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The taxonomic placement of the Miocene Patagonian frog *Wawelia gerholdi* (Amphibia: Anura)

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The Miocene frog *Wawelia gerholdi*, from northern Patagonia, was previously attributed to Ceratophryidae, the clade of extant South American horned frogs, making it one of the oldest records known for this group. However, the only known specimen has juvenile traits and is strongly similar to the australobatrachian *Calyptocephalella*. We re-examined the morphology of *W. gerholdi* and provide additional anatomical information and comparisons with juvenile individuals of Ceratophryidae and *Calyptocephalella gayi*, the only extant species of *Calyptocephalella*. We reject a close relationship between *W. gerholdi* and Ceratophryidae. Furthermore, the holotype is indistinguishable from juveniles of *C. gayi* and shares with all the species of this genus a character state combination that seems unique among anurans. Therefore, we consider *Wawelia* to be a junior synonym of *Calyptocephalella*. The problematic taxonomic status of numerous fossil species of *Calyptocephalella*, together with its untested monophyly, also prompts us to provisionally consider the extinct species as a *species inquirenda* included in this genus, pending a comprehensive revision of all available remains.

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WAWELIA GERHOLDI is a fossil anuran collected from lower Miocene sediments exposed near the locality of Ingeniero Jacobacci, in the northern Patagonian province of Río Negro, Argentina (Casamiquela 1963, Bilmes *et al.* 2013). To date, only a single specimen is known: an impression of the postcranium and a skull fragment derived from a presumed juvenile individual (Casamiquela 1963, Báez & Perí 1990). This fossil has been placed in Ceratophryidae (Casamiquela 1963, Báez & Perí 1990), the extant clade of South American horned frogs, and has even been resolved as nested in this clade in recent phylogenetic analyses (Evans *et al.* 2008, 2014, Laloy *et al.* 2013). *Wawelia gerholdi*, therefore, potentially represents one of the oldest fossil ceratophryids and it has been considered evidence of the presence of Ceratophryidae in the Miocene for divergence time estimations (Marjanović & Laurin 2007). A few known stratigraphically older remains have been attributed to ceratophryids (Báez & Perí 1989, Evans *et al.* 2008, 2014) but these are presently under re-evaluation (Báez, pers. com., 2014).

Some authors have alternatively noted similarities between *W. gerholdi* and *Calyptocephalella* (Casamiquela 1963, Báez & Perí 1990), a South

American genus closely related to myobatrachoids (Frost *et al.* 2006, Pyron & Wiens 2011). This group also has a conspicuous Patagonian record at least since the Eocene (Cione & Báez 2007, Muzzopappa & Báez 2009, Muzzopappa & Nicoli 2010, Gómez *et al.* 2011). Given the potential significance of *W. gerholdi* as one of the oldest putative ceratophryids, we re-examined the holotype for additional anatomical information and compared the taxon with juvenile specimens of both Ceratophryidae and *Calyptocephalella gayi* to study its taxonomic affinities.

Material and methods

The holotype of *W. gerholdi* (MLP 62-XII-7-1, Fig. 1A) is an imprint. Therefore, a new silicon cast was prepared to examine novel information from a positive replica; it reveals more details than the cast used by previous authors. The analysis of the new cast shows that the fossil has suffered considerable damage in the preserved portion of the skull and the anterior presacral vertebrae since previous studies in the 1990s (Fig. 1). As a comparative sample, we observed dry and cleared and double-stained skeletons of relevant extant species from several herpetological collections (see below) using a Nikon SMZ 800 stereomicroscope with a drawing tube.

	<i>Wawelia gerholdi</i> MLP 62-XII-7-1	<i>Calyptocephalella gayi</i> MACN 45750	<i>Ceratophrys</i> <i>cranwelli</i> MACN 47991
Vertebral column (I–VIII)	16.3	16.0	14.2
Neural arch PV IV width/length	6.0/1.5	5.5/1.9	4.1/2.3
Length of transverse process PV IV	5.6	4.7	6.6
Femur	19.2	20.0	17.9

Table 1. Comparative measurements of *W. gerholdi* and selected juvenile specimens of *Calyptocephalella* and *Ceratophrys*. Measurements are expressed in millimetres. They were obtained directly from the cast. Only completely preserved elements were measured.

Institutional abbreviations follow Sabaj Peres (2014) with the addition of: LIHUBA, Laboratorio de Investigaciones Herpetológicas de la Universidad de Buenos Aires, Buenos Aires, Argentina; and MMH, Museo de Ciencias Naturales ‘Vicente Di Martino’, Monte Hermoso, Provincia de Buenos Aires, Argentina.

Specimens examined (*dry skeletons; †fossils): *Alsodes gargola* MACN 37845, 37930, 37951, 38942. *Atelognathus patagonicus* CENAI 1070–1; *A. reverberii* MACN 33973; *A. salai* MACN 41327; *Batrachyla antantardica* MACN 47402; *B. leptopus* MACN 38006, 41291; *B. taeniata* CENAI 6865-6, 6921; *Calyptocephalella gayi* MACN 39894–39901, 45741–7*, 45749–50, 45751*; *Ceratophrys ameghinorum*† MACN 14317–9, 14324–5, 19731, MLP 52-IX-27-11, 88-VII-20-1–2; MMH 84-1-15, 85-2-11; *C. calcarata* AMNH 177036*; *C. cranwelli* MLP 273*; FML 5472*, 5474–7*; *C. ornata* LIHUBA 1051*, MLP 137*, 247*, FML 1193*; *Chacophrys pierottii* MACN 47403*–4*; FML 1019, 9012; *Crossodactylus schmidtii* MACN 35122. *Eupsophus calcaratus* MLP 4011; *E. roseus* MACN 37976, 37979, 37981; *E. vertebralis* MACN 43704*; *Hymenochirus boettgeri* MACN 42621; *Insuetophrynus acarpicus* CENAI 6896; *Lepidobatrachus asper* FML 5469*–70*; *L. laevis* FML 13703*–4*, 13709*, 1089*; *L. llanensis* CENAI 8519, FML 420*, 1016*, 5220–1*, 1089*; *Lepidobatrachus australis* MMH 85-12-2a. *Limnomedusa macroglossa* MACN 4644, MLP 1410; *Odontophrynus achalensis* CENAI 2972, 2975, 2977; *O. americanus* CENAI 3938–9, 3939, 3942, MACN 25236, 25237; *O. carvalhoi* MNRJ 15358; *O. cordobae* CENAI 4522, MACN 26199; *O. cultripes* CENAI 9839, 9841; *O. lavillai* CENAI 5811, 6461, 5794, 6465; *O. maisuma* MLP 4828, ZVCB 1517; *O. occidentalis* MACN 24953, 26228, 26229; MLP 4385, 3916; *O. salvatori* MNRJ 27756; *Proceratophrys appendiculata* CENAI 9064; *P. avelinoi* MACN 36854, MLP 938; *P. boiei* MLP 76; *P. cristiceps* MNRJ 15358; *Rhinella major* MACN 45955; *Rhinoderma darwini* CENAI 5491; *Telmatobius bolivianus* CBF 2063, 5379; *T. marmoratus* CBF 2167, 3621, KU 164079–80*; *T. oxycephalus* FML 2867, 3836; *T. rubigo* FML 20829; *T. verrucosus* CBF 2765, 5372.

Description

Báez & Perí (1990) described *Wawelia gerholdi* in detail, and we provide only supplemental information

here. The holotype consists of the imprint of an incomplete semi-articulated skeleton in dorsal view (Fig. 1). The limited cranial components include an ornamented bone fragment with a subtriangular well-delimited portion and a poorly defined and more ventral lateral portion. The postcranium comprises an almost complete series of nine vertebrae plus the urostyle, parts of the pectoral and pelvic girdles, and some elements from both the fore and hindlimbs. We focus here on novel observations that add to or modify the description provided by Báez & Perí (1990).

The vertebral neural arches are short, broad and non-imbricate. The widest neural arch is that of the fourth presacral vertebra (PV IV), whose width is more than twice its length (Fig. 1). The preserved portions of the transverse processes (TP) on PV III and IV, suggest that they were robust and long (in its longest axis), being even longer than the sacral diapophyses. It is not possible, however, to establish their relative extension. The TP of the posterior presacral vertebrae are shorter than the sacral diapophyses, with their length decreasing slightly from PV V to PV VII. An irregular sacralization is evident in vertebrae VIII and IX, indicating that a malformation on the axial skeleton took place during the development of this individual.

The sacral diapophyses of the specimen are moderately expanded distally, but given its evident malformations, this condition can not be considered a diagnostic character. Vertebra IX is preserved rotated and in posterior view. It has a circular neural canal and two well-developed condyles for the bicondylar articulation with the urostyle. The urostyle itself is incomplete, but two cotyles are clearly exposed. A medial longitudinal groove on the dorsal surface of the urostyle indicates that it was still underdeveloped (Ridewood 1902, Marelli 1927, Kovalenko & Danylevskaia 1994, Kovalenko 1995, Púgener & Maglia 2009a, b).

A disarticulated clavicle is displaced to the left of the vertebral column (Fig. 1C, D). Although its posterior margin is obscured by other elements, it was clearly long and strongly curved. An expanded proximal articular facet for the scapula is also well exposed (Fig. 1C, D). The distal end of the left scapula is also discernible and is expanded to at least twice the diameter of the distal humeral head. Two laminar elements situated over the left TP of PV III, and the right portion of PV II–V, respectively, are here interpreted as the cleithra. The distal half of the left humerus is visible beneath the

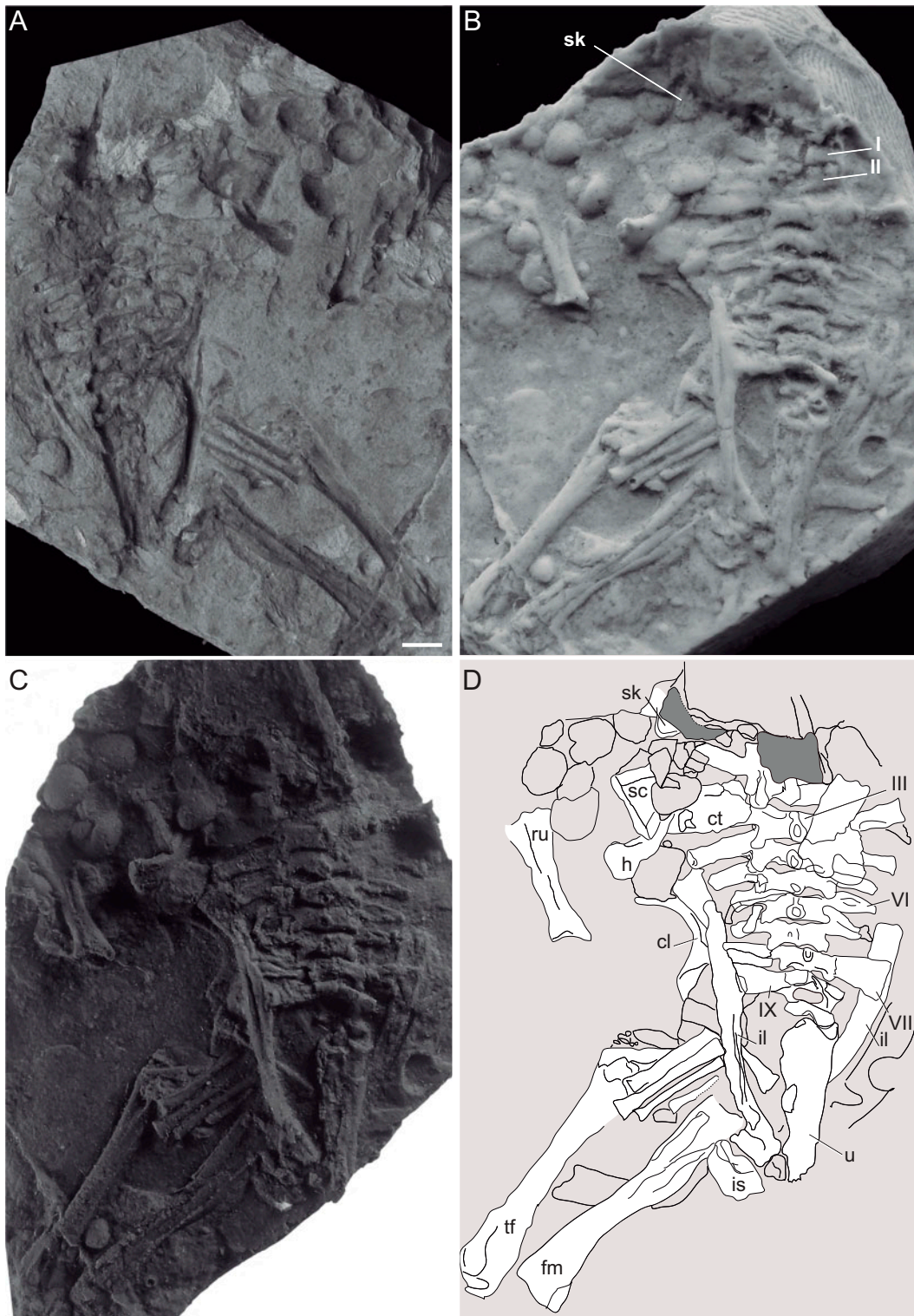


Fig. 1. *Wawelia gerholdi*. **A**, Only known specimen (MLP 62-XII-7-1). **B**, Cast prepared for the study of Báez & Perí (1990). **C**, New cast. **D**, Interpretative illustration of the new cast. Dark grey shows the area that has suffered damage. Note that part of the skull and the first vertebrae evident in the latex cast are not currently preserved in the fossil (and new cast). Abbreviations: fm, femur; h, humerus; il, ilium; is, ischium; cl, clavicle; ct, clithrum; ru, radioulna; sc, scapula; sk, skull; tf, tibiofibula; u, urostyle; Roman numerals indicate vertebral number. Scale bar = 5 mm.

scapula. This is slightly curved and has an incompletely ossified epiphysis, in which the humeral ball and epicondyles are partially unossified. Despite this, the humeral ball is conspicuous and occupied most of the distal

end of the element. A well-developed radioulna (i.e., the fusion of the radius and ulna has already occurred) is evident lateral to the humerus.

The pelvic girdle is retained close to its life position (Fig. 1). The left ilium bears a dorsal crest along most of its length. No dorsal prominence is evident, which could be a consequence of incomplete preservation of the margin of the crest. The left ischium bears an acetabular fossa and a laminar, posterodorsal expansion (Fig. 1).

Discussion

As noted by Báez & Perí (1990), *Wawelia gerholdi* possesses several characteristics that are commonly present in juvenile anurans: unfused right and left portions of neural arches of PV I and II (Fig. 1B, evident on the original cast but now damaged in the fossil); neural spines incompletely ossified (evidenced by medial depressions on the neural arches); an incompletely developed urostylar dorsal crest; and a poorly ossified humeral ball and femoral epiphyses (Fig. 1). Some of these features are evident in adults of some poorly ossified anuran taxa (e.g., *Atelognathus patagonicus*, *Leiopelma hochstetteri*; Stephenson 1952), but adults of these species also possess poorly ossified skulls. *Wawelia gerholdi*, on the other hand, has conspicuous ornamentation on the skull, which is indicative of at least some hyperossification. The ornamentation or exostosis of the skull bones is a consequence of additional bone deposition or hyperossification, which usually involves the overall skeleton. The co-occurrence in the known specimen of *W. gerholdi* of ornamented skull bones and the unossified portions of the postcranial skeleton indicates that this specimen represents an early stage of development.

The presence of sacralization in TPs of vertebrae VIII and IX, and the asymmetrical TPs on the posterior PV are interpreted as malformations of the axial skeleton. These are common in anurans and include irregular sacralization of either the eighth vertebra or urostyle (e.g., Ridewood 1902, Marelli 1927, Kovalenko & Danylevskaya 1994, Kovalenko 1995, Púgener & Maglia 2009a, b).

Previous taxonomic placements of Wawelia gerholdi

Wawelia gerholdi has been repeatedly referred to Ceratophryidae (Casamiquela 1963, Báez & Perí 1990, Evans *et al.* 2008, 2014, Laloy *et al.* 2013). Ceratophryidae includes 12 extant species within *Ceratophrys*, *Chacophrys* and *Lepidobatrachus* (Frost 2015). Its monophyly has been corroborated in phylogenetic analyses that variably include some or near all ceratophryid species (Haas 1999, Fabrezi 2006, Frost *et al.* 2006, Grant *et al.* 2006, Evans *et al.* 2008, 2014, Fabrezi & Quinzio 2008, Pyron & Wiens 2011, Faivovich *et al.* 2014). Other fossil remains have also been attributed to the group (Günther 1859, Vergnaud-Grazzini 1968, Báez & Perí 1989, Perí 1993, Rinderknecht 1998, Femicola 2001, Agnolín 2005,

Evans *et al.* 2008, 2014, Stoessel *et al.* 2008, Tomassini *et al.* 2011, Nicoli 2014).

The first referral of *W. gerholdi* to Ceratophryidae was by Casamiquela (1963). His approach was to exclude anuran groups that do not have extant species in the same habitat inferred for the fossil locality, and those that lack at least one of the following characters present in the fossil: ornamented dermal skull roof, long distal portion of the scapula, long TP of presacral vertebrae, or moderately expanded sacral diapophyses. Following this reasoning, he concluded that *W. gerholdi* was related either to *Calyptocephalella* or to Ceratophryidae but a close relationship with *Calyptocephalella* was discarded owing to its putative larger adult size and what was interpreted as a different orientation of the TP of PV III in comparison with those of *W. gerholdi*.

Báez & Perí (1990) re-analyzed *W. gerholdi*, tentatively accepting its attribution to Ceratophryidae, but repeatedly emphasized the ontogenetic immaturity of the holotype and its similarity with *Calyptocephalella* (= *Caudiverbera* in Báez & Perí 1990). These authors focused their comparisons on those groups of anurans that show some degree of dermal bone ornamentation on the skull roof. Among these, they based their association with Ceratophryidae on the TP on the anterior presacrals being longer than sacral diapophyses. This character state, which has been considered a synapomorphy of Ceratophryidae (Lynch 1971, 1982), although unquestionable as such, is not exclusive to this group and is also present in *Calyptocephalella* (Muzzopappa *et al.* 2015).

More recently, *W. gerholdi* was incorporated in a series of phylogenetic analyses, always resulting in it being nested in Ceratophryidae (Evans *et al.* 2008, 2014, Laloy *et al.* 2013). The analysis by Evans *et al.* (2008) is based on modifications of the dataset published by Fabrezi (2006). The analyses by Laloy *et al.* (2013) and Evans *et al.* (2014) are based on the same morphological dataset. This is a combination of the dataset of Báez *et al.* (2009), which is a modification of that of Fabrezi (2006) and the dataset of Evans *et al.* (2008). Evans *et al.* (2014) combined this morphological dataset with aligned molecular data obtained from the analysis by Pyron & Wiens (2011). Aspects of these studies have been questioned by Báez *et al.* (2009), Gómez *et al.* (2011) and Faivovich *et al.* (2014). Nevertheless, these analyses were not designed to explore the position of *Wawelia* in the context of the currently known anuran phylogenetic diversity and, thus, neither the taxon sampling nor the character analyses are sufficiently broad (or adequate) for this purpose. Moreover, some of the characters scored for *W. gerholdi* in these analyses are contestable (see below), and both Evans *et al.* (2008, p. 2954) and Evans *et al.* (2014, p. 45) expressed doubt over the topological positioning of *W. gerholdi* obtained in their analyses.

On the basis of the descriptions provided by Casamiquela (1963) and Báez & Perí (1990), Evans *et al.* (2008, 2014) and Laloy *et al.* (2013) scored *Wawelia* for about 10% of the characters included in the analyses. In the corrected dataset of Evans *et al.* (2014), nine characters of the 75 characters included in the analyses were scored for *Wawelia*. The cranial exostosis, scored as present for *Wawelia* by Evans *et al.* (2008), was scored as unknown by Evans *et al.* (2014). The scored characters in this later analysis include five for which we have no objections (eight presacral vertebrae [Ch. 34: 1], bicondilar sacro-urostilar articulation [Ch. 43: 0], absence of TP in urostyle [44: 1], absence of free ribs [46: 0], well-developed dorsal crest on iliac shaft [66: 1]), but four of them are problematic. These issues may reflect an inadequate appreciation for the immaturity of the only known specimen and / or an incomplete consideration of the available descriptions. The problematic scorings are:

Ch. 37. Presacral vertebrae, imbrication of posterior-most four neural arches: imbricated (37: 0). As noted by Báez & Perí (1990); *W. gerholdi* lacks imbricated neural arches, although this could be a result of its juvenile condition. This character should be scored as unknown character state.

Ch. 38. Presacral vertebrae, height of neural spines in anterior presacrals: low (38: 0). The neural spines of *W. gerholdi* are incompletely ossified. Therefore, this character should be scored as unknown character state.

Ch. 39. Presacral vertebrae, orientation of TP of the 6th presacral: nearly perpendicular to axial axis (39: 0). Although the TPs of PV VI of *W. gerholdi* are nearly perpendicular to the midline, they are asymmetrical (Fig. 1). The same trait is evident in the TP of PV VII. The posterior column of *W. gerholdi* might include irregular elongation and shape of the TP and sacral diapophyses (evident in vertebrae VIII and IX) as occurs in other anurans with atypical axial development (e.g., Kovalenko & Danylevskaya 1994, Kovalenko

1995, Púgener & Maglia 2009a, b). Therefore, we advocate scoring of this character as unknown.

Ch. 42. Sacral vertebrae, expansion of diapophyses: moderately dilated sacral diapophyses (anterior and posterior margins of sacral rib clearly divergent, distal end of rib flared by comparison with proximal end, but less than total sacral width; 42: 1). See discussion for character 39 (above).

When the data matrix is updated (supplemental files, F1-Matrix) and the phylogenetic analysis redone (see details on the supplemental files, F2-Phylogenetic analysis), the optimal topologies do not recover a close relationship between *W. gerholdi* and ceratophryids, unlike the results of Evans *et al.* (2014). There are multiple equally parsimonious positions of *W. gerholdi* within Neobatrachia (see results in the supplemental files, F2-Phylogenetic analysis).

Is Wawelia gerholdi a ceratophryid? A reappraisal of the evidence

Several osteological synapomorphies have been proposed for Ceratophryidae (Fabrezi 2006, Fabrezi & Quinzio 2008), but most involve skeletal elements not preserved in the holotype of *W. gerholdi*. Only two, non-exclusive to the family, however, can be evaluated in the fossil: the cranial exostosis and the absence of an ilial dorsal crest. *Wawelia gerholdi* presumably had cranial exostosis as indicated by the ornamented skull elements. A similar condition occurs in various anuran groups and is also present in *Calyptocephalella*, some clades of Bufonidae, Hemiphractidae, Hylidae and the ranoid *Pyxicephalus*, among others (e.g., Parker 1881, Tihen 1962, Trueb & Duellman 1978, Trueb 1970, Sheil 1999). The preserved ilion of *W. gerholdi* possesses a well-developed dorsal crest, unlike the nearly cylindrical iliac shaft of Ceratophryidae (Fig. 2B). Although a shallow ridge is evident on the anterior portion of the ilial shaft in some ceratophryids



Fig. 2. Girdles of selected anurans. **A, C**, Juvenile *Ceratophrys ornata* (FML 1193). **B, D**, *Calyptocephalella gayi* (**B**, MACN 47109; **D**, Juvenile MACN 45743). **A, B**, Pectoral girdle, ventral view; **C, D**, Pelvic girdle, lateral view. Scale bar = 3 mm.

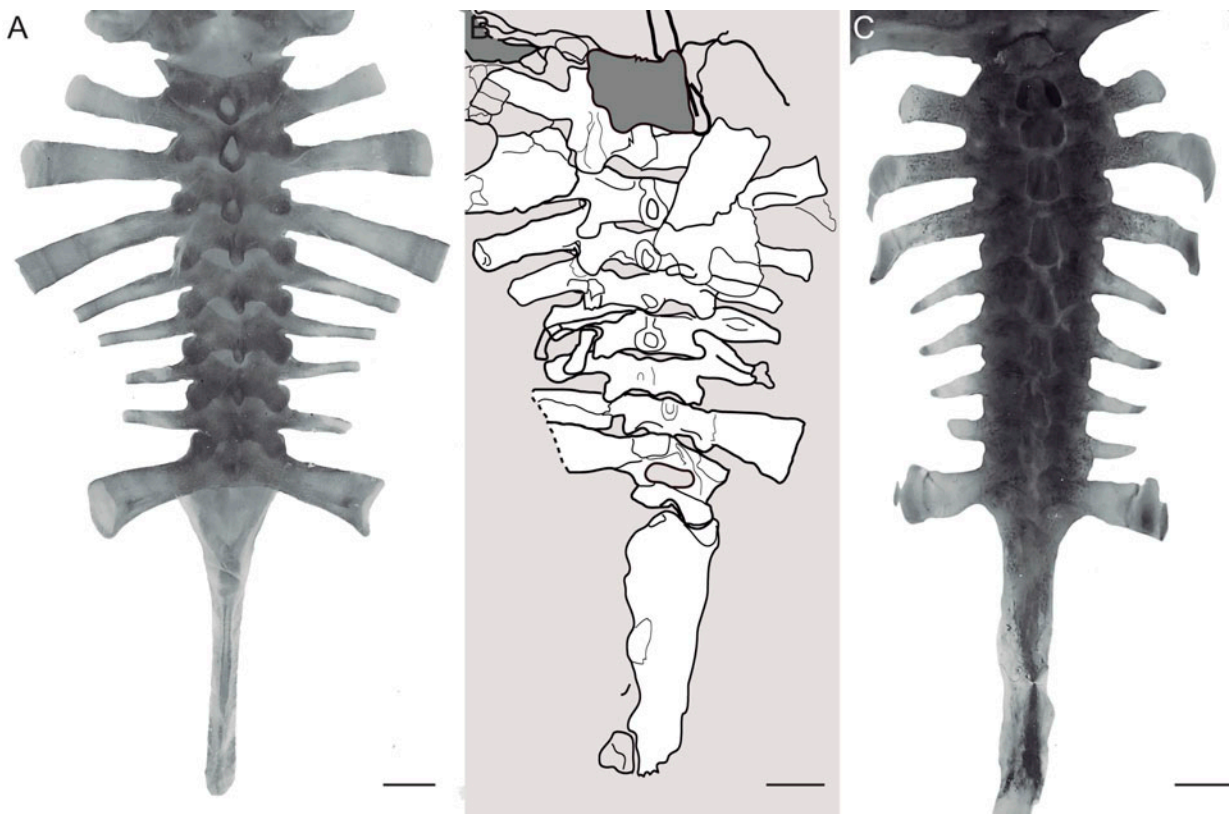


Fig. 3. Vertebral columns of selected anurans. A, Juvenile *Ceratophrys cranwelli* (MACN 47991). B, *Wawelia gerholdi* (MLP 62-XII-7-1). C, Juvenile *Calyptocephalella gayi* (MACN 45743). Scale bar = 3 mm.

[e.g., *C. cornuta* (Wild 1997) and *C. ornata* (LIHUBA 1051; FML 1193)], they never bear a dorsal crest.

Wawelia gerholdi differs from Ceratophryidae, even from juvenile specimens, in several aspects of the vertebral proportions and the morphology of the elements of the pectoral girdle. The neural arches of *W. gerholdi* are broader and shorter than those of Ceratophryidae, in which the length of the neural arch of the PV IV is less than twice its width. This condition is also visible in juvenile specimens with similar size and degree of ossification to that of *W. gerholdi* (Fig. 3A, Table I). The anterior TPs of both *W. gerholdi* and ceratophryids are longer than the sacral diapophyses (Fig. 3A, B). However, the TP length is subequal to the width of the corresponding neural arches in *W. gerholdi*; this is otherwise much greater in ceratophryids (Fig. 3A, B, Table I). Finally, although *W. gerholdi* possesses a long and strongly curved clavicle, this bone in ceratophryids is short and, in most cases, nearly straight (Fig. 2A; except for the short, slightly curved clavicle of *Chacophrys pierottii*).

Wawelia gerholdi as a juvenile of *Calyptocephalella*

Calyptocephalella is a southern South American genus of large, robust-bodied frogs with hyperossified skulls. At present, it includes four fossil and extant species. The single extant species, *C. gayi*, inhabits water-bodies of the temperate rainforest in south-central Chile (Ceï 1962). However, the fossil record indicates a past distribution of

the genus in Argentinian Patagonia, east of the Andes, at least during the Eocene–Miocene (Schaeffer 1949, Gómez *et al.* 2011; see Supplemental file F3). Even older, poorly preserved anuran remains from the Paleocene and Upper Cretaceous are also likely referable to this genus (Báez 1987, Martinelli & Forasiepi 2004, de la Fuente *et al.* 2007; see Supplemental file F3).

A series of phylogenetic analyses, based mainly on molecular data, proposed a sister-group relationship of *Calyptocephalella* and the endemic Chilean *Telmatobufo* (Frost *et al.* 2006, Pyron & Wiens 2011). This clade, Calyptocephalellidae, is closely related to Australopapuan Myobatrachoidea (Limnodynastidae + Myobatrachidae) and, thus, is placed within Australobatrachia (Frost *et al.* 2006, Pyron & Wiens 2011). No putative phenotypic synapomorphies have yet been identified for *Calyptocephalella*. Despite this, *W. gerholdi* is indistinguishable from juveniles of *Calyptocephalella gayi*. Besides their similar proportions, they also share ornamented skull surfaces, non-imbricated, broad and short neural arches whose width is about twice their length, elongate TPs in the anterior presacral vertebrae that are equal to the width of the corresponding neural arch and longer than the sacral diapophyses, an elongate and curved clavicle, and a well-developed dorsal crest above the iliac shaft (Figs 2C, D, 3C, Table I). The only observed differences between *W. gerholdi* and *C. gayi* are the teratological condition of the vertebral column in the former taxon. This character state combination does not seem to appear in other anurans, thus we

consider *Wawelia* to be a junior synonym of *Calyptocephalella*.

Fossil remains of *Calyptocephalella* are numerous but fragmentary and their taxonomic assignment is equivocal (see Supplemental file F3). In addition, monophyly of the genus has not yet been tested. In this context, we consider it preferable at present to redefine MLP 62-XII-7-1 as *Calyptocephalella gerholdi* comb. nov. species inquirenda pending a more comprehensive revision of all available material.

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Disclosure statement

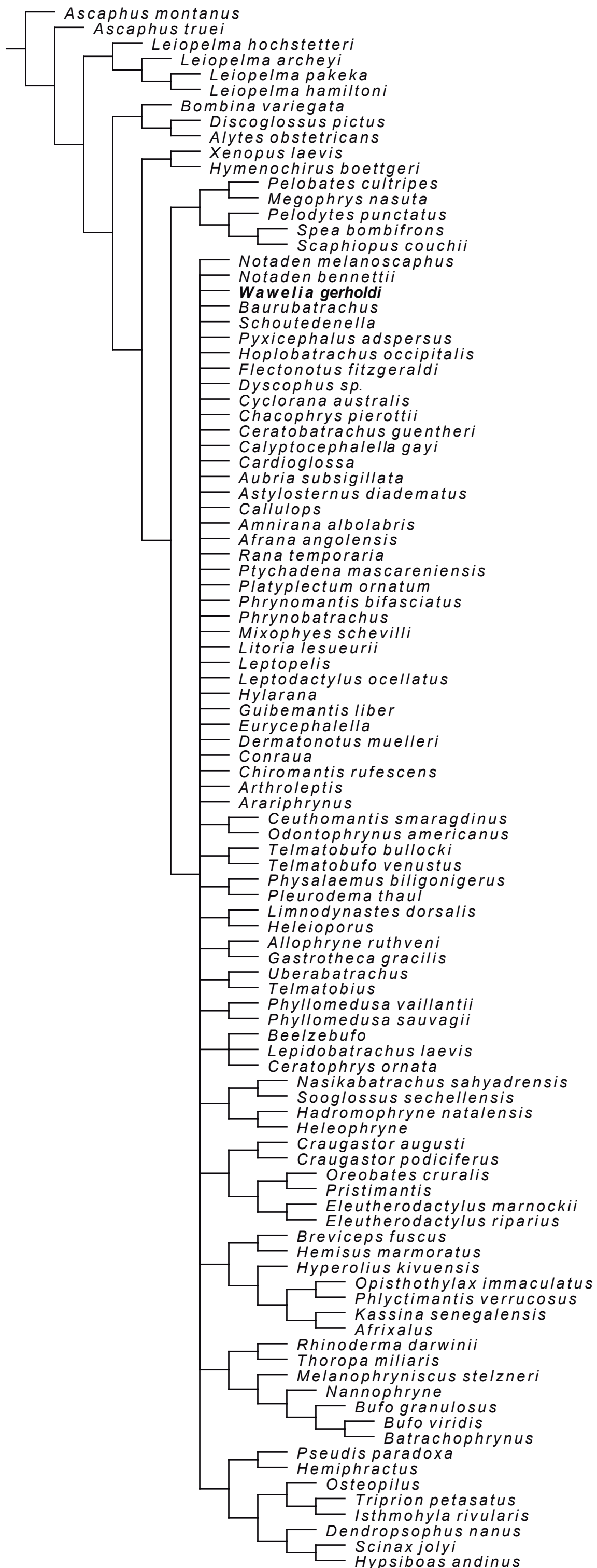
No potential conflict of interest was reported by the authors.

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Phylogenetic analysis.- The phylogenetic analysis performed on the T.N.T Willi Hennig Soci Edition (Goloboff et al., 2008) software package using the New Technology search command, using search level 15, and requesting 20 hits in the driven search. The resulting topologies were then submitted to a final round of TBR. The analysis resulted in 114 most parsimonious trees (strict consensus provided below) of 36014 steps.



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Fossil record of *Calyptocephalella*

TAXONOMIC ASSIGNMENT	PROCEDENCE	REFERRED MATERIAL	REFERENCE
Leptodactylidae <i>indet.</i> ; a close affinity with <i>Calyptocephalella</i> (as <i>Caudiverbera</i>) is mentioned in the discussion.	(1) Bajo de Santa Rosa Loc., Allen Fm. (Upper Cretaceous). Río Negro, Argentina	MACN-PV RN 1063, 1066,1069	Martinelli & Forasiepi 2004
“Leptodactylidae”; considered possibly related to <i>Calyptocephalella</i> (as <i>Caudiverbera</i>) in the discussion.	(2) Los Alamitos Loc., Los Alamitos Fm. (Upper Cretaceous). Río Negro, Argentina	MACN-RN 160	Báez 1987 de la Fuente <i>et al.</i> 2007
<i>cf. Calyptocephalella</i> (as <i>Caudiverbera</i>)	(3) Punta Peligro Loc., Salamanca Fm. (Paleocene). Chubut, Argentina	MACN-CH 1625	Bonaparte <i>et al.</i> 1993
? <i>Calyptocephalella</i> (as <i>Caudiverbera</i>)	(4) Las Flores Fm. (Paleocene–Eocene). Chubut, Argentina	Repository not mentioned Not described / not illustrated	Báez 2000
<i>Calyptocephalella pichileufensis</i>	(5) Río Pichileufú Loc., Huitrera Fm. (Eocene). Río Negro, Argentina	BAR85a, BAR85b	Gómez <i>et al.</i> 2011 Kramarz <i>et al.</i> 2011

<i>Calyptocephalella casamayorensis</i> (as <i>Eophractus</i>)	(6) Cañadón Hondo Loc., Sarmiento Fm. (Eocene). Chubut, Argentina	AMNH 3165 (holotype); 3164.	Schaeffer 1949 Lynch 1971
? <i>Calyptocephalella</i> (as <i>Caudiverbera</i>)	(7) Confluencia Loc., Huitrera Fm. (Eocene). Neuquén, Argentina	CP-Bar 2466-1-A & B (tadpole) Not described / not illustrated	Báez <i>et al.</i> 1990 Báez 2000 Kramarz <i>et al.</i> 2011
Calyptocephalellidae indet.	(8) Sierra Dorotea Loc., Río Turbio Fm. (Eocene). Magallanes Region, Chile	SGO.PV.6546.	Otero <i>et al.</i> 2014
<i>Calyptocephalella canqueli</i> (as <i>Caudiverbera</i>)	(9) Scarritt Pocket Loc., Sarmiento Fm. (Oligocene). Chubut, Argentina	AMNH 3429 (holotype); 3400; 3427; 3401 (tadpole). CPBA-V 14084 (tadpole)	Schaeffer 1949 Muzzopappa & Báez 2009 Muzzopappa & Nicoli 2010
<i>Calyptocephalella canqueli</i>	(10) Puesto Baibíán Loc., Sarmiento Fm. (Miocene). Chubut, Argentina	MPEF-PV1498; 1881–1890	Muzzopappa & Báez 2009

<i>Calyptocephalella canqueli</i> (as <i>Caudiverbera</i>)	(11) Gran Barranca Loc., Sarmiento Fm. (Presumably Colhue-Huapi member, Miocene). Chubut, Argentina	AMNH 3236– 3239, 3241 Not described / not illustrated	Schaeffer 1949
<i>Calyptocephalella</i> sp. (as <i>Caudiverbera</i>)	(11) Gran Barranca Loc., Sarmiento Fm. (presumably Colhue-Huapi member, Miocene). Chubut, Argentina	MACN 11656-1 – 11656-49	Báez 1977
<i>Calyptocephalella gayi</i> (as <i>Gigantobatrachus parodii</i>)	(12) Laguna Blanca Loc. (Miocene). Santa Cruz, Argentina.	MLP 59-VII-30-1 (holotype of <i>G.</i> <i>parodii</i>)	Casamiquela 1958 Lynch 1971
<i>Calyptocephalella gayi</i> (as <i>Gigantobatrachus parodii</i>)	(12) Río Guenguel Loc. (Miocene). Santa Cruz, Argentina	MLP 59-VII-30-2	Casamiquela 1958 Lynch 1971
<i>Calyptocephalella gayi</i> (as <i>Gigantobatrachus parodii</i>)	(13) Barranca de los Loros Loc., Los Loros Fm. (Miocene). Rio Negro, Argentina	MLP 61-IV-6-2	Casamiquela 1963 Lynch 1971
<i>Calyptocephalella</i> sp.	(14) Estancia La Costa Loc., Santa Cruz Fm. (Miocene). Santa Cruz, Argentina	MPM-PV 3712, 3507. CORD-PZ 1232	Fernicola & Albino 2012

<i>Calyptocephalella gayi</i>	(15) Laguna de Taguatagua SGO.PV.410–415 Loc., Laguna de Taguatagua Fm. (Upper Pleistocene). O'Higgins, Chile	Casamiquela 1976 Jiménez- Huidobro <i>et al.</i> 2009 Otero <i>et al.</i> 2014
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Numbers in brackets, numbers of Fossiliferous localities in the Map . Fm.: Formation; Loc.: Locality. Institutional Abbreviations: AMNH: American Museum of Natural History, New York, USA; BAR: Museo Paleontológico de San Carlos de Bariloche, Río Negro, Argentina; CPBA-V, Facultad de Ciencias Exactas y Naturales-Paleontología de Vertebrados (Universidad de Buenos Aires), Buenos Aires, Argentina; MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (CH, Chubut Collection, PV, Paleontología de Vertebrados, RN, Río Negro Collection), Buenos Aires, Argentina; MLP: Museo de La Plata, Buenos Aires, Argentina; MPEF-PV: Paleontología de Vertebrados, Museo Paleontológico "Egidio Feruglio", Chubut, Argentina; MPM-PV: Museo Regional Provincial “Padre Manuel Jesús Molina”, Santa Cruz, Argentina; SGO.PV: Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; CORD-PZ: Museo de Paleontología de la Universidad Nacional de Córdoba, Colección Paleozoología, Córdoba, Argentina.

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Fossiliferous localities with remains referred to *Calyptcephalella*. Localities are listed on Table in Supplementary File 3. (1) Bajo de Santa Rosa Loc., (2) Los Alamitos Loc., (3) Punta Peligro Loc., (4) Las Flores Fm., (5) Rio Pichileufú Loc., (6) Cañadón Hondo Loc., (7) Confluencia Loc., (8) Sierra Dorotea Loc., (9) Scarritt Pocket Loc., (10) Puesto Baibián Loc., (11) Gran Barranca Loc., (11) Gran Barranca Loc., (12) Río Guen-guel Loc. (13) Barranca de los Loros Loc., (14) Estancia La Costa Loc., (15) Laguna de Taguatagua Loc.