



Systematic status of the mid-Tertiary neobatrachian frog *Calyptocephalella canqueli* from Patagonia (Argentina), with comments on the evolution of the genus

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Abstract. The neobatrachian genus *Calyptocephalella* Strand, closely allied to the Australian myobatrachoids in recent molecular analyses, is now restricted to lowland water bodies of the Austral forests of Chile but had a broader distribution according to paleontological data. New, well-preserved material from the early Miocene locality Estancia Baibíán, Chubut Province, Argentina, is described herein and assigned to *Calyptocephalella canqueli* Schaeffer, a species erected on the basis of Deseadan (late Oligocene) specimens, but subsequently synonymized with the only living species, *Calyptocephalella gayi* Duméril and Bibron. Detailed comparisons suggest that *Calyptocephalella canqueli* is a valid taxon representing frogs that inhabited Patagonia east of the Andes in the late Oligocene-early Miocene; a revised diagnosis is provided for the species. Palynological evidence coupled with the presence of *C. canqueli* document that humid forests, dominated by the angiosperm *Nothofagus*, persisted near the Atlantic coast in the Miocene. Disappearance of suitable habitats owing to a marked drying trend that started in the middle Miocene may have been responsible for the demise of this anuran genus east of the Andes.

Resumen. STATUS SISTEMÁTICO DEL ANURO NEOBATRACIO *CALYPTOCEPHALELLA CANQUELLI* DEL TERCIARIO MEDIO DE LA PATAGONIA (ARGENTINA) CON COMENTARIOS SOBRE LA EVOLUCIÓN DEL GÉNERO. El género de neobatrachios *Calyptocephalella* Strand, cercanamente relacionado con los miobatracoideos australianos en recientes análisis moleculares, está actualmente restringido a los cuerpos de agua del bosque Austral en Chile aunque tuvo una distribución más amplia de acuerdo a la información paleontológica. Se describe aquí material nuevo y muy bien preservado proveniente del Mioceno temprano de la localidad Estancia Baibíán, provincia de Chubut, Argentina, el cual es asignado a *Calyptocephalella canqueli* Schaeffer, especie erigida a partir de restos deseadenses (Oligoceno tardío), pero que fuera subsecuentemente sinonimizada con la única especie viviente del género: *Calyptocephalella gayi* Duméril y Bibron. Sin embargo, en base a comparaciones detalladas, se concluye en el presente trabajo que *C. canqueli* es un taxón válido que habitó Patagonia al este de los Andes durante el Oligoceno tardío-Mioceno temprano, y se provee una diagnosis revisada. La evidencia palinológica sumada a la presencia de *C. canqueli* documenta que los bosques húmedos, dominados por la angiosperma *Nothofagus*, persistieron cerca de la costa atlántica durante el Mioceno. La desaparición de ambientes propicios debido a una marcada tendencia a la aridez que se inició en el Mioceno medio probablemente haya sido responsable de la extinción de este género de anuros al este de los Andes.

Key words. Australobatrachia. Myobatrachoidea. Gondwana. Sarmiento Formation. Deseadan. Colhuehuapian. Austral forests.

Palabras clave. Australobatrachia. Myobatrachoidea. Gondwana. Formación Sarmiento. Deseadense. Colhuehuapense. Bosques australes.

Introduction

The anuran fauna that currently inhabits the moist Austral forests, a unique biotope on the foothills of the southernmost Andes in South America, typically is thought to include the most primitive "leptodactylid" frogs (Ceï, 1962; Formás, 1979). Many

of these anuran taxa were found to be highly endemic and considered to be relicts of groups formerly widespread in Temperate South America (Formás, 1979). *Calyptocephalella* Strand, 1928, which today is restricted to the temperate region of Chile, from the Región Central (Aconcagua Province) to Puerto Montt (*i.e.*, between 30° and 42° S; Ceï, 1962), is a fine example of such an endemic taxon. The only living species, *Calyptocephalella gayi* Duméril and Bibron, 1841 (formerly *Caudiverbera caudiverbera*; see Myers and Stothers, 2006 for nomenclatorial changes), is an aquatic to semi-aquatic frog that dwells in lowland lakes, ponds, and quiet streams (Ceï, 1962). Traditio-

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nally, *Calyptocephalella* was regarded as a member of "Telmatobiinae," (Lynch, 1978; Díaz and Valencia, 1985; Lavilla, 1988; Nuñez and Formás, 2000); however, this South American "leptodactylid" subgroup, like "Leptodactylidae" in its traditional sense, is considered to be non-monophyletic (Haas, 2003; Correa *et al.*, 2006). Several recent phylogenies of amphibians based on molecular data from many taxa agree in providing an alternate phylogenetic hypothesis in which *Calyptocephalella* is closely allied to the Australian myobatrachoids (San Mauro *et al.*, 2005; Correa *et al.*, 2006; Frost, 2007), thereby drastically changing previous ideas on the evolutionary history of the genus. Owing to the absence of rigorous, broad-scale morphological analyses of neobatrachian interrelationships and the frequency of homoplasy among anurans, there are no known morphological characters to support this novel hypothesis. Furthermore, *Calyptocephalella* seldom has been included in phylogenetic studies; so, there is little information in the literature about its relationships.

Calyptocephalella has a long stratigraphic record. Although there is a significant hiatus that extends from the late Miocene to the Pleistocene (Báez, 2000; Muzzopappa, 2005), fossil remains assigned to, or possibly near to, this taxon (mostly as *Caudiverbera* discussed below) range from the uppermost Cretaceous [Los Alamos Formation, (Báez, 1987)] to the Pleistocene [Laguna de Tagua Tagua Archaeological Locality, (Casamiquela, 1976)]. These remains usually are fragmentary and known to date only from Patagonia, east of the Andes, and central Chile. This former distribution is consistent with the hypothesized sister-group relationship between the South American *Calyptocephalella*-*Telmatobufo* clade and the Australian Myobatrachoidea, because South America and Australia had some kind of geographical connection, via Antarctica, that permitted limited interchange of land vertebrates until at least the early Paleocene (Woodburne and Case, 1996; Vizcaíno *et al.*, 1998).

Paleontological exploration in central Patagonia conducted by researchers of the Museo de La Plata and the Museo Paleontológico Egidio Feruglio in 1997 led to the discovery of a new Neogene fossiliferous locality in the Sierra de La Colonia region in Chubut Province (figure 1). Lacustrine rocks well exposed at this locality, called Puesto Baibíán, yielded the natural mold of a partially articulated anuran skull. A subsequent fieldtrip to the same locality carried out by one of the authors (P.M.) produced several isolated cranial and postcranial elements, all of them also preserved as natural molds, as well as a partial skeleton of a single individual at a nearby site, Puesto Gerónimo. All these fossils can be referred to *Calyptocephalella*. They are significant be-

cause they are more complete than previous finds and they have excellent preservation, in contrast to most Cretaceous and Tertiary remains assigned to the genus. The purpose of this study is to clarify the taxonomic status of the material from Estancia Baibíán (*i.e.*, Puesto Baibíán and Puesto Gerónimo). It is the first step in elucidating the evolutionary history of this ancient anuran lineage in the context of the former land connections of South America with other Gondwanan regions and drastic climatic and environmental changes throughout the Cenozoic in high latitudes.

Systematic status of the extinct nominal species of Calyptocephalella

Several generic names have been erected for fossils considered to represent close relatives of the extant *Calyptocephalella gayi* and later synonymized with this genus (as *Caudiverbera*). Such is the case of the Eocene specimens described as *Eophractus casamayorensis* (Schaeffer, 1949) and those interpreted as representatives of the miocene *Gigantobatrachus parodii* (Casamiquela, 1958). Lynch (1971) considered the latter taxon, together with the Oligocene-Miocene *Calyptocephalella canqueli* Schaeffer, 1949, as subjective junior synonyms of *Calyptocephalella gayi* (as *Caudiverbera caudiverbera*). Also, he accepted *E. casamayorensis* as the only valid extinct species of *Calyptocephalella*, although he neither gave any explanation for this assignment, nor provided diagnostic characteristics to distinguish this species from *C. gayi*. In contrast, Sanchiz (1998) listed *casamayorensis*, *canqueli*, and *parodii* as extinct species of *Calyptocephalella*. Last, *Teracophrys* Ameghino, 1899 (Ameghino, 1900-1902) must be added to the list of synonyms of *Calyptocephalella*, because the Miocene remains assigned to the former subsequently were referred to the latter (Báez, 1977).

Geological and paleoenvironmental setting

The fossil site is located on the southwestern slope of the Sierra de La Colonia, southern Somuncurá Massif, Chubut Province (figure 1). The fossiliferous beds are part of a non-marine sequence composed mainly of 12 m of reddish-brown claystones, which disconformably overlies the uppermost section of the La Colonia Formation (G. Cladera, pers. comm., 2003). Sedimentological features suggest that the depositional environment at Puesto Baibíán evolved from a fluvial setting at the bottom, represented by claystone and sandy beds, to a lacustrine setting, represented by several meters of

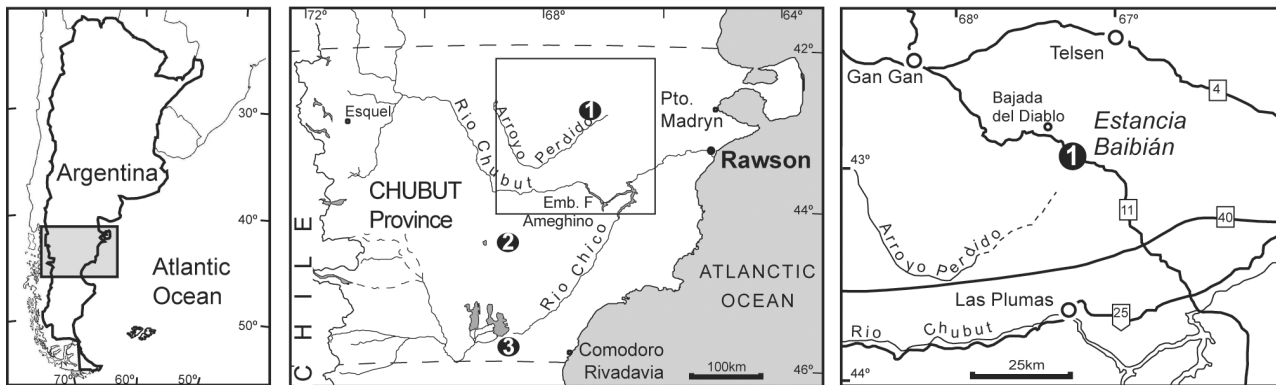


Figure 1. Geographic location of the fossiliferous localities (1) Estancia Baibíán (including Puesto Baibíán and Puesto Gerónimo sites), (2) Scarritt Pocket, and (3) Gran Barranca (modified from Archangelsky and Zamaloa 2003) / ubicación geográfica de las localidades fosilíferas (1) Estancia Baibíán (incluyendo los sitios Puesto Baibíán y Puesto Gerónimo), (2) Scarritt Pocket y (3) Gran Barranca (modificado de Archangelsky y Zamaloa 2003).

brownish, bedded siltstone (G. Cladera, pers. comm., 2003). The upper third of the lacustrine sediments contains the shaly layer that yielded the anurans and some remains of fishes (percoids?). This layer also contains a large quantity of organic filaments that range in length from 1-50 mm and lay parallel to the bedding plane. Overlying and underlying the vertebrate-bearing layer, there are 7 cm thick layers of coal from which seeds and lanceolate leaves were recovered; these three layers are traceable along at least 200 m. The depositional environment inferred from the sedimentological data is in agreement with the paleontological content. Palynological samples from the level containing the anuran and fish remains record the presence of freshwater algae, amorphous organic material, and abundant pollen of the aquatic-to-subaquatic angiosperm *Sparganiaceapollenites barungensis*, indicating sedimentation in a permanent, freshwater pond. In particular, the abundance (50%) of *S. barungensis*, a taxon that grows in the shallow margins of bodies of water, indicates that the palynological samples were taken near the former shore (M.C. Zamaloa, pers. comm. 2007; Barreda and Palazzesi, 2007).

At first, the fossiliferous sequence exposed at Puesto Baibíán was thought to be part of the underlying La Colonia Formation and, thus, of latest Cretaceous age because the upper section of this unit has yielded a Campanian-Maastrichtian marine fauna (Ardolino *et al.*, 1995). Subsequent palynological studies demonstrated that the sequence exposed at Puesto Baibíán is younger than middle Eocene, owing to the presence of *Nothofagidites* among the predominant angiosperm pollen (Archangelsky and Zamaloa, 2003). Furthermore, the microflora supports an earliest Miocene (early Aquitanian) age based on the degree of morphological diversity shown by the asteracean pollen and the presence of *Tricolpites trioblatus* (Barreda and Palazzesi, 2007).

At Puesto Baibíán, a basalt layer overlies the anuran-bearing sequence and underlies pyroclastic rocks attributed to the Sarmiento Formation (Archangelsky and Zamaloa, 2003). The latter unit crops out in the nearby Bajada del Diablo region, where a basalt flow is intercalated within Deseadan (late Oligocene) or Colhuehuapian (early Miocene) tuffs of the upper section of the Formation (Ardolino *et al.*, 1995; Ardolino *et al.*, 1999). This stratigraphical evidence points to the recognition of the anuran-bearing sequence as a fluvio-lacustrine facies of the upper section of the Sarmiento Formation, a hypothesis that should be confirmed by the radiometric dating of the basalts from Puesto Baibíán.

Material and methods

The described and comparative materials used during the study are housed in the following institutions: American Museum of Natural History, New York, USA (AMNH); Departamento de Ciencias Geológicas, Paleontología, Vertebrados, Universidad de Buenos Aires, Buenos Aires, Argentina (CPBA-V); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Museo Paleontológico "Egidio Feruglio," Trelew, Chubut, Argentina (MPEF-PV).

The fossils described herein consist mostly of the natural molds of isolated bones (figure 2.1), although actual bones of a partially articulated skeleton are also preserved (figure 2.3). Silicone rubber peelings of the molds were made (figures 2.2, 4), the illustrations of which were executed with the aid of a Zeiss Stemi SV11 binocular equipped with a camera lucida. Isolated teeth were removed from the matrix of MPEF-PV 1887 and fixed on a plate; the same procedure was applied to replacement crowns removed

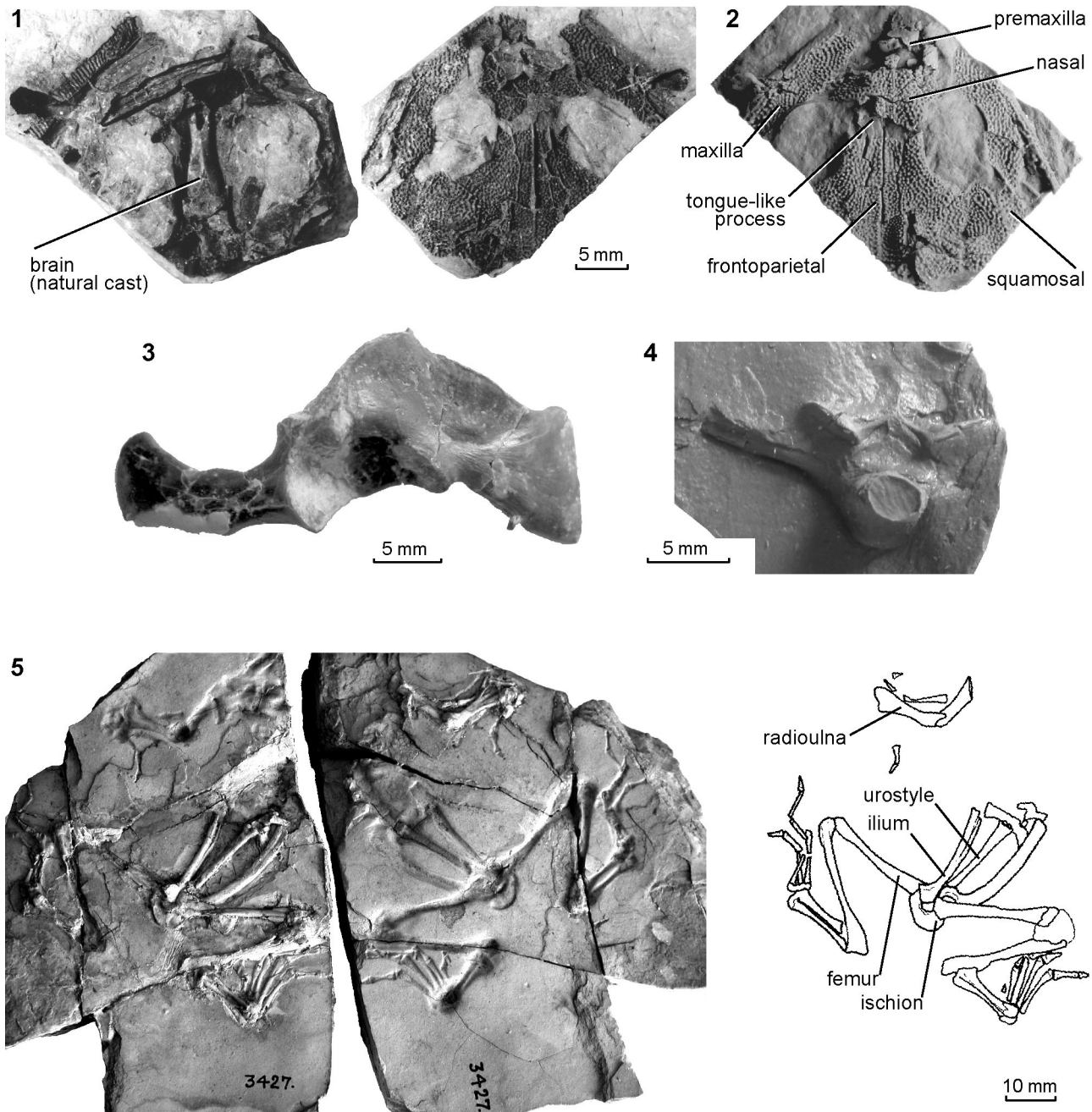


Figure 2. 1-4, *Calyptocephalella canqueli* Schaeffer, from Estancia Baibíán / *procedente de Estancia Baibíán*; 1, MPEF-PV 1498, ventral (left) and dorsal (right) impressions of the skull / *impresiones ventral (izquierda) y dorsal (derecha) del cráneo*; 2, silicone rubber peel of the dorsal impression of the same specimen / *positivo de goma siliconada de la impresión dorsal del mismo ejemplar*; 3, MPEF-PV 1887, articulated scapula and coracoid / *escápula y coracoides articulados*; 4, MPEF-PV 1883, silicone rubber peel of the impression of a 5th presacral vertebra in posterior view, condyle missing / *positivo de goma siliconada de la impresión de una vértebra presacra 5° en vista posterior, faltando el cóndilo*; 5, *C. canqueli* Schaeffer, AMNH FR 3427, from Deseadan beds at Scarritt Pocket, part and counterpart and schematic composite interpretive drawing / *procedente de estratos deseadenses de Scarritt Pocket, parte y contraparte y dibujo esquemático interpretativo compuesto*.

from dry skeletons of *Calyptocephalella gayi* for comparisons. Both sets of teeth were scanned at the SEM laboratory of the Museo Cs. Naturales "Bernardino Rivadavia," with a SEM Philips XL30 TMP. Palynological samples from the anuran-bearing bed were prepared following the standard procedure at AMEGHINIANA 46 (1), 2009

the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.

Observations of *Calyptocephalella canqueli* from the type locality (see below) are based on photographs of AMNH FR 3429 (Holotype) and 3427 (figure 2.5).

Systematic paleontology

AMPHIBIA Gray, 1825

ANURA Fischer von Waldheim, 1813

NEOBATRACHIA Reig, 1958

Calyptocephalella Duméril and Bibron, 1841

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

Calyptocephalella canqueli Schaeffer, 1949

Figures 2-4

Holotype. *Calyptocephalella canqueli* Schaeffer, 1949 AMNH FR 3429. Partial skeleton of a single individual consisting of crushed skull, right pectoral girdle and fore limb, articulated three first vertebrae, isolated vertebrae, and limb fragments.

Type locality and age. Rinconada de los López, Scarritt Pocket, Chubut Province. Deseadan (late Oligocene).

Additional material from type locality used in this study. AMNH FR 3427. Incomplete skeleton of a single individual consisting of posterior portion of axial skeleton, right forelimb, pelvic girdle, and hind limbs.

Referred material. Incomplete, partially articulated skull (MPEF-PV 1498); incomplete, partially articulated skull (MPEF-PV 1881); sphenethmoid (MPEF-PV 1882); ilium and presacral vertebra (MPEF-PV 1883); left humerus (MPEF-PV 1884); sacrum, atlas, urostyle, maxilla (MPEF-PV 1885); incomplete, disarticulated skull, and sacral vertebra (MPEF-PV 1886); disarticulated premaxilla, portion of maxilla, frontoparietal, quadratojugal, sphenethmoid, otic capsules, mandible, left humerus, proximal portion of right humerus, scapula, and coracoid (MPEF-PV 1887); left clavicle (MPEF-PV 1888); left maxilla (MPEF-PV 1889); tibiofibula (MPEF-PV 1890).

Locality and horizon. Puesto Baibíán (S 43°00'29" W 067°38'02") and Puesto Gerónimo (S 42°59'49.7" W 67°37'56.7"), Estancia Baibíán, 10 km SE Bajada del Diablo on Provincial Route 11, Chubut Province, Argentina. Upper third of the lacustrine sequence exposed at Estancia Baibíán (Sarmiento Formation?), early Miocene.

Emmended diagnosis. Species of *Calyptocephalella* differing from *C. gayi* in proportionally narrower adult orbit, larger and more rounded posterolateral projection of squamosal, shorter scapula (140% the length of the coracoid), ilium with wider ventral acetabular expansion and preacetabular zone.

Description. The following description is a composite that is based on all of the elements recovered at Estancia Baibíán. We consider all of these elements, which belong to at least five adult individuals, to represent a single taxon that shows comparable size-

range and degree of ossification with the living *Calyptocephalella gayi*.

The skull is relatively flat, wider than long, and has an approximately triangular outline in dorsal aspect. The orbits are longer than wide and oval. Both dermal and endochondral elements are well ossified. Despite the extensive ossification, no fusion was observed between dermal bones, or between the latter and endochondral elements, even though the available specimens belong to adult individuals.

The roofing bones are ornamented with relatively low conical tubercles that are moderately separated from each other and are distributed over the entire surface of each bone (figure 2.2). The nasals and the *partes dentalis* of the maxillae, however, have a series of deep pits along their margins, probably resulting from the fusion of adjacent tubercles, as suggested by Lynch (1971).

The external surface of the premaxilla is smooth, except for some irregular shallow furrows on the alary process. The latter process is approximately rectangular; when in natural position, the alary processes were close to each other and their medial margins were parallel. The *pars palatina* has a distinct palatine process and a lateral expansion for the articulation with the *pars palatina* of the maxilla. The notch resulting between these two processes has the shape of an asymmetrical V, the medial border being steeper than the lateral.

The maxilla has a high *pars facialis* that forms the lateral margin of the orbit (figures 2.1-2 and 3.1-2). On its inner side it bears a groove between the *pars facialis* and the ascending maxillary palatine process for the articulation with the nasal. Posterior to the orbit, the *pars facialis* forms a high zygomatic process that articulates broadly with the zygomatic ramus of the squamosal by means of a deep groove on the internal surface of the zygomatic process of the maxilla. The well-developed *pars palatina* forms a projecting shelf, except for a portion at the level of the ventral margin of the orbit where it flattens against the inner surface of the *pars facialis*; this causes the reduction of the sulcus for the palatoquadrate bar (MPEF-PV 1889), or even its absence (MPEF-PV 1885). At the level of the pterygoid process formed by the *pars palatina*, on the inner side of the *pars facialis*, there is a distinct longitudinal crest that probably roofed the *processus pterygoideus* of the palatoquadrate cartilage in life. Dorsal to this crest, an anteriorly directed, funnel-shaped channel penetrates deep into the bone. The maxillary tooth row extends from the anterior end of the bone to the anterior half of the articular facet for the quadratojugal.

The teeth are pedicellate and bicuspid; the crowns are conical and distinctly arched lingually (figure 3.13). The main cusp is sharp distally and bears a ca-

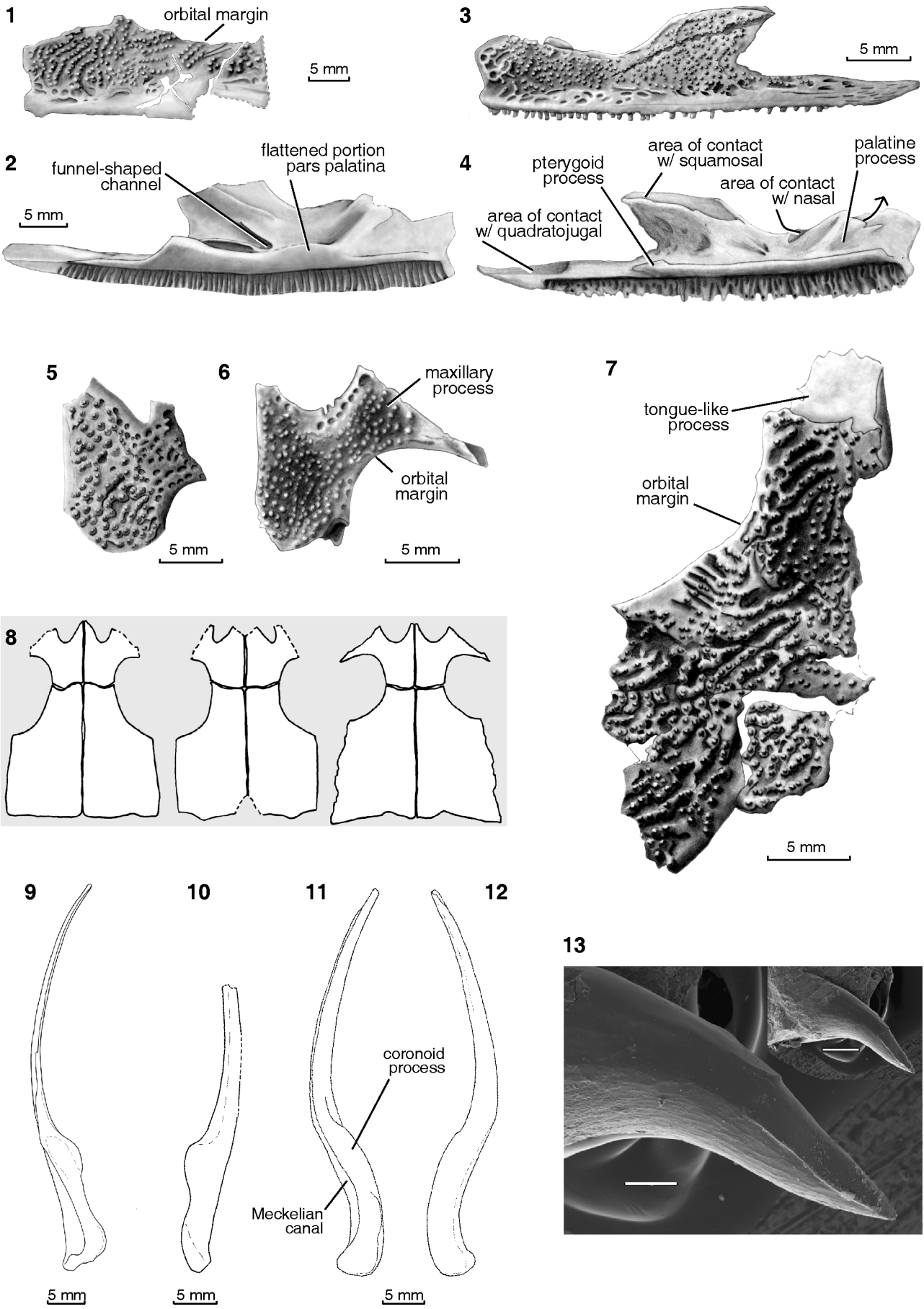
rina along its tip. Labially and in a somewhat more basal position, there is a second, lower cusp that completely overlaps the main cusp and is visible owing to its slightly protruding margin.

The nasal (figure 3.5) is roughly quadrangular. Its posterior half overlaps the most anterior portion of the sphenethmoid and an anterior process of the frontoparietal. Laterally, the nasal is in contact with the maxilla by means of a wide maxillary process that forms the anterior margin of the orbit. The nasal-frontoparietal suture is either perpendicular to the midline (MPEF-PV 1886) or slightly V-shaped (MPEF-PV 1498). The frontoparietals (figures 2.1-2 and 3.7) articulate with one another along their mid-lengths, thereby resulting in the absence of a frontoparietal fontanelle. A smooth tongue-like process that extends from the anterior margin of each frontoparietal underlies the most posterior portion of the corresponding nasal and rests on the posterior half of the sphenethmoid. Posterolaterally, the frontoparietal overlaps the entire otic capsule and the medial portion of the *crista parotica*, and articulates broadly with the otic plate of the squamosal forming a parasagittal suture. A distinct flange, the *lamina perpendicularis*, projects ventrally from the ventral surface of the frontoparietal; this flange overlaps the dorsolateral surface of the braincase and the most dorsal part of the anterior wall of the otic capsule (MPEF-PV 1887). The dorsal surface of the frontoparietal extends laterally beyond the *lamina perpendicularis* to form an extensive supraorbital flange. The squamosal has an extensive otic plate, which articulates with the frontoparietal, medially, and with the zygomatic process of the maxilla, anterolaterally. The vomers floor the anterior palate, medial to the choanae. Each vomer has a wide anterior portion that nearly reaches the maxilla-premaxilla articulation; a posterolaterally directed, acuminate process, herein interpreted as the prechoanal process, arises from this portion. Fragments of bone next to the sphenethmoid and posterior to the prechoanal process might represent a postchoanal process. The presence of teeth or odontoids cannot be determined owing to in-

complete preservation of the vomer. Posterior to the vomers and slightly anterior to the orbitonasal foramina, there is a pair of elongate impressions with rounded medial ends on the ventral surface of the sphenethmoid in MPEF-PV 1881 and 1882; these are interpreted as palatines (neopalatines *sensu* Trueb, 1993). The parasphenoid is T-shaped; its rounded anterior end has an irregular border and reaches a point slightly anterior to the palatines. The anterior portion of the cultriform process of the parasphenoid is narrow, but becomes slightly wider along the posterior half of the orbit, where it extended under the cartilaginous portion of the floor and most ventral part of the lateral walls of the braincase. The alae of the parasphenoid are not preserved; however, the irregular lateral margins of the corpus of the bone, as well as the occurrence of a flange that overlaps the most ventral part of the anterior wall of the otic capsule, indicate their presence. The mandible is represented by the angulosplenic and dentary (figure 3.9). Owing to the preservation, it was not possible to assess whether the mentomeckelians were present. The anterior end of the angulosplenic reaches near the mandibular symphysis; its posterior part is rather straight, robust, and bears a well-developed coronoid process. The dentary extends along the mandibular arcade from the symphysis to the level of the coronoid process.

The sphenethmoid is completely covered by the extensive nasals and frontoparietals. Anteriorly, the sphenethmoidal ossification invades the *septum nasi* and the olfactory capsules, including parts of the *planae antorbitales*, *tectum nasi*, and *solum nasi*; as a result, the orbitonasal and olfactory foramina are completely surrounded by bone. The anterior and posterior limits of the sphenethmoidal ossification, however, vary among the available specimens in part depending on their age. In all preserved specimens, the dorsal surface of the sphenethmoid lacks an emargination for the frontoparietal fenestra. The exoccipital and the prootic are also well ossified and indistinguishably fused to one another. In one individual (MPEF-PV 1881), it is evident that the prootic ossifi-

Figure 3. Comparative morphology of skull bones / morfología comparada de huesos craneanos; **1, 2, 5, 7, 9, 10** and **13**, *Calyptocephalella canqueli* Schaeffer; **1**, MPEF-PV 1498, partial maxilla in external view / maxilar incompleto en vista externa; **2**, MPEF-PV 1888, partial maxilla in internal view / maxilar incompleto en vista interna; **5**, MPEF-PV 1886, right nasal in dorsal view / nasal derecho en vista dorsal; **7**, MPEF-PV 1881, left frontoparietal in dorsal view / frontoparietal izquierdo en vista dorsal; **9**, MPEF-PV 1887, left angulosplenic in dorsal view / angulosplenic izquierdo en vista dorsal; **10**, holotype / holotipo, AMNH FR 3429, right angulosplenic (reversed) in ventral view / angulosplenic derecho (invertido) en vista ventral; **13**, MEF-PV 1887, SEM photograph of maxillary tooth in lateral view, scale bars: 100 μ (left) and 250 μ (right) / fotografía tomada con MEB de diente de maxilar en vista lateral, escalas: 100 μ (izquierda) y 250 μ (derecha); **3, 4, 6, 11** and **12**, *Calyptocephalella gayi* Duméril and Bibron; **3**, MACN 39076, maxilla in external view / maxilar en vista externa; **4**, MACN 39076, maxilla in internal view / maxilar en vista interna; **6**, MACN 39076, right nasal in dorsal view / nasal derecho en vista dorsal; **11**, CPBA-V 1052, left angulosplenic in dorsal view / angulosplenic izquierdo en vista dorsal; **12**, CPBA-V 1052, left angulosplenic in ventral view / angulosplenic izquierdo en vista ventral; **8**, comparative morphology of articulated nasals and frontoparietals of *C. canqueli* (left from holotype and center from MPEF-PV 1498) and *C. gayi* (right) / morfología comparada de nasals y frontoparietales articulados de *C. canqueli* (izquierda basada en el holotipo y centro basada en MPEF-PV 1498) y *C. gayi* (derecha).



cation invaded the *tectum synoticum*, forming an almost complete bony roof to the posterior braincase. Lateral to the inner ear region, there is an extensively ossified *crista parotica*, which is distally expanded. Its dorsal surface is flat, whereas its ventral surface is deeply excavated midlaterally to form a roof for the middle ear cavity. The ventral surface of the inner ear region is not preserved in any specimen; this prevents description of the shape and occurrence and position of foramina. The occipital condyles, along with other parts of the exoccipitals, are poorly preserved. The columella is represented in one specimen (MPEF-PV 1498) by the proximally expanded, rod-like portion of the ossified *pars media plectri*.

The vertebrae are disarticulated and represent only a small portion of the entire column. The atlas has a relatively flat centrum, bearing two anterior oval cotyles separated by a narrow notch (Type II of Lynch's [1971] classification of atlases) and a posterior condyle. Another presacral vertebra, interpreted as possibly the fifth owing to its long, slender, slightly posteriorly directed transverse processes, and high neural spine, has a procoelous centrum (figure 2.4). The sacral vertebra (figure 4.1) has a flattened, procoelous centrum and diapophyses that are moderately expanded distally and posteriorly directed. Posteriorly, the sacral centrum bears two condyles for the articulation with the closely set cotyles of the urostyle (MPEF-PV 1886). A high dorsal crest extends along the preserved portion of the latter element. The presence of one nerve foramen at the base of the dorsal crest on the left side indicates that at least one postsacral neural arch was formed during development.

The scapula (figures 2.3 and 4.6) is a stout and quadrangular bone. Its maximum length (from the *pars acromialis* to the posterolateral angle of the shaft) is four thirds the maximum length of the long axis of the coracoid. The scapula has an expanded *pars acromialis*, which is separated from the comparatively less-developed *pars glenoidalis* by a deep notch. A conspicuous, laminar crest occurs on the leading edge of the scapular shaft. The posterior margin of the scapula is thick and slightly posteriorly directed. The coracoid (figures 2.3 and 4.6) is robust; it is moderately expanded at both ends, with the sternal end being somewhat more expanded than the glenoidal end. At its midlength, the diaphysis of the coracoid bears remarkable symmetrical expansions anteriorly

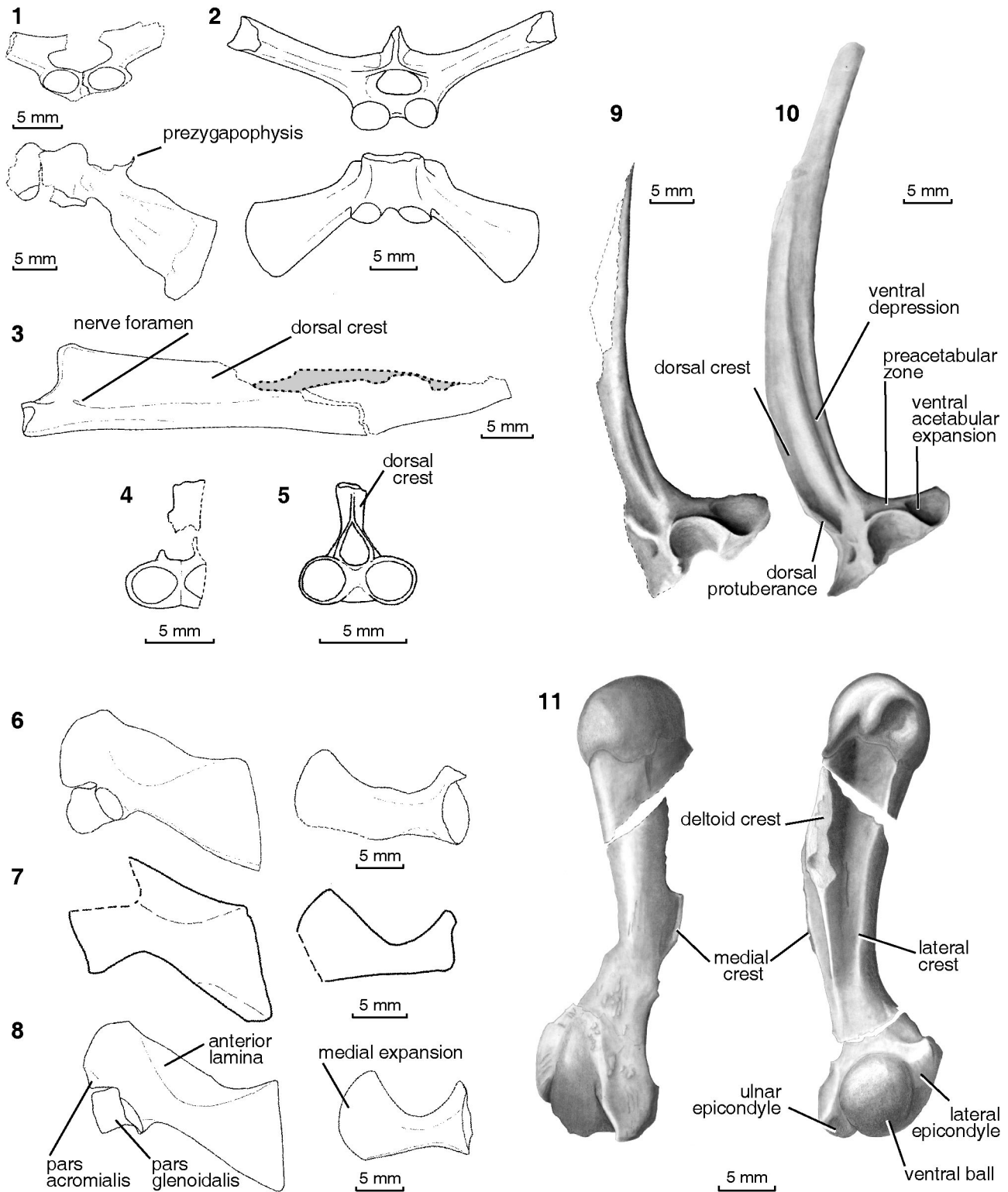
and posteriorly. The clavicle is well ossified and anteriorly curved. The humerus (figure 4.11) bears a conspicuous deltoid crest along the anterior two thirds of the ventral surface of the diaphysis. This crest is slightly displaced medially and, together with a medial crest, forms a rather deep channel for the tendon of the m. coracoradialis. The distal end of the humerus bears a protuberant, well-ossified ventral ball (= *eminentia capitata*).

A right ilium (MPEF-PV 1883) is the only preserved element of the pelvic girdle (figure 4.9). This bone has a long, mediolaterally flattened, and slightly ventrally curved shaft. A dorsal crest was probably present, indicated by a longitudinal groove on the inner side of the iliac shaft. On the lateral side of the shaft there is a distinct ventral depression that extends longitudinally along its posterior third. The corpus of the ilium is broad with wide supracetabular and ventral acetabular expansions, and wide preacetabular zone (*sensu* Lynch, 1971). On the supracetabular expansion, an ovoid dorsal protuberance extends diagonally from the preserved dorsal margin to the base of the extruded dorsal margin of the acetabulum. The tibiofibula, the only recovered element of the hind limb, is slightly curved and has a foramen for the anterior tibial artery at the midlength of the diaphysis.

Comparisons

The combined occurrence of bicondylar sacro-urostyler articulation, procoelous holochordal vertebrae, and wide scapula is consistent with referral of the remains from Estancia Baibián (EB) to Neobatrachia. Furthermore, these fossils may be attributed to the neobatrachian genus *Calyptocephalella* because of the features they share in common with this taxon - viz., the similar shape and extension of the roofing skull elements, which are broadly in contact to form a casque that covers the neurocranium, and the tuberculated ornamentation. As in adults of *C. gayi*, the sphenethmoid lacks an emargination for the frontoparietal fenestra, there is no frontoparietal fontanelle, the lateral margin of the orbit is formed by the maxilla, the wide maxillary *pars dentalis* bears pedicellate, bicuspid teeth, the flat sacral diapophyses are moderately expanded distally, and the quadrangular scapula has a well-developed flange on its

Figure 4. Comparative morphology of postcranial bones / *morfología comparada de huesos postcraneanos*; **1, 3, 4, 6, 7, 9** and **11**, *Calyptocephalella canqueli* Schaeffer; **1**, sacral vertebra / *vértebra sacra*, MPEF-PV 1885, in posterior view (above) / *en vista posterior (arriba)*, MPEF-PV 1886 in ventral view (below) / *en vista ventral (abajo)*; **3**, MPEF-PV 1885, urostyle in left lateral view, restored parts from the right side in gray / *urostilo en vista lateral izquierda, partes reconstruidas en base al lado derecho en gris*; **4**, MPEF-PV 1885, urostyle in anterior view / *urostilo en vista anterior*; **6**, MPEF-PV 1887, left scapula (left) and coracoid (right) in ventral view / *escápula (izquierda) y coracoid*



coides (derecha) izquierdos en vista ventral, 7, holotype / holotipo, AMNH FR 3429, right scapula (left) and coracoid (right) in dorsal view / escápula (izquierda) y coracoides (derecha) derechos en vista dorsal; 9, MPEF-PV 1883, right ilium in acetabular view / ili6n derecho en vista acetabular; 11, MPEF-PV 1884, left humerus in dorsal (left) and ventral (right) views / h6mero izquierdo en vistas dorsal (izquierda) y ventral (derecha); 2, 5, 8 and 10, *Calyptocephalella gayi* Dum6ril and Bibron, CPBA-V 1433; 2, sacral vertebra in posterior (above) and ventral (below) views / v6rtebra sacra en vistas posterior (arriba) y ventral (abajo); 5, urostyle in anterior view / urostilo en vista anterior; 8, left scapula (left) and coracoid (right) in ventral view / escápula (izquierda) y coracoides (derecha) izquierdos en vista ventral; 10, right ilium in acetabular view / ili6n derecho en vista acetabular.

anterior edge. However, the allocation of the fossils at the species level demands scrutiny not only of the skeleton of the living *C. gayi*, but also of other fossil remains attributed to the genus.

Preliminarily, Muzzopappa and Báez (2004) suggested that the remains from EB might represent the poorly known Eocene *Calyptocephalella casamayorensis*, partly owing to the former interpretation of the bearing sediments as being Eocene in age. The only known elements (incomplete maxillae and nasal, and one presacral vertebra) of *C. casamayorensis* are insufficient to make significant comparisons either with *C. gayi* or with the remains from EB, but it is noteworthy that all available skull bones have an ornamentation consisting of deep pits. In contrast, every dermal roofing bone recovered at EB, including those representing individuals of sizes within the size-range of *C. casamayorensis*, bears conical tubercles on its external surface. Also the comparably sized adult skulls of *C. gayi* examined have a tuberculated ornamentation pattern, although somewhat different from that of the bones from EB (figures 3.1, 3, 5-7). Thus, the ornamentation pattern suggests that the species present in EB is not *C. casamayorensis*.

Although *Calyptocephalella canqueli* from Deseadan (late Oligocene) beds at the neighboring locality of Scarritt Pocket was synonymized with *C. gayi* (Lynch, 1971), it seems pertinent to include the holotype and a specimen referred to this fossil taxon in the comparisons (figure 2.5). Other incomplete remains that were considered to represent new fossil taxa (discussed above) are in need of revision and were considered too fragmentary to establish meaningful comparisons at this point. In the original description, Schaeffer (1949) stressed the close relationship of *C. canqueli* with *C. gayi*. Nevertheless, he considered that a taxonomic separation was warranted based on the wider nasal bridge between the orbit and the naris, the narrower (*i.e.* longer than wide) adult orbit, and the relatively shorter and less rounded posterolateral projection of the otic plate of the squamosal in the former. The nasal from EB has a bridge of similar proportions to that of *C. gayi* (figures 3.5-6) but the anterior projection of this bone is distinctly wider, a feature correlated with a narrower exonarial notch, than in all of the other examined taxa. Also, the skulls from EB and *C. canqueli* have proportionally shorter postorbital regions and larger orbital lengths than that of the living species (figure 3.8). Additionally, in both fossil forms the maxillary *pars facialis* at the level of the orbit is significantly higher than that of *C. gayi*; hence, the orbits are markedly oval in contrast to the rather circular orbits of *C. gayi*. In addition to the higher *pars facialis*, the maxilla from EB is further distinguished from that of *C. gayi* in having a flattened *pars palatina* at the level

of the orbit instead of being shelflike (figures 3.2, 4). Also at this level, the palatine process forms an angle (42-48°) with the horizontal plane that is wider than in *C. gayi* (15-25°). We were unable to examine these latter features in *C. canqueli* because the mandible overlaps the inner side of the maxilla in the only specimen available for the examination of this trait.

The specimens from EB and *C. canqueli* are more densely ornamented than is the extant species, probably because the tubercles are lower and have wider bases than in *C. gayi*. In addition, the angulosplenials of these fossil forms lack the distinctive sigmoid shape that characterizes that of *C. gayi* and bear better-developed coronoid processes than do the latter (figures 3.9-12); these differences may indicate changes in the musculature involved in the opening and closing of the mouth. Also, the jaw articulation is more anterior in the fossils than in *C. gayi*.

The neurocranium is heavily ossified in all examined species of *Calyptocephalella*, a characteristic shared with its sister taxon, *Telmatobufo*. In the specimens from EB (especially in MPEF-PV 1881), the complete ossification of the roof of the braincase suggests the absence of chondrocranial fenestrae, both frontoparietal and parietal. This remarkable feature also occurs in the larval chondrocranium of *C. gayi* (Parker, 1881; Reinbach, 1939) and in a few other anurans, such as *Ceratophrys cornuta* (Wild, 1997), *Ceratophrys ornata*, and *Lepidobatrachus laevis* (Haas, 2003). We were unable to assess the condition for *Calyptocephalella canqueli* because the neurocranium is not exposed dorsally.

In regard to the postcranial skeleton, the sacral vertebra from EB differs from that of the living species in having more dorsoventrally flattened condyles and less dorsally directed diapophyses (figures 4.1-2). The urostyle from EB bears a high dorsal crest along most of its length (figure 4.3) unlike the urostyle of the living species, the crest of which markedly decreases in height at the anterior third of the bone. Schaeffer (1949:54) described the dorsal crest on the urostyle of *C. canqueli* as a "strongly developed dorsal ridge". The urostylar cotyles are not as distinctly separated from one another as they are in the living species (figures 4.4-5); instead, they are narrowly separated in both fossil forms. It is noteworthy that Schaeffer (1949) stated that the urostyle of *C. canqueli* has two condyles. Even though two balls are evident at the proximal end of this element, they certainly correspond to the condyles of the incompletely preserved sacral vertebra. There are some significant differences in the proportions of the pectoral girdle of the compared taxa (figures 4.5-8). While the scapula is 40% longer than the coracoid in *C. canqueli* and the species from

EB, it is about 65-80% in *C. gayi*. The glenoid of the scapula is obliquely oriented in the species from EB, whereas it is almost perpendicular to the *pars glenoidalis* in *C. gayi*; this results in a wider glenoid cavity in the former than in the latter. The condition of *C. canqueli* could not be established because the head of the humerus obscures the glenoid cavity in the holotype, the only specimen available for assessing this trait. The humerus from EB is rather more robust than that of *C. gayi*, although both have similarly conspicuous cristae along their respective diaphyses.

The ilium from EB has the supra-acetabular and ventral acetabular expansions and the preacetabular zone much wider than that of *Calyptocephalella gayi*. *C. canqueli* seems to have had a similarly wide ventral acetabular expansion and preacetabular zone; unfortunately, the supra-acetabular expansion is obscured by the femur and this makes it difficult to assess its width. All three forms have iliac shafts bearing a dorsal crest, as inferred from the presence of a groove on the inner side of the ilium in the fossil specimens. The position of the dorsal protuberance of the ilium differs markedly among these taxa: it extends across the supra-acetabular expansion to reach the dorsal margin of the acetabulum in the fossil from EB, but is restricted to the margin of the posterior end of the dorsal crest, and consequently it does not reach the acetabulum in *C. gayi*. As noted above, in the specimen of *C. canqueli* that preserves the pelvic girdle, the femur overlaps the dorsal portion of the ilium and this obscures the dorsal protuberance. The iliac shaft of both fossil forms is less curved than that of *C. gayi*, and the ventral depression extending across the posterior third of the iliac shaft described above for the fossil from EB is also present in *C. canqueli*. The ilium of *C. gayi* shows a comparable depression, although it is much shorter and has a different orientation.

Discussion and conclusions

The remains from Estancia Baibián and those from Scarritt Pocket agree in most anatomical aspects discussed above; the lack of significant differences suggests that these materials represent a single species. In contrast, these fossils differ from adults of the living *Calyptocephalella gayi* in several traits, although they resemble immature individuals of this species in having larger orbits and a more anterior articulation of the lower jaw, as noted by Schaeffer (1949). Other features, such as the straight posterior portion of the angulosplenial, the well-developed coronoid process, the high coracoid/scapula ratio, the relatively straight iliac shaft, the wide iliac ex-

pansions, and the closely set cotyles on the urostyle, are present neither in adult nor in juvenile individuals of *C. gayi*. Hence, the available evidence does not support the referral of the materials from Estancia Baibián and Scarritt Pocket to the living species; instead, it suggests that they represent a distinct species for which the binomen *C. canqueli* is resurrected. The discovery of additional specimens, however, will permit further comparisons to test this identification.

Calyptocephalella canqueli and the evolution of the genus

Calyptocephalella has been considered a species-poor genus (Formás, 1979) with only one extant and one extinct species, according to Lynch (1971). The present study suggests that the lineage may have undergone more cladogenetic events than generally thought during its long evolutionary history, although with little osteological differentiation. In this regard it is worthy of note that the low diversity of Calyptocephalellidae (*Calyptocephalella* + *Telmatobufo*, *sensu* Frost, 2007) strikingly contrasts with its speciose sister group, Myobatrachchoidea (Myobatrachidae + Lymnodynastidae), which includes 120 species inhabiting a broad range of environments and showing radical variations from basic anuran lifestyle (Littlejohn *et al.*, 1993). Paleontological data attest to their presence in Australia at least since the early Eocene (Sanchiz, 1998), whereas a putative record from the lower Paleogene of India needs to be substantiated (Rocek and Rage, 2000). Remains from Patagonia ascribed to the lineage represented by *Calyptocephalella*, however, indicate that calyptocephalellids and myobatrachoids had diverged by the latest Cretaceous, in agreement with the early (130 My, Roelants *et al.*, 2007) or late Cretaceous (90 My, Wiens, 2007) estimation for this event based on chronologically calibrated molecular phylogenies. The close affinity of *Calyptocephalella* to the Australian myobatrachoids was discovered thanks to the survival of one species of this genus. Morphologists, as yet, have never suggested this relationship which, in contrast, was recovered by many phylogenetic analyses based on molecular characters (e.g., Correa *et al.*, 2006; Frost, 2007; Roelants *et al.*, 2007). The drastic morphological divergence of myobatrachoids and calyptocephalellids from the ancestral stock from which they originated, together with the absence of extinct or extant basal representatives, makes it difficult to trace their history back using morphological data alone, whereas molecular sequences seem to have retained evidence of deep ties.

Divergence of the common ancestors of calyptocephalellids and myobatrachoids, the Australobatrachia *sensu* Frost *et al.* (2006), from the rest of the hylids was proposed as a relatively early event, estimated as latest Jurassic (Roelants *et al.*, 2007) or middle Cretaceous (Wiens, 2007), of neobatrachian evolution. Most palaeogeographical reconstructions of Gondwana break-up show persisting connections between South America-Antarctica-Australia that may have permitted some overland dispersals at least until the earliest Paleocene (Woodburne and Case, 1996; Vizcaíno *et al.*, 1998). Moreover, Antarctica may have acted as a center of diversification for australobatrachians, considering the mild climatic conditions that prevailed there throughout the Cretaceous and Palaeogene (Poole and Cantrill, 2006).

At present, *Calyptocephalella gayi* is distributed in the northern temperate region west of the Andes, associated with the *Nothofagus* forest. The earliest record of the lineage, however, is from the Campanian-Maastrichtian of Patagonia (Báez, 1987), when a warm climate prevailed in high latitudes and nothofagacean forests were not widespread on the continent but had already become the dominant component of the Antarctic vegetation (Poole and Cantrill, 2006). Subsequent northern expansion of the temperate forests was likely related to climatic cooling and these forests were still dominating the flora of eastern Patagonia (Barreda and Palazzesi, 2007) when *Calyptocephalella canqueli* was living there in still water bodies near the Atlantic coast. An extensive Atlantic transgression together with a marked climatic drying trend that began by the middle-late Miocene (Ortiz-Jaureguizar and Cladera, 2006) may have reduced suitable freshwater habitats, including breeding sites. This shrank in geographic range probably contributed to the demise of the calyptocephalellid lineage on the eastern plains of southern South America, although it survived west of the Andes to the present day.

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References

- Ameghino, F. 1900-1902. L'age des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* L (1900): 109-130, 145-165, 209-299; L1 (1901): 20-39, 65-91; L2 (1901): 145-165, 244-250; L4 (1902): 161-180, 220-249, 283-342.
- Archangelsky, A. and Zamalao, M.d.C. 2003. Primeros resultados palinológicos del Paleógeno del sector oriental de la Sierra La Colonia, provincia del Chubut, Argentina. *Revista del Museo Argentino de Ciencias Naturales*, n.s. 5: 119-123.
- Ardolino, A.A., Franchi, M.R., Remesal, M. and Salani, F. 1999. La sedimentación y el volcanismo terciarios en la Patagonia Extraandina. 2. El volcanismo en la Patagonia Extraandina. *Instituto de Geología y Recursos Minerales, Geología Argentina Anales* 29: 579-612.
- Ardolino, A.A., Busteros, R., Cucchi, M., Franchi, M.R., Lema, H. and Remesal, M. 1995. Cuerpos alcalinos básicos paleógenos del sur de Somún Curá (Argentina) y su marco estratigráfico. En: *Paleógeno de América del Sur*, Publicación Especial N°3 Asociación Paleontológica Argentina, Argentina, pp. 7-22.
- Báez, A.M. 1977. Sobre *Teracophrys* (Anura, Leptodactylidae) *nomina nuda* de la Formación Colhué Huapi (Oligoceno Superior), provincia del Chubut, República Argentina. *Revista de la Asociación Geológica Argentina* 22: 145-151.
- Báez, A.M. 1987. Anurans. In: J.F. Bonaparte (ed.), *The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina*, *Revista de Museo Argentino de Ciencias Naturales Bernardino Rivadavia - Paleontología*, pp. 121-130.
- Báez, A.M. 2000. Tertiary anurans from South America. In: H. Heatwole and R. Carroll (eds.), *Amphibian Biology*, Surrey Beatty & Sons, Chippin Norton, pp. 1388-1401.
- Barreda, V. and Palazzesi, L. 2007. Patagonian vegetation turnovers during the Paleogene-Early Neogene: origin of arid-adapted floras. *The Botanical Review* 73: 31-50.
- Casamiquela, R.M. 1958. Un anuro gigante del Mioceno de Patagonia. *Revista de la Asociación Geológica Argentina* 13: 171-183.
- Casamiquela, R.M. 1976. Los vertebrados fósiles de Tagua-Tagua. *1° Congreso Geológico Chileno* (Santiago de Chile), *Actas* 1: C87-C102.
- Cei, J.M. 1962. *Batrachios de Chile*. Ediciones de la Universidad de Chile, Santiago de Chile, 128 pp.
- Correa, C., Veloso, A., Iturra, P. and Méndez, M.A. 2006. Phylogenetic relationships of Chilean leptodactylids: a molecular approach based on mitochondrial genes 12S and 16S. *Revista Chilena de Historia Natural* 79: 435-450.
- Díaz, N.F. and Valencia, J. 1985. Larval morphology and phenetic relationships of the Chilean *Alsodes*, *Telmatobius*, *Caudiverbera* and *Insuetophrynus* (Anura: Leptodactylidae). *Copeia* 1985: 175-181.
- Duméril, A.-M. and Bibron, G. 1841. *Erpétologie générale ou Histoire Naturelle complète des Reptiles*. Librairie encyclopédique de Roret, Paris, 793 pp.
- Formás, R.J. 1979. La herpetofauna de los bosques temperados de Sudamérica. In: W.E. Duellman (ed.), *The South American herpetofauna: its origin, evolution and dispersal*, Museum of Natural History, University of Kansas, Kansas, pp. 341-369.
- Frost, D.R. 2007. *Amphibian Species of the World: an online reference*. American Museum of Natural History, New York, USA. 2007.
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Hass, A., Haddad, C.F.B., De Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Molder, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D. and Wheeler, W. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 370 pp.
- Haas, A. 2003. Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura). *Cladistics* 19: 23-89.
- Lavilla, E.O. 1988. Lower Telmatobiinae (Anura: Leptodactylidae): generic diagnoses based on larval characters. Occasional

- Papers of the Museum of Natural History. The University of Kansas* 124: 1-19.
- Littlejohn, M.J., Roberts, J.D., Watson, G.F. and Davies, M. 1993. Family Myobatrachidae. In: C.G. Glasby, G.J.B. Ross and P.L. Beesley (eds.), *Fauna of Australia* Volume 2A Amphibia and Reptilia, Australian Government Publishing Service, Australia, pp. 1-46.
- Lynch, J.D. 1971. *Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs*. University of Kansas, Lawrence, 238 pp.
- Lynch, J.D. 1978. *A re-assessment of the telmatobiine leptodactylid frogs of Patagonia. Occasional Papers of the Museum of Natural History*. The University of Kansas 72: 1-57.
- Muzzopappa, P. 2005. [Restos de Caudiverbera (Anura, Neobatrachia) en una nueva localidad Paleógena de Patagonia Central, y la validez de las especies casamayorenses y deseadenses del género. Tesis de Licenciatura, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina, 61 pp. Unpublished.].
- Muzzopappa, P. and Báez, A.M. 2004. Evidencia de una nueva especie de *Caudiverbera* (Anura, Neobatrachia) en el Eoceno de Puesto Baibíán, provincia del Chubut. *Ameghiniana Suplemento Resúmenes* 41: 57R.
- Myers, C.W. and Stothers, R.B. 2006. The myth of *Hyla* revisited: the frog name *Hyla* and other commentary on *Specimen medicum* (1768) of J. N. Laurenti, the father of herpetology. *Archives of natural history* 33: 241-266.
- Núñez, J.J. and Formás, R.J. 2000. Evolutionary history of the Chilean frog genus *Telmatobufo* (Leptodactylidae): an immunological approach. *Amphibia-Reptilia* 21: 351-356.
- Ortiz-Jaureguizar, E. and Cladera, G.A. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments* 66: 498-532.
- Parker, W.K. 1881. On the structure and development of the skull in the Batrachia. Part 3. *Philosophical Transactions of the Royal Society of London* 172: 1-266.
- Poole, I. and Cantrill, D.J. 2006. Cretaceous and Cenozoic vegetation of Antarctica integrating the fossil wood record. In: J.E. Francis, D. Pirrie and J.A. Crame (eds.), *Cretaceous-Tertiary High-Latitude Palaeoenvironments, James Ross Basin, Antarctica*, Geological Society, London, Special Publications, pp. 63-81.
- Reinbach, W. 1939. Untersuchungen über die Entwicklung des Kopfskeletts von *Calyptocephalus gayi*. *Jenaische Zeitschrift Für Naturwissenschaft* 72: 211-362.
- Rocek, Z. and Rage, J.-C. 2000. Tertiary anurans of Europe, Africa, Asia, North America, and Australia. In H. Heatwole and R. Carroll (eds.), *Amphibian Biology*, Surrey Beatty & Sons, Chippin Norton, pp. 1332-1387.
- Roelants, K., Gower, D.J., Wilkinson, M., Loader, S.P., Biju, S.D., Guillaume, K., Moriau, L. and Bossuyt, F. 2007. Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 104: 887-892.
- San Mauro, D., Vences, M., Alcobendas, M., Zardoya, R. and Meyer, A. 2005. Initial diversification of living amphibians predated the breakup of Pangea. *The American Naturalist* 165: 590-599.
- Sanchiz, B.J. 1998. *Salientia. Handbuch der Paläoherpetologie*. Verlag Dr. Friederich Pfeil, München, 275 pp.
- Schaeffer, B. 1949. Anurans from the early Tertiary of Patagonia. *Bulletin of the American Museum of Natural History* 93: 41-68.
- Strand, E. 1928. Miscellanea nomenclatorica zoological et palaeontologica I-II. *Archiv für Naturgeschichte* 92: 30-75.
- Trueb, L. 1993. Patterns of cranial diversity among the Lissamphibia. In: J. Hanken and B.K. Hall (eds.), *The Skull*, University Chicago Press, Chicago, pp. 255-343.
- Vizcaíno, S.F., Pascual, R., Reguero, M.A. and Goin, F.J. 1998. Antarctica as background for mammalian evolution. In: *Paleógeno de América del Sur y de la Península Antártica*, Publicación Especial N° 5 Asociación Paleontológica Argentina, Argentina, pp. 199-209.
- Wiens, J.J. 2007. Global patterns of diversification and species richness in amphibians. *The American Naturalist* 170: S86-S106.
- Wild, E.R. 1997. Description of the adult skeleton and developmental osteology of the hyperossified Horned frog, *Ceratophrys cornuta* (Anura: Leptodactylidae). *Journal of Morphology* 232: 169-206.
- Woodburne, M.O. and Case, J.A. 1996. Dispersal, vicariance, and the Late Cretaceous to Early Tertiary Land Mammal biogeography from South America to Australia. *Journal of Mammalian Evolution* 3: 121-161.

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