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A NEW CALYPTOCEPHALELLIDAE (ANURA, NEOBATRACHIA) FROM THE UPPER CRETACEOUS OF PATAGONIA, ARGENTINA, WITH COMMENTS ON ITS SYSTEMATIC POSITION

[Una nueva Calyptocephalellidae (Anura, Neobatrachia) del Cretácico Superior de la Patagonia, Argentina, con comentarios sobre su posición sistemática]

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ABSTRACT: The living genus *Calyptocephalella* is currently represented by the species *C. gayi*, geographically restricted to Chile, and several extinct Cenozoic species from Argentine Patagonia. In the present paper, a species of *Calyptocephalella* is described from the Late Cretaceous (Campanian-Maastrichtian) of Río Negro province, Argentina. The new taxon shows a unique combination of apomorphic and plesiomorphic features, and represents the oldest record for the calyptocephalellids. Present analysis indicates that calyptocephalellids are composed by the genera *Calyptocephalella*, *Gigantobatrachus*, and *Beelzebufo*. The genus *Gigantobatrachus* is revalidated, and a new species of the genus coming from the Paleocene of Patagonia, is described. The genus *Beelzebufo* is currently represented by the species *B. ampinga*, from the Latest Cretaceous of Madagascar. Although this taxon was previously referred to Ceratophryidae, present analysis suggests calyptocephalellid affinities for this genus. A brief overview of Late Mesozoic anurans from India sheds doubts about the occurrence of putative Laurasian-like taxa anuran taxa in the Latest Cretaceous of that continent, and most of these specimens are considered as indeterminate neobatrachians or as nearly related to calyptocephalellids, suggesting a wider distribution of this anuran clade during the Mesozoic.

Key words: *Calyptocephalella*, Ceratophryidae, Calyptocephalellidae, Gondwana, India, Cretaceous.

RESUMEN: El género viviente *Calyptocephalella* se encuentra actualmente representado por la especie *C. gayi* geográficamente restringida a Chile, así como diversas especies extintas de la Patagonia argentina. En el presente artículo, una nueva especie del género *Calyptocephalella* es descripta para el Cretácico tardío (Campaniano-Maastrichtiano) de la Provincia de Río Negro, Argentina. La nueva especie puede ser diagnosticada sobre la base de una combinación de caracteres apomórficos y plesiomórficos, y representa el registro más antiguo para los Calyptocephalellidae. El presente análisis indica que Calyptocephalellidae se encuentra compuesta por los géneros *Calyptocephalella*, *Gigantobatrachus* y *Beelzebufo*. El género *Gigantobatrachus* es revalidado, y una nueva especie del género proveniente del Paleoceno de Patagonia es descripta. El género *Beelzebufo* se encuentra representado por la especie *B. ampinga*, proveniente del Cretácico tardío de Madagascar. Este taxón ha sido originalmente referido a Ceratophryidae, sin embargo, el presente análisis sugiere afinidades con Calyptocephalellidae. Una breve revisión de los anuros del Mesozoico tardío de India arroja dudas acerca de la ocurrencia de posibles taxones de filiaciones laurásicas, y dichos especímenes son aquí considerados como neobatracios indeterminados o cercanamente relacionados a los Calyptocephalellidae. Esto, en conjunto con materiales procedentes del Cretácico de África, sugieren una distribución geográfica más amplia para el clado durante el Mesozoico tardío.

Palabras clave: *Calyptocephalella*, Ceratophryidae, Callyptocephalellidae, Gondwana, India, Cretácico.

INTRODUCTION

The fossil record of Mesozoic anurans is South America is highly biased. Basal anurans of the clade Pipidae have been recorded from several localities in outcrops from the Mid-to Late Cretaceous of Brazil and Argentina (see BÁEZ, 2000). The finding of fossil mesozoic neobatrachian anurans is scarcer than that of Pipidae. In fact, only nearly complete specimens have been recorded from the Early and Late Cretaceous of Brazil (e.g., BÁEZ & PERÍ, 1990; BÁEZ *et al.*, 2009a). In Argentina, the fossil record of Mesozoic anurans is still very patchy. Fossil Pipidae have been indicated on the basis of incomplete skeletons from the Mid-Cretaceous (Cenomanian) of Neuquén and Río Negro provinces (BÁEZ, 2000; BÁEZ *et al.*, 2000, 2007). In addition, coming from the Late Cretaceous

(Santonian) of Northwestern Argentina, a large number of specimens belonging to the pipid *Saltenia ibanezi* Reig, 1959 have been described in detail (BÁEZ, 1981; BÁEZ & PUGÉNER, 1998). Additional isolated pipid remains were cited and described at several fossiliferous localities from the Latest Cretaceous (Campanian-Maastrichtian) of Río Negro province (BÁEZ, 1987; MARTINELLI & FORASIEPI, 2004).

Regarding the neobatrachian record, only very fragmentary and often dissociated and incomplete remains have been described from diverse localities from Campanian-Maastrichtian beds of Patagonia, Argentina. These specimens were assigned to the polyphyletic "Leptodactylidae" (*sensu* FROST *et al.*, 2007) and have been regarded as nearly related to the living Chilean genus *Calyptocephalella* Strand 1928 (BÁEZ, 1987; DE LA FUENTE *et al.*, 2007). This brief picture clearly shows the rather incomplete nature of the anuran fossil record in South America.

In the present paper, several new specimens belonging to a new anuran taxon nearly related to living *Calyptocephalella* are described in detail. These remains, mostly isolated bones, have been reported in several Late Cretaceous outcrops of Northwestern Patagonia, and are described below.

MATERIALS AND METHODS

Present phylogenetic analysis was based on a data matrix of 104 characters and 69 taxa. Most taxa comprised in the data matrix follows those included by FABREZI (2006) and EVANS *et al.* (2008) with the sole addition of *Beelzebufo ampinga, Calyptocephalella satan, C. pichileufensis, C. canqueli, Gigantobatrachus parodii* y *G. casamiquelai*. Characters employed in the present phylogenetic analysis were extracted from FABREZI (2006), EVANS *et al.* (2008), and BÁEZ *et al.* (2009), which mostly followed characters employed by other previous authors (e.g., Lynch, 1971, 1978; WIENS *et al.*, 2005; SCOTT, 2005; Appendix 1). Characters 0 to 80 were extracted from EVANS *et al.* (2008), whereas characters 81-103 are based on other published references and personal observations. The dataset (Appendix 2) was analyzed using the heuristic search of NONA (GOLOBOFF, 1993). Each search round consisted of 1000 random-addition sequence Wagner builds followed by tree bisection reconnection (TBR) branch swapping with a hold of 100. Assumption of equal weight resulted in 2 equally parsimonious trees of 675 steps (RI = 60; CI = 21). Strict consensus tree was of 699 steps resulted in a highly resolved Calyptocephalellidae (see below).

LOCALITY AND HORIZON

The material here described was found by members of the Museo Municipal de Lamarque, Río Negro province, Argentina, at Cerro Tortuga fossiliferous locality at the Santa Rosa Basin (see NOVAS *et al.*, 2009, fig. 1), a locality with extensive outcrops belonging to the Campanian-Maastrichtian (Late Cretaceous) Allen Formation (LEANZA *et al.*, 2004). This area yielded numerous fossil vertebrates including several ornithurine birds (CLARKE & CHIAPPE, 2001; AGNOLIN, 2010A; AGNOLIN & NOVAS, 2011), abelisaurid, titanosaurid, and dromaeosaurid dinosaurs (CORIA, 2001; MARTINELLI & FORASIEPI, 2004, NOVAS *et al.*, 2009), leptodactylid and pipid frogs, chelid turtles, sphenodontid lizards, and madtsoid snakes (CLARKE & CHIAPPE, 2001; CORIA, 2001; HOPE, 2002; MARTINELLI & FORASIEPI, 2004; NOVAS *et al.*, 2009), as well as fossil mammals (Rougier *et al.*, 2009). Fossil vertebrates also include a large variety of fossil fishes, including amiiforms, aspidorhynchids, siluriforms similar to Diplomystidae, lepisosteids, percichthyid perciforms, dipnoan ceratodontiforms, and batoids (BRITO, 1997; MARTINELLI & FORASIEPI, 2004; APESTEGUIA *et al.*, 2007; AGNOLIN, 2010b; BOGAN *et al.*, 2010).

Among available amphibian specimens collected at the fossiliferous locality here reported, there are some isolated bones belonging to a minute Pipidae and several specimens referable to a single large neobatrachian taxon. Similar association has also been reported for other Campanian-Maastrichtian localities at Argentine Patagonia (e.g. BAJO DE SANTA ROSA, LOS ALAMITOS, LA COLONIA; BÁEZ, 1987). At the Cerro Tortuga fossiliferous locality the Pipidae are represented by an isolated opisthocoelous vertebra (MML 871), and the distal end of humerus (MML 856) which typically shows an eminentia capitata with its sagittal plane coinciding with that of the bone shaft (BÁEZ, 1987, fig. 2). A more precise taxonomic assignation of the specimens is not possible due to its incomplete and dissociated nature of available material.

In addition to pipids, a large neobatrachian with robust proportions and heavily sculptured cranial remains is very common at the fossiliferous locality. These specimens are interpreted as belonging to a single anuran species due to its similarities in size, structure, form, external ornamentation in the case of skull bones, and character congruence. The individuals are here interpreted as belonging to a new species of the living genus *Calyptocephalella*, and are described at following.

SYSTEMATIC PALEONTOLOGY

Anura Merrem, 1820

Neobatrachia Reig, 1958

Hyloidea Stannnius, 1856

Calyptocephalellidae (Reig, 1960a)

Calyptocephalella Strand, 1928

Calyptocephalella satan nov. sp.

Holotype. MML 870, right incomplete maxilla.

Etymology. *Satan*: Evil, in order to emphasize the large size and morphology of the new anuran here described.

Diagnosis. Calyptocephalellidae diagnosable on the basis of the following combination of characters (autapomorphies marked by asterisk): 1) relatively well-developed pterygoid process of the maxilla, 2) unsculptured alveolar region of the labial face of the maxilla dorsoventrally narrow*, 3) premaxilla with anterior portion of palatine shelf well defined in lingual view, 4) atlantal cotyles bean-shaped*, 5) unfused atlas and second presacral vertebra, 6) strong anteroposterior extension of sacral vertebral diapophyses*.

Referred material. MML 847, complete atlas; MML 848, complete atlas; MML 849, fragmentary left squamosal; MML 851, incomplete fragment of skull roof; MML 850, presacral vertebral centrum; MML 851, incomplete fragment of skull roof; MML 854, incomplete sacral centrum; MML, 855, mid-portion of right maxilla; MML 857, incomplete left frontoparietal; MML 858, incomplete posterior portion of right maxilla; MML 859, incomplete right frontoparietal; MML 860, incomplete urostyle; MML 862, presacral vertebral centrum and incomplete sacrum; MML 863, incomplete left maxilla; MML 864, incomplete right squamosal; MML 865, incomplete right maxilla preserving tooth bases; MML 866, right radius-ulna without its distal end; MML 867, two distal ends of right humeri; MML 868, fragmentary urostyle; MML 869, incomplete right frontoparietal; MML 872, incomplete left premaxilla; MML 875, complete atlas; MML 886, fragmentary sacrum.

In addition to the specimens here described, previous authors cited, described, mentioned, and illustrated several bones that are here referred to *C. satan*. These include a left ilium, three distal humeri, three incomplete maxillae, and a fragmentary right squamosal described by BÁEZ (1987; MACN-RN 160) as coming from the Late Cretaceous (Campanian-Maastrichtian) Los Alamitos Formation, at Los Alamitos Ranch, Río Negro province, Argentina. This author identified such specimens as belonging to a *Calyptocephalella*-like innominate taxon.

Additional specimens referable to *C. satan* were described by Martinelli & Forasiepi (2004) as coming from the Allen Formation (Campanian-Maastrichtian), at Bajo de Santa Rosa locality, Río Negro province, Argentina. The specimens consist on a fragmentary right maxilla (MACN-RN 1063), twenty three incomplete skull bones, including highly incomplete maxillae and frontoparietals (MACN RN 1069), and a right humerus lacking its proximal end (MACN RN 1066). All these specimens were correctly identified by Martinelli & Forasiepi (2004) as belonging to an innominate *Calyptocephalella*-like anuran. I also refer to *C. satan* several specimens interpreted by Martinelli & Forasiepi (2004) as indeterminate anurans, including five incomplete presacral vertebrae (MACN RN 1067), five incomplete angulosplenials (MANC RN 1068), and a complete radius-ulna (MACN RN 1070).

González Riga (1999) described the distal end of a right humerus of a large "leptodactylid", coming from the Late Cretaceous Loncoche Formation (Campanian-Maastrichtian), at Ranquil Có fossiliferous locality, Mendoza province, Argentina. This specimen is also referable to *C. satan*.

DESCRIPTION

Among the available bones, there are different sized specimens, representing large to very large individuals. The external cranial elements of the Patagonian fossil anuran show a distinctive, coarse pit-and-ridge sculpture that, in conjunction with the large size and robustness of the bones, permits attribution of different elements to a single large hyperossified anuran species along Allen Formation and coeval stratigraphic units. Accordingly, the description and reconstruction of the new species is based on > 30 bones coming from a single locality. These bones include several cranial roofing bones, braincase, vertebrae, and limb elements.

Detailed comparison of available specimens with other anurans indicate that the skull of *C. satan* was probably wider or as wide as long, with very thick and sutured skull roof bones.

Premaxilla. A single incomplete left premaxilla is represented in the collections (MML 872, fig. 4). The pars dentalis, as occurs in *Calyptocephalella* and *Beelzebufo*, is dorsoventrally expanded, and exhibits traces of 8 alveoli. No teeth has been preserved. The bone, as in *Calyptocephalella* species*, B. ampinga*, and ceratophryids differs from most remaining cranial bones in having a smooth external surface, lacking any trace of exostotic ornamentation (Reig, 1960a; Perí, 1993; Evans *et al.*, 2008). As occurs in living *C. gayi*, *C. satan* shows a palatine shelf that conforms a dorsoventrally tall and longitudinally extended "step-like" structure (see Lynch, 1971); on the contrary, in *B. ampinga* and ceratophryids this palatine shelf is reduced (Asher & Krause, 1998; Evans *et al.*, 2008). The alary processes of the premaxilla are dorsally

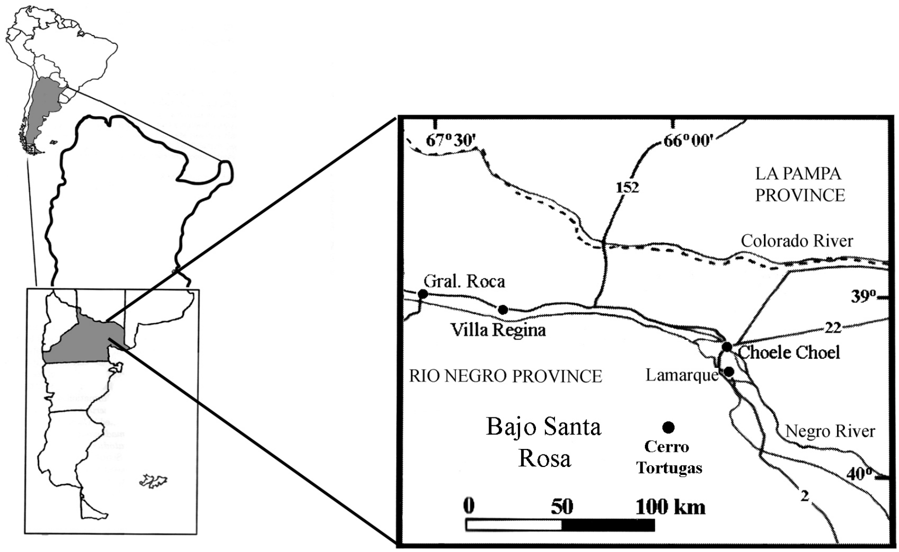

Figure 1. Map indicating fossiliferous locality where the holotype of B. satan *was found. Modified from Martinelli & Forasiepi (2004).*

oriented, and are poorly differentiated from the main body of the bone, a condition that recalls that of *Calyptocephalella,* and ceratophryids (CASAMIQUELA, 1958; LYNCH, 1971; BÁEZ, 1977; PERI, 1993; EVANS *et al.*, 2008). The very large posterior process suggests a tightly interlocking premaxilla-maxilla contact, a condition also observed in *Calyptocephalella, B. ampinga, Gigantobatrachus*, and ceratophryids (CASAMIQUELA, 1958; MUZZOPAPPA & BÁEZ, 2009; EVANS *et al.*, 2008).

Maxilla. Several maxillary fragments (MML, 855, 858, 863, 865, 870, fig. 5) allow reconstructing most features of this bone. As in most roofing bones of the skull, the external surface of the maxilla is covered by an extensive ornamentation with a honeycomb pattern of thin ridges and broad pits. The pits become smaller and shallower towards the alveolar margin. Near the posterior end of the bone the ornamentation is composed by very elongate pits and grooves. The smooth alveolar margin is taller at the anterior portion of the bone, a condition resembling *B. ampinga, Calyptocephalella* and *Gigantobatrachus* (SCHAEFFER, 1949; CASAMIQUELA, 1958, 1963; EVANS *et al.*, 2008; MUZZOPAPPA & BÁEZ, 2009). However, in *C. satan*, the mid-portion of the maxilla shows a dorsoventrally reduced and narrower alveolar margin, which is almost covered by exostotic ornamentation, a condition that is here considered as a probable autapomorphy of this taxon. At the posterior end of the bone the alveolar margin becomes dorsoventrally taller, being separated from the external surface of the

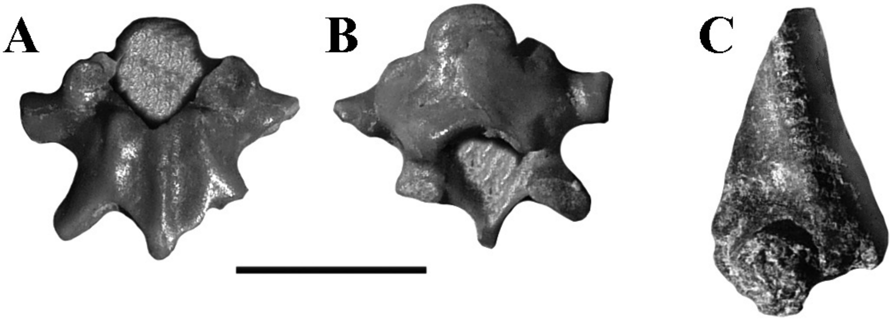

Figure 2. Indeterminate Pipidae. ***A-B****, presacral vertebra (MML 871) in* ***A****, dorsal, and* ***B****, ventral views.* ***C****, incomplete distal end of right humerus (MML 856) in ventral view.* ***Scale bar****, 2.5 mm.*

maxilla by a longitudinal groove, a condition also present in *B. ampinga* and *Gigantobatrachus* (CASAMIQUELA, 1958; EVANS *et al.*, 2008).

The teeth of the upper arcade were not preserved, thus the morphology of teeth crowns cannot be assessed. The pars dentalis is dorsoventrally tall, and tooth bases are subvertical and parallel each other, a condition typical of Calyptocephalellids, including *B. ampinga* (EVANS *et al.*, 2008).

In lateral view the maxilla is dorsoventrally tall, a condition similar to that of Calyptocephalellids and ceratophryids (PERI, 1993; EVANS *et al.*, 2008; MUZZOPAPPA & BÁEZ, 2009). The maxilla conforms the ventral margin of the orbit, as occurs in *Calyptocephalella, Gigantobatrachus*, and probably *B. ampinga* (CASAMIQUELA, 1958; LYNCH, 1971; MUZZOPAPPA & BÁEZ, 2009). In *Gigantobatrachus* the maxilla is dorsoventrally narrower, and the orbit is smaller and more deeply inserted in the upper margin of the maxilla (CASAMIQUELA, 1958). In *C. pichileufensis* the orbital margin of the maxilla is shallower than in other species of the genus, including *C. satan* (GÓMEZ *et al.*, 2011).

The palatine shelf is very well-defined and step-like, a derived condition shared with *Calyptocephalella, Gigantobatrachus,* and *B. ampinga* (CASAMIQUELA, 1958; LYNCH, 1971; EVANS *et al.*, 2008; MUZZOPAPPA & BÁEZ, 2009). The palatine shelf is very well developed along all its length, and conforms a poorly developed pterygoid process towards the posterior end of the bone, a condition similar to that of *Calyptocephalella gayi* and *Gigantobatrachus* (CASAMIQUELA, 1958; MUZZOPAPPA & BÁEZ, 2009, fig. 5 I-L). In *C. canqueli*, "*C. rugosa*", and *C. casamayorensis* the pterygoid process is very well developed and wing-like (BÁEZ, 1977; SCHAEFFER, 1949; MUZZOPAPPA & BÁEZ, 2009), whereas in ceratophryids, the palatine process of the maxilla is much more reduced, being nearly absent (LYNCH, 1971; PERI, 1993). The ascending ramus for the

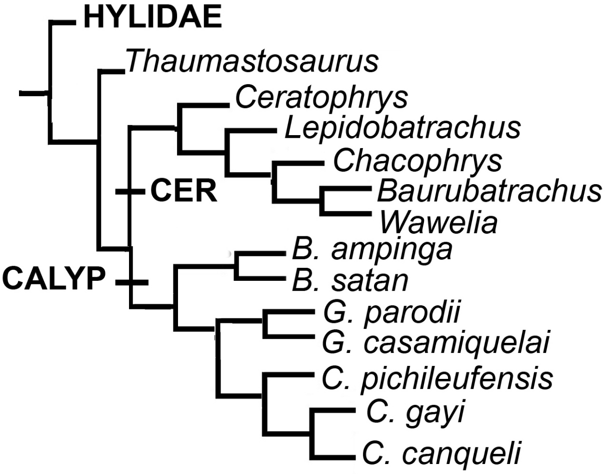

Figure 3. Simplified cladogram showing phylogenetic relationships among Hyloidea. ***Abbreviations****: B,* Beelzebufo*; C,* Calyptocephalella*; Calyp, Calyptocephalellidae; Cer, Ceratophryidae; G,* Gigantobatrachus.

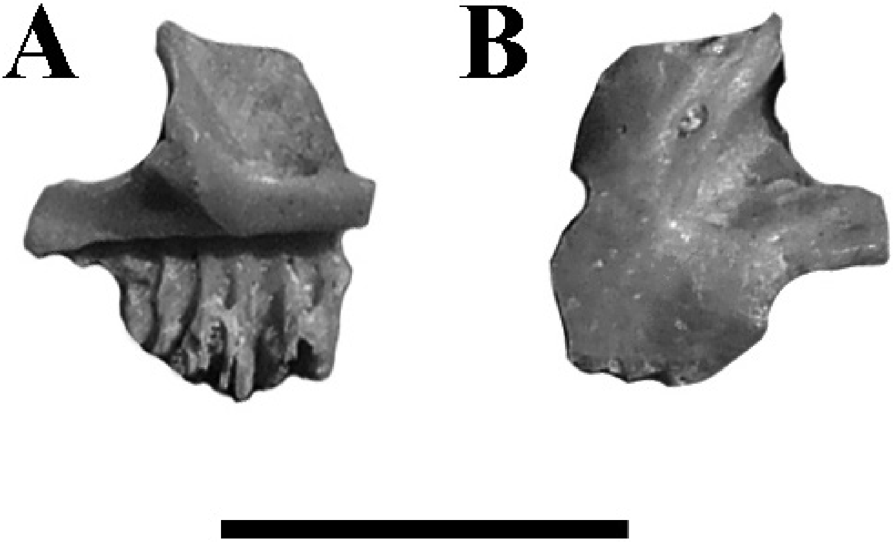

Figure 4. Calyptocephalella satan, *left premaxilla (MML 872) in* ***A****, medial, and* ***B****, lateral views.* ***Scale bar****, 2 mm.*

squamosal is very well developed and laminar, a condition recalling *Calyptocephalella, Gigantobatrachus,* and *B. ampinga* (Casamiquela, 1958; Evans *et al.*, 2008; Muzzopappa & Báez, 2009). At the base of this ramus exists a funnel-shaped canal, similar to that present in *C. canqueli* and *C. gayi*, but different from the subcircular fossa present in *Gigantobatrachus* (Casamiquela, 1958; Muzzopappa & Báez, 2009).

Frontoparietal. Several incomplete specimens (MML 857, 859, 869, fig. 6) allow an accurate reconstruction of the bone. This element exhibits a straight medial articulation for the opposite element, indicating the absence of fusion of frontoparietals, a condition similar to Calyptocephalellids (Muzzopappa & Báez, 2009), but different from that of ceratophryids (Peri, 1993). A distinctive longitudinal ventral lamina projects ventrally from the frontoparietals to overlap the dorsolateral wall of the braincase, as occurs in other *Calyptocephalella* species (Muzzopappa & Báez, 2009). The dorsal portion of the frontoparietals extends laterally and conforms the orbital margin, which is very thin and weakly ornamented. The orbital margin is gently concave, a condition similar to that of *C. pichileufensis* (Gómez *et al.*, 2011), whereas in *C. gayi* and *C. canqueli* the orbits are strongly concave (Muzzopappa & Báez, 2009).

Squamosal. This bone is represented by two fragmentary specimens (MML 849, MML 864, fig. 7). The dorsal surface of the squamosal conforms a posterior otic plate, very similar to that of *Calyptocephalella,* and *B. ampinga* (Evans *et al.*, 2008; Muzzopappa & Báez, 2009), whereas in *C. pichileufensis* the otic plate is subrectangular in contour (Gómez *et al.*, 2011). The rear of the bone lacks ornamentation, a condition similar to *B. ampinga* (Evans *et al.*, 2008), whereas in remaining Calyptocephalellids and ceratophryids this margin is ornamented.

Atlas. There are three isolated atlas (MML 847, 848, 875, fig. 8) representing three different sized individuals. The atlas is invariably free, being unfused to the second presacral vertebra, in contrast with *B. ampinga*, *Ceratophrys*, and some specimens of *C. gayi*, in which both vertebrae are firmly fused (Reig, 1960a; Lynch, 1971; Evans *et al.*, 2008). The neural spine is transversely expanded and very robust. The anterior articular cotyles of the atlas are bean-shaped, and are in contact at its base, contrasting with the condition of *C. gayi*, in which both cotyles are ventrally separated (Lynch, 1971; Evans *et al.*, 2008). The posterior articular condyle of the centrum is very well developed.

Presacral vertebrae. All available presacral vertebrae are procoelous (fig. 9), and lack any sign of notochordal pit, both features being diagnostic of Neobatrachia (Gómez *et al.*, 2011). The vertebral centrum is dorsoventrally low and transversely expanded, being elliptical in contour. This condition differs from that of *C. casamayorensis* (Schaeffer, 1949) in which the vertebral centrum is subcircular in outline (Casamiquela, 1958). The neural canal is transversely wide. The diapophyses are well-fused to the neural arch and

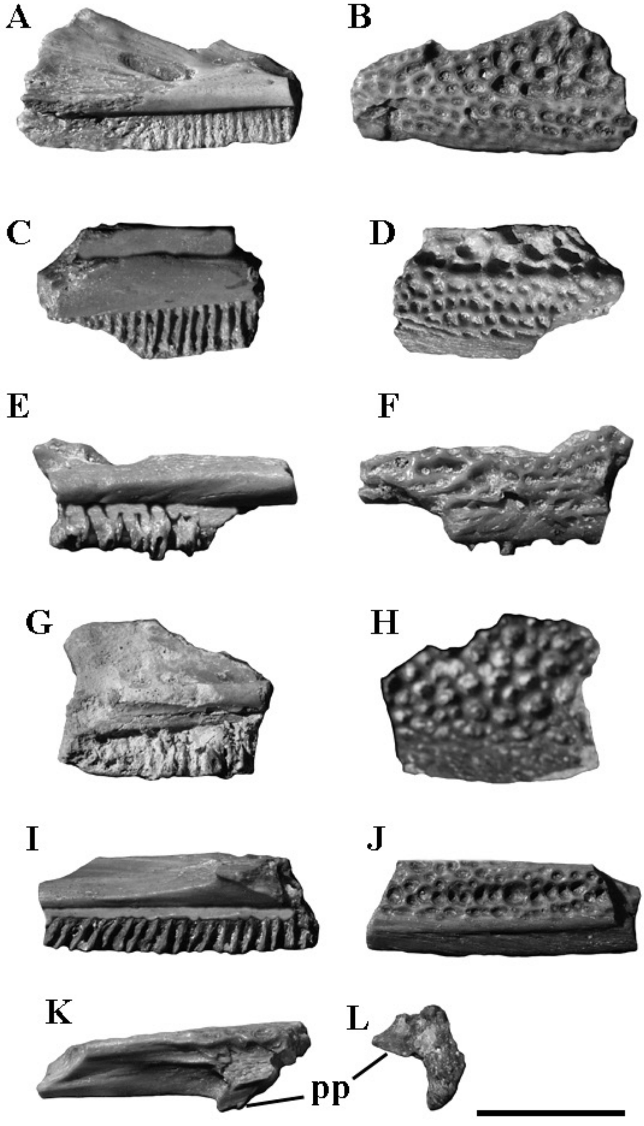

Figure 5. Calyptocephalella satan*, maxillae.* ***A-B****, MML 870 (holotype specimen) left incomplete maxilla in* ***A****, medial, and* ***B****, lateral views.* ***C-D****, MML 858, incomplete posterior portion of right maxilla in* ***C****, medial, and* ***D****, lateral views.* ***E-F****, MML 865, incomplete right maxilla in* ***E****, medial, and* ***F****, lateral views.* ***G-H****, MML, 855, mid-portion of right maxilla in* ***G****, medial, and* ***H****, lateral views.* ***I-L****, MML 863, posterior portion of left maxilla in* ***I****, medial,* ***J****, lateral,* ***K****, dorsal, and* ***L****, posterior views.* ***Abbreviations****, pp, pterigoid process.* ***Scale bar****, A-B, E-L, 5 mm; C-D, 2,5 mm.*

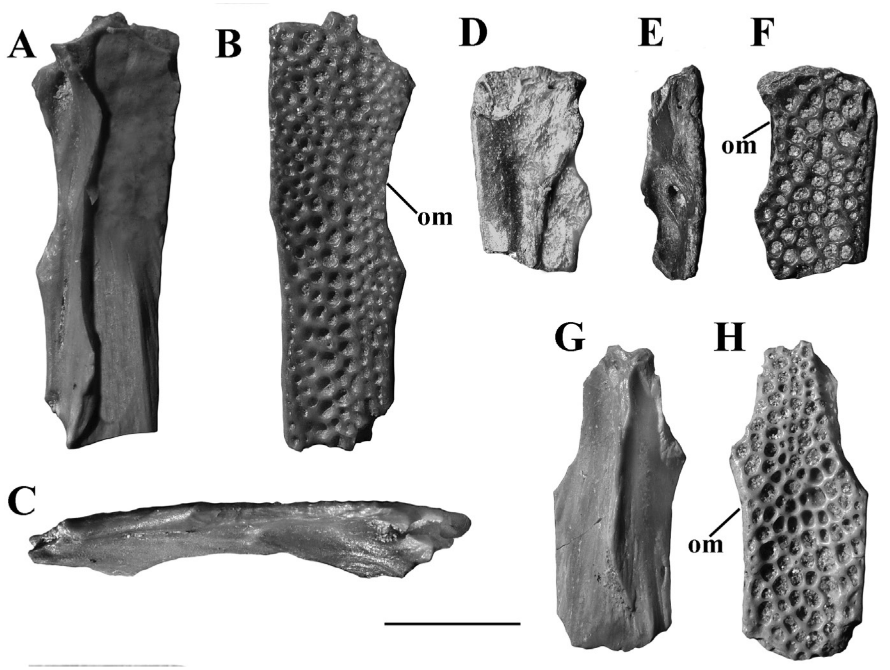

Figure 6. Calyptocephalella satan*, frontoparietals. **A-C**, MML 857, incomplete left frontoparietal in **A**, ventral, **B**, dorsal, and **C**, lateral views. **D-F**, MML 859, incomplete right frontoparietal in **D**, ventral, **E**, lateral, and **F**, dorsal views. **G-H**, MML 869, incomplete right frontoparietal in **G**, ventral, and **H**, dorsal views. **Abbreviations:** om, orbital margin. **Scale bar**, 5 mm.*

are oriented anteriorly, a morphology recalling that of *Calyptocephalella* and *Gigantobatrachus* (CaSAMIQUELA, 1958).

Sacrum. Available sacral elements (MML 854, 862, 886, fig. 10 A-D, F-H) are very incomplete, but allow recognizing main anatomical features. The anterior articular surface of the centrum is elliptical in contour, strongly concave, transversely wide, and dorsoventrally low. The posterior articular surface shows two prominent condyles, as diagnostic of Neobatrachia (GÓMEZ *et al.*, 2011). The sacral diapophyses are dorsoventrally low, and very distally expanded, a condition ususally considered synapomorphic of ceratophryids, being also present in *B. ampinga* (BÁEZ & PERI, 1989; EVANS *et al.*, 2008). On the contrary, in calyptocephalellids the distal expansion of the diapophyses is moderate (EVANS *et al.*, 2008). In *C. satan* the diapophyses are much more expanded than in remaining calyptocephalellids and in ceratophryids, being very anteroposteriorly widened since its basal portion, and its distal end appears to be even more widened. Sacral diapophyses are slightly posteriorly oriented.

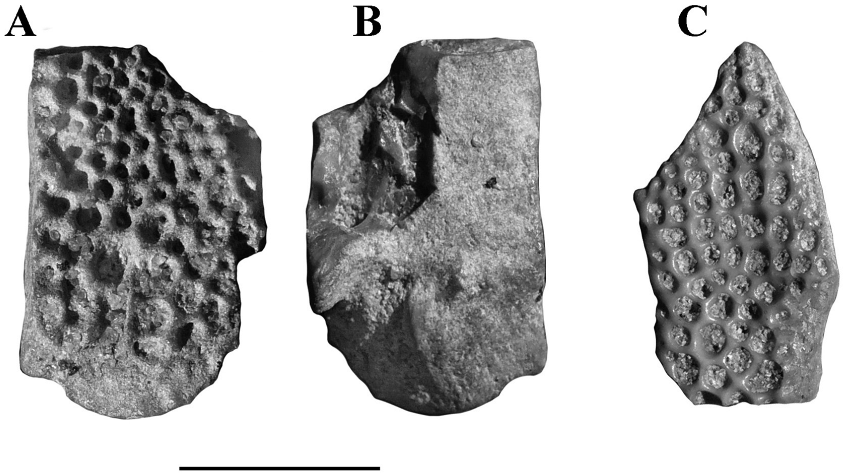

Figure 7. Calyptocephalella satan*, squamosals. **A-B**, MML 864, incomplete right squamosal in **A**, dorsal, and **B**, ventral views. **C**, MML 849, highly incomplete left squamosal in dorsal view. **Scale bar**, 5 mm.*

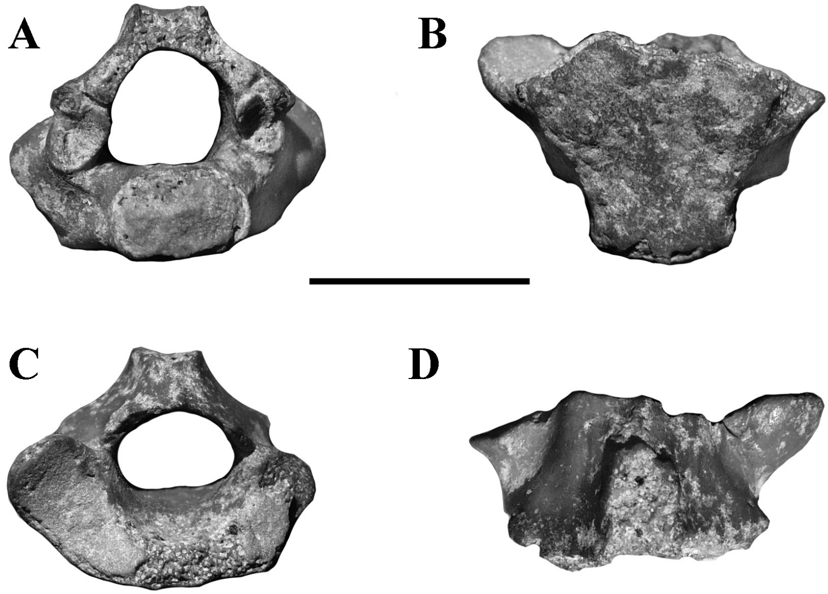

Figure 8. Calyptocephalella satan*, complete atlas (MML 875) in **A**, posterior, **B**, ventral, **C**, anterior, and **D**, posterior views. **Scale bar, 5 mm.***

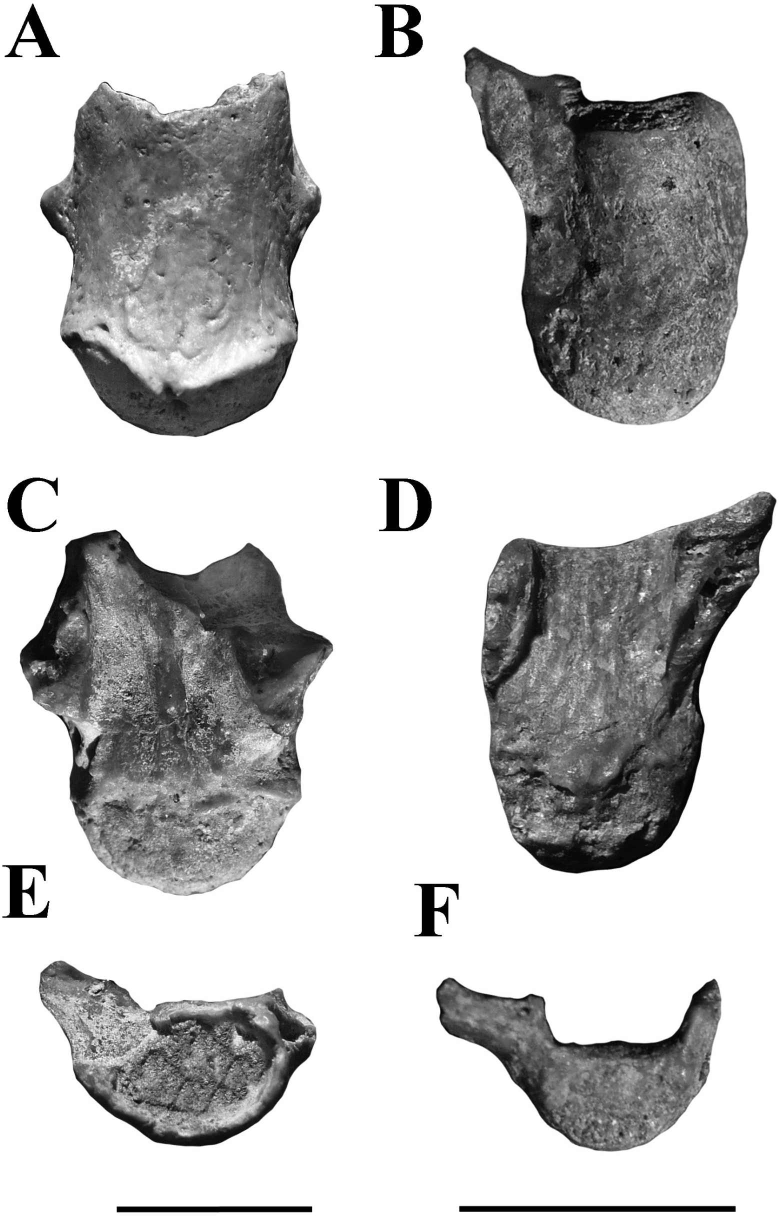

Figure 9. Calyptocephalella satan*, presacral vertebrae. **A, C, E**, MML 850 incomplete presacral vertebra in **A**, ventral, **C**, dorsal, and **E**, anterior views. **B, D, F**, MML 862 incomplete presacral vertebra in **B**, ventral, **D**, dorsal, and **F**, anterior views **Scale bar**, 5 mm.*

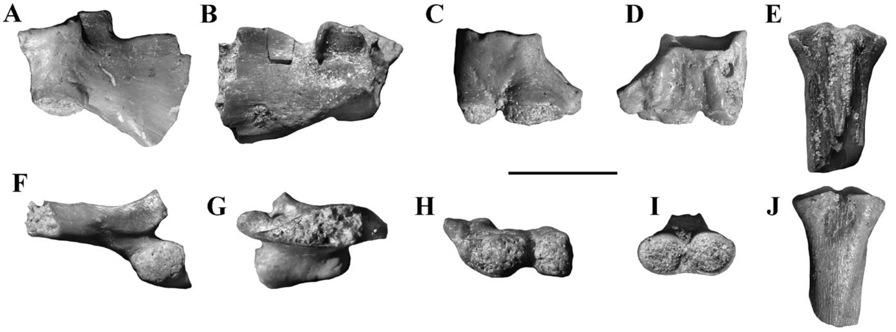

Figure 10. Calyptocephalella satan*, sacrum and urostyle.* ***A-B, F-G****, MML 862 incomplete sacrum in* ***A****, ventral,* ***B****, dorsal,* ***F****, posterior, and* ***G****, left lateral views;* ***C-D, H****, MML 886, highly incomplete sacrum in* ***C****, ventral,* ***D****, dorsal, and* ***E****, posterior views;* ***E, I-J****, MML 868, incomplete urostyle in* ***E****, dorsal,* ***I****, anterior, and* ***J****, ventral views.* ***Scale bar****, 5 mm.*

Urostyle. The urostyle is known by incomplete specimens (MML 860, 868), and its morphology is poorly known (fig. 10 E, I-J). This stout bone lacks transverse processes and shows a transversely expanded proximal articular end. The proximal cotyles are ellipsoidal in contour and both are subequal in size and morphology, whereas in *Gigantobatrachus* these cotyles are strongly asymmetrical (CASAMIQUELA, 1963). The urostylar spine is not complete, but its preserved portion indicates that it was very robust and transversely wide, with an expanded neural canal. Although incompletely preserved, the urostyle of *C. satan* appears to be extremely shortened, contrasting with the condition exhibited by Ceratophryidae (REIG, 1960b).

Humerus. This element of the skeleton is represented by two distal ends (MML 867, fig. 11 A-F) which show stout diaphyses and very robust epiphyses. Lateral and medial epicondyles are distally blunt and subequal in distal extension, showing gently convex external margins. The margins of the epicondyles are flange-like and are very similar in morphology to that of *C. gayi*, but in the latter species both epicondyles are much more transversely expanded (BÁEZ, 1991). The distal articular ball is protuberant and well-ossified, very large and subcircular in contour, and it is proximally delimited by a shallow and indistinct ventral fossa. The olecranon scar is elongated and laterally positioned.

Radius-ulna. The fused radius and ulna is very robust, a condition recalling that of remaining calyptocephalellids (MML 866, fig. 11 G). The bone is stouter than in ceratophryids (Peri, 1993), but thinner than in *C. canqueli* (Schaeffer, 1949). The olecranon process is robust and well extended proximally.

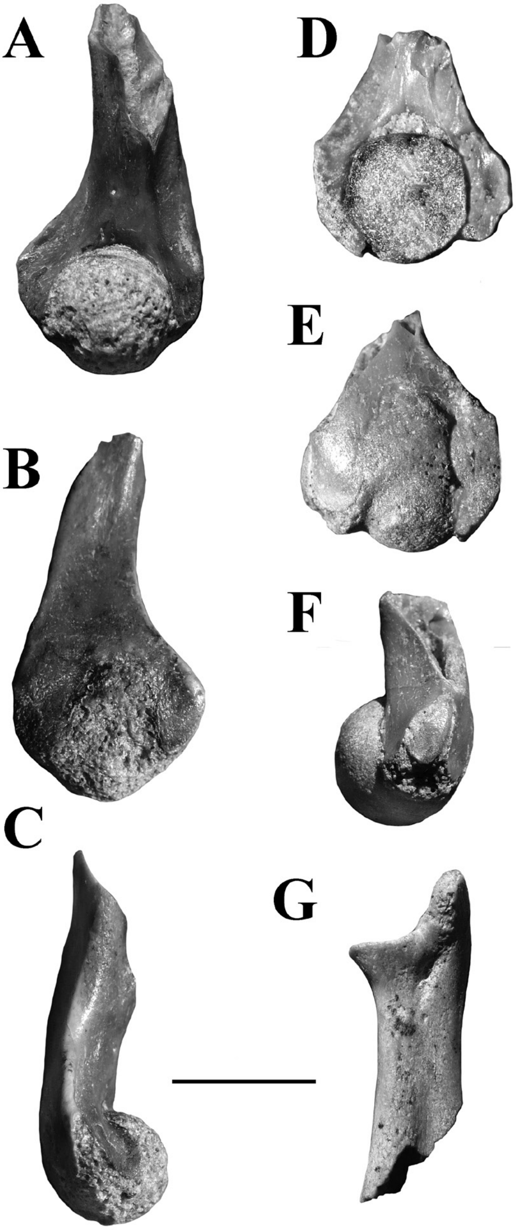

Figure 11. Calyptocephalella satan *humerus and radius-ulna.* ***A-C,*** *MML 867, distal end of right humerus in* ***A****, ventral,* ***B****, dorsal, and* ***C****, lateral views.* ***D-F,*** *MML 867, distal end of right humerus in* ***D,*** *ventral,* ***E,*** *dorsal, and* ***F,*** *medial views.* ***G****, MML 866, right radius-ulna without its distal end.* ***Scale bar****, 1 cm.*

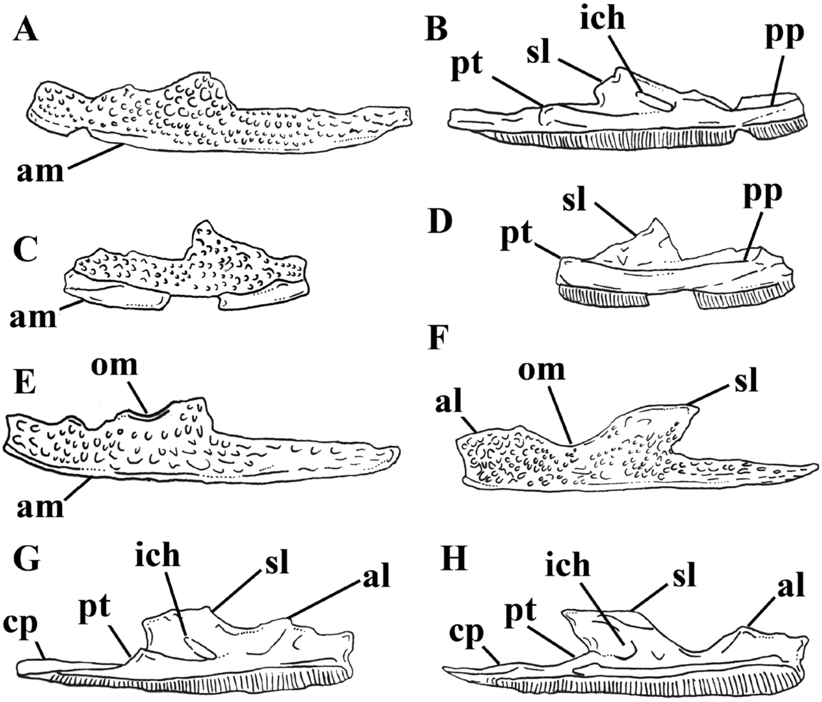

*Figure 12. Left maxillae of different Calyptocephalellid genera. **A-B**,* Calyptocephalella satan *in **A**, lateral, and **B**, medial views. **C-D**,* Beelzebufo ampinga *in **C**, lateral, and **B**, medial views. **E**,* Gigantobatrachus parodii *in lateral view. **F, H**,* Calyptocephalella gayi *in **F**, lateral, and **H**, medial views. **G**,* Calyptocephalella canqueli *in medial view. C, D modified from Evans* et al. *(2008); E, modified from Casamiquela (1958); F-H modified from Muzzopappa & Báez (2009). **Abbreviations**: al, anterior lamina; am, alveolar margin; cp, caudal process; ich, internal channel; om, orbital margin; pp, palatine.*

DISCUSSION

PHYLOGENETIC POSITION AND COMPARISONS OF THE NEW TAXON

Phylogenetic analysis here conducted resulted in a resolved phylogenetic position for *Calyptocephalella satan*. This taxon is clearly nested within the Calyptocephalellidae clade, among Hyloid neobatrachians. Available specimens of *Calyptocephalella satan* clearly indicate its neobatrachian affinities, as suggested by presacral vertebrae with nearly equally developed transverse processes, holochordal vertebral centra, bicondylar sacrococcygeal articulation, monovertebral sacrum with the base of the diapophyses subcircular/ovoidal in cross section, and possible absence of free dorsal ribs (REIG, 1958; MUZZOPAPPA & BÁEZ, 2009). Several features distinguish *C. satan* from the Ranoidea, including distally expanded sacral vertebrae, anterior presacral vertebrae with transverse processes elongate, transverse processes of posterior presacral vertebrae shortened, sacral vertebra with well-developed postzygapophyses, and atlantal cotyles closely approximated medially, a combination of characters shared by *C. satan* and Hyloidea (LYNCH, 1971; BÁEZ & PERI, 1989).

Moreover, among hyloid neobatrachians, *C. satan* could be included within calyptocephalellids on the basis of the following synapomorphies: 1-presence of dorsoventrally extended pars dentalis of premaxilla and maxilla, 2-step-like palatine shelf of maxilla, 3-high and laminar ascending process of maxilla, 4-transverselly expanded articular surface of presacral vertebrae centra, 5-dorsally oriented sacral diapophyses, and 6-symmetrical distal end of humerus (Appendix 3; see below). Among calyptocephalellids, *C. satan* is included within the crown-group (*Calyptocephalella* + *Gigantobatrachus*) on the basis of the presence of very well-developed dorsal iliac crest, and short urostyle (Appendix 3).

Moreover, *C. satan* shows a combination of features that allow its referral to the genus *Calyptocephalella* including a poorly defined alary process of the premaxilla, very dorsoventrally tall orbital margin of the maxilla, atlas unfused to second presacral vertebra, and very robust and stout radius-ulna. In addition to these gross similarities, *C. satan* shares with the genus *Calyptocephalella* the derived presence of a funnel-like canal on the medial side of the maxilla (fig. 12), and a medially tilted dorsal crest of ilium, both unambiguous synapomorphies of the genus (Appendix 3).

There is a large amount of features that allow distinguishing *C. satan* from the genus *Beelzebufo*. In *C. satan*, as in other *Calyptocephalella* species and probably *Gigantobatrachus*, the pterygoid process of the maxilla in medial view, is wing-like, much more developed than in *Beelzebufo* (MUZZOPAPPA & BÁEZ, 2009). In *B. ampinga* the anterior portion of the palatine process of the maxilla is absent, whereas in *C. satan*, other *Calyptocephalella* species, and *Gigantobatrachus* such process is present (CASAMIQUELA, 1958; MUZZOPAPPA & BÁEZ, 2009). Another difference between *B. ampinga* and *C. satan* consists on their external maxillary ornamentation. In fact, in *B. ampinga*, as well as in *Calyptocephalella* and *Gigantobatrachus* species, the alveolar margin at the labial maxillary face shows a dorsoventrally tall unsculptured surface (SCHAEFFER, 1949; CASAMIQUELA, 1958; EVANS *et al.*, 2008; MUZZOPAPPA & BÁEZ, 2009). In contrast, in *C. satan* the alveolar margin is dorsoventrally reduced at the mid-level of the maxilla, a probable autapomorphy of this taxon (fig. 12).

C. satan may be further distinguished from *B. ampinga* in having unfused first and second presacral vertebrae. Fusion between the first and second presacral vertebrae was considered as a synapomorphic character shared by

Beelzebufo and *Ceratophrys* by EVANS *et al.* (2008). However, it must be noted that the fusion between the first and second vertebrae is variable among ceratophryids and calyptocephalellids. In fact, the fusion between both vertebrae is not exclusive of *Ceratophrys* and *Beelzebufo*, but is also present in old-adult individuals of *Ceratophrys, Lepidobatrachus*, and *Calyptocephalella gayi*. In this way, this trait was considered by LYNCH (1971) as a character probably reflecting senility. In this way, although the lack of fusion between both vertebrae is considered as a character that allows distinguishing *C. satan* from *B. ampinga*, this feature may be regarded only as a tentative diagnostic character.

B. ampinga shows a very derived premaxilla, reminiscent to that of Ceratophryidae (EVANS *et al.*, 2008). In fact, in *B. ampinga* the premaxilla exhibits narrow pars dentalis in lingual view, a reduced palatine shelf, and a flat labial surface (EVANS *et al.*, 2008). On the contrary, *C. satan* shows a plesiomorphic premaxilla, very similar to that seen in *Calyptocephalella* and *Gigantobatrachus* (CASAMIQUELA, 1958). In fact, in *C. satan* as in the later taxa the premaxilla exhibits a well-developed palatal shelf, a dorsoventrally tall pars dentalis, and the external surface of the bone exhibits a deep anterior concavity.

The other calyptocephalellid genus to which *C. satan* must be compared is *Gigantobatrachus*. *C. satan* is a species of very large size, being slightly smaller than *Gigantobatrachus* species (CASAMIQUELA, 1958). However, *C. satan* differs from this genus in having a more developed squamosal lamina, wider and shallower orbital margin of the maxilla, dorsoventrally taller and transverselly compressed proximal end of urostyle, and medially tilted dorsal margin of ilium (CASAMIQUELA, 1958, 1961; Appendix 3; see below). In addition, species of *Gigantobatrachus* (CASAMIQUELA, 1958; see below) shows a conspicuous external sculpture of cranial bones, being composed by very deep pits, separated by strong ridges, that differ from the shallower, proportionally smaller, and less defined pits and ridges exhibited by *Calyptocephalella* species, including *C. satan*.

Regarding *Calyptocephalella* species, *C. satan* is clearly distinguished from remaining taxa included in this genus on the basis of the combination of characters reported in the diagnosis of the species (see above). Moreover, *C. satan* differs from *C. pichileufensis* in several features, including rounded distal margin of squamosal, opened temporal fossae, very large and anteriorly positioned orbital margin on the frontals, and several minor details exhibited by the maxilla (GÓMEZ *et al.*, 2011). *C. satan* differs from the poorly known *C. casamayorensis* in a large amount of features, including a different pattern on skull roof ornamentation (reticulate in *C. canqueli*), and in having ellipsoidal (rather than subcircular) anterior articular surface of vertebral presacral centrum (Schaeffer, 1949). *C. satan* may be distinguished from *C. canqueli* and *C. gayi* in several minor details regarding maxillary morphology, including a dorsoventrally taller posterior process of the maxilla and relativelly poorly developed and less wing-like pterygoid process (MUZZOPAPPA & BÁEZ, 2009). The maxilla in *C.*

canqueli and *C. gayi* is also taller and stouter than in *C. satan*. Furthermore, the funnel-like medial canal of the maxilla in *C. gayi* is poorly defined and less developed than in *C. canqueli* and *C. satan* (MUZZOPAPPA & BÁEZ, 2009). Finally, *C. satan* differs from *C. rugata* (AMEGHINO, 1901) in having antero-dorsally inclined presacral and sacral diapophyses, squamosal not ventrally oriented, and more gracile and delicate premaxilla (see BÁEZ, 1977).

Within calyptocephalellids, *C. satan* exhibits some autapomorphic features not seen in remaining taxa of the clade. In *C. satan* the sacral diapophyses dialted, a condition that is present in calyptocephalellids and ceratophryids (see REIG, 1960a,b; LYNCH, 1971). However, *C. satan* differs from the latter taxa in, showing a unique fan-shaped contour of transverse processes (fig. 10). In addition, in *B. ampinga* as well as most species of *Calyptocephalella* atlantal cotyles that are extremely elongate and transversely compressed. On the contrary, in *C. satan* the atlantal cotyles are more robust and bean-shaped, probably constituting an autapomorphy for the species.

PHYLOGENETIC RELATIONSHIPS AND COMPOSITION OF CALYPTOCEPHALELLIDAE

The relationships among and within neobatrachians are still a large matter of debate (see FROST *et al.*, 2007). In this way, the relationships of *Calyptocephalella* and its kin, within Hyloidea are still in state of flux. REIG (1960a) indicated that *Calyptocephalella* was a very peculiar taxon, and considered it as clearly separable from remaining "leptodactylids" (currently considered as a polyphyletic taxon; see FROST *et al.*, 2007) within a subfamily of its own: Calyptocephalellinae. Several early authors considered *Calyptocephalella* as nearly related to the genus *Ceratophrys* and its kin (i.e. Ceratophryidae) (e.g., NOBLE, 1931; CASAMIQUELA, 1963; FABREZI, 2006; EVANS *et al.*, 2008) or as nearly allied to *Telmatobius*, and hence only distantly related to ceratophryids (e.g., LYNCH, 1971; NÚÑEZ & FORMÁS, 2000). However, most recent phylogenetic analyses, aminly based on molecular evidence indicate that *Calyptocephalella* may be related to Australian Myobatrachidae (e.g., SAN MAURO *et al.*, 2005; CORREA *et al.*, 2006; FROST *et al.*, 2007). Present morphological analysis indicates that *Calyptocephalella* is well nested within the Hyloidea, as a member of the Calyptocephalellidae. Although the analysis of suprafamiliar clades among neobatrachians is beyond the scope of the presen paper, it is worth to note that *Calyptocephalella* and its kin resulted as the sister group of ceratophryids, as advocated by early authors (see synapomorphies uniting calyptocephalellids and ceratophryids in Appendix 3). Moreover, the putative ceratophryid genus *Thaumastosaurus*, from the Early Tertiary of Europe was recovered as basal to both clades, sharing with these taxa four unambiguous morphological synapomorphies (see Appendix 3). Within Calyptocephalellidae, three different genera are here recognized, namely *Calyptocephalella* Strand, 1928, *Gigantobatrachus* Casamiquela, 1958, and *Beelzebufo* Evans *et al.*, 2008.

On its original definition, REIG (1960a) coined the Calyptocephalellinae (as a subfamily of a polyphyletic "Leptodactylidae") in order to emphisize the distinctiveness of the living species *C. gayi* Duméril & Bibron, 1841. This author also included within this group the extinct genera *Eophractus* SCHAEFFER, 1949, and *Gigantobatrachus* Casamiquela, 1958, and suggested that both were doubtfully separable from *Calyptocephalella*. Following REIG'S (1960a) suggestion, HECHT (1963) considered the Calyptocephalellidae as composed by the single genus *Calyptocephalella*, with its junior synonyms *Eophractus* and *Gigantobatrachus*. LYNCH (1971) in his revision of the family "Leptodactylidae" considered that the genus *Calyptocephalella* was composed only by the species *C. gayi* (which included as junior synonyms *C. canqueli,* and *Gigantobatrachus parodii*) and *C. casamayorensis*. This criterion was followed by some posterior authors (BÁEZ & GASPARINI, 1977; GASPARINI & BÁEZ, 1974). Later, SANCHIZ (1998) followed the criterion of Lynch, but also recognized as valis the Neogene species *Calyptocephalella parodii*. This point of view was followed by most recent authors (MUZZOPAPPA & BÁEZ, 2009; MUZZOPAPPA & NÍCOLI, 2010; GÓMEZ *et al.*, 2011), and is adopted here with some modifications. Present analysis suggests that *Gigantobatrachus* is a valid genus, including the species *G. parodii* (included within *Calyptocephalella* by Sanchiz, 1998) and a new taxon here described (see below). In addition, the Miocene species *C. rugata* is also considered as a valid taxon of *Calyptocephalella*.

In fact, AMEGHINO (1901) named, but not described, anuran remains from the Sarmiento Formation (Colhuehuapian; Lower Miocene; PASCUAL *et al.*, 1996) of Chubut province, Argentina. Ameghino coined the new genus *Teracophrys*, with the species *T. rugata* and *T. vermiculata,* without figuring nor describing them. Later, BÁEZ (1977) reviewed the original material of Ameghino collection, and concluded that all belonged to a single, probably extinct *Calyptocephalella* species. In this way, BÁEZ (1977) considered *Teracophrys,* with the species *T. rugata* and *T. vermiculata* as *nomen vanum*. As noted by BÁEZ (1977) Miocene material of *Calyptocephalella* may be distinguished from other species of the genus (including living *C. gayi*) by a unique combination of characters, including subhorizontally oriented diapophyses on presacral and sacral vertebrae, presacral diapophyses not posteriorly oriented, robust neural spines, lateral margin of squamosal ventrally oriented, esphenethmoid with anterolateral osseous ridges, robust and dorsoventrally tall premaxilla, and pterigoid process of maxilla medially expanded (see BÁEZ, 1977). This combination of features allow considering the Miocene *Calyptocephalella* as a valid taxon, and due to the laws of priority, this species is provisionally named here as *C. rugata* (AMEGHINO, 1901).

In this way, following previous authors and present investigation, the genus *Calyptocephalella* is here considered as composed by the living species *C. gayi*, and the extinct taxa *C. casamayorensis* (SCHAEFFER, 1949) (Eocene, Chubut province, Argentina; SCHAEFFER, 1949; LYNCH, 1971), *C. pichileufensis*

GÓMEZ *et al.*, 2011 (Eocene, Río Negro province, Argentina; GÓMEZ *et al.*, 2011), *C. canqueli* Schaeffer, 1949 (Oligocene-Miocene, Chubut province, Argentina; SCHAEFFER, 1949; MUZZOPAPPA & BÁEZ, 2009; MUZZOPAPPA & NÍCOLI, 2010), *C. rugata* (Ameghino, 1901) (Lower Miocene, Chubut province, Argentina; BÁEZ, 1977), and *C. satan* nov. (Latest Cretaceous, Río Negro and Mendoza provinces; present paper).

The monotypic genus *Beelzebufo* was coined by Evans and collaborators (EVANS *et al.*, 2008) in order to include the species *B. ampinga*. This taxon is known by several incomplete and disarticulated cranial and postcranial bones, coming from the Maevarano Formation (Maastrichtian; Latest Cretaceous) of Madagascar (ASHER & KRAUSE, 1998; EVANS *et al.*, 2008). *Beelzebufo* was considered by EVANS *et al.* (2008) as pertaining to the family Ceratophryidae, as the sister genus of the extant *Ceratophrys*. However, in contrast to EVANS *et al.* (2008) present phylogeny results in the inclusion of *Belzeebufo* within Calyptocephalellidae. In fact, this genus shares with remaining calyptocephalellids several features, including the morphology of the medial and lateral faces of the maxilla, vertebral and sacral features (Appendix 3; see below). In the present analysis, *Beelzebufo* constitutes the sister-group of crown-group calyptocephalellids.

The ceratophryid affinities of *Beelzebufo* were sustained by EVANS *et al.* (2008) on the basis of the following putative synapomorphies: 1-exostosed skull-roofing bones, 2-unicuspid teeth, 3-postero-lateral parietal expansion, 4-absence of a projecting palatine shelf on the adult premaxilla and anterior maxilla, and 5-posterolaterally expanded frontoparietals (see LYNCH, 1971; WILD, 1997). However, characters 1, 3, 5 are also clearly present in most *Calyptocephalella* species (REIG, 1960a; GÓMEZ *et al.*, 2011). Regarding character 2, it cannot be properly observed in available *Beelzebufo* specimens. In fact, EVANS *et al.* (2008) reported only a single maxillary fragment with preserved teeth. The specimen shows sharp tooth tips preserved in the broken tooth bases. The teeth of *Calyptocephalella* and *Gigantobatrachus* (CASAMIQUELA, 1958; LYNCH, 1971) are fang-like, similar to that of Ceratophryidae, but show a very small cuspid at the base of each tooth that overlaps the main cusp, whereas in ceratophryids this additional cusp is absent (PERI, 1993). Due to the absence of well-preserved tooth bases, we consider that the presence of double or single cusped teeth cannot be assessed in *B. ampinga* (in consequence, in the present data matrix the character state 12 in *B. ampinga* is regarded as uncertain). Moreover, the morphology of the pars dentalis in Ceratophryidae is rather different from that seen in *Beelzebufo*, suggesting a different tooth morphology. In fact, in ceratophryids, fang-like teeth show an acrodont implantation, and consequently the pars dentalis is very low (PERI, 1993). On the contrary, in pleurodont anurans, including *Calyptocephalella* and *Gigantobatrachus* the pars dentalis is dorsoventrally tall, and the labial surface of premaxilla and maxilla is ventrally extended (PERI, 1993, fig. 12). The latter condition is also seen in *Beelzebufo*, reinforcing the hypothesis that this genus probably lacked the acrodont fang-like teeth typical of ceratophryids. Finally, character 4 (i.e., absence of palatal process on premaxilla) stands as a probable *Beelzebufo* + Ceratophryidae synapomorphy; however, in the present analysis this condition is considered as convergently acquired between both taxa.

In addition, Evans *et al.* (2008) indicated that *Beelzebufo* resembled *Ceratophrys* and *Chacophrys* in having a tightly interlocking premaxilla-maxilla contact (character 82). However, this condition is also seen in Calyptocephalellidae, being well developed in *Calyptocephalella* and *Gigantobatrachus* (CASAMIQUELA, 1958). EVANS *et al.* (2008) included *Beelzebufo* as the sister genus of *Ceratophrys* by having two derived characters: 1-cervical cotyles continuous in ventral midline, and 2-posession of posttemporal fenestrae. Moreover, the later character was also employed by EVANS *et al.* (2008) in order to distinguish *Beelzebufo* from *Calyptocephalella* and its kin. Regarding the first character, the presence of ventrally continuous atlantal cotyles is not unique to *Ceratophrys* and is clearly present in remaining ceratophryid genera (PERÍ, 1993). This character may still stand as a synapomorphy shared between Ceratophryidae and *Beelzebufo* species; however, present analysis indicates that it may be better considered as a homoplasy. Regarding the second character (i.e. presence of a posttemporal fenestra), this feature has been regarded as synapomorphic for the genus *Ceratophrys* by previous authors (PERÍ, 1993). On the contrary, in *Calyptocephalella* and other anurans, the otic plate of the squamosal and the laterally expanded frontoparietal flush on the occipital plane, lacking any sign of posttemporal fenestrae (see LYNCH, 1971; EVANS *et al.*, 2008, fig. 3P). However, presence of posttemporal notch is also seen in *C. pichileufensis* (GÓMEZ *et al.* 2011). In this way, presence of posttemporal fenestrae is here considered as convergently acquired by Calyptocephalellidae and Ceratophryidae.

EVANS *et al.* (2008) pointed out that *Beelzebufo ampinga* differed from remaining ceratophryids in having 1-pit-and-ridge cranial ornamentation, 2-unsculptured posterior tip of squamosal ramus, and 3-patent cranial sutures. Features 1 and 3 are clearly present in the Calyptocephalellid *Calyptocephalella*, as well as in *Thaumastosaurus* (RAGE & ROCEK, 2007). The character 2 is also seen in *C. satan*, and may constitute a derived feature, convergently acquired by both taxa.

Regarding character 1, the kind external ornamentation has been proven not to be a character of high taxonomic value. In fact, the external ornamentation of skull roof bones appears to be variable along the ontogeny of caliptocephalellid taxa (CASAMIQUELA, 1958). In *C. canqueli* from the early developmental stages onward, these bones are ornamented with shallow pits, and with subsequent individual growth, this kind of ornamentation changes to a tuberculated pattern (MUZZOPAPPA & NÍCOLI, 2010). On the other hand, in *C. gayi* the tadpoles bear sparse tubercles along the frontoparietal surface, and at adult stages the external ornamentation is composed by pits and ridges (MUZZOPAPPA & NÍCOLI, 2010).

CASAMIQUELA (1958) indicated that the external reticulated ornamentation of adult specimens of *C. casamayorensis* resembled the morphology seen in tadpoles or juvenile individuals of other calyptocephalellid species. This suggests that *C. casamayorensis* may constitute a neotenic species. The same may be probably applied to the species *C. canqueli*, which resembles juveniles of *C. gayi* in external ornamentation, as well as, several osteological features (e.g., poorly expanded lateral maxillary process on nasals, very large orbits, anterior articulation of the lower jaw; MUZZOPAPPA & BÁEZ, 2009). This suggest that paedomorphosis may have played an important role in calyptocephalellid diversification and speciation. Accordingly, the morphology of the external ornamentation among calyptocephalellids may not be a highly useful diagnostic character.

EVANS *et al.* (2008) also indicate that general proportions of different skull bones, as well as general aspect of the cranium of *B. ampinga*, were strikingly similar to that of ceratophryids. However, because several available skull bones of this species are incompletely known and belong to different individuals, several aspects of the reconstruction of the cranium made by EVANS *et al.* (2008) may be partially re-interpreted in a different way. These authors conceived a very large maxillary process of nasals, not very different from that occurring in the living calyptocephalellid species *C. gayi* and the extinct *C. pichileufensis* (MUZZOPAPPA & BÁEZ, 2009; GÓMEZ *et al.*, 2011). However, EVANS *et al.* (2008) reconstructed the maxillary process of nasals as contacting the maxilla and squamosal, a condition very different to that of calyptocephalellids, but similar to ceratophryids. Nevertheless, there is no evident articular surface for the squamosal contact in the maxillary process of nasals, and thus the contact between the nasal and squamosal is uncertain, as recognized by Evans *et al.* (2008). If the anterior squamosal process is reinterpreted as lacking articulation with the nasals, the orbit appears to be laterally delimited by the maxilla, as occurs in *Calyptocephalella*, and not by the nasal and squamosal as exhibited by ceratophryids. In addition, EVANS *et al.* (2008) reconstructed the frontoparietals as proportionately narrow and anteroposteriorly shortened, as similar to ceratophryids. However, no complete frontoparietal bone is available among the bones assigned to *B. ampinga* (EVANS *et al.*, 2008, Supplementary Information). In this way, the skull of *Beelzebufo* may be alternatively reconstructed as *Calyptocephalella*-like, contrasting with EVANS *et al.* (2011) reconstruction. Concluding, the ceratophryid affinities of *B. ampinga* rest on very weak evidence and conflictive characters, and calyptocephalellid affinities for this taxon appear to stand on more robust evidence.

Present analysis also recognizes *Gigantobatrachus* as a valid genus of Calyptocephalellidae, following the original proposal of CASAMIQUELA (1958; 1963). In fact, the type-species *G. parodii* differs from remaining Calyptocephalellids in having a very large size, sphenethmoid bone showing longitudinal wing-like lateral processes, a very low teeth number (less than 6 premaxillary and 45 maxillary teeth), dorsoventrally low maxilla with a proportionally small and deeply concave orbital margin (fig. 12), dentary not laterally compressed, and dorsal longitudinal crest of ilium not medially oriented (medially tilted in *Calyptocephalella*) (CASAMIQUELA, 1958, 1963). The type species of the genus *Gigantobatrachus* is the Miocene taxon *G. parodi* Casamiquela, 1958, which is represented by several incomplete individuals belonging from different fossiliferous localities (CASAMIQUELA, 1963). The genus *Gigantobatrachus* was recovered in the present analysis as the sister group of *Calyptocephalella*, both conforming a clade sustained by three synapomorphies: 1-presence of very well-developed dorsal iliac crest, 2- urostyle as long as presacral column, and 3- short and curved clavicle (see Appendix 3). This clade includes all living and extinct calyptocephalellid species from South America.

In Paleocene sediments from the “Banco Negro Inferior” of Punta Peligro locality, Chubut province, Argentina, several specimens of a very large *Calyptocephalella*-like taxon has been briefly described (BÁEZ, 1991; BONAPARTE *et al.*, 1993). In the description of these specimens, Bonaparte and collaborators (BONAPARTE *et al.*, 1993) indicate that these isolated bones very probably belonged to a a new undescribed gigantic species of the genus *Calyptocephalella*, and recognized that it was probably related to *C. parodii* (*Gigantobatrachus* herein).

In agreement with such proposal, the specimens described by BONAPARTE *et al.* (1993) clearly belongs to Calyptocephalellidae in having the following combination of characters: a very heavy external cranial ornamentation composed of pits and ridges, step-like palatal shelf, very tall pars dentalis of maxilla, presacral vertebrae with depressed centra and very wide neural canal, and ilium with a very well developed dorsal longitudinal crest. Moreover, these specimens belong to the genus *Gigantobatrachus* because of its gigantic size (the largest known taxon within the family), external ornamentation composed by very deep and wide pits separated by strong osseous ridges (see CASAMIQUELA, 1958), proximal articular end of urostyle strongly dorsoventrally compressed and transversally expanded (unambiguous synapomorphy of *Gigantobatrachus*; Appendix 3), and very small and deeply concave orbital margins of the maxilla (unambiguous synapomorphy of *Gigantobatrachus*; Appendix 3). However, some differences with available material of *G. parodii* suggest that the Paleocene specimens belong to an unnamed species of the genus, which is described as follows:

Gigantobatrachus casamiquelai nov. sp.

Holotype. MACN CH-1625a, incomplete posterior portion of right maxilla (BONAPARTE *et al.*, 1993, fig. 2E).

Diagnosis. Species of the genus *Gigantobatrachus* distinguishable from *G. parodii* on the basis of the following characters (autapomorphies followed by an asterisk): 1) maxilla with dorsoventrally expanded palatal shelf*, 2) maxilla with dorsoventrally low pars dentalis*, 3) distal end of humerus with medial epicondyle distally extended and separated from the humeral articular ball by a deep groove and notch, 4) very prominent distal articular ball of humerus, 5) ventrally keeled presacral vertebrae*.

Referred material. BONAPARTE *et al.* (1993) reported diverse specimens referable to *G. casamiquelai* including incomplete maxillae and skull-roof bones, 3 incomplete angulosplenials, a single presacral vertebra, proximal urostyles, distal humeri, incomplete tibiofibula, and a left ilium. All these specimens were described by BONAPARTE *et al.* (1993), and its description will not be repeated here.

BÁEZ (1991) briefly described a fragmentary maxilla from the Lower Paleocene at Las Flores locality (Chubut province, Argentina) that may be also referred to *G. casamiquelai*, on the basis of external sculpture, morphology of pars dentalis, and large size.

Etymology. The species is dedicated to the argentine naturalist Rodolfo M. CASAMIQUELA (1932-2008) whom originally described the genus *Gigantobatrachus*.

In addition to the above mentioned genera and species there are some isolated fossil specimens from Patagonia that may also be referred to Calyptocephalellidae. TAUBER (1999) reported from the Santa Cruz Formation (Early-Mid Miocene) of the Santa Cruz province, an isolated maxilla as *Caudiverbera* sp. (plate 1, figs. 10-11). The specimen may be referred to Calyptocephalellidae on the basis of a strongly ornamented labial surface with a tall and smooth alveolar margin, dorsoventrally tall pars dentalis in lingual view, extensive and shelf-like palatine process, and the presence of a high maxillary ascending process. This combination of characters indicates that the specimen clearly belongs to a *Calyptocephalella*-like taxon. Moreover, BÁEZ (2000) reported abundant *Calyptocephalella* remains from several localities of the Early Miocene Santa Cruz Formation, at Santa Cruz province. In addition, abundant Calyptocephalellid remains have been recovered in different outcrops of the slightly older Pinturas Formation (Early lower Miocene), at Río Pinturas locality, Santa Cruz province, Argentina (MACN Pv, *pers. obs.*), which indicate the abundance of Calyptocephalellids until Early Miocene outcrops.

AMEGHINO (1899) briefly described the species *Saniwa australis* as belonging to the lizard genus *Saniwa*, of the family Varanidae. Ameghino based the species on two incomplete vertebral centra coming from Colhuehuapian beds (Lower Miocene) of Chubut province, Argentina. This author distinguished the new species on the basis of very wide vertebral centrum and the absence of ventral longitudinal keel (AMEGHINO, 1899). Later, GASPARINI *et al.* (1986) reinterpreted *S. australis* as belonging to an indeterminate anuran. A brief overview of the holotype (MACN A-5805) of *Saniwa australis* corroborates anuran affinities for this specimen. Moreover, the transversally expanded and dorsoventrally low vertebral articular centra, very wide neural canal, and ventrally smooth centrum suggest Calyptocephalellid affinities for the specimens. Additionally, it lacks the transverselly expanded posterior condyle seen in *Saniwa* and other varanids (KRISTER *et al.*, 2008). In this way, *Saniwa australis* Ameghino, 1899 is considered here as an *nomen dubium*, representing an indeterminate Calyptocephalellidae.

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

Present phylogenetic analysis invites to review several isolated anuran specimens that have important palaeobiogeographical implications, and several taxa that may be referred to the Calyptocephalellidae clade.

ISOLATED CALYPTOCEPHALELLID REMAINS FROM GONDWANAN LANDMASSES

ASHER & KRAUSE (1998) reported the presence of a possible Pelobatidae from the Latest Cretaceous (Maastrichtian) Maevarano Formation of Madagascar. These authors explained the presence of a typically laurasian taxon in Madagascar by two different hypotheses. On one hand, pelobatids may have reached Madagascar from Asia via the Indian subcontinent. On the other hand, pelobatids origin may have predated the fragmentation of Pangea, and members of this group may have been more widely distributed than currently realized. ASHER & KRAUSE (1998) based the presence of a pelobatid in Madagascar on a single isolated atlas that resembled Pelobatidae in the combination of having solid, procoelous centrum, lacking nothochordal canal and transverse processes, having atlantal cotyles nearly in touch ventrally, and being unfused with the second presacral vertebra. However, such combination of characters is not unique to pelobatids, but is also present in most neobatrachians, including *Beelzebufo,* and *Calyptocephalella*. Moreover, in general aspect and proportions the bone is indistinguishable from *Calyptocephalella* and *C. satan* in being very transversely expanded. Thus, the isolated Malagasy atlas may be better identified as Neobatrachia cf. Calyptocephalellidae. In this way, the reassignment of this specimen tends to invalidate the palaeobiogeographic hypotheses about early pelobatid distribution proposed by ASHER & KRAUSE (1998).

RAGE & DUTHEIL (2008) reported from the Cenomanian Kem Kem beds (Upper Cretaceous) of Morocco an incomplete posterior portion of skull roof, incomplete maxilla and ilium of a large non-pipid indeterminate anuran. The specimens show a combination of characters suggestive of calyptocephalellid affinities. In fact, the individuals exhibit ridge and pit external cranial ornamentation, dorsoventrally deep pars dentalis on maxilla, step-like palatine shelf at the maxilla, completely fused braincase, reduced subtemporal fossae, occipital arterial foramina developed as a wide foramen that opens medially to a subvertical ridge, a wide and deep condyloid fossa lateral to the occipital condyle where a large jugular foramen opens, and ilium with broad supracetabular and preacetabular expansions, and very large acetabulum (see LYNCH, 1971; RAGE & ROCEK, 2007). This combination of characters suggests that the Kem Kem anuran remains belongs to an anuran with affinities to Calyptocephalellidae.

It must be pointed out that JONES *et al.* (2003) also reported isolated ilia from the Early Cretaceous of Morocco as belonging to the Laurasian clade Discoglossidae. However, these specimens are very poorly preserved, and the combination of traits exhibited by these remains (e.g., posterodorsally extended supra-acetabular expansion, morphology of dorsal tuberosity) is not exclusive of discoglossids, being also present in calyptocephalellid and ceratophryid anurans. In this way, these incomplete specimens may be better regarded as Neobatrachia indet.

BÁEZ (1991) reported from the Early Paleogene of Bolivia several disarticulated anuran specimens of dubious affinities. However, some of these bones appear to be related to Calyptocephalellid anurans. As for example, isolated ilia resemble *Calyptocephalella* in several morphological features, including the presence of a well-developed longitudinal crest in the dorsal margin of the iliac shaft, and the very large iliac shaft-ventral acetabular expansion angle (see BÁEZ & NÍCOLI, 2004; see also LYNCH, 1971). In the same way, isolated vertebrae are similar to that of *Calyptcephalella* in having the cotyles of the atlas nearly confluent at the base, and very short transverse processes on posterior presacral vertebrae (LYNCH, 1971). Moreover, HOFFSTETTER (1968) cited presence of *Calyptocephalella*-like anurans from the Oligocene of Bolivia, although these records are far from certain (BÁEZ, 2000). If these records are confirmed, they could belong to the first South American fossil of Calyptocephalellids north to Argentina. This indicates that, although calyptocephalellids were probably present in Cretaceous and Paleogene outcrops of northern South America, they constituted only a minor component of these batrachofaunas.

FOSSIL ANURANS FROM THE LATE CRETACEOUS-PALEOGENE OF INDIA

In addition, the recognition of several new calyptocephalellid taxa and the phylogenetic analysis here performed also helps to understand some incongruences of the anuran fossil record. Regarding the Mesozoic record, previous reports of different anuran clades in India indicates a peculiar amphibian fauna. In fact, the record mainly consists on fragmentary and isolated bones, with the single exception of the genus *Indobatrachus* (NOBLE, 1930), which is represented by several specimens preserved on slabs.

Frogs from the Intertrappean sediments within the Cretaceous-Tertiary Deccan Trap volcanic episode in peninsular India are represented by the families Discoglossidae, Myobatrachidae, Pelobatidae, and possibly Hylidae (NOBLE, 1930; JAIN & SAHNI, 1983; SPINAR & HODROVA, 1985; PRASAD & RAGE, 1991, 1995, 2004). This faunal assemblage is currently considered as a mixture of Gondwanan and Laurasian faunistic elements (PRASAD & RAGE, 2004; PRASAD *et al.*, 2010) with a dominant influence of Laurasian-like taxa (SAHNI *et al.*, 1981; 1982; SAHNI & BAJPAI, 1991; CHATERJEE & RUDRA, 1996; PRASAD, 2008). Putative Laurasian anuran clades are represented by Discoglossidae and Pelobatidae, which were interpreted as immigrants for Asia after the impact between Indian subcontinent and Asiatic landmasses at the Uppermost Cretaceous (see BONAPARTE, 1999). Other authors, on the basis of this and other faunistic similarities proposed that India was never far removed from Asia (CHATERJEE & HOTTON, 1986). Faunistic evidence employed in order to sustain these proposals was based on the shared presence of several typically Asiatic taxa on India, notably including palaeoryctid-like mammals and pelobatid and discoglossid frogs (see BONAPARTE, 1999; PRASAD *et al.*, 2010). However, it is worthy to note that Indian mammals previously referred to the Laurasian Palaeoryctidae or as basal Euarchonta were recently considered by some authors as related to some mammals currently referable to the Gondwanan clade Afrotheria (see BOYER *et al.*, 2009; PRASAD *et al.*, 2010; SEIFFERT, 2010). In this way, the only tetrapod clades exhibiting “clear” Laurasian affinities are the frog families Pelobatidae and Discoglossidae (but see BAJPAI, 2010).

The Pelobatidae were first reported by SAHNI *et al.* (1982) from the Intertrappean beds from Deccan (Maastrichtian). These authors sustained the identification mainly on the basis of a fragmentary ilium, incomplete maxilla, and a distal humeral end. Later, JAIN and SAHNI (1983) indicated the presence of additional Late Cretaceous pelobatid remains coming from the Latest Cretaceous of Central India. Regrettably, the incomplete and isolated nature of the findings conspires against the correct identification of the anuran specimens mentioned above (see THEWISSEN, 1990; EVANS *et al.*, 2008). In fact, the remains assigned to Pelobatidae by SAHNI *et al.* (1982) show a combination of characters also present in calyptocephalellid anurans. At first hand, the ilia reported from India were considered as pelobatids mainly due to the presence of a longitudinally extended dorsal crest, a condition present in the genera *Calyptocephalella* and *Gigantobatrachus* (CASAMIQUELA, 1963; MUZZOPAPPA & BÁEZ, 2009). Moreover, the presence of a ventral longitudinal depression in such ilia reinforces calyptocephalellid affinities for the specimens (see MUZZOPAPPA & BÁEZ, 2009). The distal humerus figured by SAHNI *et al.* (1982) lacks any clear derived trait allowing its referral to a specific neobatrachian clade; however, its general morphology, including a very distally positioned ulnar epicondyle, and a smooth and proximally located lateral epicondyle recalls the genus *Calyptocephalella* (MUZZOPAPPA & BÁEZ, 2009). As recognized by SAHNI *et al.* (1982) the preserved portion of maxilla lacks any clear synapomorphic trait allowing the referral of the specimen to Pelobatidae, and consequently, they referred the specimen to this anuran group on the basis of general morphology and external ornamentation. However, the ornamentation composed by pits and grooves is already present in several anuran clades, including calyptocephalellids and ceratophryids (GÓMEZ *et al.*, 2011). Moreover, a very deep and smooth alveolar margin is another character that distinguishes the Indian specimen from Pelobatidae, and reinforces its affinities with *Calyptocephalella* and its kin. Regrettably, the incomplete nature of the available remains precludes a clear systematic assignment, and the specimens are regarded as indeterminate Neobatrachia probably related to Calyptocephalellidae.

Later, JAIN & SAHNI (1983) reported an isolated tibio-fibula, phalanges, and tarsal bones as belonging to pelobatids. However, these authors do not sustained the assignment of these specimens on the basis of discrete characters, and only remarked superficial similarities with living pelobatids. In this way, the poorly informative condition of these isolated bones, together with the absence of clear characters that may sustain pelobatid affinities for the specimens, they may be better considered as Anura indet.

In conclusion, the anuran specimens from India referred to pelobatids by previous authors, may be better re-interpreted as indeterminate anurans and neobatrachians of possible calyptocephalellid affinities.

PRASAD & RAGE (1991, 1995, 2004) included from Cretaceous-Tertiary Deccan Trap deposits several incomplete ilia that they referred to the discoglossid subclade Gobiatinae (sensu SPINAR & TATARINOV, 1986). Later, THEWISSEN & MCKENNA (1992) questioned the referral of these specimens to discoglossids, on the basis of the purported paraphyletic nature of this anuran clade, a critique that was contested by PRASAD & RAGE (1995); lately ASHER (1995), based on the morphological disparity of iliac morphology seen in diverse living discoglossid doubted on the taxonomic assignment of the Indian specimens. PRASAD & RAGE (1991, 1995, 2004) referred isolated ilia to Gobiatinae Discoglossidae on the basis of a posterodorsally extended supra-acetabular expansion, and the morphology of the dorsal tuberosity. However, such combination of characters is not unique to Discoglossidae. In fact, a very well developed supra-acetabular expansion is also present in several Gondwanan taxa, including *Calyptocephalella*, and some ceratophryids (LYNCH, 1971; BÁEZ & NÍCOLI, 2004). In this way, available data suggests that the referral of these ilia to Discoglossidae in ambiguous, and that these specimens may be considered as indeterminate anurans, as soon as, new and more informative specimens became available.

In addition, in the Deccan Intertrappean beds, no single amphicoelous or opisthocoelous vertebra has been reported, and all available vertebral specimens appear to belong to procoelous Neobatrachia, an anuran clade that includes taxa more derived than discoglossids (PRASAD & RAGE, 2004). Although this latter statement is based on negative evidence, the absence of non-procoelous vertebrae in the fossiliferous localities from India also argues against the presence of discoglossids in such sedimentary outcrops.

The genus *Indobatrachus* is currently composed by three different species represented by several partial specimens (SPINAR & HODROVA, 1995). The taxon was formerly referred to Bufonidae (NOBLE, 1930), and lately to Myobatrachidae by LYNCH (1971). LYNCH (1971) included *Indobatrachus* within myobatrachids because of the shared presence of bicotylar coccyx, dilated sacral diapophyses, shortened transverse processes of the presacral vertebrae, and possibly free intervertebral discs. However, most of these features are diagnostic of Neobatrachia, rather than to a less inclusive clade (REIG, 1958), and due to the absence of derived characters present in *Indobatrachus*, GÓMEZ *et al.* (2011) desestimated myobatrachid affinities for the genus. Other authors proposed phylogenetic relationships of *Indobatrachus* with Sooglosidae or Nasikabatrachidae, based uniquely on biogeographic reasons, and did not supported their asseveration with derived characters (e.g., BIJU & BOSSUYT, 2003).

On the contrary, *Indobatrachus* shares the presence of broadly dilated sacral diapophyses with *Calyptocephalella* and Ceratophryidae (LYNCH, 1971). Moreover, *Indobatrachus* shares with *Calyptocephalella* very broad and short pectoral and appendicular bones, short and stout scapula with an expanded anterior lamina and extended acromion, and laminar sacral diapophyses (REIG, 1960a; GÓMEZ *et al.*, 2011). However, *Indobatrachus* differs from *Calyptocephalella* and related taxa in lacking strongly fused and deeply ornamented cranial bones (NOBLE, 1930). The characters reported above suggest that *Indobatrachus* may be related to Calyptocephalellidae; however, although the fossil genus resembles calyptocephalellids in postcranial features, it still lacks some calyptocephalellid apomorphies (e. g. cranial exostotic bones). In this way, only a detailed reestudy of available specimens, as well as an abarcative phylogenetic numerical analysis, may indicate the exact taxonomic position of *Indobatrachus*, which is here considered as Neobatrachia indet. cf. Calyptocephalellidae.

As indicated above, with the exclusion of the families Pelobatidae and Discoglossidae from the Mesozoic faunas of India, previously proposed faunistic similarities between this landmass and Asia during the Cretaceous tend to blur. In this regard, and contrasting with some proposals (see PRASAD *et al.* 2010), faunistic evidence does not contradict the traditional view of an Eocene collapse between Asia and India, as previously advocated by other authors (BOSSUYT & MILINKOVITCH, 2001).

COMMENTS ON EVANS *ET AL.* (2008) ARTICLE

Referral of *Beelzebufo ampinga* to the Ceratophryidae prompted EVANS *et al.* (2008) to propose that this phylogenetic relationship provides strong support for the hypothesis that proposes that physical links between Madagascar, India, and South America existed until Late Cretaceous times (HAY *et al.*, 1999). This contrasts with conventional palaeogeographical hypotheses that propose an Early Cretaceous separation of such landmasses (SMITH *et al.*, 1994). However, present referral of *Beelzebufo* to Calyptocephalellidae, together with the presence of possible Calyptocephalellid-related taxa in Africa by Mid-Cretaceous times (see below) weakens the palaeobiogeographical hypothesis expressed by EVANS *et al.* (2008). On the other hand, the existence of calyptocephalellids or related taxa in Cretaceous beds of South America, Africa, Europe, Madagascar, and possibly India, indicates that this anuran clade was probably widely distributed along Europe and Gondwanan landmasses during such time frame.

In agreement with calyptocephalellid affinities of *Beelzebufo*, molecular analyses provided Late Palaeogene to Early Neogene origins for Ceratophryidae (MAXSON & RUIBAL, 1988; ROELANTS *et al.*, 2007; WIENS, 2007). The exclusion of *Beelzebufo* from Ceratophryidae is clearly compatible with such molecular data. RUANE *et al.* (2011) on the basis of molecular divergence and statistical support questioned the referral of *Beelzebufo* to Ceratophryidae, although these authors did not propose alternative relationships for the later taxon. Present change in the taxonomic position of *Beelzebufo* appears to be more congruent with such molecular data and statistics.

COMMENTS ON DYNAMICS OF SOUTHERN SOUTH AMERICAN BATRACHOFAUNAS

Dynamic of vertebrate faunas during the Mesozoic and Tertiary has been studied by several different authors, who focused mainly on reptile faunal assemblages for the Mesozoic time span (BONAPARTE, 1986, 1996; LEANZA *et al.*, 2004; NOVAS, 2009) and on mammalian faunas for Cenozoic times (PASCUAL & ORTIZ JAUREGUIZAR, 2007). However, different studies have also analyzed ichthyofaunal evolution during Late Mesozoic-early Tertiary times (ARRATIA & CIONE, 1996; CIONE & BÁEZ, 2007; AGNOLIN, 2010a). Regarding amphibians, some previous reports attempted an explanation for the evolution of the southern South American batrachofaunas (ESTES & REIG, 1973; GASPARINI & BÁEZ, 1974; ESTES & BÁEZ, 1985; BÁEZ, 2000; CIONE & BÁEZ, 2007). The fossil Cretaceous and Cenozoic amphibian record of southern South America is restricted to anuran taxa, lacking records of caecilians and salamanders (GASPARINI & BÁEZ, 1974).

Based on the present analysis, three main paleobatrachofaunal assemblages may be recognized that succeeded each other along the Late Mesozoic and Tertiary times. The first palaeobatrachian fauna may be termed as the "ancient assemblage" (following the concept of VUILLEUMIER, 1968). This association is represented by a large array of Andean-Antarctic batrachofaunal elements (*sensu* CEI, 1980) together with pipid anurans (BÁEZ, 2000). This first stage is composed by pipids and calyptocephalellid anurans. In fact, in early Late Cretaceous (Cenomanian-Turonian) outcrops, several pipids and *Calyptocephalella*-like taxa have been reported (BÁEZ, 1986; BÁEZ *et al.*, 2000, 2007; LEANZA *et al.*, 2004), and no remains of other anuran groups have been recognized in Patagonian sediments. Latest Cretaceous (Campanian-Maastrichtian) localities also yielded a similar taxonomic composition, being represented by pipid and calyptocephalellid specimens in several Patagonian localities (BÁEZ, 1987; MARTINELLI & FORASIEPI, 2004; present paper). Early Paleocene localities from Patagonia also exhibit the same taxonomic composition, and several calyptocephalellids have been reported, including gigantic *Gigantobatrachus*, and smaller *Calyptocephalella*, as well as some pipids (BONAPARTE *et al.*, 1993; but see BÁEZ, 2000). This anuran assemblage is highly reminiscent to that observed along Cretaceous outcrops. Due to the absence of extinct anuran clades at the Cretaceous/Paleogene boundary, the Late Cretaceous-Early Tertiary massive extinction event may have no important consequences on Patagonian anuran faunistic associations. Moreover, the presence of calyptocephalellids and pipids is a recurrent association recovered until Eocene-Oligocene times along Patagonian fossiliferous localities (SCHAEFFER, 1949; BÁEZ, 1991, 2000; CIONE & BÁEZ, 2007). In addition, *Telmatobius*-like taxa has also been reported from Eocene and Oligocene beds of Patagonia (BÁEZ & FERNÍCOLA, 1999; BÁEZ, 2000). This probably indicates a relative stability among batrachofaunal taxonomic composition during the Cretaceous-Oligocene time span.

As pointed out above, Cretaceous-like batrachofaunal associations were present along the Paleogene and early Neogene. In fact, although *Calyptocephalella* and *Gigantobatrachus* are still recorded until Late Miocene times (BÁEZ, 2000; CIONE & BÁEZ, 2007; present paper), *Telmatobius*-like taxa and pipids disappear from the Patagonian fossil record since the earliest Miocene. *Telmatobius*-like taxa are currently restricted in geographical distribution to Andean and Sub-Andean regions (CEI, 1980). Due to the stenoic nature of pipids and telmatobiids, the colder and dryer climatic conditions of Patagonia during the Miocene (ZACHOS *et al.*, 2001) may be the main responsibles for the retraction and regional extinction of these anuran clades. The presence of typically dry and xeric-adapted taxa, such as ceratophryids (see LYNCH, 1971; CIONE & BÁEZ, 2007) in the Miocene and post-Miocene fossil record of Patagonia reinforces this hypothesis (CASAMIQUELA, 1963; AGNOLIN, 2006; FERNÍCOLA & VIZCAÍNO, 2006; see also TAUBER 1999, a premaxilla and maxilla identified as Leptodactylidae indet., pl. 1, figs. 1-9). In this way, depauperated Neogene

Patagonian batrachofaunas were composed by calyptocephaellid and ceratophryid anurans. The coexistence of calyptocephalellid and ceratophryid taxa constitutes a clear non-analogous faunistic assemblage that probably characterized Middle-Late Miocene times. It must be noted that living *C. gayi* is currently an obligate inhabitant of lentic environments (DONOSO BARROS & REIG, 1960a), but during Neogene times extinct representatives of the genus (i.e. *C. rugata, Gigantobatrachus*sp.) were probably more tolerant to dryer habitats than living forms. Thus, the peculiar Miocene anuran association is here considered as a "second palaeobatrachian assemblage".

Regrettably, in Argentinian Patagonia, post-Miocene outcrops are not widely exposed, and no single anuran remain has been published from that time span. On the contrary, anurans are well represented in the Plio-Pleistocene beds from the Pampean Region. This Pliocene "modern batrachofauna" is composed by living genera of the clades Ceratophryidae (i.e., *Ceratophrys, Lepidobatrachus*; FERNÍCOLA, 2004; TOMASSINI *et al.*, 2011), and BUFONIDAE (i.e. *Rhinella*; CASAMIQUELA, 1967; GASPARINI & BÁEZ, 1974). These anurans probably reached Pampean and Patagonian assemblages due to the southern expansion of Chacoan environments during the "Southern Plains Age" (PASCUAL *et al.*, 1996). In fact, *Ceratophrys* and *Lepidobatrachus* are represented by species related or belonging to Northern South American taxa (AGNOLIN, 2006; TOMASSINI *et al.*, 2011), and *Rhinella* is recorded since Oligocene times in Bolivia (BÁEZ & NÍCOLI, 2004). These data suggest that most of the post-Miocene taxa that composed southern South American batrachofaunas were probably northern immigrants for more humid and template environments, and that these anurans reached the austral regions by Pliocene times.

As a conclusion, three main batrachofaunal assemblages may be recognized in the Late Mesozoic-Holocene time span at Patagonia. The first one, is regarded here as the "ancient assemblage", composed by pipids, calyptocephalellids, and *Telmatobius*-like taxa during Cenomanian-Oligocene times. This fauna was composed by taxa inhabitant of temperate and relatively humid environments. The "second batrachofaunal assemblage" includes a non-analogous Calyptocephalellidae-Ceratophryidae association, which occurred along the Miocene period. This assemblage is also characterized by the disappearance of pipids and *Telmatobius*-related taxa, and by the presence of xeric-adapted anurans. It must be pointed out that pipids belonging to putatively extinct Patagonian lineages have been recently reported in several Pleistocene beds from the Pampean region, indicating its survival in temperate areas (BÁEZ *et al.*, 2009b; BOGAN & JOFRÉ, 2009). The third batrachofaunal assemblage constitutes the "modern batrachofauna" and is characterized by the dominance of northern immigrant taxa, including ceratophryid and bufonid genera, which appear to have distributed southwards by post-Miocene times. It must be pointed out that this age may be also characterized by the notable retraction of the otherwise abundant calyptocephalellids in Patagonia

(*Calyptocephalella* re-appears in the fossil record in the Latest Pleistocene of Chile; CASAMIQUELA, 1976).

However, the succession of assemblages here proposed appears to be restricted at the southern cone of Argentina. In Tertiary beds of northern South America (i.e. Bolivia, Brazil), pipids are scarce or nearly absent (with the single exception of "*Xenopus*" *romeri*; ESTES, 1975), and no unambiguous calyptocephalellid has been recorded (ESTES, 1970; BÁEZ *et al.*, 2009). From Late Cretaceous to Early Tertiary times several hylids, bufonids, and leptodactylids, among other neobatrachians, have been recorded in extensive outcrops of Bolivia and Brasil (ESTES, 1970; ESTES & REIG, 1973; BÁEZ, 1991, 2000; BÁEZ *et al.*, 2009a), being totally absent in Cretaceous and Paleogene outcrops of Patagonia and Pampas of Argentina. This indicates important faunistic differences between northern and southern South America by Cretaceous-Paleogene times. A similar difference of faunal composition, between both regiones has also been proposed for dinosaurs (APESTEGUÍA, 2002; NOVAS, 2009), and dipnoans (AGNOLIN, 2010).

Present analysis allow to discuss some previous hypotheses regarding the current composition and distribution of southern South America living anuran faunas. The current distribution of frogs in the far south of South America has been explained by the means of three different hypothesis: 1) Depauperate hypothesis (DARLINGTON, 1965), 2) "Ancient assemblage" hypothesis (CEI, 1962), and 3) "Complex history" hypothesis (VUILLEUMIER, 1968). The first of them suggests that the amphibians of forested Patagonia may constitute a depauperate fauna composed by poorly differentiated representatives of existing widespread South American groups. The second one indicates that the frogs of *Nothofagus* woods are a relict of an ancient Tertiary batrachofauna that survived in these forested areas and remained separated from remaining South America by ecological barriers. The third hypothesis indicates that this batrachofauna consists on the sum of the histories of different elements composing them. In this hypothesis, VUILLEUMIER (1968) recognized 4 different anuran stocks, several of which arrived at late Neogene times, whereas others derived from Early Tertiary taxa.

Present proposal does not perfectly match any of these hypotheses. On the basis of the fossil record and distribution of different taxa only two main anuran components may be recognized among living taxa. The first component consists on survivors of taxa that were widely distributed among Gondwana (e. g., *Calyptocephalella, Telmatobius*-like taxa; see LYNCH, 1971; VAN DER MEIJDEN *et al.*, 2007). The other faunistic component is formed by the genera *Rhinella* and *Pleurodema*, which entered to the Patagonian region by Plio-Pleistocene times, probably when Chacoan-like environments expanded southwards.

In addition, the fossil neobatrachian record suggest that Pleistocene climatic events have no major impacts on the taxocenosis of the Patagonian anuran composition. In fact, Pleistocene events (including the "refugium effect") may have driven the distribution of taxa within Patagonia, but may have not affected its taxocenosis, a pattern also observed in Pleistocene paleoherpetofaunas from the Pampean Region of Argentina (SCANFERLA *et al.*, 2009; AGNOLIN & JOFRÉ, 2011).

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APPENDIX 1. CHARACTER LIST

Sin embargo, los resultados obtenidos en este trabajo, así como el reanálisis de la evidencia presentada por PARDIÑAS *et al.* (1996), indican que el conjunto de taxones registrados para la citada localidad fosilífera constituye una asociación típica de los actuales ambientes mixohalinos bonaerenses. Una asociación ictiofaunística semejante a la descripta se encuentra actualmente en la desembocadura del río Quequén Salado, varios kilómetros río abajo del yacimiento pleistocénico aquí estudiado. En este aspecto, es RINGUELET (1944) quien remarca las particularidades de dicha asociación ictiológica para ambientes mixohalinos del río Quequén Salado. Este autor indica: "En el río Quequén Salado se produce lo que se llama una mezcla de faunas. Los peces del mar como la corvina negra *Pogonias cromis*, la blanca *Micropogonias furnieri*, la lisa o *Mugil platanus*, los lenguados del género *Paralichthys* y las lengüitas, entran por la boca del río y se mezclan con peces de agua dulce, bagres sapos *(Rhamdia quelen)* por ejemplo. Este fenómeno es un tema que puede ocupar mucho tiempo en los desvelos de un naturalista… por ser de utilidad la determinación de los lugares de desove, de penetración máxima y de tantas cuestiones más" (RINGUELET, 1944).

0. Nasal shape: 0 - triangular and large; 1 - reduced to a narrow slip of bone.
1. Nasals medial contact: 0 - fused or in contact; 1 - moderately to widely separated.
2. Cranial exostosis: 0 - absent; 1 - present.
3. Dorsal exposure of sphenethmoid: 0 - invisible dorsally; 1 - visible dorsally.
4. Ventral configuration of sphenethmoid: 0 - a single bone; 1 - consisting of two element.
5. Frontoparietals medial contact: 0 - no medial contact; 1 - slightly separated; 2 - sutured or fused.
6. Supraorbital alae: 0 - absent; 1 - present.
7. Frontoparietals: 0 - parallel sided; 1 - posterior end is wider than anterior end.
8. Parieto-squamosal arch: 0 - absent; 1 - present.
9. Interfrontal: 0 - absent; 1 - present.
10. Otic ramus of squamosal: 0 - absent or rudimentary; 1 - overlapping crista parotica; 2 - overlapping crista parotica and otoccipital.
11. Zygomatic ramus of squamosal: 0 - short or absent; 1 - moderately developed; 2 - long, reaching maxilla.
12. Teeth: 0 - absent; 1 - bicuspid; 2 - monocuspid.
13. Shape of anterior, premaxillary, margin of maxilla: 0 - concave; 1 - straight.
14. Shelf on pars palatina of premaxilla: 0 - present; 1 - reduced; 2 - absent.
15. Orientation of processus alaris of premaxillae: 0 - parallel; 1 - divergent.
16. Pars facialis of maxilla: 0 - low; 1 - high.
17. Anterior ramus of pterygoid: 0 - long, reaching antorbital planum; 1 - short.
18. Pterygoid rami: 0 - well differentiated; 1 - posterior and medial rami forming a plate.
19. Prevomer: 0 - absent or unpaired; 1 - incomplete, without odontophore; 2 - complete.
20. Anterior process of prevomer: 0 - long, reaching the premaxilla-maxilla articulation; 1 - reduced, not reaching premaxilla-maxilla articulation.
21. Quadratojugal: 0 - absent or reduced; 1 - entire, but not contacting maxilla; 2 - articulated or fused to maxilla.
22. Palatine: 0 - absent; 1 - present.
23. Fangs in lower jaw: 0 - absent; 1 - forming a plate of dentary; 2 - a spur-like projection formed by dentary and mentomeckelian bones.
24. Mentomeckelian bone: 0 - absent; 1 - distinct from dentary; 2 - fused to dentary.
25. Ceratohyalia: 0 - continuous; 1 - discontinuous.
26. Ceratohyalia processes: 0 - absent; 1 - anteromedial processes; 2 - anteromedial and anterolateral processes.
27. Anterolateral process of hyoid plate: 0 - absent; 1 - pointed; 2 - dilated distally; 3 - expanded.
28. Posterolateral process of hyoid plate: 0 - absent; 1 - present.
29. Posteromedial process ossification: 0 - ossification present on a cartilaginous stalk; 1 - ossification abuts directly on the hyoid; 2 - ossification invades the hyoid.
30. Posteromedial epiphyses: 0 - cartilaginous; 1 - ossified.

31. Posteromedial ridge of posteromedial process: 0 - absent; 1 - present.
32. Parahyoid bone: 0 - absent; 1 - small ossification; 2 - transverse bar.
33. Endochondral ossifications in the hyoid: 0 - absent; 1 - present.
34. Number of presacral vertebrae: 0 - eight; 1 - seven.
35. Shape of eighth vertebra: 0 - opisthocoelous; 1 - procoelous; 2 - biconcave.
36. Cervical cotylae arrangement: 0 - contiguous; 1 - separated.
37. Sacral vertebra and urostyle: 0 - articulated; 1 - fused.
38. 8th presacral and sacral vertebrae: 0 - separated; 1 - fused.
39. Neural arches: 0 - imbricate; 1 - non-imbricate.
40. Neural spines: 0 - low; 1 - high; 2 - flattened.
41. Relative length of transverse processes: 0 - decreasing gradually in caudal direction; 1 - decreasingly abruptly from IV vertebra in caudal direction.
42. Sacral transverse processes: 0 - widely expanded; 1 - moderately dilated; 2 - with anterior and posterior margin subparallel.
43. Ribs: 0 - absent; 1 - present.
44. Dorsal shields: 0 - absent; 1 - two ossifications; 2 - complex formed by a set of plates.
45. Orientation of transverse processes of 8th presacral vertebra: 0 - perpendicular to axial axis; 1 - markedly forward; 2 - absent.
46. Omosternum: 0 - cartilaginous; 1 - ossified not forked; 2 - ossified, forked; 3 - absent.
47. Metasternum: 0 - absent; 1 - cartilaginous; 2 - proximal ossified style.
48. Coracoid: 0 - entire medial margin; 1 - perforated medial margin.
49. Clavicle: 0 - well developed; 1 - reduced; 2 - absent.
50. Epicoracoid: 0 - widely overlapping; 1 - slightly overlapping; 2 - fused; 3 - absent, coracoids with medial union (firmisterny).
51. Scapula: 0 - short; 1 - long.
52. Dorsal crest on iliac shaft: 0 - absent; 1 - present.
53. Epipubis: 0 - absent; 1 - present.
54. Femoral crest: 0 - absent; 1 - present.
55. Intercalary element: 0 - absent; 1 - present.
56. Tarsal sesamoidea: 0 - absent; 1 - cartilage sesamoidea; 2 - os sesamoidea tarsale.
57. Distal tarsal 3 and distal tarsal 2: 0 - free; 1 - fused.
58. Distal tarsal 1: 0 - absent; 1 - present.
59. Prehallux: 0 - one spherical proximal element; 1 - two elements, the distal one enlarged; 2 - three or more elements; 3 - two elements, the distal one hypermorphic.
60. Shape of terminal phalanx of toe IV: 0 - straight; 1 - curved.
61. Distal tip of terminal phalanx of toe 4: 0 - knob-like; 1 - pointed; 2 - notched; 3 - T-shaped; 4 - Y-shaped.
62. Ventral spine of toe IV: 0 - absent; 1 - present.
63. Subarticular sesamoidea of toes: 0 - absent; 1 - present.
64. Postaxial carpals (ulnare and distals 5 and 4): 0 - unfused; 1 - ulnare free, 5 and 4 fused; 2 - ulnare free, 3, 4 and 5 fused; 3 - ulnare and 5 fused, 4 free.
65. Preaxial carpals (element Y and distal 2): 0 - unfused; 1 - 2 and Y fused; 2 - element Y, distal 2 and 3 fused.
66. Prepollex: 0 - one spherical proximal element; 1 - two elements, the distal one enlarged; 2 - three or more elements; 3 - two elements, the distal one hypermorphic.
67. Shape of terminal phalanx of finger IV: 0 - straight; 1 - curved.
68. Distal tip of terminal phalanx IV: 0 - knob-like; 1 - pointed; 2 - notched; 3 - T-shaped; 4 - Y - shaped.
69. Ventral spine of finger IV: 0 - absent; 1 - present.

70. Subarticular sesamoidea of finger IV: 0 - absent; 1 - present.
71. Carpal torsion: 0 - absent; 1 - present.
72. Parotoid glands: 0 - absent; 1 - present.
73. Bidder organ: 0 - absent; 1 - present.
74. Development: 0 - direct; 1 - larval.
75. Spiracle in larva: 0 - pair; 1 - single and sinistral; 2 - single and medial; 3 - single, medial and posterior.
76. Keratinised jaws in larva: 0 - absent; 1 - present.
77. Keratodonts in larva: 0 - absent; 1 - present.
78. Sexual dimorphism in size: 0 - females larger than males; 1 - females equal or smaller than males.
79. Sexual dimorphism in finger length: 0 - absent; 1 - present.
80. Heterochronic traits related to size: 0 - absent; 1 - noticeable paedomorphic traits; 2 - noticeable peramorphic traits.

NEWLY ADDED CHARACTERS.

81. Pars dentalis of premaxilla and maxilla: 0 - dorsoventrally low; 1 - dorsoventrally tall (BÁEZ, 1977).
82. Tightly interlocking premaxilla-maxilla contact (peg-and-socket): 0 - absent, free contact; 1 - present (EVANS *et al.*, 2008).
83. Palatine shelf of maxilla: 0 - developed as a bump or ridge-like; 1 - step-like (discussed in detail by LYNCH, 1971).
84. Maxilla with pterygoid process of palatine shelf: 0 - well-devepoed; 1 - reduced or very poorly developed (LYNCH, 1971).
85. Very well developed and laminar ascending squamosal process on maxilla: 0 - absent; 1 - present (MUZZOPAPPA & BÁEZ, 2009).
86. Ascending squamosal ramus of maxilla in internal view showing: 0 - rounded depression; 1 - a funnel-like canal (MUZZOPAPPA & BÁEZ, 2009).
87. Nasal-frontoparietal contact: 0 - absent or extremely narrow; 1 - transversely broad (LYNCH, 1971).
88. Maxillary process of nasal bone: 0-maxillary process splint-like or slightly developed as a subtriangular knob; 1 - very large maxillary process laterally extended and widely contacting the maxilla (GÓMEZ *et al.*, 2011).
89. Occipital arterial foramen developed as a wide foramen that opens medially to a subvertical ridge: 0 - absent, or present as an opened groove; 1 - present (RAGE & ROCEK, 2007) (carotid foramina of LYNCH, 1971).
90. Wide and deep condyloid fossa lateral to the occipital condyles where a large jugular foramen opens: 0 - absent; 1 - present (RAGE & ROCEK, 2007).
91. Posttemporal fenestrae: 0 - absent; 1 - present (LYNCH, 1971).
92. Presacral vertebral centra: 0 - subcircular or ovoidal in contour; 1 - transversely wide and dorsoventrally depressed, being elliptical in contour (CASAMIQUELA, 1963).
93. Atlas and second presacral vertebra: 0 - unfused; 1 - fused (EVANS *et al.*, 2008).
94. Sacral diapophyses: 0 - subhorizontal; 1 - strongly dorsally oriented (REIG, 1960a).
95. Sacral diapophyses: 0 - laminar; 1 - thick (Ceratophryidae; GÓMEZ *et al.*, 2011).
96. Urostyle length compared to total presacral length: 0 - lower; 1 - subequal (REIG, 1960a,b).
97. Proximal end of urostyle dorsoventrally compressed and transversally expanded: 0 - absent; 1 - present.
98. Shaft/ventral acetabular expansión angle: 0 - less than or subequal to 90°; 1 - more than 90° (BÁEZ, 1987).

99. Dorsal crest of ilium: 0 - straight; 1 - medially deflected (CASAMIQUELA, 1963).
100. Ilium with very expanded and broad supracetabular and preacetabular expansions: 0 - absent; 1 - present (LYNCH, 1971).
101. Scapula: 0 - relatively elongate, with a well-defined and constricted scapular shaft; 1 - sub-cuadrangular in contour with a well-developed flange on its anterior surface (MUZZOPAPPA & BÁEZ, 2009).
102. Clavicle: 0-elongate and straight, or gently curved; 1 - short and strongly curved (REIG, 1960a).
103. Distal epicondyles of humerus: 0 - distally acute, with the medial epicondyle much more developed than the lateral one; 1 - distally blunt, which brings the distal end of the humerus a nearly symmetrical contour (BÁEZ & NÍCOLI, 2004).

APPENDIX 2. DATA MATRIX

Bombina	110101010100110000021200100311001100100000010101000000100011000000100000001211000000000000000000000000000
Afrana	110101001011110000021210100111000002000010200012001010000112111020100001001111002000000000000000000000000
Afrixalus	000112010011110000011210102200000002100100200121002000010111121010112101001111001000000000000000000000000
Allophryne	010102000011011001011000100211000001100100100031000100100100030020003001001111000000000000000000000000000
Amnirana	110101000011110000021210102111000002000000200012001110000112030020102001001111000000000000000000000000000
Arthroleptis	010101010011110000011210101301000001100100200021002110001111000111100011000???0100000000000000000000000000
Callulops	0000?20000010100000212101000010?00011001001001?102301?00?112140?20204??1000---??0000000000000000000000000
Astylosternus	000102010011110011021210101211000002000100200021002110001113111020100001001111000000000000000000000000000
Aubria	001002000022200010020211200211000002000010200022111010000111101021100001001111102000000000000000000000000
Batrachophrynus	1001000000000000100101102???????0011000002001010000?00?1??00??2??00??10?11111?000000000000000000000001000
Bufo_granulosus	001000111020012010021210100211000001100010100131000000100112000020200001111111000000000000000000000000000
Bufo_viridis	010100010010010010011000100211000001100000100131000000100112000020200001111111000000000000000000000000000
Cardioglossa	000102010011010001011210101301000002100100200021002110001010000110000011001111011000000000000000000000000
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Chacophrys	001002111022212010020212200012102001000021100101000110100113000020100001001111000010000111100001001010000
Chiromantis	110102000011110000021210102211000002100100200022002110111101140020314001001111000000000000000000000000000

Conraua	010102000011110000020211200211000002000110200022001110001112000020200001001111000000000000000000000000000
Cyclorana	0001110000121000100202102??1????00110012010000?00011?10?1??00??2??00??10?11111?000000000000000000000000
Dendrosophus	000100010010110100011210100111000001100100100101000100010112110020311001001111001000000000000000000000000
Dyscophus	000012000000110100020210010?????000210010010011100310000?11200??20?000?10013000?000000000000000000000000
Flectonotus	01010000000111100010211101001110000011001001001010000000101111100201110010000???00100000000000000000000000
Heleioporus	11010100000001001100202l0?022110?00011001?1100101?00?0???1???0??2???0??11011111?00000000000000000000100000
Hemiphractus	00110211102221001002021200?????00001001102000010001 0??1?1000??20?00??1000---0?000000000000000000000000
Hoplobatrachus	0000020010211000110212112002110000020001102001220011000011121010201001010011110020000000000000000000000000
Hymenochirus	000002101001012201 10?00000???1????101100010?0131002010002110000032000000000100000000000000000000000000000000
Hyperolius	010111010011110000011210102100000002100100200121002100011111121010112101001111000000000000000000000000000
Hypsiboas	000100010011110001021210100111000001100100100101000100010112110020311001001111000000000000000000000000000
Isthmohyla	000000000011110001021110100111000001100000100231000000010113110020111001001111000000000000000000000000000
Kassina	000112010011110000011210103100000002100000200121002100011111121110112111001111000000000000000000000000000
Lepidobatrachus	0010021110222120100202122100121020010000[123]11001010001001001130000201000010010100020100001111100[01]0100101000
Leptodactylus	0001020000[123]1110001020210100111000001100010100102000000000112000020200101001111100[023]000000000000000000001000
Leptopelis	110102100011110000020210101101000002100100200011002110111111110010111001001111000000000000000000000000000
Limnodynastes	1101?1000000111010021 2?01012110000111000001001010021 0?10?11?010???101??10011111?000000000000000000000000
Litoria	110101100001100001020210 2??????0?0110010010002100010011?11?110?202110?1?011110?000000000000000000000000
Megophrys	1?11020000111101000202102000110000011100000020010001 0?000113010010101?010011000?2000000000000000000000000
Melanophryniscus	000002111010010010011000100311000001100000100001001000101112000020100001001111000000000000000000000000000
Mixophyes	000102000001110111021210?01111000001100 1?0100?010?0?0???1???0??2???0??10011111?00000001000000000000000000
Odontophrynus	00010201000010001002021010111100000110001010013100010010111300002010000100111110000000000100000000000101000
Opisthothylax	010111000011110000011210102100000002100100200021002100110111110010111001001111000000000000000000000000000
Osteopilus	00100211001210000102021010?????000110010010 01??00010011?1??010?20?01??10011110?2000000000000000000000000
Pelobates	00100210001210010002020 0[123]10????00011100010001020 0000?00??1200??00100??1??11110?0000000000000000000000000
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Phrynobatrachus	1101020000111101000112101003110100021001002000[123]200201000011[123]0200201020010011110000000000000000000000000
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Phyllomedusa	0101001000211100000[123]0[123]1010001100000110000010000[023]100000001011211002011100110111100[123]0000000000000000000000
Physalaemus	0001010100101100000202101013110000011000001001020001000001130000201000010011110000000000000000000000000
Pleurodema	0001010100111100000210101012110000011000001001020001001011120000201000010011110000000000000000000100000
Pseudis	000102010012110100020210100211000001100010100101000000011111000020100101001111000000000000000000000000000
Ptychadena	1101020000111100000212001001110000?10100020012201201000011211102031110100111100000000000000000000000000
Pyxicephalus	0010021000222000100202121002110000020000102001220031101001120010201000010011111020000000000000000000000
Rana	0001020000001100000002102????10000021001002000120031100001 1100?0201000?10011110?0000000000000000000000
Rhinoderma	0101100000110101000111001001110000010001001001010010000001100000200000010011110010000000000000000000000
Spea	0101001000111101100200001103110000010100110001010000001000130000001000010011110000000000000000000000000
Scaphiopus	0010021110221100110200001103110000010100110001010000001000130000001000010011110000000000000000000000000
Schoutedenella	0001010100000111010112101013010000011001002001211021100011100201120020110000???0110000000000000000000000
Scinax	0001010000111100000212101001110000011001001001010000001101121200202120010011110010000000000000000000000
Telmatobius	1100020000002000100202101????2000001100100200101000001?10?11200??20100??1?0111101000000000000000000000000
Telmatobufo	11010[123]000001110?1002021??00111000001100100100101000000??0?1?[123]?1??20??0??110??0?1?0?0000000?000000000000000
Triprion	001102101?021100010202101 0?????00011000200001010010 0?01?1??010020101?010011111?000000000000000000000000
Xenopus	1000020000212102001 0?000000??1000000110011010101001001000111110000000000000100000000000000000000000000000
Beelzebufo_ampinga	0010?2111022??2011???21???????????1000???1???????00?????????????????????????211110011??111100000??0?
C_satan	??1??211??????1?1?????????????????1000???1???????10?????????????????????????111011???-1101110111??1
Baurubatrachus	0010??1???22?1??10???2???????????01000001100 00?00?11?????????????????????????000000011??0?000???0?01?
Thaumastosaurus	001102100012[123]1??000???1???????????????????1??????????????????????????????????????00000011110???????????
Wawelia	??1?????????????????????????????0????00110?0?0????1??????????????????????????????????????0010???????
C_gayi	0010021110221000100202 11[123]0?????00011001101001010011101001100100201 01?010011110?2111011111101[01]1010111111
C_canqueli	0010021110221000100202 11[123]0???????011001101001??00111010011001002010 1?0?????????111011111?0101010111111
C_pichileufensis	00100211102210?01????2???????????01?001101001?????11???????????????????????????11101?11??010?010???111

G_parodi	??100???????10001??????1???????????1???????????????11????????????????????????????111010?????1????1?0?11?
G_casamiquelai	??1????????????????????1???????????1???????????????1???????????????????????????1?10???????1????1101??0

APPENDIX 3. CHARACTER DIAGNOSES OF SELECTED NODES

Characters in bold indicates unambiguous synapomorphies

Thaumastosaurus+(Ceratophryidae+Calyptocephalellidae): 87-1, 88-1, 89-1, **90-1**.

Ceratophryidae+Calyptocephalellidae: 8-1, 10-2, 16-1, **82-1**.

Ceratophryidae: 12-1, 23-2, 41-1, 61-0, 68-0, 95-1.

Calyptocephalellidae: **81-1**, **83-1**, **92-1**, **94-1**.

Gigantobatrachus + *Calyptocephalella*: 52-1, **85-1**, 102-1.

Gigantobatrachus: **97-1**.

Calyptocephalella: **88-1**, **99-1**, **103-1**.