A glimpse at the ontogeny of the fossil neobatrachian frog *Calyptocephalella canqueli* from the Deseadan (Oligocene) of Patagonia, Argentina

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Two fossil tadpoles collected in the Deseadan levels (Oligocene) at the Scarritt Pocket locality of central Patagonia are studied herein. These specimens, which show different degrees of skeletal development, have been assigned to the neobatrachian *Calyptocephalella canqueli* based on the morphology of the frontoparietals and the presence of adult specimens of this fossil species at the same locality. The concurrent analysis of three developmental stages (Gosner Stages 35/36 and 38/39, and adult) has provided significant data about the ontogeny of this species, including the change of the pattern of exostosis of the frontoparietals, from a pitted to a tuberculated pattern, and the corroboration of the inclusion of two neural arches in the formation of the urostyle. This evidence will shed light on developmental mechanisms that might be involved in the evolution of the genus *Callyptocephalella*.

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Introduction

Calyptocephalella (formerly *Caudiverbera*, see Russell and Bauer 1988; Myers and Stothers 2006 for nomenclatorial changes) is an endemic South American genus of neobatrachian frog characterized by the extensive ossification of the skull and the tubercular ornamentation of the roofing bones. The single living species, *Calyptocephalella gayi*, is restricted to the temperate region of Chile, from the Región Central (Aconcagua Province) to Puerto Montt (i.e., between 30° and 42° S) (Cei 1962). However, fossil remains recovered from sediments that range from the uppermost Cretaceous (Los Alamitos locality, in Rio Negro, Argentina (Báez 1987) to the Pleistocene (Laguna de Tagua, Tagua archeological locality, in Chile (Casamiquela 1976; Jiménez-Huidobro et al. 2009) have been assigned, or considered related, to *Calyptocephalella* (mostly as *Caudiverbera*).

Calyptocephalella canqueli is one such fossil species erected by Schaeffer (1949) from a few, well-preserved articulated remains from the Deseadan Scarritt Pocket locality in central Chubut, Argentina (Fig. 1). Although the validity of the species was questioned by Lynch (1971), Muzzopappa and Báez (2009) recently revalidated *C. canqueli* based on a revision of the original specimens and the analysis of new

fossil material from a new locality, Puesto Baibián, also in Chubut (Fig. 1).

Calyptocephalella has been traditionally considered a close relative of other South American neobatrachian taxa (Lynch 1971, 1978; Formas 1979; Formas et al. 2001). However, several recent phylogenetic analyses based on molecular data (San Mauro et al. 2005; Correa et al. 2006; Frost et al. 2006) resulted in a sister taxon relationship between *Calyptocephalella* and the South American genus *Telmatobufo,* with this monophyletic clade positioned within the Australian myobatrachoids.

Two well-preserved, undescribed specimens from the Scarritt Pocket locality that we interpret to be tadpoles of *Calyptocephalella canqueli* are described herein. One of these specimens was recovered by George Gaylord Simpson in 1934 and deposited in the collection of the American Museum of Natural History, labeled as "frog?". The other specimen was collected by Justino Hernández, Galileo Scaglia, and Julio Contreras in 1964 and deposited in the collection of Vertebrate Paleontology, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. The examination of this material reveals aspects of the ontogeny of this extinct taxon. Moreover, work underway (by PM) on the ontogeny of the extant *C. gayi* provides a fairly complete developmen-
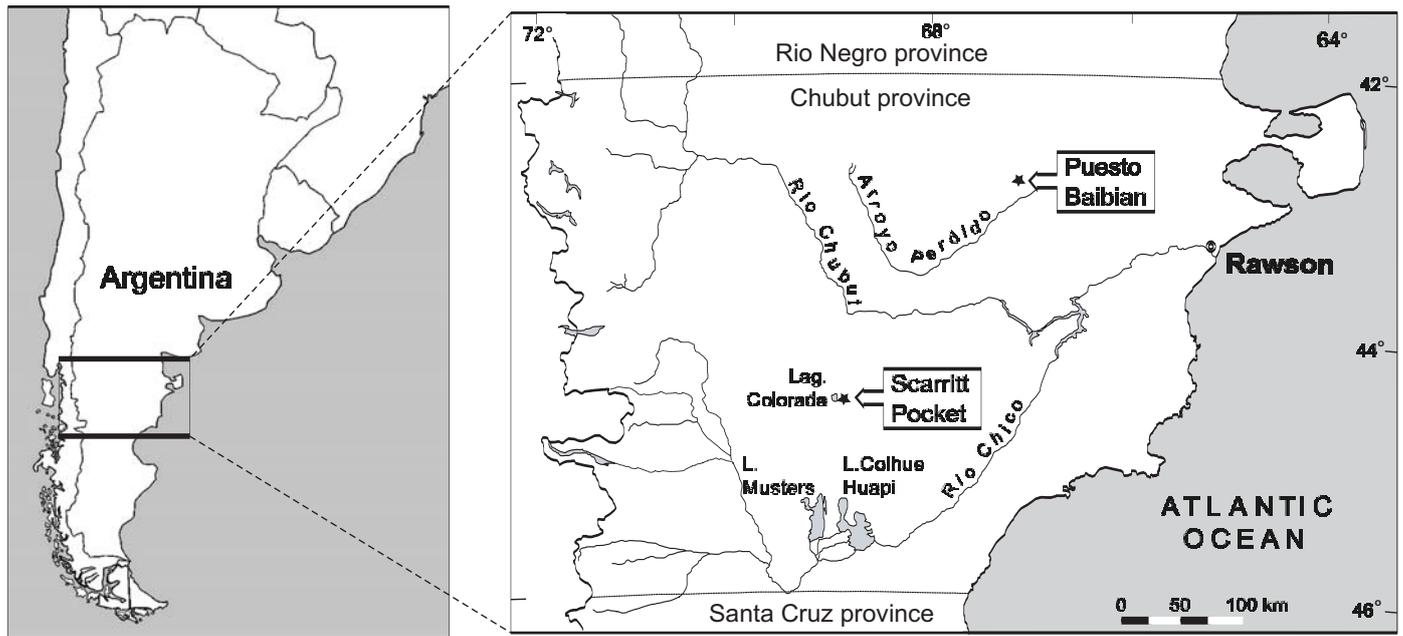
Fig. 1. Location map showing the paleontological localities Scarritt Pocket and Puesto Baibián (Sarmiento Group, Deseadan) in Chubut, Argentina.

tal series for comparison (see Table 1). The description of the ontogeny of *Calyptocephalella canqueli* represents the first results of ongoing research into the osteological development of the species of *Calyptocephalella*.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; FCEN-PV, Facultad de Ciencias Exactas y Naturales-Paleontología de Vertebrado (Universidad de Buenos Aires), Ciudad Autónoma de Buenos Aires, Argentina.

Other abbreviation.—PV, presacral vertebra.

Geological setting

The locality of Scarritt Pocket (Fig. 1) is near the center of the Chubut province, about 90 km south of the town of Paso de Indios. The pocket is a small embayment on the west side of the Sierra or Meseta Canquel located in the southwestern part of a larger embayment, locally known as the Rinconada de López. The locality Scarritt Pocket extends along the slope of the Meseta for approximately 0.5 km. The sediments within the pocket represent the infilling of a topographic low, the walls of which are of a probable volcanic origin (Simpson 1934; Chafee 1952). The deposits consist of a thin series of laminated bentonites, accumulated in a small, shallow, and probably ephemeral lake, and a thicker filling of ashes that grade into heavy breccia near the crater walls (Simpson 1934). Marshall et al. (1986) estimated the age of the Scarritt Pocket sediments from about 23.4 Mya to about 21.0 Mya, according to the K/Ar datings of several basalts and tuffs that bound the pocket. However, Flynn and Swisher (1995) stated

Table 1. Specimens of *Calyptocephalella gayi* from Pucón, Chile available for the comparisons. All of the specimens are cleared and stained following the procedure of Taylor and Van Dyke (1985).

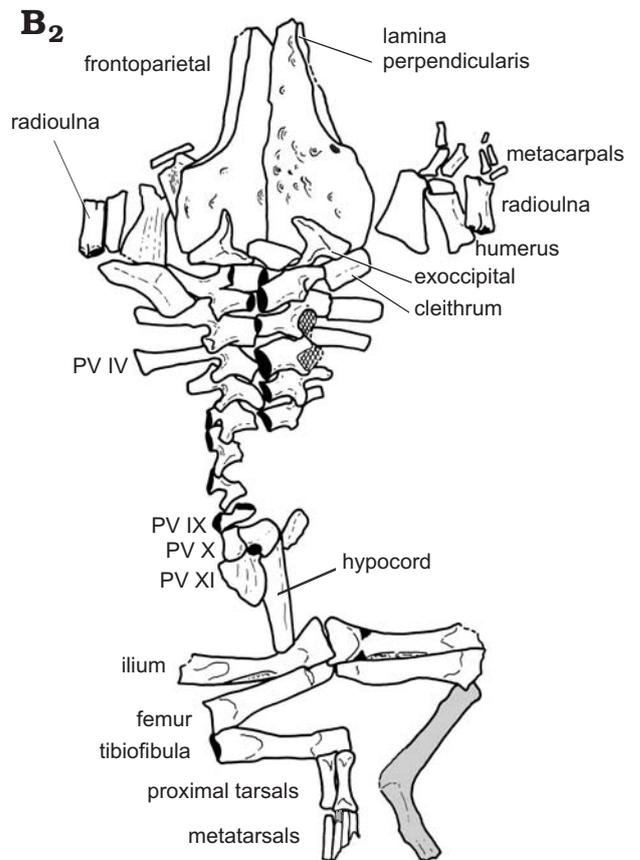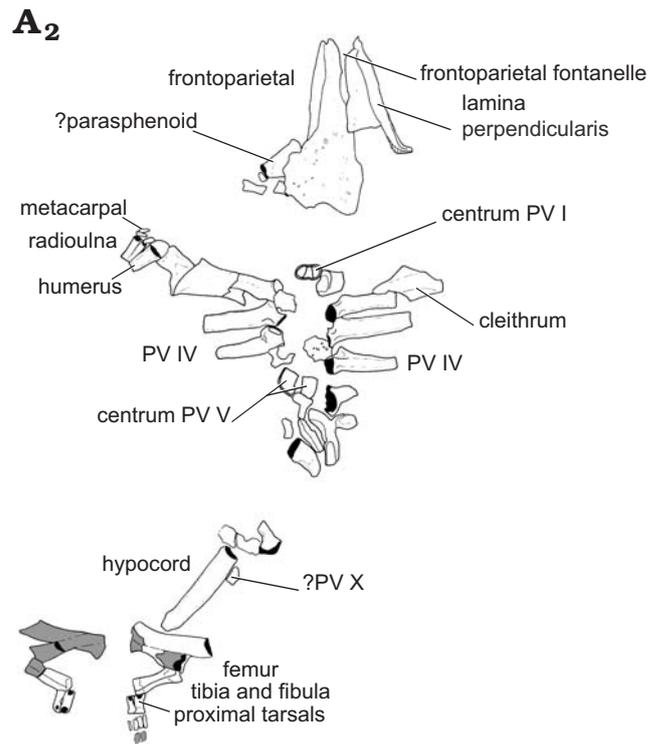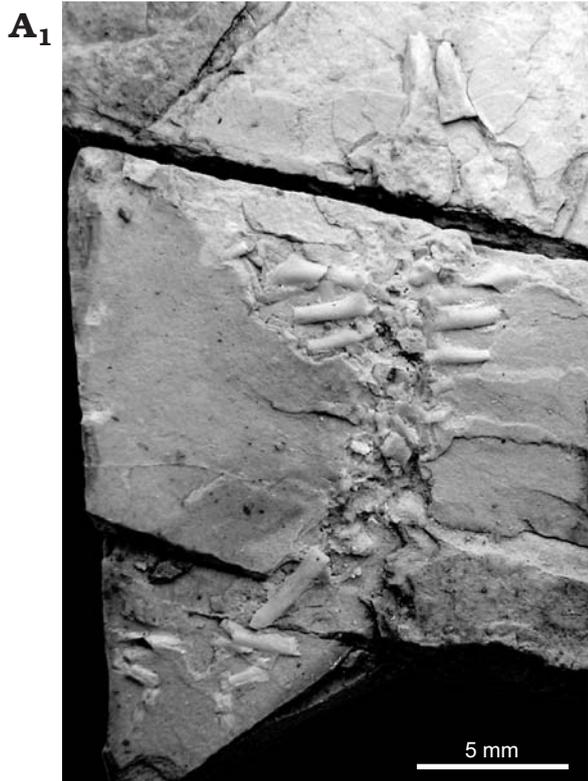| Specimen number		Gosner Stage
MACN 39894	I	34
	II	34
	III	34
	IV	35
MACN 39895	I	35
	II	35
	III	35
	IV	35
	V	36
MACN 39896	I	36
	II	36
	III	36
	IV	36
	V	36
MACN 39897	I	37
	II	37
	III	37
MACN 39898	I	38
	II	38
	III	38
	IV	38
MACN 39899	I	38
	II	39
MACN 39900	I	40
MACN 39901	I	41
	II	43

Fig. 2. Tadpoles of australobatrachid frog *Calyptocephalella canqueli* Schaeffer, 1949 from Scarritt Pocket locality, Deseadan (Oligocene), Argentina. **A**. FCEN-PV 14084, GS 35/36. **B**. AMNH 3401, GS 38/39. Photographs (A₁, B₁) and outline drawings (A₂, B₂). PV, presacral vertebra.
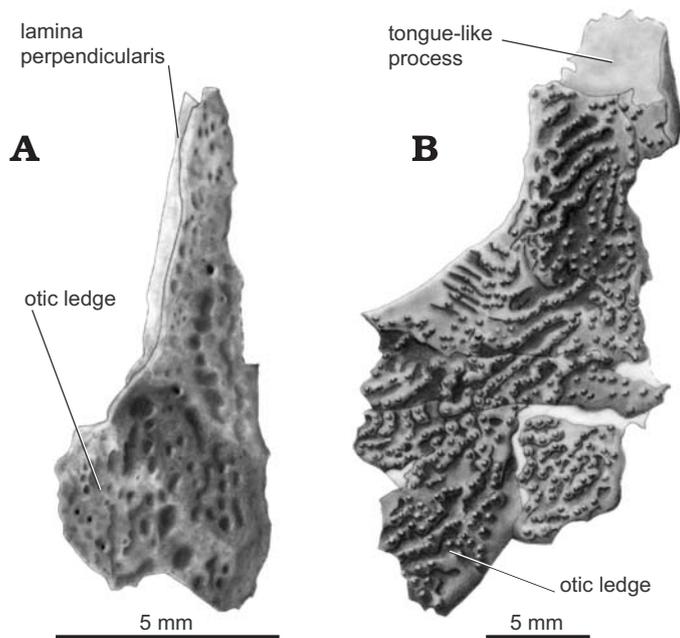
Fig. 3. Frontoparietal and sculpturing development of australobatrachid frog *Calyptocephalella canqueli* Schaeffer, 1949 from Scarritt Pocket (**A**) and Puesto Baibián (**B**) localities, Deseadan, Argentina. **A**. FCEN-PV 14084, GS 35/36. **B**. MPEF-PV 1881, adult.

that Swisher had obtained new ^{40}Ar/^{39}Ar dates from aliquots of the same samples dated by Marshall et al. (1986) ranging from about 27 to 29 Mya. The sequence is included in the Sarmiento Group and was deposited during the latest Deseadan, according to both the mammalian fossil fauna and the K/Ar dating (Chafee 1952; Marshall et al. 1986).

Systematic paleontology

Amphibia Gray, 1825

Anura Fischer von Waldheim, 1813

Neobatrachia Reig, 1958

Australobatrachia Frost, Grant, Faivovich, Bain, Haas, Haddad, De Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006

Calyptocephalellidae Reig, 1960
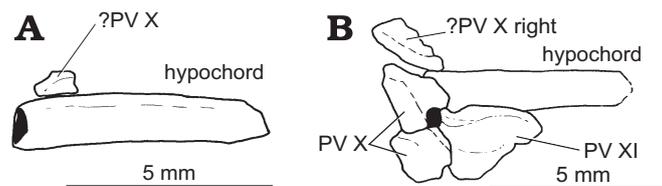
Genus *Calyptocephalella* Strand, 1928

Type species: *Calyptocephalella gayi* Duméril and Bibron, 1841.

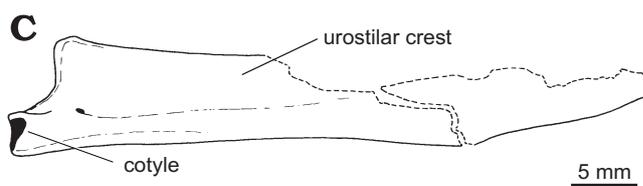## *Calyptocephalella canqueli* Schaeffer, 1949
Figs. 2–6.

Material.—FCEN-PV 14084 and AMNH 3401, well-preserved fossil tadpoles.

Description.—The specimens (Fig. 2) are largely articulated and exposed in dorsal view. Most cranial and postcranial elements are preserved as actual bones, but some are preserved as moulds. The approximate lengths of the specimens, measured from the anterior tip of frontoparietals to the posterior margin of the ilia, are 4.3 cm (FCEN-PV14084) and 3.3 cm (AMNH 3401). Even though AMNH 3401 is relatively shorter, it belongs to a later developmental stage than FCEN-PV14084, according to its higher degree of ossification—particularly in the axial and appendicular regions of the skeleton.

FCEN-PV 14084: The only visible skull bones are the frontoparietals and, probably, the parasphenoid (Fig. 2A). The frontoparietals are extensive and likely covered most of the braincase of the living tadpole. The dorsal surface of these elements is sculptured with shallow pits which are more abundant in the posterior half of the bone (Fig. 3A). Their anterior ends are pointed and together form the V-shaped margins of a frontoparietal fontanelle, which extends along one half of the length of the frontoparietals. Posterior to the fontanelle, the medial margins of these bones are parallel to the saggital line, but it is not clear whether these margins were in contact along the midline. The posterior half of each frontoparietal projects laterally, partially covering the dorsal surface of the auditory capsules. Ventrally, each frontoparietal bears a deep lamina perpendicularis, which in life covered the dorsolateral portion of the braincase and the anterodorsal wall of the otic capsule. A bone that underlies the frontoparietals is identified as the parasphenoid owing to its relative position and laminar nature; the poor preservation of this bone does not provide more details.

Six presacral vertebrae are recognized (Fig. 2A), although they show an unequal degree of development and ossification. Presacral vertebra (PV) I is represented by the articular portion of the right half of the neural arch and by its centrum, which at this stage and from a dorsal view is composed of two crescent-shaped ossifications still unfused medially (some cartilage seems to be preserved, filling the space between the ossifications). The following three vertebrae (PV II–IV) are represented by the pedicles of the neural arches, the bases of the prezygapophyses, and the transverse processes. The transverse processes of PV II are robust and mostly laterally di-

Fig. 4. Urostyle development of *Calyptocephalella canqueli* Schaeffer, 1949 from Scarritt Pocket (**A**, **B**) and Puesto Baibián (**C**) localities, Deseadan (Oligocene), Argentina. **A**. FCEN-PV14084, GS 35/36. **B**. AMNH 3401, GS 38/39. **C**. MPEF-PV 1885, adult. PV, presacral vertebra.
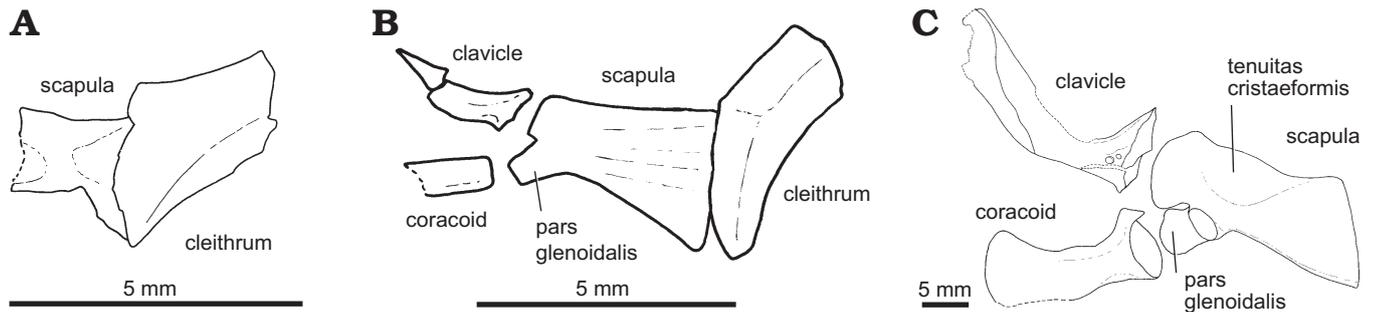
Fig. 5. Pectoral girdle development of *Calyptocephalella canqueli* Schaeffer, 1949 from Scarritt Pocket (**A**, **B**) and Puesto Baibián (**C**) localities, Deseadan (Oligocene), Argentina. **A**. FCEN-PV 14084, GS 35/36. **B**. AMNH 3401, GS 38/39. **C**. MPEF-PV 1887 (scapula and coracoid) and MPEF-PV 1888 (clavicle), adult.
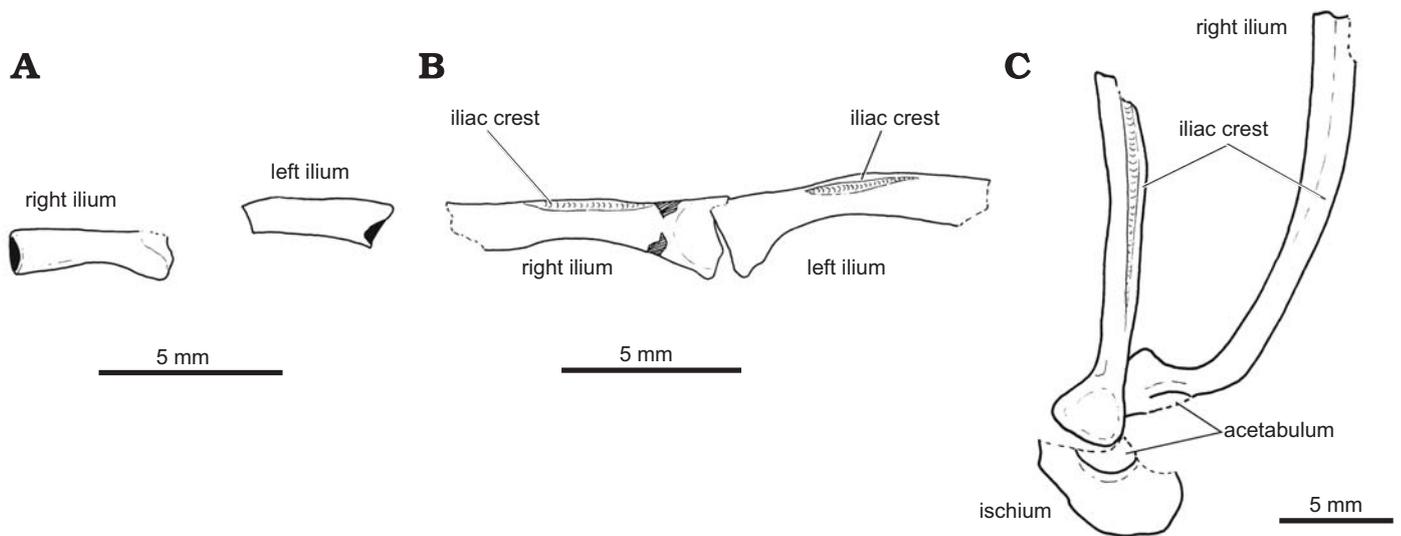

Fig. 6. Pelvic girdle development of *Calyptocephalella canqueli* Schaeffer, 1949 from Scarritt Pocket locality, Deseadan (Oligocene), Argentina. **A**. FCEN-PV 14084, GS 35/36. **B**. AMNH 3401, GS 38/39. **C**. AMNH 3427, adult.

rected. PV III bears the longest and most robust transverse processes (length:width, 3:1); they are perpendicular to the notochordal axis and have a constant width throughout their length. The processes of PV IV are more slender and taper distally. The PV V shows only the right transverse process, which is short and blunt. No other transverse process is visible. The centrum of PV V is also preserved, evidenced by two semi-oval ossifications not fused medially from a dorsal aspect. The PV VI is fragmentary; posterior to this vertebra there are small pieces of bone that cannot be attributed to any specific vertebra. The postsacral region is represented by what seems to be one neural arch and a well-ossified, robust hypochord (Fig. 4A). The hypochord is as long as four presacral vertebrae and is oval in cross section.

The pectoral girdle is divided into two halves which, along with their corresponding forelimbs, are placed on either side of the axial skeleton, as it is evidenced from the preserved left half. The pectoral girdle is represented by the right and left cleithra and the left scapula (Fig. 5A). The cleithrum is a wide and relatively thick lamina with straight anterior and concave posterior margins, shorter proximally than distally. Across the cleithrum there is a low keel that extends from the medial to the distal end. The scapula is poorly developed and poorly preserved; its proximal end is slightly longer than the distal one. The forelimb is represented by the left humerus, the radioulna and three metacarpals. The humeral diaphysis is well ossified, while the rather rounded proximal end shows a granulose texture that suggests its cartilaginous condition. The radius and ulna are already fused, although a shallow sulcus between them hints at a recent fusion. This compound element is approximately as long as the humerus, with which it articulates. Metacarpals are cylindrical elements.

The articulated pelvic girdle and hind limbs are displaced from the axial axis to the left side. The pelvic girdle (Fig. 6A) is represented by the shaft of the ilium, presumably the only ossified element of the girdle by this stage. The iliac shafts, which are oval in cross section, are poorly developed and slightly shorter than the hypochord. Posterior and ventral to these elements, the femur, tibia, fibula, and proximal tarsals are preserved. All of them are poorly developed, although their diaphyses are already ossified. The femur is a little shorter than the ilium. The tibia and fibula are still two separate elements of a length approximately similar to that of the femur. The proximal tarsals are very short (about 1/3 the

length of the fibula) and their epiphyses are wider than their diaphyses, as in adults. Posteriorly, four cartilaginous metatarsals and two proximal phalanges have left their impressions on the sediment.

AMNH 3401: The frontoparietals are similar, both in shape and ornamentation, to those of FCEN-PV 14084. However, these bones are more expanded laterally to form well-developed supraorbital flanges (Fig. 2B). There are two triradiated bones overlapping the posterior end of frontoparietals interpreted as the exoccipitals, exposed in posterior view. No foramina are visible. The axial skeleton consists of eleven pairs of neural arches and a hypochord. The laminae of the neural arches are not imbricated, but they are well developed and ossified, especially those of the anterior four presacral vertebrae. However, none of the neural arches is ossified at the midline; thus each is preserved as two separate halves. All presacrals have ossified pre- and postzygapophyses, although their mutual articulation obscures their morphology. PV II–V bear transverse processes similar to those of FCEN-PV 14084; the transverse processes of the PV VI are short—approximately one third the length of those of the anterior presacrals. No other transverse process is evident. Posterior to the last distinct neural arch (IX), three pieces of bone are interpreted to constitute two postsacral neural arches (Fig. 4B), which would ultimately form the anterodorsal portion of the urostyle. Neural Arch X is broken into two pieces. It is a tall element that forms posteriorly the anterior margin of the foramen intervertebralis. Neural Arch XI is triangular, its dorsal margin taller anteriorly than caudally. The anterior margin forms the posterior border of the foramen intervertebralis. Even though these neural arches are well developed, it is not clear whether they are already fused to each other, although they certainly are not fused to the hypochord, and thus no urostyle is yet formed in this specimen. The hypochord (Fig. 4B) is robust and relatively as long as that of FCEN-PV 14084.

The contralateral halves of the shoulder girdle are located on both sides of the skull (Fig. 2B), indicating that they were still occupying almost a single plane. The cleithrum (Fig. 5B) is relatively longer than that of FCEN-PV 14084. Its proximal end is blunt and the distal end is pointed; thus, the anterior margin is shorter than the posterior one. A keel projects mediolaterally across the dorsal surface of this bone. The scapula (Fig. 5B) is stocky and subtriangular, being wider laterally than medially and having a straight anterior margin. The shaft is about 1.5 times broader than long and the surface of this element bears slight transversal ridges. The preserved right coracoid (Fig. 5B) is represented by the ossified diaphysis. The clavicle (Fig. 5B) is moderately curved with a rounded medial end. Its lateral end possesses a blunt facet that ultimately would have articulated with the scapula. The forelimbs are represented by short humeri, presumably with cartilaginous condyles, and radioulnae (the radius and ulna are clearly fused to one another; Fig. 2B).

The only preserved bony elements of the pelvic girdle are the illia oriented transverse to the vertebral column (Fig. 2B). The corpus of the ilium (Fig. 6B) is already ossified but its

preservation in medial view prevents the description of any morphological feature other than its triangular shape. The slightly curved iliac shafts are as long as five vertebrae. They bear a low iliac crest over the dorsal margin at the centre of the shaft. The femora are preserved parallel to the ilia and are almost the same length of the latter. The tibia and fibula are already fused forming the tibiofibula, although its dual origin is still evident. The tibiofibula is as long as the femur. Elongated proximal tarsals, representing approximately one half of the tibiofibular length, and four metatarsals are also preserved.

Stratigraphic and geographic range.—Sarmiento Group, Deseadan (Oligocene); Scarritt Pocket, Chubut, Argentina.

Results and discussion

The assignment of these fossils to *Calyptocephalella*, and specifically to *Calyptocephalella canqueli*, relies on the general morphology of the frontoparietals of the specimens (herein considered to belong to tadpoles; see Degree of development), the resemblance to the tadpoles of *Calyptocephalella gayi*, and the presence of adults of *C. canqueli* at the same locality. The Deseadan beds at Scarritt Pocket have yielded a taxonomically diverse anuran assemblage (Schaeffer 1949; Chafee 1952), within which *C. canqueli* is the only taxon hitherto recorded that shows an extensive ossification and ornamentation of the skull. *Neoprocoela* and *Eusophus*, the other taxa thus far described from this unit, have slender skull elements and frontoparietals that only barely meet at the midline (Schaeffer 1949). *Calyptocephalella* is a genus with an extensively ossified and ornamented skull. The dermal roofing bones of the cranium are broadly in contact forming a kind of helmet. Adult specimens of both species, *C. gayi* and *C. canqueli*, show a tubercular ornamentation over the nasals, frontoparietals, squamosals, and maxillae (Parker 1881; Reinbach 1939; Schaeffer 1949; Reig 1960; Lynch 1971; Muzzopappa and Báez 2009). From early developmental stages onward, the tadpoles of *C. gayi* bear large frontoparietals, although initially these bones are ornamented with shallow pits (Parker 1881; Reinbach 1939; PM personal observation) and subsequently the ornamentation changes to tubercles (Reinbach 1939; PM personal observation); this change of ornamentation pattern appears to happen in *C. canqueli* as well, according to the evidence provided in the present study (Fig. 3).

Degree of development.—The degree of development, ossification, and arrangement of the bony elements indicate that the individuals studied were larval tadpoles by the time they were preserved. The only skull elements present are the frontoparietals and probably the parasphenoid and the exoccipitals (Fig. 2). Although the lack of evidence is not evidence in itself, the generally superb preservation of the specimens suggests that if any other element was ossified, then it should have been preserved. Accordingly, we conclude that these were most probably the only well-ossified elements of the skull. In Recent anuran tadpoles the frontoparietals, para-

sphenoid, and exoccipitals are usually the first skull elements to ossify and they appear early in development, although their order and timing differs among taxa (generally between Gosner Stages 33 and 39) (e.g., Hanken and Hall 1984, 1988; Wild 1997, 1999; Pugener and Maglia 1997; Maglia and Púgener 1998; Haas 1999; Sheil 1999; Yeh 2002; Banbury and Maglia 2006).

In both specimens the anterior presacral vertebrae are better developed and more ossified than the posterior vertebrae (more evident in FCEN-PV 14084). Also, the neural arch laminae are not fused at the midline (Fig. 2) and the postsacral neural arches are not fused to the hypochord (Fig. 4A, B). In extant anurans, during development the axial skeleton develops and ossifies cranio-caudally (Mookerjee 1931; Pugener and Maglia 2009). The first elements of the vertebrae to form are the neural arch pedicles; later, upward and lateral growth forms the transverse processes, and upward and medial growth generates the laminae. Generally, the two halves of the neural arch lamina meet medially by the end of metamorphosis. The urostyle is formed from postsacral neural arches (the number of neural arches involved is variable according to the species) and a ventral hypochord. The postsacral neural arches ossify dorsally from the pedicles, and meet along the midline by means of a cartilaginous bridge only after the right and left halves have fused with the contiguous neural arch—when more than one is present. As the notochord erodes, the hypochord moves upward to the neural arches, to which it fuses before the end of metamorphosis (Mookerjee 1931; Mookerjee and Das 1939; Branham and List 1979; Ročková and Roček 2005; Pugener and Maglia 2009). The unequal degree of ossification between the anterior and posterior presacrals, the underdeveloped neural arch laminae, and the lack of fusion between the postsacral vertebrae and the hypochord, clearly indicate the immature (premetamorphic) stage of the *Calyptocephalella canqueli* individuals.

The elements of the anterior appendages are poorly developed in both of the examined specimens of *C. canqueli* (Fig. 5A, B). In addition, they are situated lateral to the skull and arranged in a coplanar position (Fig. 2). During the initial stages of development, each half of the pectoral girdle and its corresponding forearm form inside the opercular chamber (e.g., Altig and McDiarmid 1999); therefore, they are placed lateral to and at the same level with the posterior parts of the skull and arranged in an almost coplanar position. Later, the forelimbs rotate ventrally, below the head, until they emerge from the sacs through the spiracle and the body wall. This emergence is considered the signal that identifies the onset of metamorphosis (Gosner Stage 42). Thus, the pectoral girdle elements get reorganized and adopt their adult relative positions, i.e., cleithrum dorsal, scapula ventrolateral, and clavicle and coracoid ventral to the vertebral column. Hence, based on the poor development of the elements of the pectoral girdle and forelimbs, their placement lateral to the skull, and their arrangement in a coplanar position, it can be inferred that they were still inside the opercular chamber and had not attained the adult

position, indicating the premetamorphic stage attained by the fossil individuals.

In both immature *C. canqueli* specimens the pelvic girdles, represented by the ossified ilia, are lateral and perpendicular to the axial column (Fig. 6A, B); moreover, they neither meet posteromedially nor articulate with the diapophyses of the sacral vertebra. In addition, the ilial shafts are short (especially in FCEN-PV 14084). In extant anurans, during the larval period the pelvic girdle experiences important positional changes. For most of larval life, the ilia are detached from the axial skeleton and remain ventral to and beyond the posterior end of the vertebral column. In dorsal view, they are nearly perpendicular to the axial column. Later, they rotate from a vertical to a more horizontal position as they approach one another until their distal ends get in contact and finally fuse (Green 1931; Ročková and Roček 2005). In the adults, the ilia are parallel to the urostyle, to which they are intimately related by several muscles, and their anterior ends articulate with the sacral diapophyses (Green 1931; Emerson 1979, 1982; Ročková and Roček 2005). Thus, the degree of development and the position of the ilia also point to a relatively early stage of development for the fossil specimens.

Additionally to the previous mentioned features, from the description it becomes evident that FCEN-PV 14084 belongs to a younger developmental stage than AMNH 3401. In order to estimate the Gosner (1960) stages to which these individuals might belong, we compared the degree of development of their hind limbs with those of different stages of the available cleared and stained ontogenetic series of *Calyptocephalella gayi* (see Appendix 1). The hind limbs were chosen because their external appearance is the main feature applied to determine the different Gosner stages throughout the larval period. Hence, based on the presence of at least 4 metatarsals and the relative length of the long bones (Fig. 2A), it can be concluded that FCEN-PV 14084 had attained a Gosner Stage (GS) 35/36 and that AMNH 3401 had attained a GS 38/39, according to the length of the proximal tarsals and their relative length to the femur and tibiofibula (Fig. 2B).

Ontogeny and comparisons.—Several ontogenetic traits of *C. canqueli* emerge from the specimens described herein and the adult specimens already known for the species. Previous morphological descriptions of adult skeletons of *C. canqueli* (Schaeffer 1949; Muzzopappa and Báez 2009) are used as source information and, when appropriate, adult anatomical features will be mentioned. Little is known about the osteogenesis and development of other australobatrachians, the clade in which *Calyptocephalella* is nested (Correa et al. 2006; Frost et al. 2006; Roelants et al. 2007), thus preventing any comparisons with its closest relatives. Nonetheless, it is interesting to compare some of the changes in *Calyptocephalella* with those of other hyperossified taxa (although not phylogenetically close), such as *Ceratophrys cornuta*, *Chacophrys pierrotti*, and *Pyxicephalus adspersus*.

The ornamentation of the frontoparietals of *Calyptocephalella canqueli* changes through development. The exostosis goes from a pitted ornamentation in the larva—present at least until GS 38/39—to a tubercular type in the adult (Fig. 3). In *Calyptocephalella gayi* a similar change of ornamentation occurs during the metamorphosis (Reinbach 1939; PM personal observation), when the tadpoles bear disperse tubercles instead of pits over the frontoparietal surface. It is noteworthy that neither the skull roofing bones of *Ceratophrys cornuta* nor those of *Chacophrys pierrotti* show exostosis until postjuvenile stages, when they develop the adult tubercular pattern (Wild 1997, 1999). In contrast, *Pyxicephalus adspersus*, which has a "pillarlike" ornamentation on the adult frontoparietals, does exhibit exostosis by GS 36 (Sheil 1999), although the pattern has not been specified.

In *C. canqueli* the frontoparietal fontanelle remains open until at least GS 38/39. The fontanelle is absent in adults, in which the anterior ends of the frontoparietals meet along the midline and a tongue-like projection underlies the posterior portion of the nasals (Fig. 3B). Most of the described Australian australobatrachians have slender frontoparietals, which are not in contact to one another along the midline or with the nasals even in adults. However, frontoparietals do meet medially in adults of some taxa (e.g., *Adelotus brevis*, *Lechriodus fletcheri*, *Myxophies fasciolatus*, *Uperoleia rugosa*, *Uperoleia laevigata*; Parker 1940; Stephenson 1964; Lynch 1971; Davies 1984, 1989), but their ontogeny is unknown, except for *Uperoleia laevigata*. In this latter species the frontoparietals meet along the midline after the end of the metamorphosis (Davies 1989). In other hyperossified taxa, although phylogenetically distant to *Calyptocephalella*, the closure of the fontanelle also occurs late in ontogeny. For example, in *Pyxicephalus adspersus* it takes place at GS 46 (Haas 1999), while in *Ceratophrys cornuta* (Wild 1997) and *Chacophrys pierrotii* (Wild 1999) it occurs postmetamorphically. Other morphological changes in the frontoparietals of *C. canqueli* are related to the growth of the projection of the lateral margins, resulting in more conspicuous supraorbital flanges and longer otic ledges in adults (Fig. 3B). The latter structure contacts widely with the otic plate of the squamosal in the adult (Schaeffer 1949; Muzzopappa and Báez 2009). Finally, it is evident that the lamina perpendicularis of the frontoparietal is already deep by GS 35/36 (see Fig. 2A).

Regarding the axial skeleton of *C. canqueli*, the first three pairs of transverse processes are remarkably well ossified by GS 35/36. The ossification of the zygapophyses and the lateral aspects of the neural arch laminae, as well as that of the transverse processes of the posterior presacral vertebrae, occurs between the GS 35/36 and GS 38/39. Although little is known about the adult vertebral column of this species, Schaeffer (1949) noted that the transverse processes of PV III are robust, and a putative adult PV V from the Puesto Baibián locality has long, slender, and slightly posteriorly directed transverse processes (Muzzopappa and Báez 2009). Two distinct postsacral neural arches are well developed by GS 38/39, indicating that at least two neural arches are involved in the formation of the urostyle. This corroborates what Muzzopappa and Báez (2009) suggested based on a distinct foramen at the base of the crest on the adult urostyle (Fig. 4C).

The morphological changes of the pectoral girdle (Fig. 5) that can be noticed between GS 35/36 and GS 38/39 include growth of the cleithrum and ossification of the scapula. The diaphysis of the latter is already ossified by GS 35/36, and between Stages 35/36 and 38/39 it extends over the pars glenoidalis. However, there is no evidence of the development of the tenuita cristaeformis, a feature that has been described in the adult (Muzzopappa and Báez 2009; Fig. 5C). Additionally, during this developmental period the onset of the ossification of the coracoid and the clavicle took place. In the pelvic girdle (Fig. 6), the development of the iliac crest, which is high in the adult specimens (Fig. 6C), as well as the ossification of the iliac corpus, also starts between GS 35/36 and GS 38/39. The ischium is remarkably well-ossified in adults (Fig. 6C), but it is not present by GS 38/39. The ossification of this element probably occurs near to the end of metamorphosis as in most anurans (Wild 1997, 1999; Maglia 1998; Trueb et al. 2000; Banbury and Maglia 2006; Pugener and Maglia 2009). Finally, the onset of the fusion of radius and ulna occurs previous, but close, to the GS 35/36 and that of tibia and fibula takes place between the two preserved developmental stages.

This brief insight into the development of the fossil *C. canqueli*, along with the study of the development of the living *C. gayi*, will be integrated in the near future (in comparing the ontogeny of these two species, for instance, *C. gayi* shows a delayed development of the axial skeleton with respect to the hind limbs; PM unpublished data) and allow us to draw conclusions about the evolution of the genus.

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