# A fossil ceratophryid anuran from the Late Miocene of west-central Argentina

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**Abstract.** Remains of a Miocene anuran referable to Ceratophryidae, the clade of South American horned frogs, are described. This material is especially relevant because few pre-Pliocene fossils have been ascribed to Ceratophryidae and, in most cases, their taxonomic allocations are controversial. As far as the preserved bones can be evaluated, the fragmented Miocene fossil described here exhibits all the phenotypic synapomorphies proposed for Ceratophryidae. The remains also share some features with various recent ceratophryid species. Additionally, they possess a series of characters not observed in other Ceratophryidae. The exclusive combination of character states observed in the fossil material indicates that it represents a new species. However, the species cannot be named until relationships among ceratophryid frogs are resolved and the position of the fossil within the clade can be assessed; it is possible that it might be nested in an extant genus.

Key words. Maxillary osteology, Ceratophryidae, Loma de las Tapias Formation, San Juan Province.

## Introduction

Ceratophryids, the so-called "horned frogs" of South America, are characterized by their robust, thickset, broad head and body, and short limbs. Currently, 12 extant species are recognized in three genera (*Ceratophrys*, *Chacophrys*, and *Lepidobatrachus*) (Frost 2014). Several phylogenetic analyses that included some of these species were performed on molecular (Darst & Cannatella 2004, Correa et al. 2006, Pyron & Wiens 2011), morphological (Haas 1999, Fabrezi 2006, Evans et al. 2008, Fabrezi & Quinzio 2008, Laloy et al. 2013), and combined data sets (Frost et al. 2006, Grant et al. 2006, Evans et al. 2014). In each of these analyses, the included ceratophryid species emerged as a monophyletic clade with high support values.

Probably as a consequence of their robust build, the fossil record of Ceratophryidae is markedly more abundant than that of anurans in general (Günther 1859, Ameghino 1899, Rovereto 1914, Rusconi 1932, Casamiquela 1963, Vergnaud-Grazzini 1968, Marshall & Patterson 1981, Baéz & Perí 1989, Báez & Perí 1990, Perí 1993, Rinderknecht 1998, Contreras & Acosta 1998, Fernicola 2001, Agnolín 2005, Evans et al. 2008, Stoessel et al. 2008, Tomassini et al. 2011, Evans et al. 2014, Nicoli 2014). Despite the well-documented diversification of South American anurans by the Cretaceous (Báez et al. 2009, Báez et al. 2012), most fossil ceratophryids are not known from before the Late Cenozoic. Only a few pre-Pliocene fossil remains have been referred to Ceratophryidae, and most taxonomic allocations – the Cretaceous *Baurubatrachus pricei* (Baéz & Perí, 1989; see Evans et al. 2008, Evans et al. 2014 for taxonomy) from Brazil; *Beelzebufo ampinga* (Evans et al., 2008, Evans et al. 2014) from Madagascar; and the Miocene *Wawelia gerholdi* (Báez & Perí, 1990) from north Patagonia – are questionable and under review (Nicoli et. al. own unpubl. data, A.M. Báez pers. comm.)

The single other pre-Pliocene fossil attributed to Ceratophryidae is a fragmentary maxillary arch from the Late Miocene sediments of San Juan Province in west-central Argentina (Contreras & Acosta 1998). When this material was examined by previous workers, there was a significant amount of sediment that adhered to the fossil, obscuring most of it. The fossil was not described and its taxonomic allocation to Ceratophryidae was not well justified. This material was recently cited as representative of *Ceratophrys* sp. (Contreras & Baraldo 2011). Herein, the properly prepared fossil is described and its taxonomic position discussed by means of comparisons with various ceratophryid taxa.

## Material and methods
### Institutional abbreviations

Acronyms follow those of Sabaj Peres (2014) with the addition of MMH: Museo de Ciencias Naturales "Vicente Di

Martino," Monte Hermoso, Argentina; and PVSJ: Museo de Ciencias Naturales, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan.

## Geological setting

The fossil anuran was collected from sediments of the Loma de las Tapias Formation, exposed in the Ullum Valley, in the south of San Juan Province in west-central Argentina (Contreras 1981, Serafini et al. 1986, Contreras & Baraldo 2011; Fig. 1). This formation has been interpreted as being deposits of a brained fluvial system (Contreras et al. 2001, Contreras & Baraldo 2011). The anuran was recovered from the upper member of this unit, the Albardón Member, in association with an important assemblage of mammals (Assemblage B sensu Contreras & Baraldo 2011) attributed to the Huyaquerian South American Land Mammal Age (Contreras 1981, Contreras et al. 2001, Contreras & Baraldo 2011). The age of this assemblage, calculated based on biostratigraphy, magnetostratigraphy, and zircon dating, is considered between 7.80 and about 6.5 Mys., which places it in the Late Miocene (Bercowski et al. 1986, Contreras & Baraldo 2011, Cohen et al. 2013; updated).

## Systematic Palaeontology

Anura Fischer von Waldheim, 1813
Ceratophryidae Tschudi, 1838
genus and species indeterminate

Material – PVSJ 284, a fragment of an articulated left maxillary arch (partial mentomeckelian, dentary, angular, premaxilla, and maxilla) (Fig. 2).

Locality and age – Faunistic Assemblage B, Albardón Sandstone Member, Loma de las Tapias Formation (Late Miocene). Ullum Valley, San Juan Province, Argentina.

Taxonomic remarks – Ceratophryidae is distinguished from all other non-ceratophryid anuran taxa by the following combination of characters: (1) cranial exostosis; (2) non-pedicellate teeth; (3) lack of distinguishable pars palatina in the anterior region of the maxilla; (4) mentomeckelian indistinguishably fused to dentary; (5) mentomeckelian forming a large, acute, and robust medial fang; (6) mentomeckelian large, reaching the level of the premaxilla-maxilla articulation and in contact with angular; (7) dentary high, protruding dorsally from the level of the angular margin; and (8) dorsal (occlusal) margin of dentary crenulate.

## Description

The dentate premaxilla and maxilla bear a reticulate, "pit and ridge" ornamentation (Fig. 2A). Teeth are visible only in lateral view because the lingual side is obscured by the articulated mandible. The long, fanglike teeth are attached to the ventral margin (partes dentales) of the bones. The homogeneous ossification and texture of the bones and the teeth and their state of preservation (broken at different levels) suggest that the teeth are non-pedicellate (Figs 2A, 3A). However, no complete teeth are preserved so that the number of terminal cusps cannot bequantified. The tooth that is best preserved lacks an additional cusp on its labial face (Fig. 2A).

A small fragment of the premaxilla is preserved and found to be articulated with the maxilla. The pars dentalis of the maxilla is visible laterally as a short, acuminate process (Figs 2A, 4A) that overlaps the ventral and labial
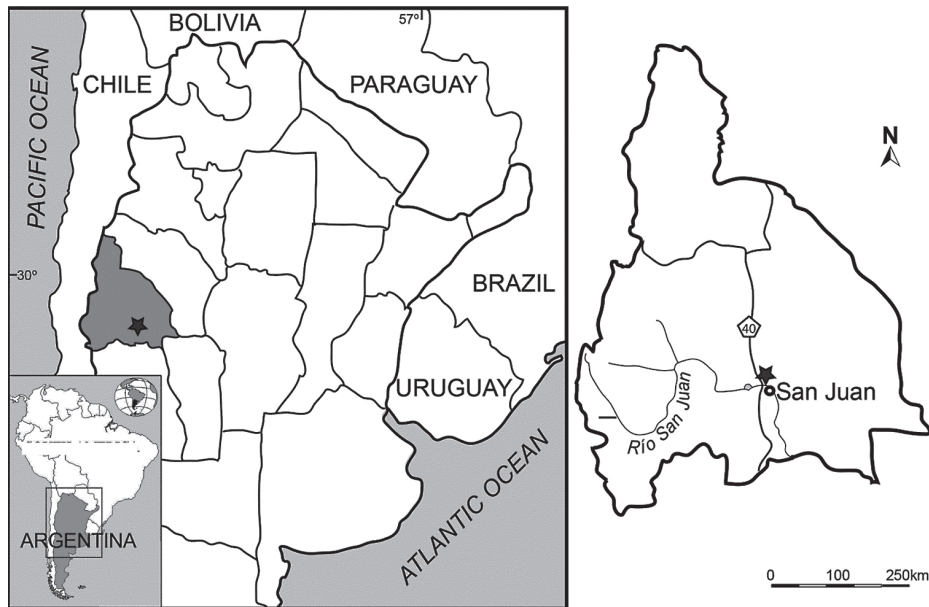


Figure 1. Map showing locality (indicated by a star) of the fossil Ceratophryidae (PVSJ 284).

surfaces of the pars dentalis of the premaxilla. On the labial surface, the premaxilla can be seen as having a triangular process that overlaps the maxilla (Fig. 4A). This maxillary and premaxillary processes appear perfectly juxtaposed with one another. In lingual view, the premaxilla bears a maxillary process of the pars palatina. The short, subtri-angular process overlaps the lingual surface of the maxilla, and terminates at the level of the first maxillary tooth; the major axis of the process parallels the margin of the max-illa (Figs 1B, 5A).

The maxilla, even though incompletely preserved, has a high pars facialis (Fig. 1A). In lingual view, it lacks a dis-tinguishable pars palatina, except for the pterygoid process that is developed in the posterior region of the preserved

bone (Figs 1B, 5A). Anteriorly, a fragment of bone that is oval in cross-section projects over the internal surface of the maxilla and is fused to it (Figs 1B, 5A). By its relative position, it may represent an ossification of the lateral nasal cartilages (cartilago oblique + planum terminalis + paries nasi + crista subnalis sensu ROCEK, 2003), and perhaps the anterior part of the vomer in the region of the maxilla. A second bone, likewise fragmentary, is in contact with the maxilla near the anterior end on the pterygoid process (Figs 1B, 5A). It seems to be the lateral portion of the ossi-fied planum antorbitale and possibly the neopalatine that reach the maxilla. Posteriorly, the subtriangular pterygoid process articulates with a laminar bone that seems to cor-respond to the distal portion of the anterior ramus of the
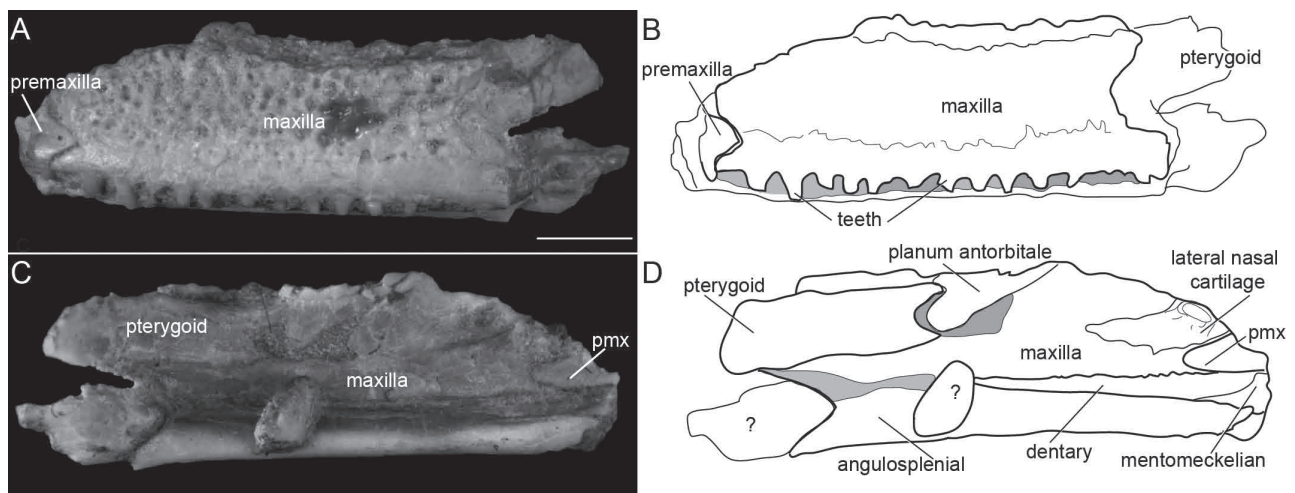


Figure 2. Miocene Ceratophryidae from west-central Argentina (PVSJ 284). A) labial view; B) lingual view. Scale bar = 5 mm.
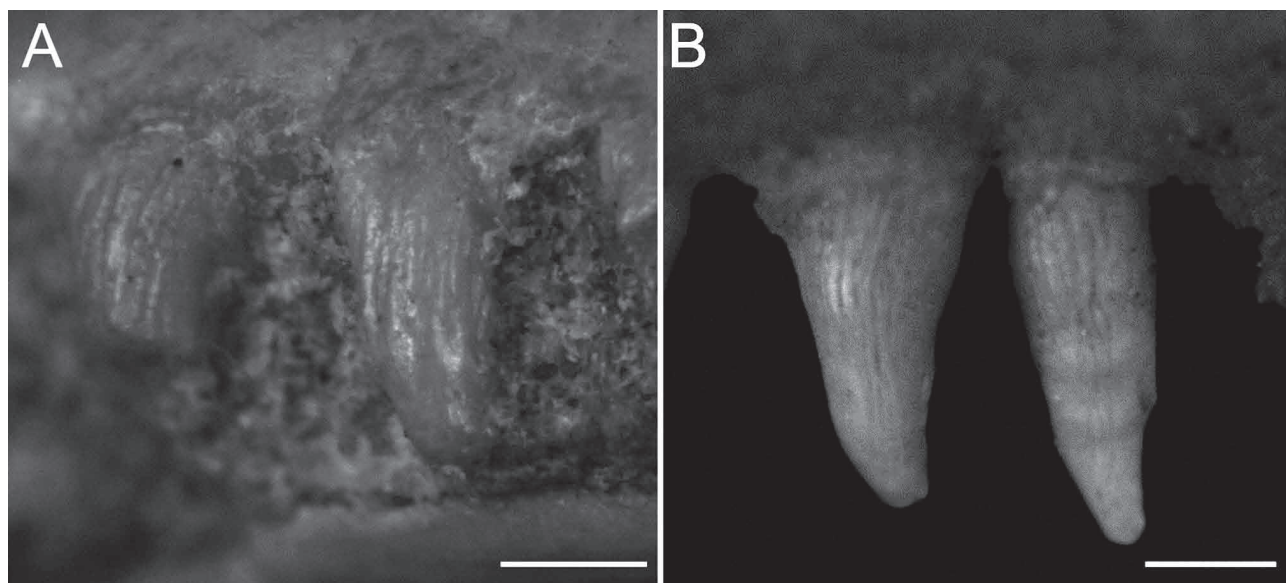


Figure 3. Detail of the teeth of the fossil, A) PVSJ 284) and one extant Ceratophryidae, B) *Ceratophrys ornata* FML 1193). Scale bar = 0.5 mm.

pterygoid. The anterior pterygoid ramus terminates at the level of the presumed planum antorbitale (Figs 1B, 5A).

The angular, dentary, and mentomeckelian bones are evident in the fragment of the articulated, preserved mandible. The angular forms the ventral and lingual faces of the mandible. This robust bone, with rounded surfaces, reaches the mentomeckelian anteriorly. The robust, laminar, and high dentary forms the labial face of mandible. It is firmly articulated with the angular, which overlaps more of its lingual face. A portion of dentary is observed, however, protruding dorsally to the angular margin. In some regions, the dorsal margin of the dentary is crenulated; thus, the dorsal (occlusal) face of the mandible consists of a high, laminate, crenulated bone. The mentomeckelian bone extends to the articulation of the premaxilla and maxilla, and articulates with the angular. Medially, it forms a robust, acute fang. It overlies the laminar dentary, from which it is distinguished by its distinct shape and volume; however, a distinct suture between the dentary and mentomeckelian is not evident and the exact limits are difficult to establish, indicating that these bones are fused. Given that the angular

and mentomeckelian bones articulate, Meckel's cartilage would not have been exposed.

Two unidentifiable fragmentary bones, presumed not to belong to the maxillary arcade, adhere to the fossil. The fragile state of preservation of the fossil precluded the removal of these elements.

### Discussion

Despite the fragmentary condition of PVSJ 284, the preserved bones of the fossil that can be evaluated exhibit all the proposed synapomorphies of Ceratophryidae, as follows: (1) cranial exostosis (FABREZI, 2006, Ch. 2; FABREZI & QUINZIO, 2008, Ch. 62); (2) non-pedicellate teeth (FABREZI & QUINZIO 2008, Ch. 69); (3) mentomeckelian and dentary fused (FABREZI 2006, Ch. 24; FABREZI & QUINZIO 2008, Ch. 74); and (4) presence of a fang in the lower jaw (FABREZI & QUINZIO 2008, Ch. 75). None of these characters is exclusive to Ceratophryidae, and they are present in other anurans. Thus, cranial exostosis, the contact of the
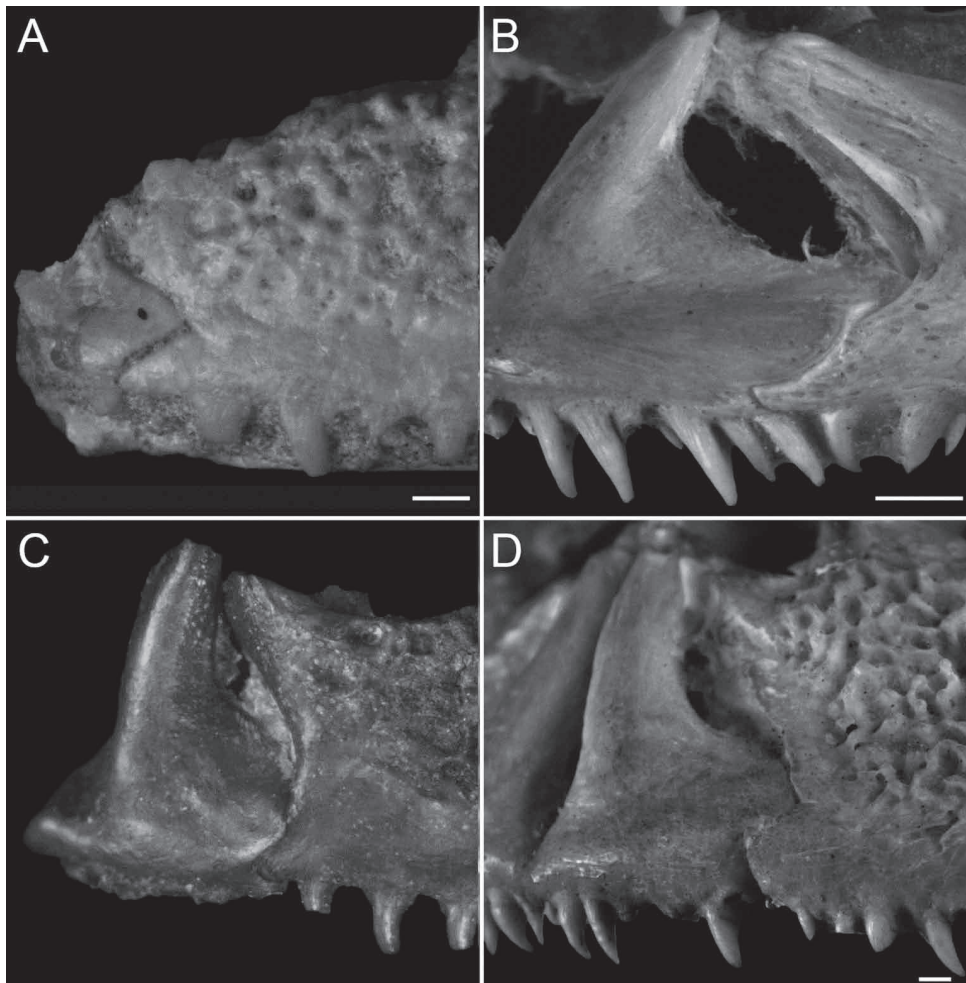


Figure 4. Detail of the premaxilla-maxilla articulation of selected Ceratophryidae in labial view. A) fossil (PVSJ 284); B) *Ceratophrys ornata* (FML 1193); C) *Chacophrys pierottii* (MACN 47403); D) *Lepidobatrachus laevis* (FML 13703). Scale bar = 1 mm.

pars facialis with the surrounding bones, and the pattern of dermal ornamentation occur in anuran groups such as Callyptocephalellidae, Hemiphractidae, Hylidae, Lophioilini, and Pelodryadinae, and ranoid Pyxicephalidae. Similarly, fusion of the mentomeckelian bones with the dentary is relatively common among anurans, although the limits of mentomeckelian and dentary usually are evident.

In contrast, the presence of fangs in the lower jaw is less common. In the ceratophryids, the fused mentomeckelian and dentary form a robust fang that projects dorsally. This exclusive condition, described as a character state by Fabrezi (2006; Ch. 23: 2, a spur-like projection formed by dentary and mentomeckelian bones) is an exclusive synapomorphy of Ceratophryidae in her phylogenetic analysis. Unfortunately, the status of this character in PVSJ 284 cannot be properly evaluated owing to the articulated and incomplete preservation of the mandible. However, it is evident that the mentomeckelian projects as a robust, large fang, which is an unusual condition among anurans. Although other anurans (e.g., Odontophrynidae) possess mentomeckelian medial fangs, they are tiny and delicate. The lower jaw of the ranoid *Pyxicephalus* sports a robust anterior fang (slightly lateral to the symphysis), but it is formed by the dentary (Sheil 1999). Similarly, the presence of non-pedicellate teeth is unusual in anurans; they have been observed in Pipidae (Smirnov & Vasil'eva 1995), Ceratophryidae (Fabrezi 2001) and some ranoid taxa (e.g., *Pyxicephalus*). According to Smirnov & Vasil'eva (1995), fanglike, non-pedicellate teeth result from a mineralisation of the labile zone between pedicel and crown.

Ceratophryids also differ from all other anurans in the absence of a distinguishable pars palatina on the premaxilla and in at least the anterior region of the maxilla (Fig. 5). This condition was evaluated in phylogenetic analyses only with regard to the premaxilla (Ch. 14 in Fabrezi 2006), rendering it an exclusive synapomorphy for the group (Fabrezi 2006). The premaxilla of PVSJ 284 is not preserved well enough to identify the presence or absence of a pars palatina, but it is at least absent in the anterior portion of the preserved maxilla.

The ceratophryid mandible is also distinguished by its high, crenulate-ended dentary and the extension of the mentomeckelian bones (with these latter reaching the level of the premaxilla-maxilla articulation and articulating with the angular). All these features are present in PVSJ 284.

The two monotypic Cretaceous fossil genera allocated to Ceratophryidae differ from PVSJ 284. The single specimen of *Baurubatrachus pricei* has now been re-prepared and its description is currently being revised (Báez pers. comm.); however, we already know that it possesses a well-developed pars palatina (Baéz & Perí 1989). Likewise, the published photographs of the lingual side of the maxilla of *Beelzebufo ampinga* (Evans et al. 2008, Evans et al. 2014) show that it has an anterior facet to receive a maxillary process (the "dorsal maxillary process" of Evans et al. 2014). In addition, some concavities and irregular regions of the lingual face of the pars facialis of *B. ampinga* were interpreted as articular facets for the vomer and neopalatine (Evans et al. 2014); these facets, as well as the presumably facet for the maxillary process of the premaxilla, are notably distant from the ventral margin of the maxilla, whereas in PVSJ 284, these articulations lie close to the ventral margin of the maxilla.

The single known specimen of the Miocene *Wawelia gerholdi* is an imprint of the postcranium and a small piece
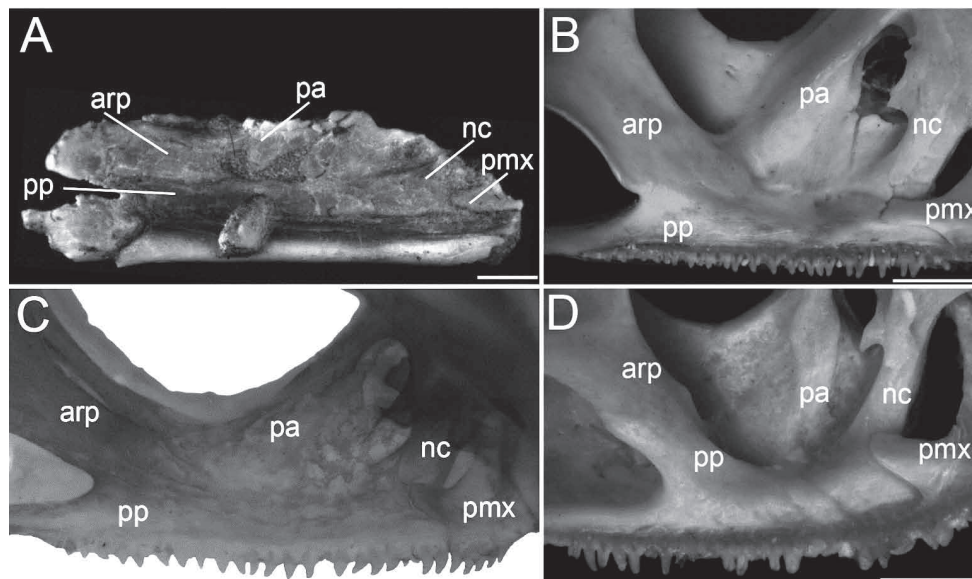


Figure 5. Labial views of maxillary arches of selected ceratophryid anurans. A) Miocene fossil (PVSJ 284); B) *Ceratophrys cranwelli* (FML 5477); C) *Chacophrys pierottii* (FML 9012); D) *Lepidobatrachus llanensis* (FML 5221). arp – anterior ramus of pterygoid; pa – ossification of the planum antorbitale; pmx – premaxilla; nc – ossification of the lateral nasal cartilages; pp – pterygoid process of maxilla. Scale bar = 5 mm.

of the cranium of a juvenile frog that has been referred to Ceratophryidae (Casamiquela 1963, Báez & Perí 1990, Evans et al. 2008, Evans et al. 2014). The preserved skull remains of this specimen are extremely fragmentary and poorly preserved; moreover, the fossil has suffered some damage from handling for its most recent description (pers. obs.). There are no common elements of *W. gerholdi* and PVSJ 284 that could be compared. However, the re-description of *W. gerholdi* (Nicoli et al. own unpubl. data) provides additional anatomical information that demonstrates the differences between it and ceratophryids and suggest that *W. gerholdi* is incorrectly included in this clade.

None of the few osteological synapomorphies proposed for extant ceratophryid genera (Fabrezi 2006, Fabrezi & Quinzio 2008) involve the regions preserved in PVSJ 284. However, several osteological characters that vary amongst ceratophryid species were not considered in the phylogenetic analysis. Consequently, the relationships of the species within Ceratophryidae are unresolved. The different phylogenetic approaches included different and limited ceratophryid taxon samplings and produced competing hypotheses about the relationships within Ceratophryidae and among ceratophryids and other anurans (Haas 1999, Darst & Cannatella 2004, Fabrezi 2006, Correa et al. 2006, Grant et al. 2006, Evans et al. 2008, Fabrezi & Quinzio 2008, Pyron & Wiens 2011, Laloy et al. 2013, Frost 2014, Evans et al. 2014). Therefore, the significance of a presence or absence of characters shared by the fossil and some ceratophryid taxa is difficult to evaluate.

For example, in PVSJ 284, the labial process of the premaxilla is triangular and pointed, whereas this process is broad and nearly round in all other Ceratophryidae (Fig. 4). In addition, the entire margin of the labial process is in contact with the maxillary pars facialis, forming a suture between both elements in PVSJ 284 (Fig. 4A). In contrast, in most ceratophryids the pars facialis usually is only in contact with the margin of the premaxillary labial process and forms a suture in the ventral region (Fig. 4). The dorsal part of the pars facialis is not directed medially at the level of the labial process of the premaxilla; instead, it projects dorsomedially to form a process directed at the alary processes (Figs 4B, C). The pars facialis is in contact with parts of the dorsal portion of the labial process of the premaxilla only in *Lepidobatrachus laevis*, which has proportionally shorter alary processes than other ceratophryids (Fig. 4D).

Similarly, all ceratophryids (and PVSJ 284 as well) possess a process in the region of the pars dentalis of the maxilla that covers the anterolateral part of the premaxilla (Fig. 4A). In PVSJ 284, this process is distinctly asymmetrical, being developed on both the labial and ventral faces of the bone. No premaxillary teeth can be observed lateral to the level of the medial end of this maxillary process (Fig. 4A). In contrast, in all ceratophryids examined this maxillary process overlaps the premaxilla thus that one or two premaxillary teeth (or dental positions) are visible lateral to the medial end of this process (Fig. 4). Moreover, in almost all observed Ceratophryidae (Appendix) the maxil-

lary process is nearly symmetrical and only developed on the labial face of the bone (Fig. 4). The process is generally broad and rounded in *Lepidobatrachus* and *Ceratophrys,* and tiny and triangular in *Chacophrys* (Figs 4C, D). One juvenile *Ceratophrys ornata* (FML 1193) possesses an asymmetric, acuminate process that resembles that of PVSJ 284 (Fig. 4B).

The lingual aspect of the maxillary process of the premaxilla of PVSJ 284 also differs from those of other ceratophryids. In *Ceratophrys,* the process is bar-shaped with a subquadrangular end; the process is long, reaching the level of the fourth maxillary tooth (Fig. 5B). In *Lepidobatrachus*, the short maxillary process only extends to the level of the first or second maxillary tooth; this process is broad and poorly distinguished from the remaining bone (Fig. 5D). The maxillary process of *Chacophrys* resembles that of *Lepidobatrachus*, even hough the process is slightly more elongated and pointed (Fig. 5C). Both *Lepidobatrachus* and *Chacophrys* possess asymmetrical maxillary processes that are dorsally directed and clearly different from the nearly symmetrical process of PVSJ 284, the long axis of which nearly parallels the margin of the bone (Figs 5A, C, D).

The posterior part of the maxillary arch of PVSJ 284 resembles those of *Ceratophrys* and *Chacophrys* (and differs from *Lepidobatrachus*) in the presence of a subtriangular pterygoid process (bar-shaped in *Lepidobatrachus*; Fig. 5). In addition, the anterior ramus of the pterygoid extends along the pars palatina of the maxilla to the level of the planum antorbitale, whereas in *Lepidobatrachus* (Fig. 5), the anterior ramus articulates with the pars palatina of the maxilla only at the pterygoid process.

In summary, PVSJ 284 is likely to represent a new ceratophryid species, based on the presence of all the synapomorphies proposed for Ceratophryidae that can be evaluated in these remains, in addition to other derived characteristics of ceratophryids. In addition, PVSJ 284 possesses a suite of characters that have not been observed in other Ceratophryidae. However, positioning the species within the Ceratophryidae is impossible at present, owing to the lack of resolution of phylogenetic relationships within this family. The species could be closely related to (or even nested in) any of the extant ceratophryid genera. Its placement must therefore await inclusion in a phylogenetic analysis based on all of the observed osteological variation in Ceratophryidae. Such an analysis is underway and includes broad taxon sampling of Ceratophryidae and outgroups and is based on multiple data sets. When this analysis is complete, the taxonomic position of the new fossil species within the Ceratophryidae will have revealed itself, and until that time, I will not assign a name to PVSJ 284.

to discuss the anatomy and taxonomy of the fossils under study, and S. Reuil skilfully prepared the fossil specimen. J. Faivovich (MACN), D. Frost (AMNH), A. Kramarz (MACN), E. Lavilla and S. Kretzschmar (FML), N. Sánchez (MMH), L. Trueb (KU), and J. Williams (MLP) allowed the examination of material under their care. C. Deschamps (MLP) kindly provided valuable information about the geological context of the fossil. Funding for this project were provided by the Agencia Nacional de Promoción Científica y Técnica (PICTs 1895/11, 227/12, 404/13), the Consejo Nacional de Promoción Científica y Técnica (PIP 889/12), and Grant # 2013/50741-7, São Paulo Research Foundation (FAPESP).

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## Appendix

Specimens examined for comparisons. Most of them are clear and stained specimens, the dry skeletons are denoted with an asterisk. Fossils are denoted with a †.

*Alsodes gargola* MACN 37845, 37930, 37951, 38942. *Atelognathus patagonicus* CENAI 1070–1; *A. reverberii* MACN 33973; *A. salai* MACN 41327. *Batrachyla antantardica* MACN 47402; *B. leptopus* MACN 38006, 41291; *B taeniata* CENAI 6865–6, 6921. *Calyptocephalella gayi* MACN 45741–3*. *Ceratophrys ameghinorum*† MACN 14317–9, 14324–5, 19731, MLP 52-IX-27-11, 88-VII-20-1–2; MMH 84-1-15, 85-2-11; *C. calcarata* AMNH 177036*; *C. cranwelli* MLP 273*; FML 5472*, 5474–7*; *C. ornata* MLP 137*, 247*, FML 1193*. *Chacophrys pierottii* MACN 47403*–4*; FML 1019, 9012. *Crossodactylus schmiti* MACN 35122. *Eupsophus calcaratus* MLP 4011; *E. roseus* MACN 37976, 37979, 37981; *E. vertebralis* MACN 43704*. *Hymenochirus boettgeri* MACN 42621. *Insuetophrynus acarpicus* CENAI 6896. *Lepidobatrachus asper* FML 5469*–70*; *L. laevis* FML 13703*–4*, 13709*, 1089*; *L. llanensis* CENAI 8519, FML 420*, 1016*, 5220–1*, 1089*; *Lepidobatrachus* sp.† MMH 85-12-2a. *Limnomedusa macroglossa* MACN 4644, MLP 1410. *Macrogenioglottus alipioi* CFBH 4261*. *Odontophrynus achalensis* CENAI 2972, 2975, 2977; *O. americanus* CENAI 3938–9, 3939, 3942, MACN 25236, 25237; *O. carvalhoi* MNRJ 15358; *O. cordobae* CENAI 4522, MACN 26199; *O. cultripes* CENAI 9839, 9841; *O. occidentalis* MACN 24953, 26228, 26229; MLP 4385, 3916; *O. lavillai* CENAI 5811, 6461, 5794, 6465; *O. maisuma* MLP 4828, ZVCB 1517; *O. salvatori* MNRJ 27756. *Proceratophrys appendiculata* CENAI 9064; *P. avelinoi* MACN 36854, MLP 938; *P. boiei* MLP 76. *P. cristiceps* MNRJ 15358. *Rhinella major* MACN 45955. *Rhinoderma darwini* CENAI 5491. *Telmatobius bolivianus* CBF 2063, 5379; *T. oxycephalus* FML 2867, 3836; *T. marmoratus* CBF 2167, 3621, KU 164079–80*; *T. rubigo* FML 20829; *T. verrucosus* CBF 2765, 5372.