





CALYPTOCEPHALELLA (ANURA, AUSTRALOBATRACHIA) REMAINS FROM RÍO SANTA CRUZ (EARLY–MIDDLE MIOCENE, SANTA CRUZ FORMATION), SANTA CRUZ PROVINCE, ARGENTINA

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| STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS OF THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) ALONG THE RÍO SANTA CRUZ, SOUTHERN PATAGONIA, ARGENTINA | NOTOUNGULATA AND ASTRAPOTHERIA (MAMMALIA, MERIDIUNGULATA) OF THE SANTA CRUZ FORMATION (EARLY–MIDDLE MIOCENE) ALONG THE RÍO SANTA CRUZ, ARGENTINE PATAGONIA | ANALYSIS OF THE EARLY–MIDDLE MIOCENE MAMMAL ASSOCIATIONS AT THE RÍO SANTA CRUZ (PATAGONIA, ARGENTINA) |



CALYPTOCEPHALELLA (ANURA, AUSTRALOBATRACHIA) REMAINS FROM RÍO SANTA CRUZ (EARLY–MIDDLE MIOCENE, SANTA CRUZ FORMATION), SANTA CRUZ PROVINCE, ARGENTINA

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Key words. Calyptocephalellidae. *Calyptocephalella canqueli*. Neobatrachia. Neogene. Barrancas Blancas Locality. **Palabras clave.** Calyptocephalellidae. *Calyptocephalella canqueli*. Neobatrachia. Neógeno. Localidad Barrancas Blancas.

RECENT systematic prospecting in the classic localities of the Santa Cruz Formation (SCF) along Río Santa Cruz have produced a vast collection of vertebrate fossil remains (Fernicola *et al.*, 2014; Cuitiño *et al.*, 2016; Fernicola *et al.*, 2019). The assemblage includes bones of anurans recovered from the two easternmost localities, Barrancas Blancas (Estancia Aguada Grande and Estancia Santa Lucía) and Segundas Barrancas Blancas (Estancia Cordón Alto) (Fig. 1). Outcrops of the SCF have already yielded anuran remains at Estancia La Costa, in the Atlantic coast, which were assigned to *Calyptocephalella* Strand, 1928 by Tauber (1999) and Fernicola and Albino (2012) (see Fernicola *et al.*, 2019: figs. 1 and 4). *Calyptocephalella*, whose record is conspicuous and the most common among extinct anuran genera from Patagonia, has a heavily ossified skull, and inhabited these terrains from the Late Cretaceous (Báez, 1987; Martinelli and Forasiepi, 2004; Agnolín, 2012) to the Miocene (Tauber, 1999; Muzzopappa and Báez, 2009; Fernicola and Albino, 2012; Nicoli *et al.*, 2016). Nowadays, only one representative of this genus, *C. gayi* Duméril and Bibron, 1841, survives along southern central Chile (Cei, 1962), living in ponds, lakes and quiet streams.



Figure 1. Map of Río Santa Cruz with the prospected localities and estancias mentioned in the text. **BB**, Barrancas Blancas; **SBB**, Segundas Barrancas Blancas; **YH**, Yaten Huageno; **Ea**., Estancia. Modified from Fernicola *et al.* (2014).

The aim of this contribution is to present the results of investigations on anuran remains from the SCF in Río Santa Cruz. They represent the first anuran record from the original localities of the SCF from which Florentino Ameghino (1889) erected the "Piso Santacruceño" (Fernicola *et al.*, 2014).

The osteological terminology follows that of Trueb (1973), except for the terms fontanella and fenestra, which are used according to Gaupp (1896) as follows: fontanella for openings between dermal bones, and fenestra for openings in the chondrocranium.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; CFA-AN, Colección Fundación Azara, CABA, Argentina; FCEN, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, CABA, Argentina; MACN-HE, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", División Herpetología, CABA, Argentina; MPEF-PV, Museo Paleontológico "Egidio Feruglio", Trelew, Province of Chubut, Argentina; MPM-PV, Museo Regional Provincial "Padre Manuel Jesús Molina", Río Gallegos, Province of Santa Cruz, Argentina.

SYSTEMATIC PALEONTOLOGY

Anura Fischer, 1813 Neobatrachia Reig, 1958 Australobatrachia Frost *et al.*, 2006 Calyptocephalellidae Reig, 1960

Genus Calyptocephalella Strand, 1928

Type species. Calyptocephalella gayi Duméril and Bibron, 1841. Recent, south and central Chile.

> Calyptocephalella cf. canqueli Schaeffer, 1949 Figure 2.1–3

Holotype. Calyptocephalella canqueli Schaeffer, 1949 AMNH FR 3429.

Type locality and age. Rinconada de los López, Scarritt Pocket, Province of Chubut. Late Oligocene (Deseadan). *Referred material.* MPM-PV 20025, a left frontoparietal and fragments of both left and right maxillae.



Figure 2. 1–3, *Calyptocephalella* cf. *canqueli*, MPM-PV 20025; 1, frontoparietal, dorsal (left) and ventral (right) views; 2–3, maxillae (fragments), external (left) and internal (right) views. Black arrowheads indicate tongue-like processes; purple surfaces indicate scars left by the squamosal's tongue-like process; the purple arrow indicates the channel for the occipital artery. Scale= 5 mm.

Locality and horizon. Eastern section of Barrancas Blancas (Estancia Aguada Grande), Río Santa Cruz, Province of Santa Cruz, Argentina. Low energy fluvial deposits of Early Miocene (Santacrucian), Santa Cruz Formation (Cuitiño *et al.*, 2016; Cuitiño *et al.*, 2019).

Description. A complete left frontoparietal and fragments of both maxillae constitute, so far, the best preserved remains of anurans recovered from Río Santa Cruz. As they were found close to each other in the field, they are considered to belong to a single individual. Even though these are the only elements that were recovered, several scars imprinted on their surfaces provide significant information regarding the cranial morphology of the specimen. All three elements bear pustular ornamentation on their external surface, the pustules being wide-based, close to one another and not arranged in any particular way. Neither traces of fusions nor coosifications were observed in any of these bones.

The frontoparietal (Fig. 2.1) is a large and conspicuous bone that reached the uttermost posterior border of the neurocranium, extended laterally over the orbit by means of a wide supraorbital flange (whose anterior margin makes the lateral and posterior segments of the orbit), and medially articulated the frontoparietal of the opposite side along its whole length. The supraorbital flange bears two contact facets for articulation with the adjacent squamosal: a triangular scar on the posterolateral portion imprinted by the squamosal, well seen in ventral aspect (purple triangle in Fig. 2.1), and a thin, semicircular tongue-like process (pointed with a black arrowhead in Fig. 2.1), which extends anterior to the aforementioned scar. So, the articulation between the frontoparietal and squamosal is rather complex. Another tongue-like process extends from the anterior end of the frontoparietal, for articulation with the nasal. On the ventral surface of the bone, a conspicuous lamina perpendicularis runs from the anterior border of the frontoparietal up to the level of the otic capsule, where it turns posterolaterally. One can also discern a posterior orifice of the canal through which the occipital artery entered the bone, and another foramen located anteriorly, through which it entered the orbit (purple arrow in Fig. 2.1). It is apparent that the canal for the occipital artery was rather short.

The left and right maxillae (Fig. 2.2-3) are only repre-

sented by their orbital and postorbital regions. The external surface bears the same type of ornamentation than that of the frontoparietal, except for the pars dentalis, which is covered by faint ridges parallel to the ventral margin of the bone. On the inner surface, distinct pars facialis, pars palatina and pars dentalis are recognized. The pars facialis is high all along the preserved portion; the anterior section corresponds to the orbital region and its dorsal border constitutes the margin of the orbit, while the posterior section is much higher even and conforms an ample postorbital process (which is not completely preserved on the right side, but complete on the left side). At the level of the orbit, the pars facialis and pars palatina have approximately the same depth, both being higher than the pars dentalis. Noteworthy, there is some intraindividual variation regarding the relative proportions of the pars facialis and the pars palatina when comparing right and left maxillae: the pars facialis is slighly shorter than the pars palatina in the right maxilla, but it is the opposite in the left one. On the inner surface of the postorbital process, a wide and triangular facet can be recognized, in which the tongue-like process projected from the squamosal inserted. Below the orbit, the pars palatina is thicker and more rounded than posteriorly, where —even if it is partially broken— it is evident that it was step-like (*i.e.*, it makes a right angle with both the pars facialis and pars dentalis). Several vertical septa on the inner surface of the pars dentalis indicate the presence of pedicellate teeth along the maxilla. However, neither the total number of tooth position nor the morphology of the teeth can be inferred from these maxillary fragments.

DISCUSSION

The information provided by the specimen MPM-PV 20025 and the scars recognized on it allow the asserting that it belonged to a toothed and casque-headed anuran with frontoparietals completely covering the braincase and meeting in a straight suture along the midline, while leaving no fontanella frontoparietale anteriorly. Also, it is clear that the anterior and lateral tongue-like processes of each frontoparietal were overlapped by the corresponding nasal and squamosal and, moreover, that the squamosal inserted its own tongue-like process below the frontoparietal. These evidences indicate that the frontoparietal had extensive contacts with adjacent elements. Similarly, the squamosal had a steady and straight contact with the maxillary postorbital process by means of a triangular tongue-like process, which took part in the formation of the zygomatic bridge. Despite the scanty record, consisting of three fragmentary bones of the skull roof, MPM-PV 20025 is confidently assigned to the genus *Calyptocephalella*. This assignment is based not only on the overall morphology of each bone and their ornamentation, but also on the presence and position of the tongue-like processes preserved on the frontoparietal, and those inferred for the squamosal. This type of contact between dermatocranial elements by means of tongue-like processes is also observed in extant *C. gayi* (Muzzopappa and Báez, 2009, Muzzopappa, 2013; Fig. 3.1) and in other extinct species of Calyptocephalella (e.g., C. casamayorensis Schaeffer, 1949 and C. canqueli, Schaeffer, 1949; Muzzopappa and Báez, 2009). Such structures, which reinforce contacts between dermal bones, were not found in any other group of frogs (either phylogenetically close or distant) with casqued dermal skull (e.g., Pelobates Wagler, 1830, Roček, 1981; Böhme et al., 1982, Rhinella arenarum (Hensel), pers. obs. CFA-AN-36, 133, 298), except for some Ceratophryidae (Perí, 1993; pers. obs. FCEN uncatalogued-35) and for some Latonia von Meyer, 1843 (Roček, 1994). However, the placement of the tongue-like processes in species of Ceratophrys Wied-Neuwied, 1824 is different to that of Calyptocephalella (Fig. 3.2-5); for instance, the nasal, instead of the frontoparietal, bears the tongue-like process for the contact of these two dermal bones. Also, in Ceratophrys, the maxilla has no orbital margin, as it is excluded from the orbit, and several tongue-like processes are developed for the tripartite articulation between the maxilla, the nasal and the squamosal (Fig. 3.4). In Latonia, the frontoparietals are fused along the midline and in broad contact with the nasals, either by interdigitation, as occurs in L. nigriventer (Mendelssohn and Steinitz) (Biton et al., 2016), or by the overlap of the tongue-like process ("anterior horns" by Roček, 1994, fig. 7) projected from the anterolateral margin of the frontoparietal, as it happens in L. seyfriedi von Meyer, 1843 (Syromyatnikova et al., 2019). Besides, frontoparietals of *Latonia* do not contact the squamosals.

When the frontoparietal MPM-PV 20025 is compared with that of other species of *Calyptocephalella* for which



Figure 3. 1, 3, 5, *Calyptocephalella gayi*, MACN-HE 45745; 2, 4, 6, *Ceratophrys ornata*, FCEN uncatalogued (35); schematic comparative drawings of articulated (left) and disarticulated (right) elements of the skull to expose the tongue-like processes; 1, right half of the skull; 2–3, nasal and frontoparietal; 4–5, nasal, maxilla and squamosal. Hatched areas indicate the tongue-like processes.

this element is preserved, its similarity with the frontoparietal of *C. canqueli*, from the Late Oligocene Scarritt Pocket (Schaeffer, 1949: fig. 2, AMNH 3429) and the Late Oligocene-Early Miocene of the Puesto Baibián (Muzzopappa and Báez, 2009: fig. 1, MPEF-PV 1498, 1881, 1886) localities, becomes obvious when regarding the proportions and the pustular ornamentation. As in *C. canqueli*, the frontoparietal of MPM-PV 20025 differs from that of *C. gavi* in having a longer orbital portion and a shorter postorbital portion, which may indicate a more posterior placement of the orbit. The well-preserved tongue-like process projecting from the frontoparietal towards the squamosal differs from that of *C. gayi* in being laterally broader and antero-posteriorly shorter in the fossil specimen (see Fig. 2.1 versus Fig. 3.1). The orbit of the Eocene *C. pichileufensis* Gómez, Báez and Muzzopappa, 2011 is antero-posteriorly longer and latero-medially narrower than in *C. canqueli*; furthermore, the frontoparietal in this species does not contact the squamosal, hence there is no postorbital bridge (Gómez et al., 2011). No other species of Calvptocephalella, nor Gigantobatrachus parodii Casamiquela, 1958 (formerly in synonymy with *Calyptocephalella* but recently recovered as a separate genus, still within Calyptocephalellidae, Agnolín, 2012), preserved frontoparietals to establish comparisons. The comparisons of maxillae MPM-PV 20025 with other species of *Calvptocephalella* and *Gigantobatrachus parodii*, show, aside from variations in the ornamentation patterns, significant differences in the morphology of the pars palatina and the length of the postorbital process, which imply different morphologies of both the zygomatic bridge and the orbit. As was the case with the frontoparietal, the preserved portions of the maxillae are similar to those of *C*. canqueli (Schaeffer, 1949: fig. 2, AMNH 3429; Muzzopappa and Báez, 2009: fig. 1, MPEF-PV 1498, 1885, 1889), the pars facialis, pars palatina and pars dentalis having the same proportions and still the same extension of the postorbital process. In addition, the pars palatina of MPM-PV 20025 is flattened at the level of the orbit, a feature restricted to C. canqueli (Muzzopappa and Báez, 2009), within the genus *Calyptocephalella*. When comparing the maxillae of MPM-PV 20025 with *C. casamayorensis* from the Eocene of Chubut (Schaeffer, 1949), similar maxillary proportions and length of the postorbital process are observed. However, there are differences in the pitted ornamentation and in the step-like pars palatina below the orbital portion of *C. casamayorensis*. Differences are more significant with *C. gayi*, regardless of sharing the pustular ornamentation. In *C. gayi*, the postorbital process is longer, the pars palatina is step-like below the orbit, the pars dentalis is deeper, and the pars facialis is shorter. Comparisons with *G. parodii* are more restricted due to the poor preservation of the maxilla: for instance, the postorbital process seems to be incomplete on its dorsal and lateral margins. The pars palatina of *G. parodii*, like in *C. gayi* and *C. casamayorensis*, is step-like below the orbit and the pars dentalis is two to three times deeper than that of MPM-PV 20025. Finally, the ornamentation is of the pitted type instead of pustular.

CONCLUSION

The presence of *Calvptocephalella* is reported for the first time in Río Santa Cruz. Its record in the Santa Cruz Formation, however, has already been described (as Calyptocephalella sp.) from the Atlantic coastal locality of Estancia La Costa (Tauber, 1999; Fernicola and Albino, 2012), synchronous according to the dates and analyses of Cuitiño et al. (2016). The specimen MPM-PV 20025, even though represented only by three cranial elements, is herein assigned to the species Calyptocephalella cf. canqueli owing to distinctive features that differentiate it from the remaining species of the genus (Muzzopappa and Báez, 2009): flattened pars palatina at the level of the orbit, dense pustular ornamentation, narrow and posteriorly delimited orbit by the postorbital bridge conformed by frontoparietal and squamosal, a shorter postorbital region and a longer antero-posterior orbital diameter, and significantly deeper pars facialis at the level of the orbit. It differs further from *C. gayi* by its shorter extension of the postorbital process of the maxilla and therefore shorter zygomatic bridge. Several of these features correlate with the shape of the orbit; the narrow and posterior position of the orbit of MPM-PV 20025 is due to the long orbital region of the frontoparietal plus the short zygomatic bridge established by the maxilla and squamosal.

The presence of *Calyptocephalella* cf. *canqueli* in the Santa Cruz Formation substantially enlarges the geographic distribution of this species, thus far recorded in the Province of Chubut (Schaeffer, 1949; Muzzopappa and Báez, 2009;

Muzzopappa and Nicoli, 2010). In agreement with data obtained from findings in Puesto Baibián (Gandolfo *et al.*, 2009) and Scarritt Pocket (Marshall *et al.*, 1986) (Province of Chubut), this form inhabited flooded zones and water bodies during warm temperate periods (Cuitiño *et al.*, 2016 and references therein). The area of the geographic distribution of *C. canqueli* is consistent with that of the extant *C. gayi* in Chile, although in different climatic conditions.

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MUZZOPAPPA: CALYPTOCEPHALELLA FROM THE RÍO SANTA CRUZ

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