion of the left maxillary arcade is preserved (Fig. 3B, E). Several dental positions are evident in the fragmentary maxilla, although no teeth are preserved. The pars palatina is not a lingually projected shelf perpendicular to the pars facialis as in most anurans, but is dorsally projected and fused with the ossification of the planum antorbitale (and neopalatine) and two elements that seem to represent the ossification

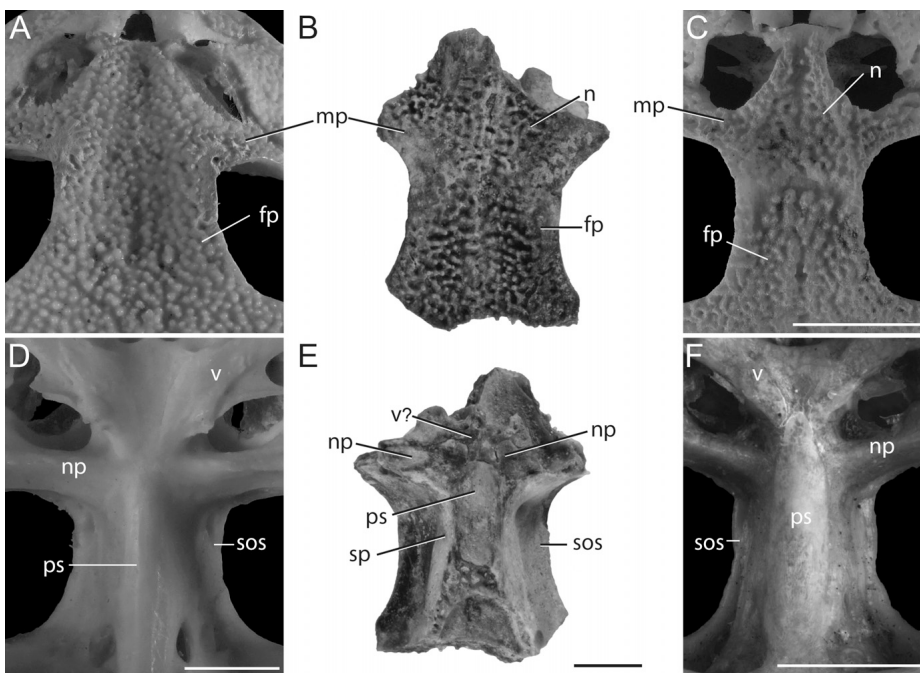
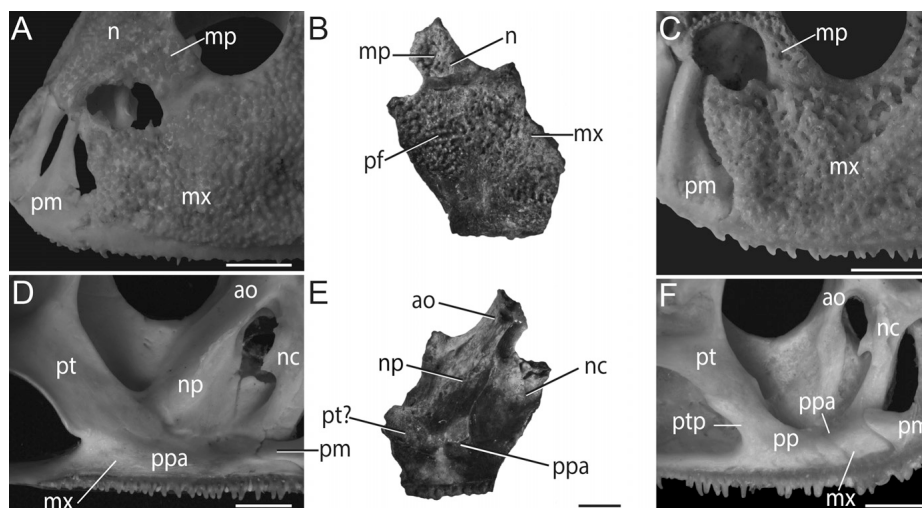


FIGURE 2. Fragment of the interorbital region of a fossil skull assigned to *Ceratophrys* compared with selected extant *Ceratophryidae*. **A, D**, *Ceratophrys cranwelli* (FML 5477); **B, E**, fossil *Ceratophrys* sp. (MD-CH-06-165); **C, F**, *Lepidobatrachus llanensis* (**C**, FML 5220; **F**, FML 1017); **A–C**, dorsal view; **D–F**, ventral view. **Abbreviations:** fp, frontoparietal; mp, maxillary process of nasal; n, nasal; np, neopalatine; ps, parasphenoid; sos, supraorbital shelf; sp, sphenethmoid; v, vomer. All scale bars equal 5 mm.

FIGURE 3. Fragment of a fossil maxilla assigned to *Ceratophrys* compared with selected extant Ceratophryidae. **A, D**, *Ceratophrys cranwelli* (**A**, FML 5472; **D**, FML 5477); **B, E**, fossil *Ceratophrys* sp. (MD-CH-06-165); **C**, *Lepidobatrachus llanensis* (FML 5222); **F**, *L. asper* (FML 5470); **A–C**, labial view; **D–F**, lingual view. **Abbreviations:** **ao**, ossifications of the planum antorbitale; **mp**, maxillary process of nasal; **mx**, maxilla; **n**, nasal; **nc**, ossifications of the nasal cartilages; **np**, neopalatine; **pm**, premaxilla; **pp**, pars palatina; **ppa**, discrete pars palatina absent; **pt**, pterygoid; **ptp**, pterygoid process. All scale bars equal 5 mm.



of the nasal cartilages (anteriorly) and the projected anterior ramus of the pterygoid (posteriorly; Fig. 3E); thus, a discrete shelf-like pars palatina is absent.

DISCUSSION AND CONCLUSIONS

Although the monophyly of Ceratophryidae (*Ceratophrys*, *Chacophrys*, and *Lepidobatrachus*) and the proposed relationships within *Ceratophrys* and *Lepidobatrachus* are well supported (Faivovich et al., 2014), the relationships among the three ceratophryid genera and the position of Ceratophryidae within Anura are still debated. Even though Faivovich et al. (2014) performed an exhaustive analysis of Ceratophryidae based on molecular data, the resulting relationships among the ceratophryid genera (i.e., the sister-group relationship of *Chacophrys* + *Lepidobatrachus*) are unsupported (jackknife frequency <50%). On the other hand, exemplars of Ceratophryidae were included in a series of broad-scale analyses of anurans, also mainly based on molecular data, which resulted in different positions within hylids (i.e., alternatively related to taxa of Alsodidae, Batrachylidae, Cycloramphidae, Hylodidae, Odontophrynidae, Rhinodermatidae, and Telmatobidae sensu Frost 2016; Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011; Fouquet et al., 2013; Pyron, 2014).

As a result of phylogenetic analyses of Ceratophryidae based on morphological information (Fabrezi, 2006; Fabrezi and Quinzio, 2008), a number of osteological synapomorphies have been proposed for the group. Only one of these synapomorphies can be evaluated in the remains studied herein: cranial exostosis (char. 2 in Fabrezi, 2006; char. 62 in Fabrezi and Quinzio, 2008). The extensive dermal ornamentation and fusion of elements present in MD-CH-06-165 indicate that the individual had an exostosed skull. This condition is not exclusive to Ceratophryidae, however, and has been observed in several anuran groups (e.g., Calyptocephalellidae, Hemiphractidae, Hylidae, Pyxicephalidae).

The absence of a shelf-like pars palatina in the anterior region of the articulated maxilla, observed in MD-CH-06-165, is an exclusive condition of Ceratophryidae that has been recently proposed as one of its possible synapomorphies (Nicoli, 2015). The maxillary pars palatina in adult ceratophryids is dorsally directed and fused with several surrounding bones. Consequently, it is not distinguishable as a discrete shelf-like element in articulated skulls. However, the sutures among the maxillary pars palatina and the other cranial elements are usually visible (Fig. 3D, F). In addition, the dorsally directed shelf of the pars

palatina is always evident when this element is disarticulated from the skull. It is interesting to note that although the absence of a maxillary pars palatina was reported in *Beelzebufo ampinga* (Evans et al., 2008, 2014), a shelf-like pars palatina is absent even in completely disarticulated maxillae in this frog (Evans et al., 2008:fig. 3D, 2014:figs. 14, 15), suggesting a different condition from that observed in ceratophryids.

On the other hand, in *Ceratophrys* and *Chacophrys*, the anterior ramus of the pterygoid fuses with the pars palatina to the level of the planum antorbitale and thus the shelf-like pars palatina is absent also in the posterior region of the bone in articulated skulls (Lynch, 1971; Nicoli, 2015; Fig. 3D). By contrast, in most *Lepidobatrachus*, except the fossil species *L. australis*, the pterygoid anterior ramus articulates with the maxillary pars palatina only through the bar-shaped palatine process; thus, the posterior portion of the pars palatina remains distally free as a discrete and dorsally directed shelf (Lynch, 1971; Nicoli, 2015; Fig. 3F). Even when the maxilla of MD-CH-06-165 is incomplete, it remains articulated with the preserved fragments of the surrounding bones. A discrete shelf-like pars palatina is absent, even posterior to the planum antorbitale, although the sutures between the dorsally directed pars palatina and other cranial bones are visible. Thus, anteriorly the pars palatina is evidently fused with the ossification of the nasal cartilages and posteriorly to a bone that presumably corresponds to the pterygoid anterior ramus (which fuses with the pars palatina and with the ossification of the planum antorbitale; Fig. 3E). This condition is considered homologous to that of *Ceratophrys*, *Chacophrys*, and *L. australis*.

The presence of a well-developed supraorbital flange, also observed in MD-CH-06-165 (Fig. 2D–F), has been proposed as a possible synapomorphy of Ceratophryidae (Nicoli, 2015). At the same time, in all taxa that have been suggested as close relatives of Ceratophryidae in different analyses (e.g., Alsodidae, Batrachylidae, Cycloramphidae, Hylodidae, Odontophrynidae, Rhinodermatidae, and Telmatobidae), the cultriform process of the parasphenoid ends posteriorly to the planum antorbitale. In all members of Ceratophryidae, this process extends more anteriorly (Fig. 2D–F), reaching the level of the planum antorbitale in *Ceratophrys* and *Chacophrys* (as in MD-CH-06-165; Fig. 2D–E) and extending to the level of the vomers in *Lepidobatrachus* (Nicoli, 2015; Fig. 2F).

No osteological synapomorphies have been proposed for *Ceratophrys*. However, the particular shape of the maxillary process of its nasals (robust, bar-shaped [Figs. 2A, 3A] vs. robust, hourglass-shaped [Figs. 2C, 3C] in *Lepidobatrachus* and slender,

sharp process in *Chacophrys* and the other close relatives when this process is present [Nicoli, 2015]) could be a synapomorphy of the genus.

In conclusion, the available evidence indicates that MD-CH-06-165 has a combination of characters exclusive of *Ceratophrys*, allowing certain attribution to this genus: cranial exostosis, robust and bar-shaped maxillary process of nasals, supraorbital shelf, absence of maxillary pars palatina (even posteriorly to the level of the planum antorbitale), and cultriform process of the parasphenoid reaching the level of the planum antorbitale. The species of *Ceratophrys* are distinguished from each other by the presence or absence of a series of skull crests, the shape of the lateral portion of the posterior dermocranium, and the presence or absence of a bony dorsal shield (Lynch, 1982; Nicoli, pers. observ.). The fragmentary condition of MD-CH-06-165 prevents evaluation of these conditions and, thus, a more precise identification within *Ceratophrys*.

Nonetheless, the material recovered in Lithofacies Association 3 (ca. 9.02–8.7 Ma) of the Arroyo Chasicó Formation certainly constitutes the oldest record of *Ceratophrys*, considering that all other fossils assigned to the genus, although mostly problematic, have been recovered in younger sediments (see Faivovich et al., 2014; Nicoli, 2014; Scanferla and Agnolín, 2015). This material could also represent the oldest Ceratophryidae, considering that the phylogenetic position of the oldest taxa attributed to this group (the Cretaceous *Beelzebufo ampinga* from Madagascar, *Baurubatrachus pricei* from Brazil, and the early Miocene *Wawelia gerholdi* from Argentina) has recently been questioned. Agnolín (2012) questioned some characters that were originally used as evidence of the putative ceratophryid identity of the first known material of *Beelzebufo*, whereas Faivovich et al. (2014) questioned the phylogenetic analyses that resulted in *Beelzebufo* being nested within Ceratophryidae. Similarly, the reparation of the single specimen of *Baurubatrachus* provides new anatomical information (e.g., presence of pedicellate teeth, maxillary pars palatina perpendicular to the pars facilis, scapula bearing a crest along its anterior edge, and long iliac shaft bearing a dorsal crest) that would allow rejecting its affinities with Ceratophryidae (Báez et al., 2005). Finally, the revision of *Wawelia* demonstrated that it is a junior synonym of the australobatrachian *Calyptocephalella* (Nicoli et al., 2016). On the other hand, the recently reported late Miocene remains from west-central Argentina attributed to Ceratophryidae were collected in sediments of the Loma de Las Tapias Formation that is considered to have been deposited between 7.8 and about 6.5 Ma and, hence, more recently than the Arroyo Chasicó Formation (Nicoli, 2016, and references therein).

At present, *Ceratophrys* is a genus that is widely distributed in South America. The extant species inhabit diverse environments, including the semiarid seasonal dry forests Caatinga and Chaco, the humid Pampean Region, and the Amazonian and Atlantic forests (see Faivovich et al., 2014, and references therein). Thus, its presence in the central part of Argentina during the late Miocene does not provide specific information regarding the local paleoenvironment. On the other hand, although the reported extant distribution of *Ceratophrys* ends ~100 km north of Arroyo Chasicó (Fig. 1), it is considered that this distribution is incompletely known (J. Faivovich, pers. comm.). Both the southernmost limit of the reported distribution of extant *Ceratophrys* and Arroyo Chasicó are included in an environmentally continuous area of the Pampean Region, making it impossible to ascertain that *Ceratophrys* does not reach the Arroyo Chasicó region today (L. Alcalde and J. Faivovich, pers. comm.).

Although a robust phylogenetic analysis of Ceratophryidae was recently performed on the basis of molecular data (Faivovich et al., 2014) and provided a framework to discuss the evolution of the group, the absence of fossils that could be used as calibration points impeded the process of establishing divergence

estimates in that analysis (Faivovich et al., 2014). This work reports the oldest record of *Ceratophrys* (and probably Ceratophryidae), on the basis of a well-supported taxonomic assignment of fossils with a well-constrained age, providing valuable evidence and a possible calibration point for molecular clock analyses of anuran evolution.

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