

In the shadow of dinosaurs: Late Cretaceous frogs are distinct components of a widespread tetrapod assemblage across Argentinean and Chilean Patagonia

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ABSTRACT

Frogs (Anura) are nowadays common and abundant constituents of terrestrial and freshwater ecosystems near globally and their fossil record shows that they were already important during Cretaceous times. However, their fossils are often very incomplete, challenging their identification, which, coupled to historical reasons, has led to their marginalization in studies of Cretaceous tetrapod assemblages. We here report on the identities of frogs from three upper Campanian–lower Maastrichtian assemblages from Chilean (Dorotea Formation) and Argentinean (Allen and Los Alamitos formations) Patagonia, with focus on humeral morphology. Records from the Dorotea Formation represent the first described Mesozoic frogs from Chile and include the southernmost record of pipids worldwide. In the three assemblages we have identified humeri of the pipid *Kuruleufenia* and of calyptocephalellid frogs, proving humeral morphology valuable in diagnosing and identifying Cretaceous frogs from Patagonia. These frogs are diagnostic components of the South American Allenian tetrapod assemblage that was widespread across Patagonia near the end of the Cretaceous.

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1. Introduction

Frogs (Anura) are nowadays common and abundant constituents of terrestrial and freshwater ecosystems near globally (Wells, 2007) and their fossil record documents that they were important in tetrapod assemblages already in the Early Cretaceous (Báez et al., 2009; Dong et al., 2013; Báez and Gómez, 2019; Gómez and Lires, 2019). Their Upper Cretaceous record also depicts frogs as a typical element of continental tetrapod faunas near worldwide, but besides some outstanding exceptions (Báez et al., 2012a; Báez and Gómez, 2018; Xing et al., 2018), it largely consists of isolated, fragmentary bones, usually found through screen-washing of sediments at microvertebrate localities (Estes and Sanchíz, 1982; Prasad and Rage, 2004; Roček et al., 2010; Company and Szentesi, 2012; Gardner and DeMar, 2013; Gardner et al., 2016; Rage et al., 2020). The known Campanian–Maastrichtian anuran fossils from Patagonia, the southernmost region of South America, also conform

to this general pattern (Báez, 1987; Martinelli and Forasiepi, 2004; Agnolin, 2012; Gómez, 2016; Novas et al., 2019; Suazo Lara, 2019) and their incomplete nature has often challenged their interpretation and identification. Because of this, but also due to historical reasons, the anuran record has typically been marginalized in studies of Cretaceous tetrapod assemblages from Patagonia, which are largely defined on the content of dinosaurs and other reptiles and, secondarily, mammals (Leanza et al., 2004; Rougier et al., 2010; Sterli et al., 2013; Gianechini et al., 2015; Alarcón-Muñoz et al., 2020; Goin et al., 2020).

It is noteworthy, however, that some isolated frog bones can be very informative, allowing reliable taxonomic assignments at the genus or species levels, although the success and accuracy of identifications varies among bones, between groups, and along the stratigraphic column (Roček et al., 2010; Pérez-Ben et al., 2014; Gardner et al., 2016). Among isolated bones, the ilium and the maxilla have long been considered 'key' elements upon which to base the identification of frogs in fossil assemblages (Sanchíz, 1998; Báez et al., 2012b; Gardner et al., 2016; Gómez and Turazzini, 2016; Muzzopappa et al., 2020), whereas vertebrae or limb elements have traditionally received little attention and often are considered of

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only limited taxonomic value (Martinelli and Forasiepi, 2004; Bastir et al., 2014; Rage et al., 2020). Nevertheless, the humerus has recently gained attention and has successfully been used in diagnosing and identifying extinct and extant frogs (Otero et al., 2014; Matthews et al., 2015; Suazo Lara et al., 2017; Blackburn et al., 2019a, 2020; Delfino, 2020; Keeffe and Blackburn, 2020; Gómez and Turazzini, 2021). When studied thoroughly, isolated and fragmentary fossils have proven useful for the taxonomic and ecological characterization of frog assemblages, as well as for inferring past environmental and climatic conditions (Roček et al., 2010; Gardner et al., 2016; Pérez-Ben et al., 2019).

We report on the identity of frogs of three upper Campanian–lower Maastrichtian assemblages from Chilean and Argentinean Patagonia with focus on humeral morphology. We provide descriptions of the first Mesozoic frogs from Chilean Patagonia, which include the southernmost record of pipids worldwide. In addition, we discuss the potential value of anurans as diagnostic components of the Allenian tetrapod fauna, widespread across Patagonia near the end of the Cretaceous.

2. Geological and palaeontological framework

The fossils reported herein mostly come from strata belonging to the Allen (upper Campanian–lower Maastrichtian), Los Alamitos (Campanian–Maastrichtian), and Dorotea (upper Campanian–Danian) formations, cropping out at several localities across Argentinean and Chilean Patagonia (Fig. 1). These sedimentary formations represent fluviallacustrine, brackish environments (Uliana and Dellapé, 1981; Andreis, 1987; Manríquez et al., 2019) that existed near the end of the Cretaceous at the onset of the Atlantic transgression when the epeiric Kawas Sea extensively flooded Patagonia (Casamiquela, 1978; Hugo and Leanza, 2001). The fossiliferous strata containing fossil frogs in the Allen, Los Alamitos, and Dorotea formations are considered to have been deposited during the late Campanian–early Maastrichtian, according to palaeontological and stratigraphic data (Andreis, 1987; Bonaparte et al., 1987; Hugo and Leanza, 2001; Alarcón-Muñoz et al., 2020; George et al., 2020). In addition, fossiliferous levels in the Dorotea Formation have been radiometrically bracketed using U–Pb at between 71.7 ± 1.2 Ma and 74.9 ± 2.1 Ma (Gutiérrez et al., 2017), agreeing with an upper Campanian–lower Maastrichtian age according to the time scale of Cohen et al. (2013, updated).

The frog-bearing levels in the Allen Formation come from the lower part of this unit and were interpreted as having been deposited in a meandering fluvial system (Artabe et al., 2004). These levels are well exposed in the area of the Trapalcó and Santa Rosa depressions, northeastern Río Negro province, Argentina, with frog-bearing localities being Cerro Tortuga, Bajo de Santa Rosa, Cerro Bonaparte, and Cerro Alberto (e.g., Martinelli and Forasiepi, 2004; Rougier et al., 2009a; Gómez, 2016). Extensive outcrops at the Trapalcó and Santa Rosa depressions have yielded pipid and calyptocephalellid frogs (Agnolin, 2012; Gómez, 2016) as part of a rich assemblage of vertebrates, also including chondrichthyan and osteichthyan (siluriforms, lepisosteiforms, ceratodontid dipnoans) fishes (Martinelli and Forasiepi, 2004; Bogan et al., 2011), non-tribosphenic mammals (Rougier et al., 2009a), chelid and meiolaniform turtles (Broin and de la Fuente, 1993; Sterli et al., 2013), non-eilenodontine sphenodontians (Apesteguía and Rougier, 2007; Apesteguía and Jones, 2012), madtsoiid and anilioid snakes (Gómez and Báez, 2006; Gómez et al., 2008; Gómez, 2011), and diverse dinosaurs including hadrosaurids, titanosaurs, abelisauroids, and birds (Martinelli and Forasiepi, 2004; Agnolin and Novas, 2012).

A similar vertebrate assemblage has long been known in the middle part of the Los Alamitos Formation (Bonaparte et al., 1987), from the south-western slope of the Cerro Cuadrado, Estancia 'Los

Alamitos', southeastern Río Negro province, Argentina, from strata interpreted as having been deposited in a fluviallacustrine, brackish setting (Andreis, 1987). Besides pipid and calyptocephalellid-like frogs (Báez, 1987), this assemblage also includes chondrichthyan and osteichthyan (siluriforms, lepisosteiforms, perciforms, ceratodontid dipnoans) fishes (Cione, 1987), non-tribosphenic mammals (e.g., Bonaparte, 1987, 2002), chelid and meiolaniform turtles (Broin, 1987; Broin and de la Fuente, 1993; Sterli et al., 2013), non-eilenodontine sphenodontians (Apesteguía, 2005), madtsoiid snakes (Albino, 1987), and hadrosaurid, titanosaur, abelisauroid, and avian dinosaurs (Bonaparte and Rougier, 1987; Powell, 1987; Salgado et al., 1997; Agnolin and Martinelli, 2009).

The presence of frogs in the Dorotea Formation has only recently been preliminary reported at the Río de Las Chinas Valley, Última Esperanza province, Chile (Suazo Lara et al., 2017; Suazo Lara, 2019). The frog-bearing levels were interpreted as deposited in a meandering fluvial system on a coastal plain (Manríquez et al., 2019) and to date has also yielded fossils of non-tribosphenic mammals (Goin et al., 2020; Martinelli et al., 2021), chelid turtles (Alarcón-Muñoz et al., 2020), and ornithischian (including hadrosaurids), titanosaur, and theropod (including birds) dinosaurs (Kaluza et al., 2018; Manríquez et al., 2019). The palaeontological content of these levels suggests a more terrestrial environment and more limited marine influence than in other parts of the Dorotea Formation (Manríquez et al., 2019; Goin et al., 2020).

Fossil frogs from Patagonia (including extra-Patagonian terrains of the Neuquén Basin; Leanza et al., 2004) are also known from broadly coeval units in Argentina, as follows (Fig. 1): Loncoche Formation (González Riga, 1999), Mendoza province; La Colonia Formation (Muzzopappa and Varela, 2014; ROG pers. observ.), Chubut province; and Chorrillo Formation (Novas et al., 2019), Santa Cruz province; the latter being continuous with the Dorotea Formation in Chile (Manríquez et al., 2019). These records also consist of isolated and fragmentary remains and have been mostly referred to calyptocephalellids or to non-pipid anurans of uncertain affinities (González Riga, 1999; Agnolin, 2012; Muzzopappa and Varela, 2014; Novas et al., 2019). Among the abovementioned units, La Colonia Formation have yielded fossils that might represent more than one non-pipid, presumably neobatrachian, taxon (Muzzopappa and Varela, 2014), but their relationships remain indeterminate.

3. Materials and methods

The fossils described here consist of fragmentary but well-preserved isolated bones, obtained mainly through screen-washing techniques. The fossils are housed at the following institutions: Colección de Paleobiología de Antártida y Patagonia (CPAP) of the Chilean Antarctic Institute, Punta Arenas, Chile; Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Buenos Aires, Argentina; and the Museo Municipal de Lamarque (MML-PV), Lamarque, Argentina. New specimens reported herein are marked with an asterisk among listed materials in the *Systematic Palaeontology* section.

While we comment on some relevant aspects of the skull and ilia of fossil frogs, our study focuses on humeral morphology because that is the only element represented in all three of the studied assemblages. Also, the humerus is commonly recovered at Upper Cretaceous localities, but its systematic value has largely been overlooked in the study of South American extant and extinct anurans. Our general anatomical terminology is mainly based on that of Gaupp (1896) and Bolkay (1919), but translated into vernacular English as in Gómez (2016) or Keeffe and Blackburn (2020) and we also provide synonyms in order to minimize misunderstandings. Our terminology for the ilium follows Gómez and Turazzini (2016).

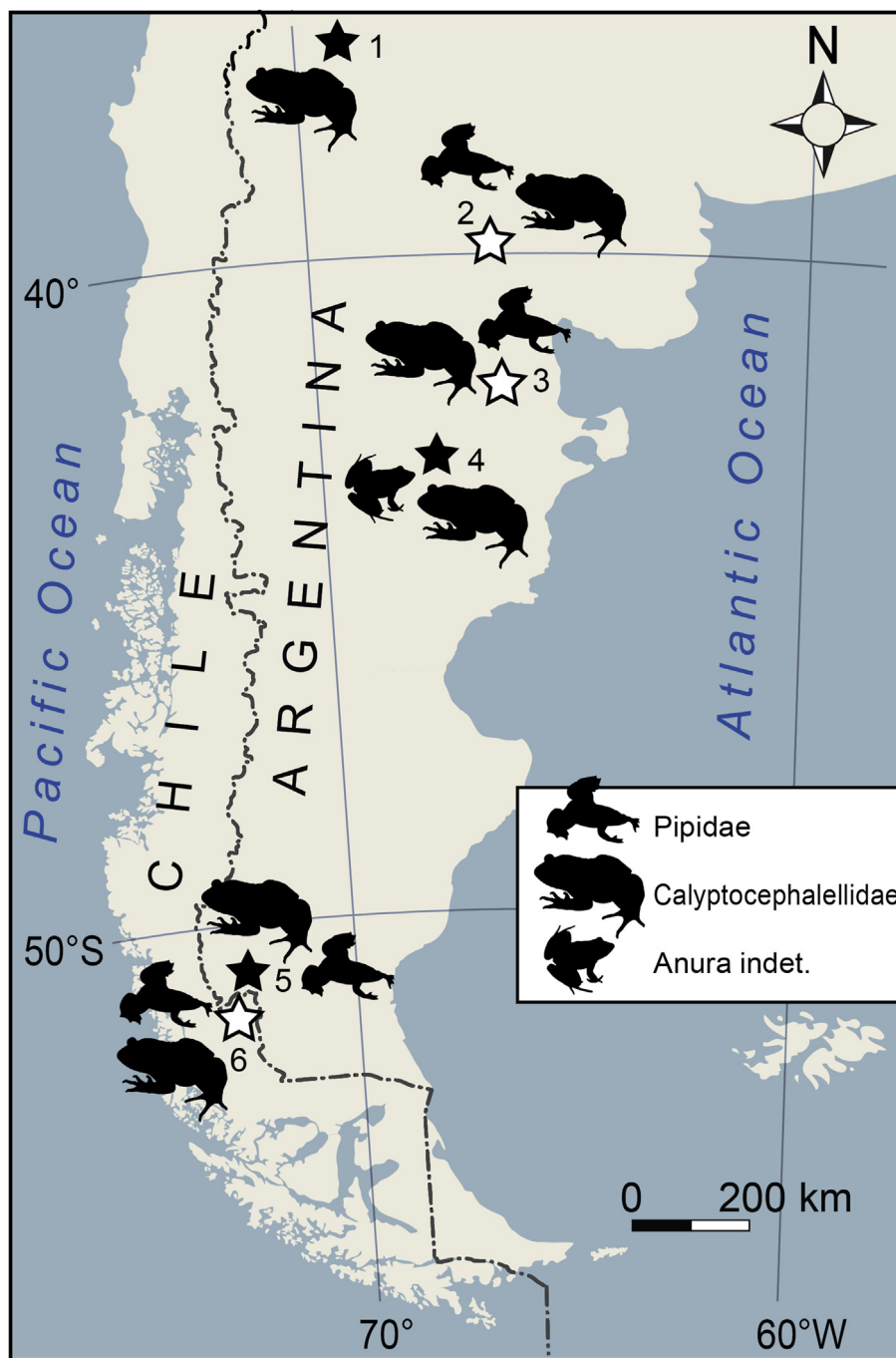


Fig. 1. Fossil record of anurans from the Campanian–Maastrichtian of Patagonia. Units: 1, Loncoche Formation, at Raquil-Co; 2, Allen Formation, at Cerro Tortuga, Bajo de Santa Rosa, Cerro Bonaparte, and Cerro Alberto; 3, Los Alamitos Formation, at Cerro Cuadrado; 4, La Colonia Formation, at El Uruguayo and nearby sites; 5, Chorrillo Formation, at La Anita; 6, Dorotea Formation, at Río de Las Chinas Valley.

For comparative purposes and visualization of the humeral morphology in relevant extant species, we generated digital three-dimensional (3D) models from X-ray computed microtomography (CT) data available at morphosource.org (Supplementary material). We obtained the 3D models using free, open source software, following the workflow outlined by Buser et al. (2020). Initial data treatment was done in Fiji/ImageJ v.1.53c (Schindelin et al., 2012) and segmentation and visualization of humeri models was performed in 3D Slicer v.4.11.2 (Fedorov et al., 2012; Kikinis et al., 2014). Additional comparative material consists of dry or cleared-and-stained skeletons (Supplementary material). Linear

measurements of the distal part of humeri in ventral view of the inter-epiphyseal maximum width (iew) and humeral ball (= eminentia capitata) maximum width (hbw) were taken digitally in Fiji.

3.1. Institutional abbreviations

AMNH – American Museum of Natural History, New York, USA; BAR – Museo Paleontológico de San Carlos de Bariloche, San Carlos de Bariloche, Argentina; CAS – California Academy of Sciences, San Francisco, USA; CFA – CEBBAD-Fundación Félix de Azara, Buenos Aires, Argentina; CPBA – Departamento de Ciencias Geológicas,

Universidad de Buenos Aires, Buenos Aires, Argentina; FCEN – Facultad de Ciencias Exactas y Naturales de la Universidad de Buenos Aires, Buenos Aires, Argentina; KU – Biodiversity Institute, University of Kansas, Lawrence, USA; MACN – Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina; MACN-PV – Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MHNG – Muséum d’Histoire Naturelle de Genève, Genève, Switzerland; MLP – Museo de La Plata, La Plata, Argentina; MML-PV – Paleontología de Vertebrados, Museo Municipal de Lamarque, Lamarque, Argentina; MPEF-PV – Paleontología de Vertebrados, Museo Paleontológico “Egidio Feruglio,” Trelew, Chubut, Argentina; MPM – Museo Padre Molina, Río Gallegos, Santa Cruz, Argentina; SAM – Iziko South African Museum, Cape Town, South Africa; SGO.PV – Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; UCHZV – Laboratorio de Zoología de Vertebrados, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile; UF – University of Florida, Florida Museum of Natural History, Gainesville, USA.

4. Systematic palaeontology

Anura Fischer, 1813

Xenoanura Savage, 1973 (= Pipoidea Ford and Cannatella, 1993)

Pipimorpha Ford and Cannatella, 1993

Pipidae Gray, 1825

Remarks. Pipids are an early diverging, but derived, group of highly aquatic anurans with a rich fossil record across their western Gondwanan distribution (Gómez and Pérez-Ben, 2019; Blackburn et al., 2019b). The earliest pipids are from the Late Cretaceous (Rage and Dutheil, 2008; Gómez, 2016), but closely related pipimorphs were already well diversified by the Early Cretaceous (Trueb et al., 2005; Gómez and Lires, 2019; Báez et al., 2021). To date, the pipid record from the Campanian–Maastrichtian of Patagonia consists of a few isolated fossils from a few localities in Río Negro province, Argentinean Patagonia, and includes a single named species (Gómez, 2016).

Kuruleufenia Gómez, 2016

Kuruleufenia xenopoides Gómez, 2016

(Figs. 2, 3A–B)

Material and occurrences. Occurrences of this taxon in the studied upper Campanian–lower Maastrichtian assemblages from Patagonia consist of isolated fragments of skull and postcranial bones from the Allen (including the holotype) and Los Alamos formations. Those from the Allen Formation were previously described and figured by Gómez (2016), when erecting this pipid genus and species. Formerly, some of these fossils were described and illustrated by Martinelli and Forasiepi (2004) as indeterminate Pipidae or Leptodactylidae. Some of those from Los Alamos Formation were described and illustrated by Báez (1987) as cf. *Xenopus* sp. Allen Formation, Cerro Tortuga, Bajo de Santa Rosa, Cerro Bonaparte, and Cerro Alberto localities, Río Negro province, Argentinean Patagonia: MACN-PV RN 1064 (Holotype), 1065, sphenethmoids; MML-PV 1057–1058, otic capsules; MML-PV 1047, 1062–1063, presacral; MML-PV 1059, sacrourostyle; MML-PV 1042, 1066, humeri; MML-PV 1060–1061, ilia. Los Alamos Formation, Cerro Cuadrado locality, Río Negro province, Argentinean Patagonia: MACN-RN 159 (bulk number), fragment of skull, presacral, ilium, humeri*, sphenethmoid*, sacrourostyle*, pelvis*.

Descriptions and remarks. The fossils from the Allen Formation, including the holotype MACN-PV RN 1064 (Fig. 2A), were described in detail by Gómez (2016) and some of the fossils from the Los Alamos Formation were previously described and illustrated as cf. *Xenopus* sp. (Báez, 1987). Here we illustrate two previously undescribed specimens (sphenethmoid and humerus: Figs. 2B and 3B, respectively) from the Los Alamos Formation and comment on the diagnostic features of these elements. The sphenethmoid is extensively ossified and completely encloses the orbitonasal foramina (= foramen nutritium of Bolkay [1919]) anteriorly (Fig. 2). The specimens from Los Alamos are broken posteriorly, so it is not possible to ascertain if the optic foramen was also completely enclosed by bone as in other pipids (Cannatella and Trueb, 1988; Gómez, 2016). As observed in the holotype MACN-PV RN 1064, sphenethmoids from the Los Alamos Formation (e.g., Fig. 2B) also show the diagnostic transverse constriction just posterior to the level of the orbitonasal foramina (Gómez, 2016). In addition, the frontoparietal fenestra extends anteriorly through a tapering embayment up to the tectum nasi, a feature considered autapomorphic of the species (Gómez, 2016).

The pipid humeri from the Los Alamos Formation also conform to the morphology of *K. xenopoides* (Fig. 3B). The humeral ball

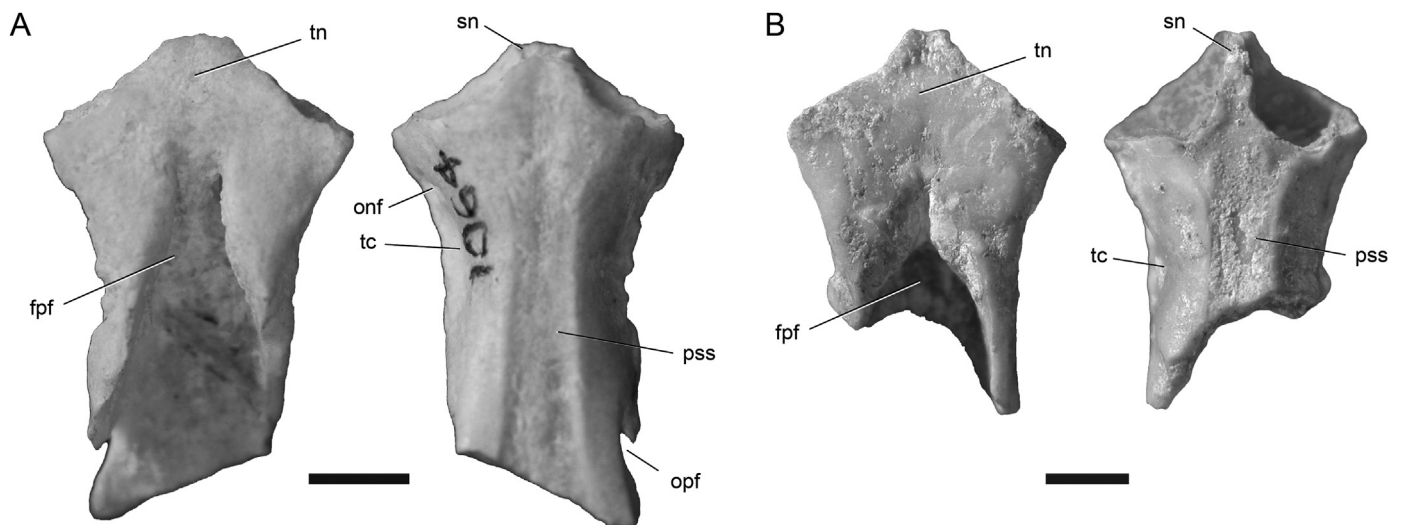


Fig. 2. *Kuruleufenia xenopoides* Gómez, 2016. Photographs of sphenethmoids in dorsal (left) and ventral (right) views: (A) MACN-PV RN 1064 (holotype) from the Allen Formation; (B) MACN-RN 159 from the Los Alamos Formation. Scale bars equal 2 mm. Abbreviations: fpf, frontoparietal fenestra; onf, orbitonasal foramen; opf, optic foramen; pss, parasphenoid scar; sn, septum nasi; tc, transverse constriction; tn, tectum nasi.

(= *eminencia capitata*) is small relative to the maximum interepicondylar width ($hbw/iww = 0.54\text{--}0.56$) and the humeral shaft (= *diaphysis*) appears to be straight and aligned with the former in all specimens, as in other pipids (Báez, 1987; Gómez, 2016). The epiphysis is well ossified and nearly symmetrical, with both epicondyles transversely expanded (a synapomorphy of Pipidae; Gómez, 2016), although the medial epicondyle (= *epicondylus ulnaris*) is more sharply pointed distally and separated from the humeral ball by a shallow groove. Most humeri from Los Alamitos preserve a fine medial crest (= *crista medialis*), although not as well developed as in MACN-PV RN 1066 (cf., Figs. 3B vs 3A), which has been regarded as autapomorphic of the species (Gómez, 2016); this subtle differences might be the result of ontogenetic variation or an incipient sexual dimorphism, as occurs in other anurans (Keeffe and Blackburn, 2020). In addition, humeri from the Los Alamitos Formation bear a large and deep triangular-shaped cubital fossa (= *fossa cubitalis ventralis*) that also show minor differences when compared to the fossils from the Allen Formation, although all specimens appear to fall within the range of variation observed in extant pipid species (ROG, pers. observ.). The remaining pipid fossils from Los Alamitos also conform to the morphology already described for the species (Gómez, 2016), but lack clear diagnostic features, although the presence of an oblique medial groove and an oblique lateral ridge on the base of the ilial shaft might entail some systematic value (Báez et al., 2012b; Gómez, 2016). Despite these elements having found isolated, their relative size, consistent morphology, and uniqueness of element morphotypes suggest that

they represent a single pipid taxon. The different bones are extensively ossified and their size, in general slightly larger than those from the Allen Formation (Supplementary material), is consistent with mature individuals of large extant pipids (Gómez, 2016).

***Kuruleufenia* sp.**
(Fig. 3C)

Material and occurrences. This taxon is recognized in the upper Campanian–lower Maastrichtian section of the Dorotea Formation, at Río de Las Chinas Valley, Última Esperanza province, Chilean Patagonia: CPAP 5881, distal end of right humerus*. This record was preliminary reported as cf. *Kuruleufenia* sp. by Suazo-Lara (2019). In addition, there is another specimen recently reported as an indeterminate pipid in the Chorrillo Formation, Santa Cruz province, Argentina (Moyano-Paz et al., 2022) that might also represent this taxon: MPM-PV-22840, a distal end of right humerus that is almost indistinguishable from CPAP 5881, although it represents a larger individual according to the originally reported size scale (Moyano-Paz et al., 2022).

Description and remarks. Although fragmentary, the humerus CPAP 5881 (Fig. 3C) is highly informative of its affinities. As with the humeri from the Los Alamitos Formation, the Chilean fossil also resembles the humeral morphology of *K. xenopoides*, though it is a little larger than any known Cretaceous pipid humeri from Argentina (Supplementary material). The epiphysis is well ossified and has both epicondyles transversely expanded, flanking a

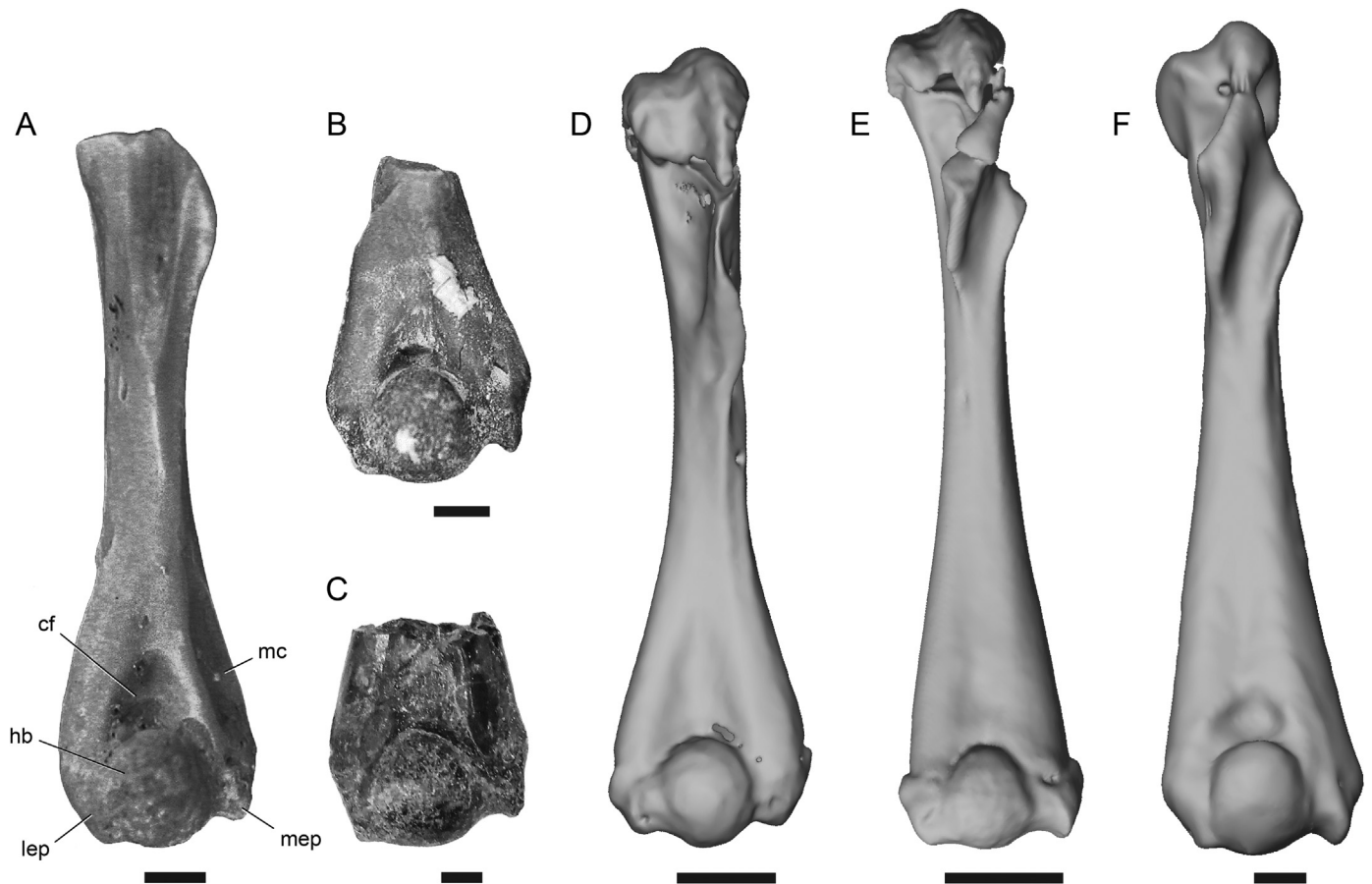


Fig. 3. Pipidae, right humeri in ventral view. *Kuruleufenia xenopoides*: (A) Allen Formation (MACN-PV RN 1066, photograph of nearly complete bone); (B) Los Alamitos Formation (MACN-RN 159, photograph of distal part); *Kuruleufenia* sp.: (C) Dorotea Formation (CPAP 5881, photograph of distal part). Extant Pipidae: (D) *Pipa parva* (UF 37924, CT scan); (E) *Xenopus clivii* (UF 92704, CT scan); (F) *Xenopus poweri* (MHNG 101781, CT scan). Scale bars equal 1 mm. Abbreviations: cf, cubital fossa; hb, humeral ball; lep, lateral epicondyle; mc, medial crest; mep, medial epicondyle.

relatively small humeral ball (hbw/iww = 0.57), as in extant pipids (Figs. 3D–F). CPAP 5881 shows the same morphology exhibited by MACN-PV RN 1066 of *K. xenopoides* from the Allen Formation (cf., Fig. 3C vs 3A), including a well-developed medial epicondyle, ending in a sharp point and separated from the humeral ball by a shallow groove, the shape and depth of the cubital fossa, and a distinct medial crest autapomorphic of that taxon (Gómez, 2016), although the epiphysis of CPAP 5881 is generally more robust. Despite CPAP 5881 having traits consistent with referral to *K. xenopoides*, we prefer to be conservative and do not go below the genus level, while we wait for more fossil material that would permit a better informed taxonomic referral.

Neobatrachia Reig, 1958

Australobatrachia Frost et al., 2006

Calyptocephalellidae Reig, 1960

Remarks. Calyptocephalellids are remnants of an ancient australobatrachian lineage, which today is restricted to water-bodies in temperate *Nothofagus* forests of south central Chile (Formas, 1979; Charrier, 2019). The group currently includes only four living species in two genera (AmphibiaWeb, 2021): *Telmatobufo* and the monotypic *Calyptocephalella*. In contrast to this restricted extant distribution, the calyptocephalellid fossil record extends across Argentinean Patagonia from the upper Campanian–lower Maastrichtian up to the Miocene (Muzzopappa, 2019). However, outside Argentinean Patagonia, previously described records are limited to the Eocene and Pleistocene of southern and central Chile, respectively (Otero et al., 2014; Labarca et al., 2020) and the Eocene of the Antarctic Peninsula (Mörs et al., 2020). Below we describe the oldest records of the group from the upper Campanian–lower

Maastrichtian of Argentinean and Chilean Patagonia, focusing on humeri.

Calyptocephalellidae indet.

(Fig. 4A–D)

Material and occurrences. Occurrences of this taxon in the studied upper Campanian–lower Maastrichtian assemblages from Patagonia consist of several isolated fragments of skull and postcranial bones from the Allen, Los Alamitos, and Dorotea formations. Many of those from the Allen Formation were described and figured by Martinelli and Forasiepi (2004) as indeterminate Leptodactylidae or Anura, and by Agnolin (2012) as a poorly diagnosed species of *Calyptocephalella* (see Muzzopappa et al., 2020). Note that Agnolin (2012) cited these fossils under different numbers (MML 847–851, 854–855, 857–860, 862–869, 872, 875, 886) than those under which are currently catalogued (see below). Those from Los Alamitos Formation were described by Báez (1987) as indeterminate Leptodactylidae, some of which were also illustrated. The record from the Dorotea Formation was preliminary reported by Suazo-Lara (2019).

Allen Formation, Cerro Tortuga and Bajo de Santa Rosa localities, Río Negro province, Argentinean Patagonia: MML-PV 875, premaxilla; MACN-PV RN 1063, MML-PV 874, 1041, 1044, 1049, 1051, 1056, maxillae; MACN-PV RN 1069, MML-PV 1035, 1045, 1055, frontoparietals; MML-PV 1050, squamosal; MACN-PV RN 1069, MML-PV 1037–1039, 1043, small fragments of skull; MACN-PV RN 1068, angulosplenials; MML-PV 873, 1033–1034, atlases; MACN-PV RN 1067, MML-PV 1036, post-atlantal presacrals; MML-PV 886, 1040, 1048, sacral vertebrae; MML-PV 876, 1046, 1054, urostyles; MML-PV 1053(1–2), humeri; MACN-PV RN 1070, MML-PV 1052,

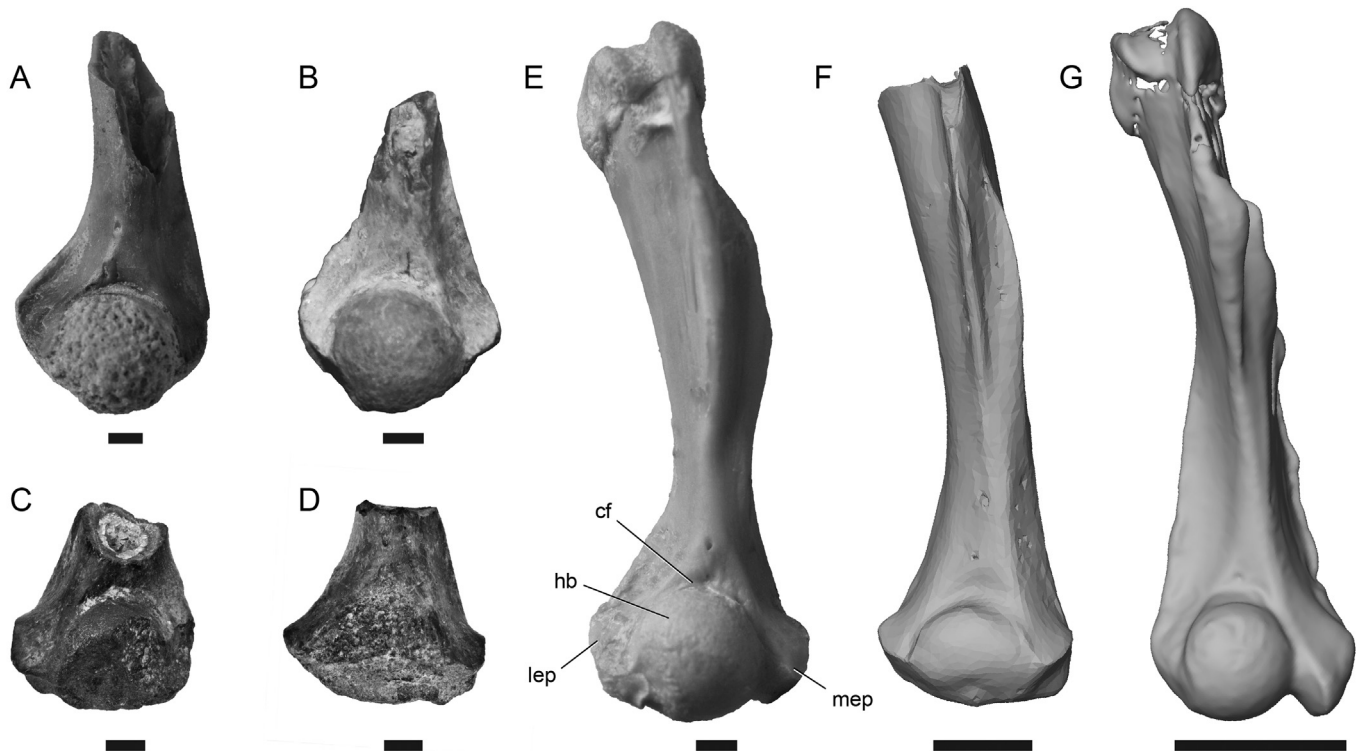


Fig. 4. Calyptocephalellidae, humeri in ventral view. *Calyptocephalella*-like humeri: (A) Allen Formation (MML-PV 1053, photograph of distal part of right element); (B) Los Alamitos Formation (MACN-RN 160, photograph of distal part of right element); (C, D) Dorotea Formation (CPAP 5878 and 5879, photographs of distal parts of left and right humeri, respectively). Extant Calyptocephalellidae: (E) *Calyptocephalella gayi* (FCEN 2066, photograph of adult right element); (F) *Calyptocephalella gayi* (CAS 10082, CT scan of subadult right element); (G) *Telmatobufo bullocki* (KU 161438, CT scan of adult right element). Scale bars equal 2 mm. Abbreviations: cf, cubital fossa; hb, humeral ball; lep, lateral epicondyle; mep, medial epicondyle.

radioulnae. Los Alamitos Formation, Cerro Cuadrado locality, Río Negro province, Argentinean Patagonia: MACN-RN 160 (bulk number), maxillae, squamosal, humeri, ilium. Dorotea Formation, Río de Las Chinas Valley, Última Esperanza province, Chilean Patagonia: CPAP 5878–5879, distal end of humeri*. In addition, there are other materials of roughly the same age that also represent this taxon: MACN-M 14, distal end of right humerus, from the Loncoche Formation, at Ranquil C6 fossiliferous locality, Mendoza province, Argentina (González Riga, 1999); MPM 21519, distal end of right humerus and MPM-PV-22841–22846, fragments of maxilla and postcranial bones from the Chorrillo Formation, Santa Cruz province, Argentina (Novas et al., 2019; Moyano-Paz et al., 2022); and several as yet undescribed fossils from the La Colonia Formation, from several sites on the southeastern slopes of the Somún Curá Massif, Chubut Province, Argentina (Muzzopappa and Varela, 2014; ROG pers. observ.).

Description and remarks. The humeri from the Dorotea Formation were preliminary reported by Suazo Lara et al. (2017). Fossils from the Los Alamitos Formation were previously described as indeterminate Leptodactylidae by Báez (1987), but considered similar to *Calyptocephalella* (as *Caudiverbera*), some of which were commented on and illustrated as calyptocephalellids by Gómez et al. (2011). Fossils from the Allen Formation at Bajo de Santa Rosa were previously described as indeterminate Leptodactylidae or Anura by Martinelli and Forasiepi (2004), whereas those from Cerro Tortuga were described as a poorly diagnosed species of *Calyptocephalella* (see Muzzopappa et al., 2020), *C. satan* Agnolín, 2012. The latter species was erected based on a fragment of maxilla, an element that was incorrectly interpreted and reconstructed by Agnolín (2012), according to Muzzopappa et al. (2020). In addition, Muzzopappa et al. (2020) noted that the features used to diagnose *C. satan* are also present in other calyptocephalellids, which raises doubts about whether the species can be reliably diagnosed. Finally, many other anatomical and methodological inaccuracies in the work of Agnolín (2012) have also been pointed out (Báez and Gómez, 2018; Muzzopappa et al., 2020). Clearly, a thorough revision of the work of Agnolín (2012) is warranted in order to elucidate the validity and extension of the *Calyptocephalella* species from the Upper Cretaceous of Patagonia. Therefore, *C. satan* should be considered *species inquirenda* awaiting a more comprehensive assessment of available fossils.

All the non-pipid fossil humeri from the upper Campanian–lower Maastrichtian assemblages studied herein represent Calyptocephalellidae (Fig. 4A–D), showing a size and morphology close to that of adults of extant *Calyptocephalella gayi* (Fig. 4E). As in the latter, the shaft of the fossil humeri strongly widens distally into a robust epiphysis. The more complete specimens show that the epiphysis is tilted laterally relative to the shaft proximo-distal axis. A large spherical humeral ball (= eminentia capitata) is flanked by similarly developed, prominent epicondyles, thus providing a rather symmetrical aspect to the distal end of the bone, presumably unique to *Calyptocephalella* among Neotropical anurans (Báez, 1987; Gómez et al., 2011; Otero et al., 2014). Relative to the epiphyseal width, the humeral ball of fossil humeri is proportionally larger ($hbw/iew = 0.63–0.65$) than in extant and most extinct calyptocephalellids (Gómez et al., 2011; Otero et al., 2014; Supplementary material). In some cases, the humeral ball is well ossified as in mature extant *Calyptocephalella* (Fig. 4E), contrasting with the condition in subadults (Fig. 4F), but several fossil specimens show epicondyles eroded or incompletely ossified distally. Medial and lateral crests are distinct towards the distal epiphysis, although the medial crest is more developed than the lateral one. The cubital fossa is shallow and crescent-shape and a nutrient foramen often pierces the bone near its proximal margin.

These fossil humeri are clearly *Calyptocephalella*-like and agree with other available skeletal elements and most previous work on these materials (Báez, 1987; Gómez et al., 2011; Agnolín, 2012). Their morphology clearly contrasts with those of the only other living calyptocephalellid, *Telmatobufo* (Fig. 4G). In the species of *Telmatobufo* available to us, the distal epiphysis is markedly asymmetrical and the medial and lateral crests are much more developed. Because the interrelationships of *Calyptocephalella*-like forms are still uncertain and the validity of some taxa is debated (Muzzopappa et al., 2020), we opt not to assign these isolated remains below the family level.

5. Discussion

Since the milestone work of Bonaparte and colleagues on the fauna from the Los Alamitos Formation (Bonaparte et al., 1987), extensive knowledge on Campanian–Maastrichtian vertebrates has been amassed from different stratigraphic units and localities across Patagonia (Leanza et al., 2004; Martinelli and Forasiepi, 2004; Rougier et al., 2010; Sterli et al., 2013; Novas et al., 2019; Alarcón-Muñoz et al., 2020). Most of this knowledge, however, has been built on findings from northern Argentinean Patagonia and the characterization of these Upper Cretaceous faunal assemblages has fundamentally been based on large dinosaur taxa (Leanza et al., 2004; Juárez Valieri et al., 2010; García and Salgado, 2012; Gianechini et al., 2015). Noteworthy, great efforts at different microvertebrate localities have contributed to a better understanding of the nature and composition of the tetrapod assemblages, mainly through the study of different reptile taxa (turtles, snakes, sphenodontians) and mammals (e.g., Leanza et al., 2004; Martinelli and Forasiepi, 2004; Apesteguía and Rougier, 2007; Gómez et al., 2008; Rougier et al., 2009a, 2009b, 2010; Sterli et al., 2013; Gasparini et al., 2015; Alarcón-Muñoz et al., 2020; Goin et al., 2020), with anurans having received increasing attention in recent years (Agnolín, 2012; Gómez and Báez, 2012; Muzzopappa and Varela, 2014; Gómez, 2016; Suazo Lara, 2019).

Tetrapod assemblages across northern Argentinean Patagonia, from lithostratigraphic units bracketed below by the Huantraiquian unconformity and above by the marine Jagüel Formation and equivalents (i.e., Loncoche, Allen, Los Alamitos, Angostura Colorada, and La Colonia formations), were defined by Leanza et al. (2004) as part of an Allenian assemblage (= “Alamitian” of Bonaparte et al., 1987; Flynn and Swisher, 1995). This assemblage was defined by the co-occurrence of several continental tetrapod taxa of typical Gondwanan lineages together with some putative Laurasian immigrants (Leanza et al., 2004). Characteristic taxa previously recognized for the assemblage are hadrosaurid and ankylosaurian ornithischians, armored small saltasaurine titanosaurs, large eutitanosaurs, large carnosaurine abelisauroids, and ornithothoracine birds (Bonaparte and Rougier, 1987; Powell, 1987; Salgado et al., 1997; González Riga, 1999; Leanza et al., 2004; Martinelli and Forasiepi, 2004; Agnolín and Martinelli, 2009; García and Salgado, 2012), coupled with the presence of non-tribosphenic mammals (e.g., dryolestoids, gondwanatheres), crocodyliforms (mesoeucrocodylians and neosuchians), chelid and meiolaniform turtles, madtsoiid and anilioid snakes, and non-eilenodontine sphenodontians (Albino, 1987; Broin and de la Fuente, 1993; González Riga, 1999; Leanza et al., 2004; Martinelli and Forasiepi, 2004; Apesteguía, 2005; Apesteguía and Rougier, 2007; Gómez et al., 2008, 2019; Rougier et al., 2009a, 2009b, 2010; Apesteguía and Jones, 2012; Sterli et al., 2013; Gasparini et al., 2015).

Anurans were not originally considered in the definition of the Allenian tetrapod assemblage (Leanza et al., 2004), although pipid and ‘leptodactylid’ frogs had been considered components of this

assemblage (Báez, 1987; Leanza et al., 2004; Martinelli and Forasiepi, 2004). Frogs previously have been reported from typical Allenian units, such as the Loncoche, Allen, Los Alamitos, and La Colonia formations (Báez, 1987; González Riga, 1999; Agnolín, 2012; Muzzopappa and Varela, 2014; Gómez, 2016), although the uncertain systematic affinities of most of these records have limited their value as defining taxa of the Allenian assemblage. Additionally, frogs were reported from other units, farther south in Patagonia, including the Chorrillo (Novas et al., 2019) and Dorotea (Suazo Lara et al., 2017; Suazo Lara, 2019) formations, the latter of which were here described.

In Argentina, fossil pipids were previously described only from the Allen and Los Alamitos formations (Báez, 1987; Martinelli and Forasiepi, 2004; Gómez, 2016). Those from the Los Alamitos Formation were originally thought to be closely allied to the extant African *Xenopus* (Báez, 1987), whereas those from the Allen Formation were recently described as an extinct species, *Kuruleufenia xenopoides*, interpreted as part of an early South American radiation within the lineage leading to *Xenopus* (Gómez, 2016). Interestingly, we identified in the fossils from the Los Alamitos Formation some diagnostic (autapomorphic) traits of *Kuruleufenia xenopoides* (Gómez, 2016) in the sphenethmoid (transverse constriction just posterior to the level of the orbitonasal foramina; frontoparietal fenestra extending anteriorly through a tapering embayment) and the humeri (medial epicondyle ending in a sharp distal point and separated from the humeral ball by a shallow groove; fine medial crest), confirming that this species is also part of the assemblage from the Los Alamitos Formation. In addition, the pipid frog from the Dorotea Formation, which represents the first pipid from Chile and the southernmost record of pipids worldwide, as well as the recently reported pipid from the Chorrillo Formation (Moyano-Paz et al., 2022), are here interpreted as an indeterminate species of *Kuruleufenia* based on the abovementioned diagnostic features of the humerus. To summarize, all currently-known pipid frogs from the upper Campanian–lower Maastrichtian of Patagonia belong to *Kuruleufenia*.

Despite ‘leptodactylid’ frogs having been considered part of the Allenian assemblage (e.g., Leanza et al., 2004), it has to be noted that several frog lineages traditionally referred as ‘leptodactylids’ (e.g., Báez, 1987; González Riga, 1999; Martinelli and Forasiepi, 2004) are not necessarily closely related to the Neotropical family Leptodactylidae under the current phylogenetic framework of anuran interrelationships (e.g., Streicher et al., 2018). Instead, known ‘leptodactylids’ from the Cretaceous–Palaeogene of Patagonia belong to Calyptocephalellidae (see Gómez et al., 2011; Agnolín, 2012), an ancient lineage within the Gondwanan clade Australobatrachia (Frost et al., 2006; Streicher et al., 2018). That family level re-assignment had previously been recognized in earlier works (Báez, 1987; Martinelli and Forasiepi, 2004), which stressed a particular resemblance to *Calyptocephalella* (as *Caudi-verbera* therein), but under an earlier systematic framework (e.g., Lynch, 1971). We confirm the presence of *Calyptocephalella*-like calyptocephalellids in the Allen and Los Alamitos formations, and, based on isolated humeri, also identified this taxon in the Dorotea Formation. This referral is mainly based on the shape of prominent epicondyles well projected at both sides of the humeral ball, a putative autapomorphic feature of *Calyptocephalella* (Báez, 1987; Gómez et al., 2011; Otero et al., 2014). These represent the oldest records of Calyptocephalellidae and accord well with most molecular-based time estimates that date the diversification of the group at some point during the Early Cretaceous (Kumar et al., 2017), implying that the early history of this lineage is as yet not documented in the fossil record.

Our study demonstrates that anurans are valuable defining taxa of the Allenian assemblage, with *Calyptocephalella*-like

calyptocephalellids and the pipid *Kuruleufenia* being the only taxa currently identified with certainty. These anurans are limited to this Patagonian assemblage and have not yet been reported elsewhere in South America (Báez et al., 2012a; Gómez, 2016; Báez and Gómez, 2018), nor they occur in older or younger Patagonian assemblages, in which known pipoids and calyptocephalellids represent different forms (Gómez et al., 2011; Gómez, 2016; Muzzopappa et al., 2020), thus reinforcing their reliability as Allenian diagnostic taxa. Furthermore, the frog records from the Dorotea Formation described herein, coupled with the already known tetrapod taxa from this Chilean unit (Manríquez et al., 2019; Alarcón-Muñoz et al., 2020; Goin et al., 2020; Martinelli et al., 2021) and the partially equivalent Chorrillo Formation in Argentina (Novas et al., 2019; Chimento et al., 2021; Moyano-Paz et al., 2022), indicate that the Allenian tetrapod assemblage reached southernmost Patagonia. The Allenian tetrapod assemblage can be recognized all across Patagonia, including its southernmost region, by the joint occurrence of *Calyptocephalella*-like calyptocephalellids and *Kuruleufenia* frogs, gondwanathere mammals, chelid turtles, madtsoiid snakes, hadrosaurid and ankylosaurian ornithischians, large titanosaurs, abelisaurid theropods, and ornithothoracine birds. The inferred ecological requirements of these anurans and other tetrapod taxa agree well with previous interpretations of the deposition of the fossil-bearing levels as occurring in fluviolacustrine environments and generally humid conditions (Andreis, 1987; Artabe et al., 2004; Manríquez et al., 2019; Novas et al., 2019). Extant members of Pipidae and *Calyptocephalella*, which nowadays do not inhabit the same region, are aquatic and there is evidence that these taxa share lacustrine environments in Argentinean Patagonia at least until the Middle Eocene (Gómez et al., 2011), implying a long history of this lifestyle for both taxa. Finally, it is worth mentioning that the frogs from the Dorotea Formation represent the first Mesozoic anurans from Chile and, in agreement with recent studies (Otero et al., 2014; Matthews et al., 2015; Blackburn et al., 2019a, 2020; Delfino, 2020), highlight the value of humeral morphology in diagnosing and identifying fossil frogs.

6. Conclusions

The identity of upper Campanian–lower Maastrichtian frogs from the Dorotea, Allen, and Los Alamitos formations of Patagonia provides evidence of a widespread anuran assemblage. Records from the Dorotea Formation represent the first described Mesozoic frogs from Chile, which include the southernmost record of pipids worldwide. Noteworthy, all currently known pipid frogs from the Campanian–Maastrichtian of Patagonia are *Kuruleufenia*. In the three assemblages we have identified humeri of *Kuruleufenia* and *Calyptocephalella*-like frogs; proving humeral morphology is valuable for diagnosing and identifying Cretaceous frogs from Patagonia. Our work shows that these frogs emerge as diagnostic components of the South American Allenian tetrapod assemblage that was widespread across Patagonia near the end of the Cretaceous. Future work on anurans from the Upper Cretaceous of Argentinean and Chilean Patagonia, including greater prospection efforts in the field as well as thorough reassessments of known fossils, will certainly improve our understanding of data presented here. Particularly relevant will be refining the taxonomy of *Calyptocephalella*-like frogs, which would allow a better grasp of the diversity of Allenian frogs.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2021.105085>.