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New clues on anuran evolution: the oldest record of an extant hyloid clade in the Oligocene of Patagonia

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New clues on anuran evolution: the oldest record of an extant hyloid clade in the Oligocene of Patagonia

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ABSTRACT

Despite the enormous diversity of the extant South American batrachofauna, its fossil record is sparse. Few pre-Neogene anuran remains have been attributed to extant taxa and, although some have been considered neobatrachians their relationships with extant groups are still mostly uncertain. In this context, a series of fossils recently collected in Oligocene sediments of central Patagonia are assigned to Odontophrynidae. This assignation is supported by an exclusive combination of characters, including extensive frontoparietals, in medial contact and deflecting posteriorly, with crescent-shaped posterolateral projections; robust pterygoid anterior ramus, reaching the planum antorbitale, projecting dorsally; notched premaxillary pars palatine; dentate vomers, narrowly separated medially; robust neopalatines, narrowly separated medially, bearing a conspicuous ridge, and with expanded lateral edges. The well-preserved fossil specimens were considered representative of a new genus and species, *Chachaiphrynus lynchi*. The presence of an Oligocene Odontophrynidae in central Patagonia, about 500 km south from the southernmost extant distribution of the group, would be associated with the more benign climate inferred in this region during the Paleogene. At the same time, this record represents the single pre-Neogene certain record of an extant clade deeply nested in Hyloidea, providing an exceptional high-quality calibration point to temporally frame the anuran phylogeny.

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Introduction

The South American batrachofauna is widely distributed and diverse. About 2000 species of hyloid anurans (sensu Pyron and Wiens [2011]; Nobleobatrachia sensu Frost et al. [2006]) occur from the north to the extreme south of the continent. Their history, however, is practically unknown given the sparseness of its fossil record. Few pre-Neogene anuran remains have been attributed to extant taxa and, although some have been considered neobatrachians, in most cases their taxonomic affinities are still uncertain (Schaeffer 1941; Tihen 1962; Lynch 1971; Estes & Reig 1973; Báez & Perí 1989; Báez 1991; Báez & Fernicola 1999; Báez 2000; Báez & Nicoli 2004; Báez et al. 2009, 2012; Nicoli 2012). A series of fossil taxa from lower-Cretaceous sediments of Brazil were considered representatives (or close relatives) of Hyloidea (Báez et al. 2009, 2012). Although the position of these fossils within the hyloids could not be established, some of them appeared deeply nested in that clade, demonstrating that the diversification of Hyloidea had already begun in the Lower Cretaceous (Báez et al. 2009, 2012). This diversity, however, is not documented in the fossil record.

Most extant South American anuran taxa do not have fossil record previous to the Neogene. Only a few pre-Neogene hyloid fossils were attributed to extant taxa and these

attributions are still controversial. Two pre-Neogene anuran species were attributed to the clade of South American horned frogs, Ceratophryidae: the Cretaceous *Baurubatrachus pricei* (Báez & Perí 1989), from Brazil, and *Beelzebufo ampinga* (Evans et al. 2008, 2014), from Madagascar; this taxonomic attribution, however, has been questioned and is currently under revision (Faivovich et al. 2014; Báez, pers. com). Isolated ilia from Oligocene sediments from Salla, Bolivia, were presumably referred to the extant genus *Rhinella* [at that time in the huge genus *Bufo* (Báez & Nicoli 2004), which subsequently was partitioned to remedy its paraphyly (Frost et al. 2006; Pramuk 2006; Chaparro et al. 2007)]; the use of the ilial morphology for taxonomical identification within Bufonidae, however, has been questioned (Bever 2005). The single specimen of the Oligocene *Neoprocoela edentata* was alternatively considered closely related with the extant genus *Telmatobius* (as *Batrachophrynus* Schaeffer 1949) or with the traditional 'Bufo' (Tihen 1962). Finally, a series of specimens from Oligocene sediments of the Scarritt Pocket locality in Central Patagonia were erroneously attributed to the extant genus *Eupsophus* and are still undetermined (Schaeffer 1949; Báez & Fernicola 1999; Nicoli 2012). No other pre-Neogene hyloid fossils were attributed to any of the numerous extant South American taxa.

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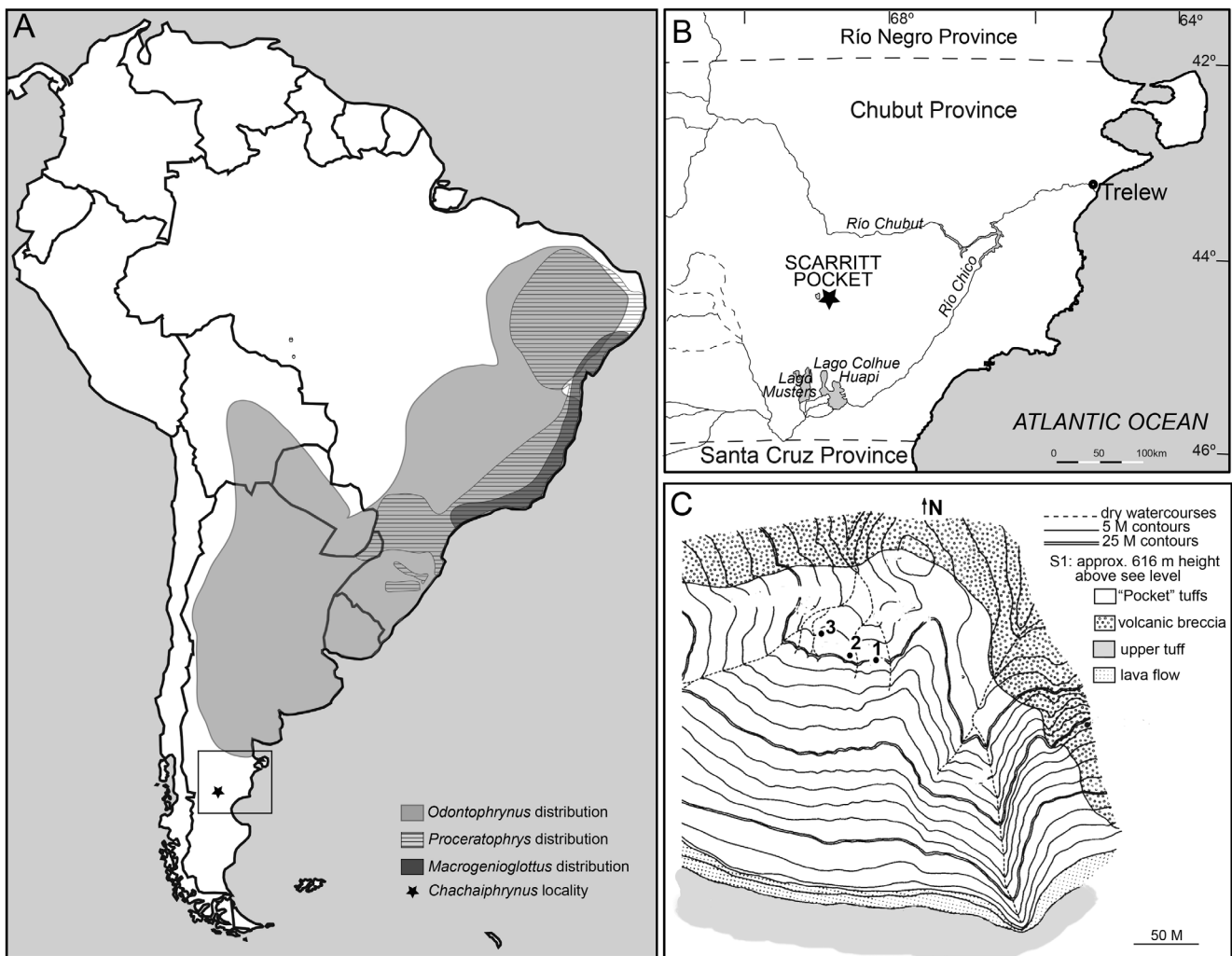


Figure 1. (A) Approximate distribution of extant and fossil Odontophrynidae (UICN 2004 slightly corrected base on Rosset et al. [2007]), open square indicate the area showed in B; (B) location of the Scarritt Pocket fossil locality in center Patagonia, Chubut Province, Argentina; (C) contour map of Scarritt Pocket looking north and down into Pocket from rim of Meseta Canquel and showing locations of the quarries that provided anuran remains (Modified from Marshall et al. [1986], determination of height above see level from GPS measurement). References: (1) Quarry 1 of Simpson; (2) Femur Site; (3) Masa site.

In the last years, a series of field trips to the fossiliferous locality Scarritt Pocket has provided an interesting collection of neobatrachian remains. Some of them represent the same taxon that was erroneously attributed to *Eupsophus* (Schaeffer 1949; Nicoli 2012). The new material provides additional evidence that allows to clarify several aspects of the skeletal anatomy and relationships of this taxon. In this paper I define and describe this new species and discuss its relationships and its significance for the knowledge of the history of the South America batrachofauna.

Geological setting

The fossil material has been collected in the locality of Scarritt Pocket, which is located near the center of the Chubut Province, Argentina (Figure 1). The pocket is a small embayment on the west side of the Sierra or Meseta Canquel located in the southwestern part of a larger embayment, locally known as Rinconada de López. The sediments within the pocket are included in the Sarmiento Formation and would have accumulated in a small, shallow, ephemeral lake that may have been formed in the crater of an extinct volcano (Simpson 1934;

Chafee 1952; Marshall et al. 1986). The deposits consist of a thin series of laminated bentonites and a thicker filling of ashes that grade into heavy breccia near the crater walls (Simpson 1934). Marshall et al. (1986) estimated the age of the Scarritt Pocket sediments to be 23.4–21.0 Myr, according to the K-Ar datings of several basalts and tuffs that bound the pocket. However, Flynn & 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 Myr (middle Oligocene).

Scarritt Pocket (SP) was discovered by G.G. Simpson in 1934, during the Second Scarritt Expedition of the American Museum of Natural History (AMNH) in Patagonia. It is well-known because of its fossil mammals attributed to the Deseadan Land Mammal Age (see Marshall et al. 1986 for a review). Most of the anuran material described here has been collected in the fossiliferous ‘Quarry 1’ of Simpson [(unpublished field notes provided by Chaffee (1952) and Marshall et al. (1986)] and two of the new specimens in recently discovered fossiliferous sites (Femur Site and Masa Site; Figure 1(C)). The anuran-bearing sediments seem to correspond to equivalent levels, consisting in

very pale-orange laminated bentonites intercalated with levels of white to grayish, pale-blue tuff.

Materials and methods

Fossil and extant skeletal material was examined using a Nikon SMZ 800 stereoscope. Photographs of extant specimens were taken with an attached Micrometrics digital camera. Fossil specimens were photographed with a Sony DSC-XZ200 digital camera.

The studied fossil material consists of several specimens preserved in slabs, some of which represent part and counterpart of the same specimen. Most specimens have cracked bones; frequently, bones are broken in different slabs and their morphology must be reconstructed. The most complete and better preserved specimens are those recently collected in SP, which are housed in the Museo Paleontológico Egidio Feruglio, Trelew, Chubut (MEF). A series of additional specimens attributable to the same species, but poorly preserved, belong to the collections of the American Museum of Natural History (AMNH) and of Vertebrate Palaeontology, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (FCEN-PV). The former (AMNH 3407; 3422; 3425–26) have been collected by G. G. Simpson and attributed by Schaeffer (1949) to the extant genus *Eupsophus*. A recent revision of this material allowed questioning that assignation (Nicoli 2012). The material housed in the FCEN (FCEN-PV 14085–14088; 14090) has been collected by Hernández, Scaglia, and Contreras in 1964 and was referred, but not figured or described, by Báez and Fernicola (1999).

Giving the vastness of the anuran diversity [Approx 6600 species (Frost 2016)], the taxonomic placement of a fossil anuran species is a serious challenge. Although several phylogenetic analyses including a relatively well-represented taxon sampling were performed (Frost et al. 2006; Grant et al. 2006; Pyron & Wiens 2011; Pyron 2014), none included osteological information. Most anuran clades are not characterised osteologically and much homoplasy is evident within the group. Performing a phylogenetic analysis including osteological data and a broad taxon sampling to rigorously test the relationships of a fossil species with all hyloid families is beyond the goals of this paper. Thus, the osteology of the fossil species was exhaustively compared with the osteology of other anurans, through examination of available specimens for comparison (see Appendix S1, Supplementary information on line) or information of the literature. Comparisons stressed anuran taxa that seem possible close-relatives with the fossil species. The osteological characters present in each group were compared with those of the closely related clades to identify putative synapomorphies. Institutional codes are those of Sabaj Pérez (2014).

Systematic palaeontology

ANURA Fischer von Waldheim, 1813

NEOBATRACHIA Reig 1958

NOBLEOBATRACHIA Frost et al. 2006

ODONTOPHRYNIDAE Lynch 1971

Chachaiphrynus **gen. nov.**

Type Species: Chachaiphrynus lynchi **sp. nov.**

Etymology: The generic name is derived from *chachai*, the voice used by the Mapuches (Patagonian native habitants) for naming an appreciated and respected old man + *phrynus*, from the Greek language, meaning toad.

Diagnosis: As for the type and only known species.

Chachaiphrynus lynchi **sp. nov.**

(Figures 2–4)

Eupsophus (non Fitzinger 1843): Schaeffer, 1949: 55, figs. 5–6 [part] (specimen misidentification).

Eupsophus (non Fitzinger, 1843; sensu Schaeffer, 1949): Báez & Fernicola 1999: 24, not figured (specimen tentative identification to the same species assigned to Schaeffer 1949 to *Eupsophus*).

Neoprocoela (non Schaeffer 1949): Báez & Fernicola 1999: 24, not figured (specimen tentative identification to *Neoprocoela*).

Holotype: MPEF-PV 10572.

Referred Material: MPEF-PV 10573–77; 10892–99 AMNH 3407; 3422; 3425–26. FCEN-PV 14085–88; 14090.

Type Locality and Age: Argentina: provincia de Chubut: Departamento Sarmiento: Scarritt Pocket (Figure 1). Middle Oligocene (Marshall et al. 1986; Flynn & Swisher 1995).

Diagnosis: This species is assigned to Odontophrynidae by the concurrence of extensive frontoparietals, in medial contact along their entire length, deflecting posteriorly and with crescent-shaped posterolateral projections that overlap the epiotic eminences; robust pterygoid anterior ramus, reaching the planum antorbitale, contacting the corresponding neopalatine and projecting dorsally; nasals with long and slender maxillary processes, contacting maxillae; otic capsules bearing prominent epiotic eminences; notched premaxillary pars palatine; dentate vomers, narrowly separated medially; robust neopalatines, narrowly separated medially, bearing a conspicuous ridge, and with lateral edges expanded and articulated with maxillae and pterygoids; sacral neural arch with a transversal crest that projects over the diapophyses; short urostyle with a high dorsal crest that nearly reaches the end of the bone; short ilial shaft; short hind limbs and knobbed terminal phalanges.

Chachaiphrynus lynchi differs from all extant Odontophrynidae in having massive and long otic capsules (length more than a third of the skull-length) and trapezoidal mentomeckelian bones without odontoid processes. It also differs from the extant species of the group in the following combination of characters: nasals in medial contact (absent in all odontophrynids except *O. lavillai* and *Macrogenioglottus*), non-contacting frontoparietals [in contact in *Proceratophrys* (except in *P. moratoi*) and *Macrogenioglottus*]; relatively short and acute-ending squamosal zygomatic ramus (long in *Proceratophrys*, contacting maxilla except in *P. moratoi*) and slender and acute-ending squamosal otic ramus (medially expanded into a subrectangular otic plate in *Proceratophrys* and *Macrogenioglottus*); absence of dermal ornamentation [present in *Proceratophrys* (except in *P. moratoi*) and *Macrogenioglottus*]; and absence of indentation in the preorbital portion of the maxillary pars facialis (present in *Odontophrynus* and *Macrogenioglottus*).

Etymology: The specific epithet honors John D. Lynch, a notable student of the South American batrachofauna, who noticed that the first collected material of *Chachaiphrynus* does not represent a member of *Eupsophus*, as it was originally considered by Schaeffer in 1949 (Lynch [1971]; see Nicoli [2012] and papers cited therein for additional details).

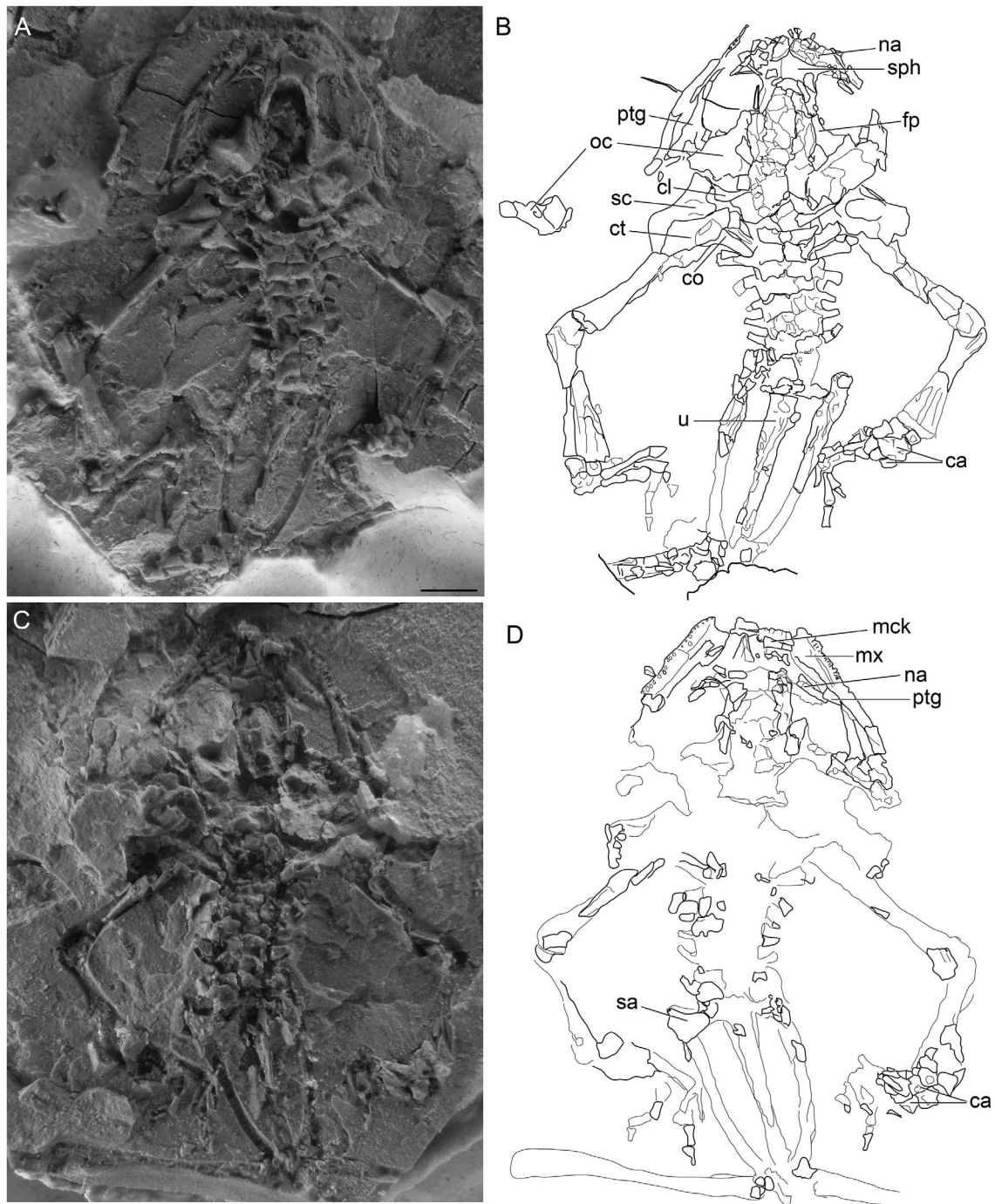


Figure 2. *Chachaiphrynus lynchi*, gen. et sp. nov., holotype, MPEF-PV 10572. (A) Photograph and (B) interpretative drawing of the slab that possesses the more ventral portion of the specimen (MPEF-PV 10572a, bearing the preserved bones in dorsal view and imprints of the ventral surfaces of not-preserved bones. A posterior fragment of the left otic capsule was mechanically removed and relocated to the left of the slab to expose the underlying elements); (C) photograph and (D) interpretative drawing of the slab that possesses the more dorsal portion of the specimen (MPEF-PV 10572b, bearing the preserved bones in ventral view and imprints of the dorsal surfaces of not-preserved bones).

Abbreviations: ca, carpal elements; cl, clavicle; co, coracoid; ct, cleithrum; fp, frontoparietal; mck, mentomeckelian bone; mx, maxilla; na, nasal; oc, otic capsule; ptg, pterygoid; sa, sacral vertebra; sc, scapula; sph, sphenethmoid; u, urostyle. Scale bar equals 3 mm.

Description

Chachaiphrynus lynchi (Figures 2–4) was a medium-sized anuran (SVL 30 to 60 mm approx. in adult specimens), having a large head that is wider than long. The relatively well-ossified skull possesses notably extensive antorbital and interorbital

regions (Figures 2 and 4). No dermal ornamentations are visible. The medial skull length is approximately equal to, or slightly shorter than, the length of the presacral vertebral column. Although hind limbs are longer than forelimbs they are relatively short.

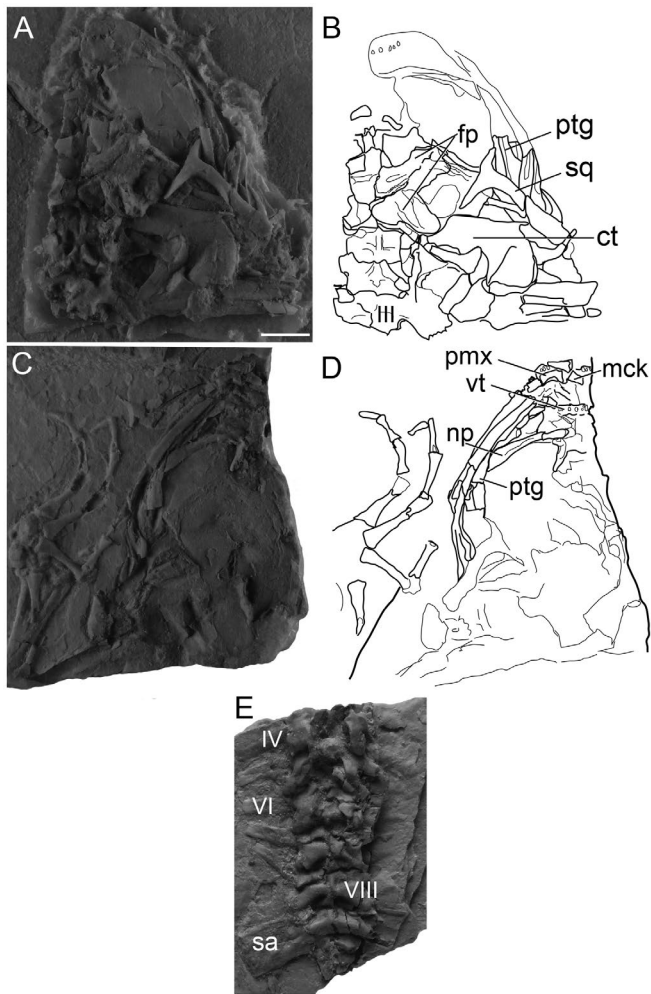


Figure 3. *Chachaiphrynus lynchi*, gen. et sp. nov., MPEF-PV 10573. (A) photograph and (B) interpretative drawing of the slab that possesses the more anterior and ventral portion of the specimen (MPEF-PV 10573a); (C) photograph and (D) interpretative drawing of the slab that possesses the more anterior and dorsal portion of the specimen (MPEF-PV 10573b); (E) photograph of the slab that possesses most of the vertebral column preserved in dorsal view (MPEF-PV 10573c). Abbreviations: ct, cleithrum; fp, frontoparietal; mck, mentomeckelian bone; np, neopalatine; pmx, premaxilla; ptg, pterygoid; sq, squamosal; vt, vomeral teeth. Scale bar equals 5 mm.

Skull

Dermal skull roof

The nasals are extensive bones that cover an important portion of the ample preorbital region (Figures 2 and 4). They are in medial contact and seem to reach the maxillary arcade and articulate with the corresponding maxilla; this latter, however, is difficult to asseverate given the kind of preservation of the fossils (see above). The nasals extend laterally in a long and slender maxillary process that may have contacted the pterygoid. The nasals are broadly distant from the frontoparietals, not contacting them.

The frontoparietals of *Chachaiphrynus lynchi* are also extensive, non-ornamented bones. As it occurs with several other bones in these fossils, frontoparietals are preserved broken in different slabs (part and counterpart) in all specimens, because of what its shape must be reconstructed (Nicoli 2012). In several specimens (e.g. MPEF-PV 10572; AMNH 3422; 3425), pieces of flat, delicate bones are preserved within the frontoparietal fontanelle (Figure 2; Nicoli 2012, figs. 5–6), which is interpreted as

consequence of postmortem crushing of frontoperitals within the neurocranium (Nicoli 2012). These pieces, as well as the pieces of frontoparietals over the ossified neurocranium, evidence median longitudinal sutures (Figures 2 and 3; Nicoli 2012, figs. 5–6). This demonstrates that they are mutually in contact along most of their length, roofing completely the frontoparietal fontanelle (Figure 4; Nicoli 2012). The reconstruction of these bones also demonstrates that frontoparietals are notably broad, and their width gradually increase posteriorly in the interorbital region (Figures 2–4; Nicoli 2012). In the otic region their lateral margins project laterally over the otic capsules, at the level of the epiotic eminences. There, the postero-lateral margins of frontoparietals seem to be crecent-shaped, as the shape of the underlie epiotic eminences (e.g. MPEF-PV 10573; Figure 3).

Maxillary arch

The maxillary arch is toothed and complete. The three partes, facialis, dentalis, and palatine, are discrete. The teeth are pedicelled, but crowns are not completely preserved.

The premaxillae are short. Few specimens preserve premaxillae in dorsal view (e.g. AMNH 3425; MPEF-PV 10572; 10897); they show a short and broad alary process. The premaxillary pars palatina is a robust and well-developed shelf perpendicular to the pars dentalis (Figures 3 and 5(D)). It is weakly notched in the central region, being expanded laterally and bearing a well-developed palatine processes medially (Figure 5(D)). A maxillary process overlapping the pars palatina of maxilla seems to be absent.

The maxillary pars facialis is deep. In the antorbital region, its width seems to be relatively constant, without a distinct preorbital process or indentation. The pars palatina is always partially obscured by the mandible, impeding assessment of the presence or shape of a pterygoid process. A slender quadratojugal contacting the maxilla is evident.

Endocranium

The sphenethmoid is a broad and entire bone. Anteriorly, it reaches about the middle of the preorbital region of the skull. An ossified septum nasi is evident in AMNH 3407 and 3425. The lateral edges of the sphenethmoid diverge posteriorly according with the lateral margins of the dermal skull roof. Dorsally, in the interorbital region, this bone defines a broad and round-ended fontanelle. This fontanelle was completely occluded by the frontoparietals, which postmortem collapsed into the neurocranium in most specimens (Nicoli 2012, fig. 2). The sphenethmoid extends laterally over the planum antorbitale and posteriorly to about the middle of the orbit.

The otic capsules are massive, their maximum length represents more than a third of the skull length. This proportion is observed in all available specimens, some of which show three-dimensionally preserved otic capsules, precluding any possibility that the observed shape is the result from deformation or crushing. The caspules have prominent epiotic eminences. The margins of the foramen magnum are completely ossified. A distinct columella is preserved in MPEF-PV 10573.

Suspensorium

The squamosals are T-shaped, with the three rami, ventral, zygomatic, and otic, well-developed (Figures 3 and 5(M)). The zygomatic ramus is relatively short (length about a quarter of the

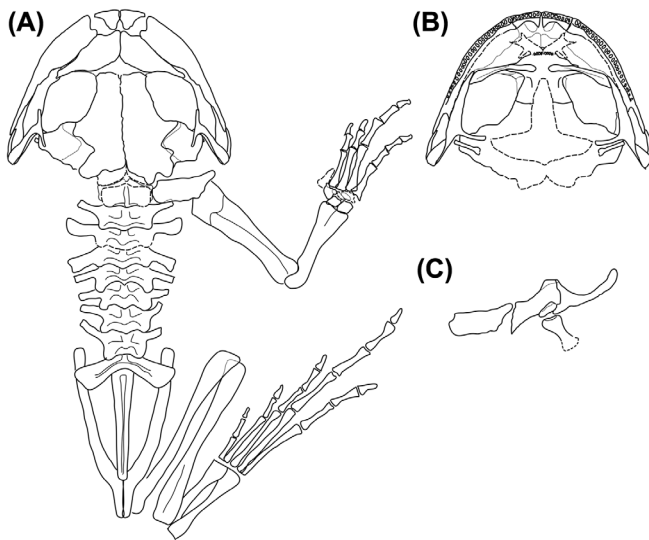


Figure 4. Reconstruction of *Chachaiphrynus lynchi*, gen. et sp. nov. (A) skeleton in dorsal view (left portion of pectoral girdle and left members omitted); (B) skull in ventral view; (C) right portion of pectoral girdle (scapula and suprascapula deflected into the ventral plane). Asymmetrical reconstruction of pair structures reflects morphological variations among different specimens. Dashed lines indicate estimations of the margins of bones.

ventral ramus length), does not contact the maxilla, and has an acute end. The otic ramus is slender, not expanded into an otic plate, and also acute ended.

The pterygoid is a robust bone. The anterior ramus is particularly robust and long, reaching the level of the planum antorbitale and contacting the neopalatine. In some specimens (e.g. MPEF-PV 10575) it is possible to observe that this ramus is projected over the dorsal surface of the skull, possibly contacting the corresponding nasal; the poor preservation or obscuring of this region in all specimens, however, impede establishment with certainty the existence of this contact.

Palate

Vomers are visible in a single specimen (MPEF-PV 10573, Figure 3), its poor preservation precludes further preparation. It is possible to observe, however, the near-perpendicular series of teeth of both vomers, so close medially as to be practically continuous. This dental series evidences that vomers are very close one to another and may be in contact.

The neopalatines are robust and long bones that extend from the maxillary arcade (where they contact with the corresponding pterygoid) to the neurocranium. Medial ends of both neopalatines are close one to another. A conspicuous ridge is evident in the ventral surface of the bone (Figure 3). The lateral edges are expanded. The parasphenoid is not preserved.

Mandible

The mandible is composed by edentate angular, dentary and mentomeckelian bones. No odontoid processes are evident. Mentomeckelian are discrete elements, about three times wider than long (Figure 5(G)). They have trapezoidal shape, without odontoids.

Axial skeleton

The vertebral column is composed of eight procoelous presacral vertebrae, sacrum and urostyle (Figures 2–4). Vertebral fusions are not observed. The vertebral centra are elongated (almost twice as long as wide) and rounded in transverse section. Neural arches are broad (at least twice as wide as long) and imbricated. In each vertebra, the posterior portion of the arch lies in a more-ventral plane than the anterior portion. The neural spines of the anterior presacrals are well-developed and broad; they are always preserved broken in different slabs impeding evaluation of their height. The transverse processes of presacrals III and IV are as wide as the sacral diapophyses and only slightly expanded distally; those of presacrals II and V–VIII are slender and narrower than the diapophyses.

The sacral neural arch shows a nearly transversal crest that projects over the diapophyses (Figure 5(J)). The sacral diapophyses are slightly expanded and robust, posterolaterally directed. The sacro-urostyler articulation is bicondylar. The urostyle is short, its length equivalent to the length of five presacrals. It lacks transverse processes and possesses a high crest that nearly reaches the end of the bone.

Appendicular skeleton

Pectoral girdle

The clavicles are robust and strongly curved bones. Their distal ends are rounded and narrowly separated (Nicoli 2012, fig. 4; Figure 4(C)). Their width is uniform in most of their length except in the proximal portion. There, the clavicles expand and articulate with the scapulae abutting the pars acromialis, without overlapping its anterior margin. The coracoid is robust; its proximal end has a robust articulation facet. The distal end is only slightly more expanded than the proximal one.

The scapula is nearly twice and a half wider than long and the shaft is slightly larger than the glenoid region (Nicoli 2012, fig. 4; Figure 4(C)). The entire bone is shorter than the clavicle. The supraescapular margin deflects posteriorly beyond the glenoid. The pars acromialis is anteriorly expanded. No cleft is evident between the partes acromialis and glenoidalis.

The cleithrum is an extensive bone; the overall shape of which is nearly rectangular in most preserved specimens, no bifurcation is evident and the lateral margin does seem to reach the scapular margin (Figures 2 and 4). However, in the large specimen MPEF-PV 10573 (Figure 3), the cleithrum seems to be more expanded posterolaterally, forming an inverted-L. The anuran cleithrum is a dermal bone that early in development invests the anterior margin of the suprascapula and then expands posteriorly onto the dorsal side of this cartilage (e.g. Pügenger & Maglia 1997; Wild 1997). Thus, morphological differences observed among fossils may be related with different degrees of ossification in individuals with different size and, presumably, age.

Forelimb and manus

The humerus is longer than radioulna, being approximately equivalent to the radioulna + metacarpal length. The humeral ball is relatively large and ossified, even in the smallest preserved specimens. The medial side of the humerus is only preserved in

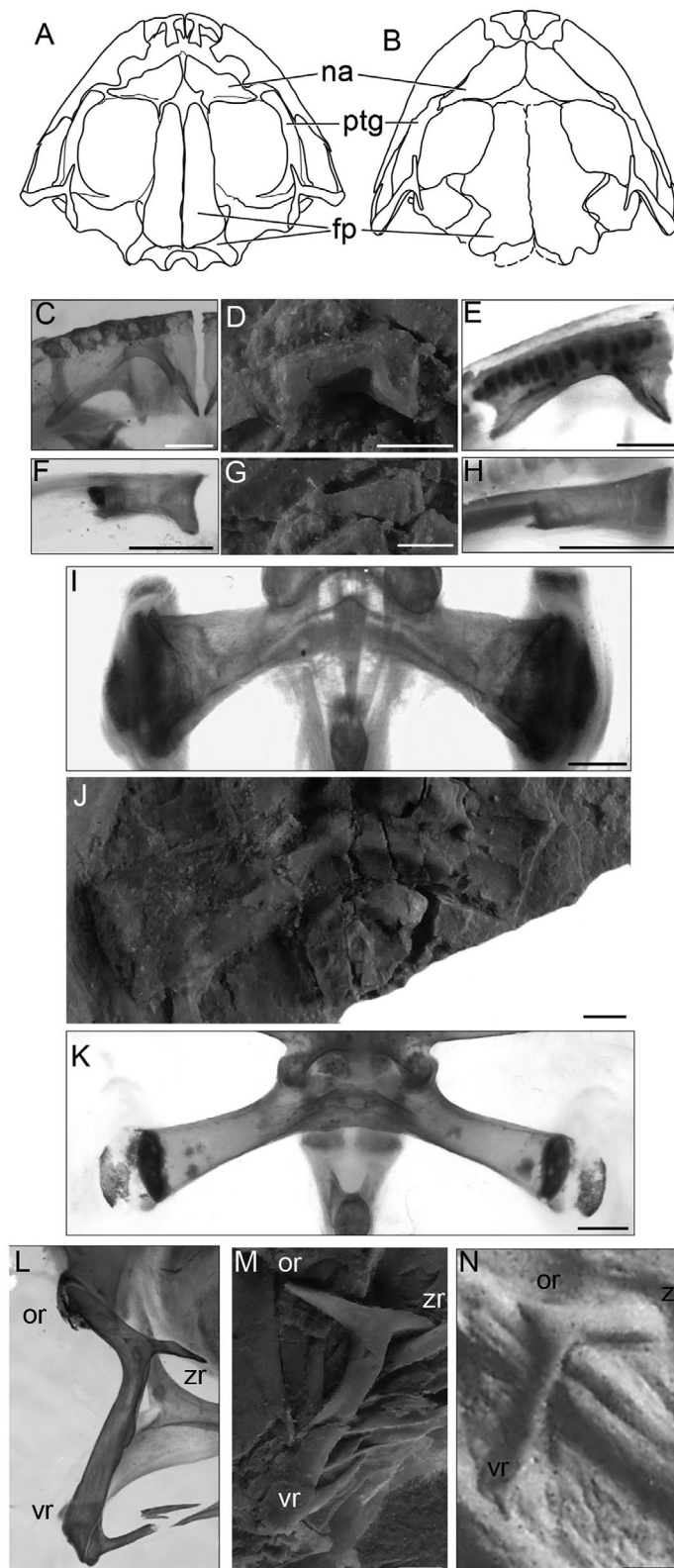


Figure 5. Skull in dorsal view of (A) *Odontophrynus achalensis* (CENAI 2972) and (B) *Chachaiphrynus lynchi*, gen. et sp. nov.; premaxilla in ventral view of (C) *Odontophrynus achalensis* (CENAI 2972), (D) *Chachaiphrynus lynchi* (MPEF-PV 10573a), gen. et sp. nov., and (E) *Limnomedusa macroglossa* (MACN 4644); mentomekelian bone of (F) *Odontophrynus achalensis* (CENAI 2972), (G) *Chachaiphrynus lynchi* (MPEF-PV 10573a), gen. et sp. nov., and (H) *Limnomedusa macroglossa* (MACN 4644); sacral vertebra in dorsal view of (I) *Odontophrynus* cf. *americanus* (MACN 49349), (J) *Chachaiphrynus lynchi* (MPEF-PV 10573c), gen. et sp. nov., and (K) *Limnomedusa macroglossa* (MACN 4644); squamosals in lateral view of (L) *Odontophrynus achalensis* (CENAI 2972), (M) *Chachaiphrynus lynchi* (MPEF-PV 10573b), gen. et sp. nov., and (N) undetermined fossil anuran from SP (CPBA-V 14089; modified and inverted from Báez and Fernicola [1999]).

Abbreviations: fp, frontoparietal; na, nasal; or, squamosal otic ramus; ptg, pterygoid; vr, squamosal ventral ramus; zr, squamosal zygomatic ramus; Scale bar equals 1 mm.

the specimen MPEF-PV 10572, which bears a high crista medialis, although it is a specimen with an approximate SVL of only 30 mm (Figure 2).

The radioulna is robust and possesses a well-developed olecranon process and a large cotyle for the humeral ball. The distal margin of the radioulna seems to be considerably more expanded than the proximal one.

The carpus is incompletely preserved in all specimens. Only four conspicuous elements are evident, but, except for the most proximal ulnare and fibulare, the disarticulated condition of the associated metacarpals impedes their certain identification. A prepollex seems to be present in MPEF-PV 10572 and AMNH 3426. The four metacarpals are short bones, being about half the length of the radioulna. In decreasing order, their lengths are IV > III > II = V. The phalangeal formula is 2-2-3-3 and the terminal phalanges are knobbed.

Pelvic girdle

The ilial shafts are as long as the presacral column and oval in cross section. No dorsal ridges or crests are evident. In some specimens it is possible to observe the presence of a well-developed, round and blunt dorsal prominence; it has an extended base and is probably laterally projected. Illia are usually preserved in medial view, impeding observation of additional features. The dorsal acetabular expansion is well developed.

Hind limb and pes

Hind limbs are relatively short. The femur is only slightly longer than the presacral column and the ilial shaft. The tibiofibula is equal or slightly longer than the femur and twice the length of the tibiale-fibulare. These latter are similarly extended and apparently not fused distally. Some ossified distal tarsals are evident, but the poor or disarticulated preservation impedes describing them. The relative size of the metatarsals is IV > V > III > II > I; the longest metatarsal is longer than the tibiale-fibulare. The phalangeal formula is 2-2-3-4-3, and the relative toe length is IV > V > III > II > I. The terminal phalanges are blunt.

Discussion

Comparisons and taxonomic placement of *Chachaiphrynus lynchi*

The concurrence of discrete neopalatines; eight procoeleous presacral vertebrae, non-expanded sacral diapophyses, bicondylar sacro-urostyle articulation, urostyle without transverse processes; long scapula, without a distinct cleft between partes acromialis and glenoidalis, and discrete and curved clavicles abutting scapulae permits attribute *Chachaiphrynus lynchi* to Hyloides (sensu Frost et al. [2006]; unnamed node of Pyron and Wiens [2011] that represents Hyloidea + Australobatrachia).

Chachaiphrynus has characteristic frontoparietals with a particular shape: they are extensive and broad bones, which are in contact along their entire medial margin, obscuring the frontoparietal fontanelle. Their lateral margins deflect posteriorly and there are fusions with the surrounding bones. Other unusual character state of *Chachaiphrynus* is the robustness and extension of the anterior ramus of pterygoid, which reaches the planum antorbitale and projects over the dorsal surface of the

skull. Relatively few living anurans possess this combination of characters. Among hyloids, these characters are observed only in Bufonidae, in Leiuperinae leptodactylids (sensu Frost 2016), and in Odontophrynidae.

Bufonidae is a well-supported, diverse clade of cosmopolitan toads (Frost et al. 2006; Pyron & Wiens 2011; Pyron 2014). Although numerous papers have described the osteology of some of its taxa (e.g. Sanders 1953; Tihen 1962; Trueb 1971; Martin 1972; McDiarmid 1972; Ruiz-Carranza & Hernández-Camacho 1976; Grandison 1978, 1980; Pregill 1981; Pramuk 2002, 2006; Baldo & Basso 2004; Coloma et al. 2007, 2010; Páez-Moscoso et al. 2011; Baldo et al. 2012; Peloso et al. 2012) the skeletons of an important portion of Bufonidae remain unknown. Among the Bufonidae with known osteology, several taxa (e.g. *Anaxyrus*, *Bufo*, *Duttaphrynus*, *Incilius*, *Nannophryne*, *Peltophryne*, *Rhaebo*, *Rhinella*, *Truebae*) possess species with frontoparietals and pterygoids with similar morphology to those of *Chachaiphrynus lynchi* (Parker 1881; Sanders 1953; Tihen 1962; Trueb 1971; Martin 1972; Pregill 1981; Pramuk 2002, 2006; Mendelson et al. 2011; pers.obs. specimen in Appendix S1, Supplementary information on line). However, all of them differ from the fossil species in having edentate maxillary arcade (synapomorphy of Bufonidae proposed by Grant et al. 2006), tiny and edentate vomers broadly separated medially; otic ramus of squamosal forming a more or less expanded otic plate; moderately to broadly expanded sacral diapophyses; and right clavicles perpendicular to midline (Parker 1881; Sanders 1953; Tihen 1962; Trueb 1971; Martin 1972; Pregill 1981; Pramuk 2002, 2006; Mendelson et al. 2011; pers.obs. specimen in the Appendix S1, Supplementary information on line).

Leiuperinae is a clade of mostly Neotropical small to medium-sized frogs that is recovered in several phylogenetic analyses (Grant et al. 2006; Pyron & Wiens 2011; Pyron 2014). Four of the five leiuperine genera (i.e. *Edalhorina*, *Engystomops*, *Physalemus*, and *Pseudopaludicola*), which are presumably monophyletic (Pyron & Wiens 2011), have species that possess several features similar to *Chachaiphrynus lynchi*. These species have nasals not contacting frontoparietals; broad frontoparietals, in contact along the midline and deflecting posteriorly, and pterygoids with well-developed anterior rami that reach the planum antorbitale and project dorsally (Lynch 1970; Cannatella & Duellman 1984; Lobo 1994, 1995, 1996a, 1996b; Nascimento et al. 2005; pers.obs. specimens in the Appendix S1, Supplementary information on line). However, these anurans possess skulls that are not wider than long; nasals lacking a well-developed maxillary processes; incomplete maxillary arcade; relatively-small, edentate, and medially-distant vomers; neopalatines broadly separated medially, without ridges; non-imbricated vertebrae; long urostyle; and long hind limbs (Lobo 1995, 1996a,b; pers.obs. specimens in the Appendix S1, Supplementary information on line).

Odontophrynidae is a widely distributed South American clade of small to medium size chubby frogs. Their monophyly has been corroborated in several phylogenetic analyses, although the relationships with other anuran taxa are still controversial (Frost et al. 2006; Grant et al. 2006; Pyron & Wiens 2011; Pyron 2014). Although, as it occurs with most anuran taxa, skeletal information was not been included in those analyses and no osteological synapomorphies have been proposed for the group, Odontophrynidae was originally recognised fundamentally on the basis of their osteology (as Odontophrynini by Lynch 1971).

Their skeletal anatomy was described or discussed in several contributions (Lynch 1971; Reig 1972; Jim & Caramaschi 1980; Izecksohn et al. 2005; Rosset et al. 2007; Prado & Pombal Jr. 2008; Rosset 2008).

Odontophrynidae shares with *Chachaiphrynus lynchi* the shape of frontoparietals and pterygoids. In this way, both taxa have extensive frontoparietals, in medial contact along their entire length, deflecting posteriorly and with crescent-shaped posterolateral projections that overlap the epiotic eminences (Figures 5(A) and (B)). Similarly, their pterygoids have a robust anterior ramus that reaches the planum antorbitale, contacting the corresponding neopalatine and projecting dorsally. Moreover, they also share an important number of additional character states: nasals bearing a long and slender maxillary process, contacting maxillae; otic capsules bearing prominent epiotic eminences; notched premaxillary pars palatine (Figures 5(C) and (D)); dentate vomers, narrowly separated medially; robust neopalatines, narrowly separated medially, bearing a conspicuous ridge, and with lateral edges expanded and articulated with maxillae and pterygoids; sacral neural arch with a transversal crest that projects over the diapophyses (Figure 5(I) and (J)); short urostyle with a high dorsal crest that nearly reaches the end of the bone; short ilial shaft; short hind limbs and knobbed terminal phalanges (Figure 5).

Most of these character states differentiate Odontophrynidae from the taxa that were alternatively considered closely related in different hypotheses: Alsodidae (*Alsodes*, *Eupsophus*), Batrachylidae (*Atelognathus*, *Batrachyla*, *Chaltenobatrachus*, *Hylorina*), Cycloramphidae (*Cycloramphus*, *Thoropa*), Hylodidae (*Crossodactylus*, *Hylodes*, *Magaelosia*), *Limnomedusa*, Rhinodermatidae (*Rhinoderma* + *Insuetophrynus*), and Telmatobiidae (Frost et al. 2006; Grant et al. 2006; Pyron & Wiens 2011; Fouquet et al. 2013; Pyron 2014). Thus, these character states are the putative, non-exclusive, synapomorphies of Odontophrynidae. The only clear exception is the shape of the terminal phalanges, which is also present in several of these taxa. The shape of the premaxilla and of the sacral vertebra and urostyle of the odontophrynids is also present in *Limnomedusa* (Figure 5), which was recovered as the sister taxon of Odontophrynidae in some phylogenetic analyses (Faivovich et al. 2005; Frost et al. 2006; Grant et al. 2006). The shape and extension of the posterolateral projections of the frontoparietals of Odontophrynidae seems to be exclusive among Hyloidea.

Special attention requires the comparison with Ceratophryidae, the clade of South America horned frogs, which is recovered as the sister-taxon of the clade including Odontophrynidae in some phylogenetic analyses (Pyron & Wiens 2011; Pyron 2014). Ceratophryidae, like Odontophrynidae, possess extensive frontoparietals, in medial contact along their entire length, and deflecting posteriorly. Their neopalatines also are narrowly separated medially, may bear a ridge, and articulate with maxillae and pterygoids; although their width is constant along their length. In addition, most ceratophryid species (except those in *Lepidobatrachus*) have vomers narrowly separated medially; although they are edentulous or with a patch of a few teeth. Moreover, the maxillary processes of the nasals of the ceratophryid monotypic genus *Chacophrys* are similar to those of the odontophrynids. They also share with Odontophrynidae the postcranial character states (sacral neural arch with a transversal

crest over the diapophyses; short urostyle with a high dorsal crest that nearly reaches the end of the bone; short ilial shaft; short hind limbs and knobbed terminal phalanges). Thus, if a sister-taxa relationship of Ceratophryidae and a clade that includes Odontophrynidae is supported, some of the putative synapomorphies of Odontophrynidae proposed above could actually be plesiomorphies or optimize ambiguously, depending on the position of Odontophrynidae.

In this way, the fossil species possesses a combination of characters exclusive of Odontophrynidae, which allows attributing *Chachaiphrynus lynchi* to this clade, even though the controversial position of Odontophrynidae within anuran impedes knowing the sequence of acquisition (and phylogenetic significance) of most of these characters.

The relative position of *C. lynchi* within Odontophrynidae, however, is uncertain. Odontophrynidae has 52 extant species in three genera: *Proceratophrys*, *Odontophrynus*, and the monotypic *Macrogenioglottus*. These latter are the most closely related, either as sister taxa (Pyron & Wiens 2011; Pyron 2014) or with *Macrogenioglottus* nested within *Odontophrynus* (Amaro et al. 2009). All extant odontophrynids have mentomeckelian bones with a medial odontoid process (Figure 5(F)). This character also differentiates Odontophrynidae from all taxa proposed as its closest related, because of what could be one of its synapomorphies. However, the mentomeckelians of *C. lynchi* are trapezoidal long bones, lacking an odontoid process (Figures 2(A)–(B) and 5(G)), like those of *Limnomedusa* (Figures 5(F)–(H)). On the other hand, some features of *Chachaiphrynus lynchi* are characteristic of *Odontophrynus* (or *Odontophrynus* + *Macrogenioglottus*) or are included within its variability: absence of dermal ornamentation, nasals in medial contact (only in *Macrogenioglottus* and *O. lavillai* among odontophrynids) and separated from frontoparietals, squamosals with a relatively short, generally acute-ending, zygomatic ramus (Figure 5(L) and (M)) and with a slender otic ramus, not expanded into an otic plate (Figure 5(L) and (M)). However, all species of *Odontophrynus* (and also *Macrogenioglottus*) possess the maxillary pars facialis indented in the preorbital portion, while *C. lynchi*, like *Proceratophrys*, lacks this indentation (Figure 5(A) and (B)). Similarly, all *Proceratophrys* and *C. lynchi* lack a maxillary process in the premaxilla, which is present in the *Odontophrynus* and in *Macrogenioglottus*.

In addition, *Proceratophrys moratoi*, recently transferred from *Odontophrynus* on the basis of molecular evidence (Amaro et al. 2009), possess a mosaic of character states from *Odontophrynus* and the other species of *Proceratophrys* (Jim & Caramaschi 1980). *Proceratophrys moratoi* shares with *Odontophrynus* and *C. lynchi* (and differs from other *Proceratophrys*) in the absence of dermal ornamentation, the lack of contact between nasals and frontoparietals, and the presence of a slender otic ramus of squamosal. The significance of this complex distribution of characters must be tested in a phylogenetic context. A phylogeny of the Odontophrynidae that includes a wide taxonomic sampling and a dense morphological data-set including osteology is in progress (Rosset, pers.com.). The inclusion of *Chachaiphrynus lynchi* in this analysis will provide a more certain idea of its phylogenetic relationships.

Several other fossil anurans have been collected in Scarrit Pocket. The Patagonian extant genus *Calyptocephalella*, closely

related with the Australasian Myobatrachoidea (sensu Frost et al. 2006), is represented in SP by adults and tadpoles of its fossils species *C. canquelli* (Schaeffer 1949; Muzzopappa & Báez 2009; Muzzopappa & Nicoli 2010). At the same time, a single specimen from SP has been considered representative of a new taxon, *Neoprocoela edentata* (Schaeffer 1949), whose relationships had been debated (Schaeffer 1949; Tihen 1962; Lynch 1971). This anuran possesses edentulous upper maxillary arcade, well-developed frontoparietal fontanelle, and dilated, triangular sacral diapophyses; differing clearly from *Chachaiphrynus lynchi*.

A third fossil anuran from SP has been considered close to the 'lower telmatobiine' sensu Lynch 1978 (Báez & Fernicola 1999), an assemblage for which there has never been any evidence of monophyly and that resulted polyphyletic in recent phylogenetic analyses (Frost et al. 2006; Pyron & Wiens 2011). It is preserved as part and counterpart of disarticulated elements (squamosal, presacral column, humeri and ilium) of a single specimen (CPBA-V 14089). Until now, the absence of preserved common elements between CPBA-V 14089 and the fossils from SP assigned by Schaeffer to *Eupsophus* sp. (referred here to *C. lynchi*) impeded determining whether these fossils represent the same species (Báez & Fernicola 1999). The new material described here provides evidence that allows comparing CPBA-V 14089 with *Chachaiphrynus lynchi*, showing that they are different species (Figure 5(M) and (N)). The squamosal of CPBA-V 14089 has a rectangular zygomatic ramus and a short otic ramus (Figure 5(N)). The ilium has a high and robust dorsal prominence and a long shaft, longer than the whole presacral column length. The vertebral column of CPBA-V 14089 has non-imbricated neural arches, at least in presacrals VI and VII (Báez & Fernicola 1999). All these character states differentiate CPBA-V 14089 from *Chachaiphrynus*.

The presence of this so incompletely known anuran taxon in SP requires being especially conservative in the identification of poorly preserved specimens from this locality. In this way, the extremely incomplete specimens AMNH 3424 and 3430, originally attributed to *Eupsophus* (Schaeffer 1949), are considered here as indeterminate. By contrast, it is possible to asseverate that the poorly preserved specimens FCEN-PV 14085–1487 [mentioned by Báez and Fernicola (1999) as possibly 'the same taxon that Schaeffer identified as *Eupsophus*' (free translation from Spanish)] and FCEN-PV 14088 and 14090 [tentatively identified as *Neoprocoela* (Báez & Fernicola 1999)] are actually *Chachaiphrynus lynchi*.

Palaeoecological significance of the presence of *Chachaiphrynus lynchi* in Patagonia during the oligocene

The extant odontophrynids have a wide distribution in South America (Figure 1(A)). Within this extensive area they occur in association with remarkably diverse environments (from moist forests, to tropical, subtropical and temperate grasslands, savannas, and shrublands; Cei 1980; Caramaschi 1996; Eterovick & Sazima 1998; Giaretta et al. 2000; Kwet & Faivovich 2001; Peiretti et al. 2002; Izecksohn et al. 2005; Rosset et al. 2006, 2007; Prado & Pombal Jr. 2008; Rosset 2008; Tiburcio et al. 2008; Rosset et al. 2009; Lisboa et al. 2010; Rolim et al. 2010). The single Odontophrynidae that reaches Patagonia and the southernmost distributed, *O. occidentalis*, has been reported at

the north of the Chubut province and in association with the Monte Biogeographic Province (Peiretti et al. 2002). Nowadays, no Odontophrynidae reaches the center of Patagonia, where is located SP, or the Steppe Biogeographic Province that now dominates this region (Figure 1(A)).

The presence of an Odontophrynidae in SP during the Oligocene is presumably associated with the more benign climate inferred in Patagonia during this time. Proxy-data (e.g. pollen grains) suggest an equable Oligocene with forest types dominating present day Patagonia (Palazzesi & Barreda 2007; Quattrocchio et al. 2011; Strömberg et al. 2013; and papers cited therein). Microtherm *Notophagus*-gymnosperm dominated forests with a fern understory (and probably some openings in the forest) would have been widespread in Patagonia during the Early Oligocene (Barreda & Palazzesi 2010). In Late Oligocene, closed forests, enriched in megatherm elements, had spread in eastern Patagonia, coexisting with the first appearance of modern shrubby and herbaceous lineages (Barreda & Palazzesi 2010). The steppe-like elements (e.g. grass and asters) were virtually absent by these times in this area (Barreda & Palazzesi 2007). The presence of odontophrynid anurans in this context is consistent with the extant distribution of the group. The aridification events of Patagonia occurred later, in the Neogene, due to the rain-shadow effect of the Andes that blocked the humid winds from the west presumably since the late Miocene onwards (Compagnucci 2011). It has been proposed that these dramatic changes caused the regional extinction of the anuran *Calyptocephalella*, amply recorded in Patagonia since the Cretaceous to the Miocene and nowadays restricted to the eastern Andean Valdivian forest (Muzzopappa & Báez 2009; Gómez et al. 2011). These climatic changes could also be the cause of the regional extinction of the Odontophrynidae.

Few interpretations of the Oligocene environment in SP in particular have been performed. Only scarce and fragmentary plants remains have been recovered in the locality, precluding any environmental inference from their analysis. Chafee (1952) analysed the putative ecological requirements of one of the most abundant mammal recovered in SP, the notungulate *Scarrittia*. He considered *Scarrittia* as a slow, ponderous browser animal, inhabitant of 'a forest habitat with plenty of vegetation for concealment and food' (Chafee 1952). The other anuran from SP with known relationships, *Calyptocephalella canqueli*, would be related with species associated to forested habitats. The single extant *Calyptocephalella*, *C. gayi*, nowadays inhabits permanent water-bodies of the Chilean Temperate Forests (Cei 1962). Likewise, the fossil *Calyptocephalella pichileufuensis* has been recovered in association with a flora indicative of climatic conditions similar to extant subtropical, or tropical montane, rainforest (Wilf et al. 2009; Gómez et al. 2011). Although the habits of each extant odontophrynid genus shows a particular tendency (see Cei 1980; Caramaschi 1996; Eterovick & Sazima 1998; Giaretta et al. 2000; Kwet & Faivovich 2001; Peiretti et al. 2002; Izecksohn et al. 2005; Rosset et al. 2006, 2007; Prado & Pombal Jr. 2008; Rosset 2008; Tiburcio et al. 2008; Rosset et al. 2009; Lisboa et al. 2010; Rolim et al. 2010; Caramaschi & Felgueiras Napoli 2012; Frost 2016), the unresolved position of *Chachaiphrynus* among the group precludes inferring its possible habits and contributing to understand the SP environment during the Oligocene.

Contribution of *Chachaiphrynus lynchi* to the knowledge of the anuran evolution

The relationships of the odontophryinids with other anurans are still controversial. Several recent phylogenetic analyses, mostly based on molecular information, have tested the relationship of anurans using relatively dense taxonomic samples and including a few Odontophrynidae (Frost et al. 2006; Grant et al. 2006; Pyron & Wiens 2011; Fouquet et al. 2013; Pyron 2014). These always resulted monophyletic, deeply nested in Hyloidea, and forming a clade with other endemic South American taxa (Frost et al. 2006; Grant et al. 2006; Pyron & Wiens 2011; Fouquet et al. 2013; Pyron 2014). These taxa, however, are not the same in all the hypotheses. Thus, whereas Alsodidae, *Limnomedusa* and Rhinodermatidae resulted in the same clade that Odontophrynidae in all the analyses, Batrachylidae, Cycloramphidae and Hylodidae are in this clade in most hypotheses, but in different positions in others (Frost et al. 2006; Grant et al. 2006; Pyron & Wiens 2011; Fouquet et al. 2013; Pyron 2014; see Blotto et al. 2013 for taxonomical clarifications of terminals in previous analyses). Finally, *Telmatobius* resulted in the clade including Odontophrynidae in the analyses of Pyron and Wiens (2011) and Pyron (2014). The odontophrynid *Chachaiphrynus lynchii*, because of its age and geographical location, could represent an interesting evidence to reconstruct the pattern of diversification of these South American anurans through the known palaeogeographical and palaeoecological history of the continent. Their unresolved phylogenetic relationships, however, impede to exploiting this evidence beyond speculative hypotheses.

By the other hand, *Chachaiphrynus* represents the oldest certain record of a South American clade deeply nested in Hyloidea and, as such, an exceptional temporal evidence of the diversification of anurans. In particular, *Chachaiphrynus* is an extraordinary potential calibration point for estimations of phylogenetic divergence time in base on molecular data. Several methods have been proposed for timescale phylogenetic trees (see Ho & Phillips 2009 for a review). Nevertheless, the calibration of this time scale is of central importance, considering that absolute ages cannot be estimates from molecular data alone. In anurans, however, the scarceness of the fossil record deprives of calibration points to these kinds of estimations. In the last decade, a series of analyses estimated the time of divergence of Hyloidea and its internal clades, but the calibration of the time scales were mostly based in temporal information attributed to external nodes (based on dated fossils with known taxonomical identity) or inferred from biogeographic events (San Mauro et al. 2005; Roelants et al. 2007, 2011; Wiens 2007; Irisarri et al. 2012; Zhang et al. 2013). This later kind of evidence is always dependent of dating phenomena that usually occurred in inaccurate times and based in assumptions of a causal relationship between cladogenesis and vicariance. Only a few holarctic putative hyloid fossils [i.e. Miocene *Bufo* sp. from Europe (Alf rez Delgado & Brea L pez 1981; Bailon & Hossini 1990); Eocene *Eleutherodactylus* sp. from the Dominican Republic (Poinar & Cannatella 1987, although see below); Miocene *Hyla* sp. from France (Bailon et al. 1988) and from Austria (Sanchiz 1998; take as ‘similar to *H. meridionalis*’ by Wiens 2007) and *H. goini* (Auffenberg 1956; Hollman 1967; take as synonymous of *H. squirella* by Wiens 2007)] have been

used as calibration points in some divergence time estimations (Roelants et al. 2007, 2011; Wiens 2007).

Without attempting to make an exhaustive analysis of these contributions, which is beyond the aim of this work, some aspects deserve to be highlighted to illustrate the current state of the knowledge. For instance, although it has been noted that improperly fossil placement can have significant effect in the estimated diversification dates (see Parham et al. 2012; Sterli et al. 2013), the taxonomical identity of the fossils used as calibration points does not seem to have been critically evaluated. Even several fossil records were obtained from reviews (e.g. Rocek & Rage 2000; Holman 2003; Rage & Rocek 2003) and not from the original papers. In this context, it is noteworthy that most of these fossils were assigned in the end of the last century to huge genera (i.e. *Bufo*, *Eleutherodactylus*, *Hyla*) that were dramatically reformulated in the last decade to resolve their paraphyly (Faivovich et al. 2005; Frost et al. 2006); nevertheless, they were used as calibration points without reconsidering their taxonomical assignation (Roelants et al. 2007, 2011; Wiens 2007). In addition, these fossils are usually fragmentary remains and their original taxonomical assignations were poorly or not discussed and based in comparisons with restricted taxonomical samplings (Auffenberg 1956; Hollman 1967; Poinar & Cannatella 1987; Sanchiz 1998). This traditional palaeontological approach, where isolated fossil elements are identified in base on its resemblance with particular, usually local, taxa, is highly questionable in the current systematic paradigm (see Bell et al. 2010; Parham et al. 2012). Taxonomical assignations should be based on shared synapomorphies, which implies a global understanding of the distribution of the morphological variation and its phylogenetic significance. On the other hand, considering a correct age of the fossils used as calibration points is evidently critical to generate reliable time-scaled phylogenies (Parham et al. 2012). It is even recommended to specified the locality and stratigraphic level (to the best of current knowledge) from which the calibrating fossils were collected as well as the reference to a published radioisotopic age and/or numeric timescale and details of numeric age selection (Parham et al. 2012). These aspects are however never discussed and the ages of fossils are usually taken from the palaeontological works. As an example, the age of the putative Eocene *Eleutherodactylus* (Poinar & Cannatella 1987), used as calibration point in some analyses (e.g. Roelants et al. 2007), has longer discussed and is still not well-defined (see Iturralde-Vinent & MacPhee 1996; Poinar & Struwe 2016, and papers cited therein).

In this context, the discovery of the relatively complete and well-represented *Chachaiphrynus lynchi*, from a known locality and stratigraphical level whose sediments were radioisotopically dated, as well as its analysis framed in a phylogenetic context and with a broad comparative taxon sampling, represents a valuable evidence to contribute to reconstruct the temporal frame of the anuran evolution.

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