



PALEONTOLOGY

Fossil fishes and anurans from the Miocene of Rio Chico and Cerro Zeballos, Chubut Province, Argentina

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Abstract: The fossil record of freshwater fishes and anurans from the Miocene in Patagonia is relatively patchy, a large number of specimens remaining undescribed. The aim of the present contribution is to describe a fossil association of percomorphacean fishes and calyptocephalellid anurans from the early to late Miocene Collón Curá Formation, at Chubut province, Patagonia, Argentina. In spite of being represented by several specimens, both anurans and fishes show a very low taxonomic diversity. This pattern matches with other fossil sites from the Cenozoic of Patagonia, as well as with the extant Patagonian batrachofaunas and ichthyofaunas. The fossil record of frogs and fishes in Patagonia is represented by few lineages that have a large evolutionary history in the area, and occasionally can be traced up to the Late Mesozoic.

Key words: Percichthyidae, Calyptocephalellidae, Miocene, Collón Curá Formation, Patagonia, Argentina.

INTRODUCTION

Fishes and anurans are intimately related with the evolution of freshwater bodies. As a result, there is often a close match between the evolutionary history of river basins and the fish lineages that inhabit them. Thus, the change of freshwater drainage and basins has a key importance for understanding the distribution and biogeography of both vertebrate groups (Reis et al. 2016). In this sense the fossil record of fishes and anurans has the potential importance to understand the reconstruction of freshwater basins in the past.

Regrettably, in contrast with the fossil record of mammals, the reports of Miocene fishes and anurans from Patagonia are scarce (Arratia & Cione 1996, Baez 2000, Cione & Baez 2007).

From the Ñirihuau Formation (early Miocene) at Río Negro and Chubut provinces indeterminate teleosts, percichthyids and

atherinopsids were reported (Feruglio 1949, Dessanti 1972, Bocchino 1964, 1971, Pascual et al. 1984), whereas percichthyids were recorded from Collón Curá Formation (middle Miocene) at Río Negro province (Casamiquela 1963). From Puerto Madryn Formation (late Miocene) at Chubut province, diverse materials of siluriforms including loricariids, and percomorphaceans were described (Cione et al. 2005).

As in the case of fishes, the record of Miocene anurans in Patagonia is saltuary. From the early Miocene, there are records of “Leptodactylidae” and specimens of the genus *Calyptocephalella* from Sarmiento, Pinturas and Santa Cruz formations at Santa Cruz and Chubut provinces (Ameghino 1901, Schaeffer 1949, Bown & Larriestra 1990, Tauber 1999, Fernicola & Vizcaíno 2006, Fernicola & Albino 2012). The genus *Calyptocephalella* is also recorded from Collón Curá Formation (middle Miocene)

at Río Negro province, and from Río Mayo Formation (late middle Miocene) at Chubut province (Casamiquela 1958, 1963, Nicoli et al. 2016). Finally, calyptocephalellids of the genera *Gigantobatrachus* and *Calyptocephalella* are recorded at Los Loros Formation (late Middle? Miocene), Río Negro Province (Casamiquela 1963, Pascual et al. 1984).

Up to the date, previous fish reports from the Collón Curá Formation are limited just to the mention of perchs, but these remain undescribed. Anurans from the same geological unit are represented only by the type specimen of *Wawelia gerholdi* that is now referred to *Calyptocephalella* (Nicoli et al., 2016). The aim of the present contribution is to describe isolated materials of fossil frogs and fishes from Collón Curá Formation (Burdigalian-Tortonian, Miocene) collected at Río Chico and Cerro

Zeballos fossiliferous sites (Martin & Tejedor 2007, González Ruiz et al. 2012), near Cushamen and Gualjaina respectively, northwestern Chubut province, Patagonia, Argentina. This is one of the few assemblages described from the Miocene in Patagonia, South America.

STRATIGRAPHIC AND GEOGRAPHIC CONTEXT

Río Chico locality

On both sides of the Chico River (Río Negro and Chubut Provinces) there are extensive Collón Curá Formation outcrops (Ravazzoli & Sesana 1977, Volkheimer & Lage 1981). Specifically, in the Calera Esparza depression (Figure 1), the sediments are extensive and subhorizontally exposed. In this area two sections of the Collón Curá Formation were described (Volkheimer &

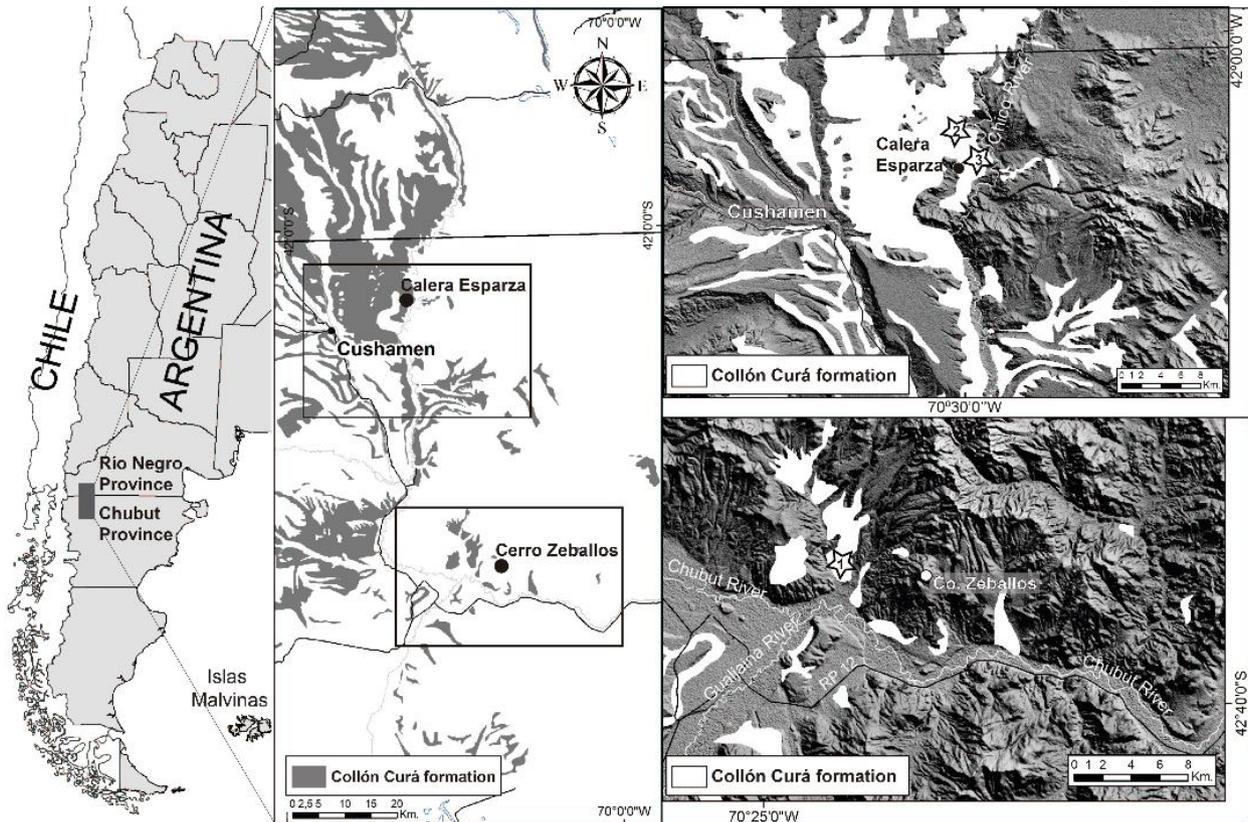


Figure 1. Map showing fossiliferous localities of Río Chico and Cerro Zeballos.

Lage 1981). The upper one of 130 m of thickness is represented by an alternation of light grey and yellowish sandstones of different granulometry. The basal 10 m of the upper section are mainly composed by silty sandstones of fine grain and greenish in colour, indicating a transition to the lower section. The latter is composed by silty sandstones and silty limestones, representing a lacustrine facies. The specimens were collected in the localities of Río Chico 2 (42° 5' 5.47" S, 70° 29' 13.7" O) and Río Chico 5 (42° 7' 1.38" S, 70° 28' 41.64" O) (Figure 1). Although there are no absolute ages for these localities, 15 km north on the Chico River, Bilmes et al. (2013, 2014) obtained an age $^{40}\text{Ar}/^{39}\text{Ar}$ of 14.86 ± 0.13 Ma (Langhian Age, Miocene) for the base of the middle section of Collón Curá Formation. The Collón Curá Formation spans from ca. 16 Ma to ca. 11 Ma (Burdigalian Age-Tortonian Age) (Brandoni et al. 2019 and references therein).

Cerro Zeballos locality

At the North of Chubut River, in front of the confluence with Gualjaina River (Chubut Province), there are extensive outcrops of the Collón Curá Formation (Lage 1982). In this area the sediments were preliminary described by Lage (1982) and Brandoni et al. (2019). In this locality, known as Cerro Zeballos (42° 34' 46.5" S, 70° 19' 55" W) (Figure 1), the sequence is homoclinal with subhorizontally disposed strata, and corresponds to volcanoclastic sediments with predominance of tuffs, chonites, and subordinate epiclastic sediments. Brandoni et al. (2019) described the section where the vertebrates were found, as a sequence of 15 m of massive tuffaceous sandstone that are ochre or yellowish in colour. These are overlaid by ca. 3 m of greenish tuffaceous mudstone, and finally epiclastic deposits of claystone, mudstone, and grainstones, with intercalated pyroclastic levels. The tuffaceous material and the presence of

rizolithes suggests a shallow and low energy system of lagoons or lakes, and a floodplain with shallow and low energy fluvial courses, probably with periods of aerial exposure. Although, there are no absolute ages for Cerro Zeballos, Brandoni et al. (2019) proposed a Tortonian Age (Miocene) for this fossiliferous association based on mammal content.

Abbreviations

LIEB-PV, Laboratorio de Investigaciones en Evolución y Biodiversidad, Paleovertebrados, Universidad de la Patagonia "San Juan Bosco" sede Esquel, Chubut, Argentina.

SYSTEMATIC PALEONTOLOGY

Acanthomorpha Rosen, 1973
 Percomorphacea Wiley & Johnson, 2010
 Centrarchiformes Bleeker, 1859
 Percichthyidae Jordan & Eigenmann, 1890
 Genus and species indeterminate
 Figures 2-6

Referred material

LIEB-PV 8000, first precaudal vertebra, 3 precaudal vertebrae, 2 caudal vertebrae, 3 articulated caudal vertebrae; LIEB-PV 8001, 9 first precaudal vertebrae, 43 precaudal vertebrae; 20 caudal vertebrae; LIEB-PV 8002, first anal pterygiophore, an incomplete ceratohyal, fragmentary left preopercular bone, incomplete left maxilla, incomplete left premaxilla, incomplete mandibular glenoid, incomplete parasphenoid, two left dentaries; LIEB-PV 8003, two left and one right dentary bones, and one right premaxilla; LIEB-PV 8004, first anal pterygiophore, 28 spines of impair fins, and 1 spine of pelvic fin; LIEB-PV 8005, first dorsal pterygiophore, two fragmentary ceratohyal, parasphenoid; LIEB-PV 8009, basioccipital;

LIEB PV 8010, 3 precaudal vertebrae, 2 caudal vertebrae (Figure 2).

Locality

Río Chico 5: LIEB-PV 8000; Río Chico 2: LIEB-PV 8001, LIEB-PV 8002, LIEB-PV 8003, LIEB-PV 8004, LIEB-PV 8005; Cerro Zeballos: LIEB-PV 8009, LIEB-PV 8010.

Description

Dentary

None of the dentaries is completely preserved, and preserved remains are restricted to the anterior third of the bone (Figure 3a-e). The preserved portion indicates that it was a subtriangular-shaped bone when viewed from the side, being slightly medially curved when viewed dorsally.

The mentonian process is prominent and robust, conforming an anteroposteriorly extended flange. Its ventral margin is ornamented by folds. A narrow longitudinal groove delimitates the dorsal edge of the mentonian process from the tooth patch. This groove posteriorly ends at the VII nerve foramen, far from the anterior margin of the dentary. The symphyseal surface is represented by two well-defined bumps that are separated from the above-mentioned longitudinal groove.

The first pit for the mandibular sensitive canal is anteroposteriorly elongate and of mid-size, being suboval in contour. There is a very small pit anterior to the second pit for the mandibular sensitive canal. The second pit is relatively large, but the incomplete nature of the specimens do not allow to recognize its precise contour. The upper foramen is small and is ogival in shape, being located within an anteroposteriorly long concavity.

In occlusal view a wide tooth patch is observed. It shows a large number of subcircular and small bases for the implantation of small villiform teeth. The tooth bases are subequal in size along all the dentary. The occlusal surface of the dentary is markedly concave, and is laterally projected, especially on its anterior end.

Premaxilla

This bone is represented by its anterior portion (Figure 3f-g). Its shape is typical to that of the Percomorphacea clade. The ascending process is very low, relatively thick and shows an anteroposteriorly wide base. The articular process is relatively thick and rounded in contour. It is separated from the ascending process by a wide and concave surface. In medial view it is ventrally delimited by a longitudinal groove.

The premaxillary ramus is transversely thick and is clearly separated from the tooth patch. In occlusal view a wide tooth patch is observed. It shows a large number of subcircular and small bases for the implantation of small villiform teeth. The tooth bases are subequal in size along all the premaxilla.

Maxilla

The maxilla is represented by a fragment of maxillary ramus of the left side (Figure 3h-i). In spite of being poorly preserved, the fragment indicates that the bone expands gradually posteriorly. The lateral surface is gently convex. In medial view it shows a deep canal that is subtriangular in contour and ends in an ogival-shaped foramen.

Preopercular

This element is represented by a fragment of the vertical limb (Figure 4d). It is laminar in cross-section and shows a dentate posterior margin.

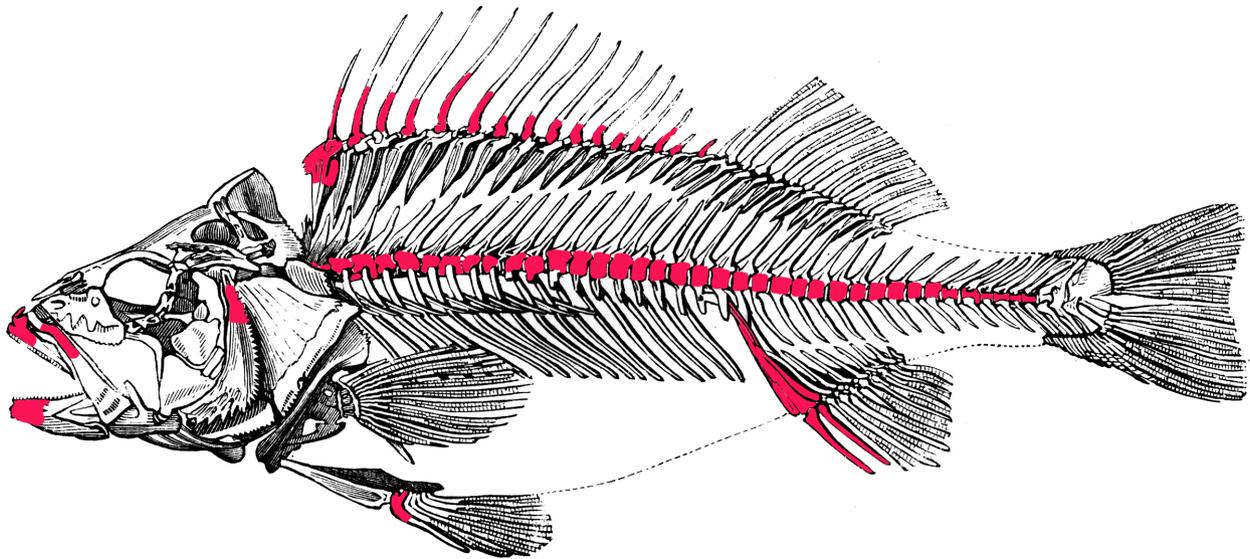


Figure 2. Sketch drawing of the skeleton of the common perch (*Perca fluviatilis*) representing a generalized percomorphacean. Shaded in red the elements here reported. Modified from Goodrich (1859).

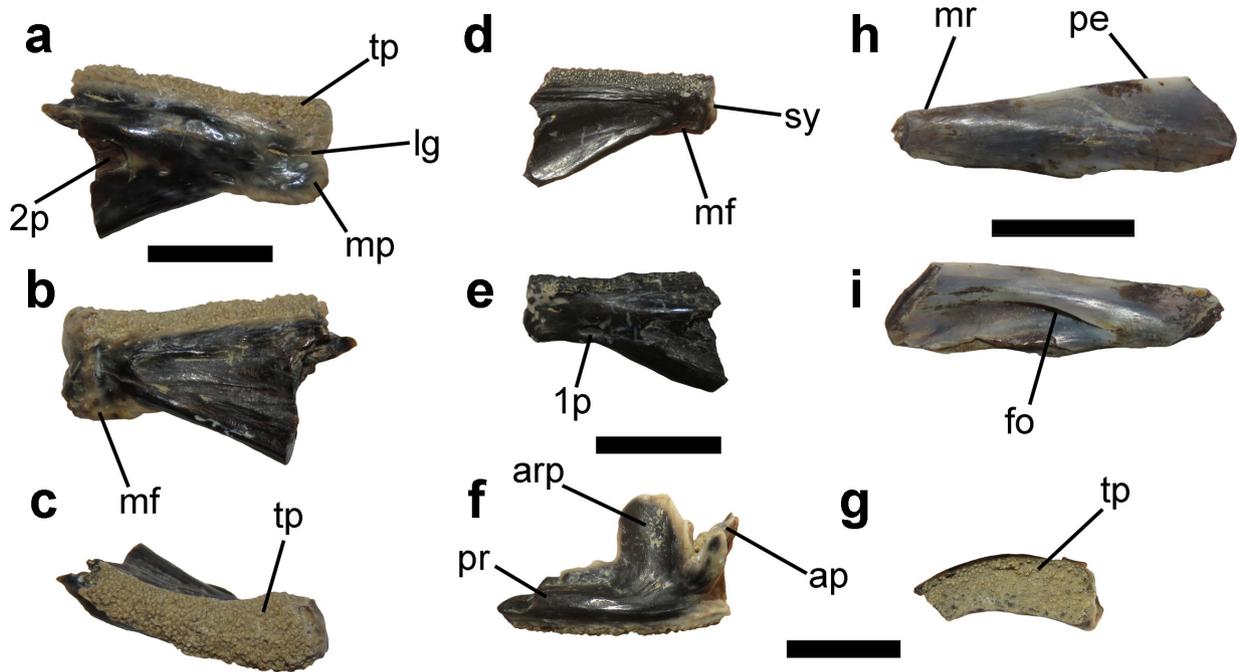


Figure 3. Percichthyidae genus and species indeterminate. Selected cranial bones. a-c, right dentary (LIEB-PV 8003) in a, lateral; b, medial; and c, occlusal views. d-e, left dentary (LIEB-PV 8002) in d, medial, and e, lateral views. f-g, right premaxilla in f, lateral, and g, occlusal views. h-i, left maxilla (LIEB-PV 8002) in h, lateral; and g, medial views. References: ap, ascending process; arp, articular process; fo, medial foramen; lg, longitudinal groove; mf, mentonian flange; mp, mentonian process; mr, maxillary ramus; pe, posterior expansion; pr, premaxillary ramus; sy, dentary symphysis; tp, tooth patch; 1p, first pit for the mandibular sensitive canal; 2p, second pit for the mandibular sensitive canal. Scale bar: 1 cm.

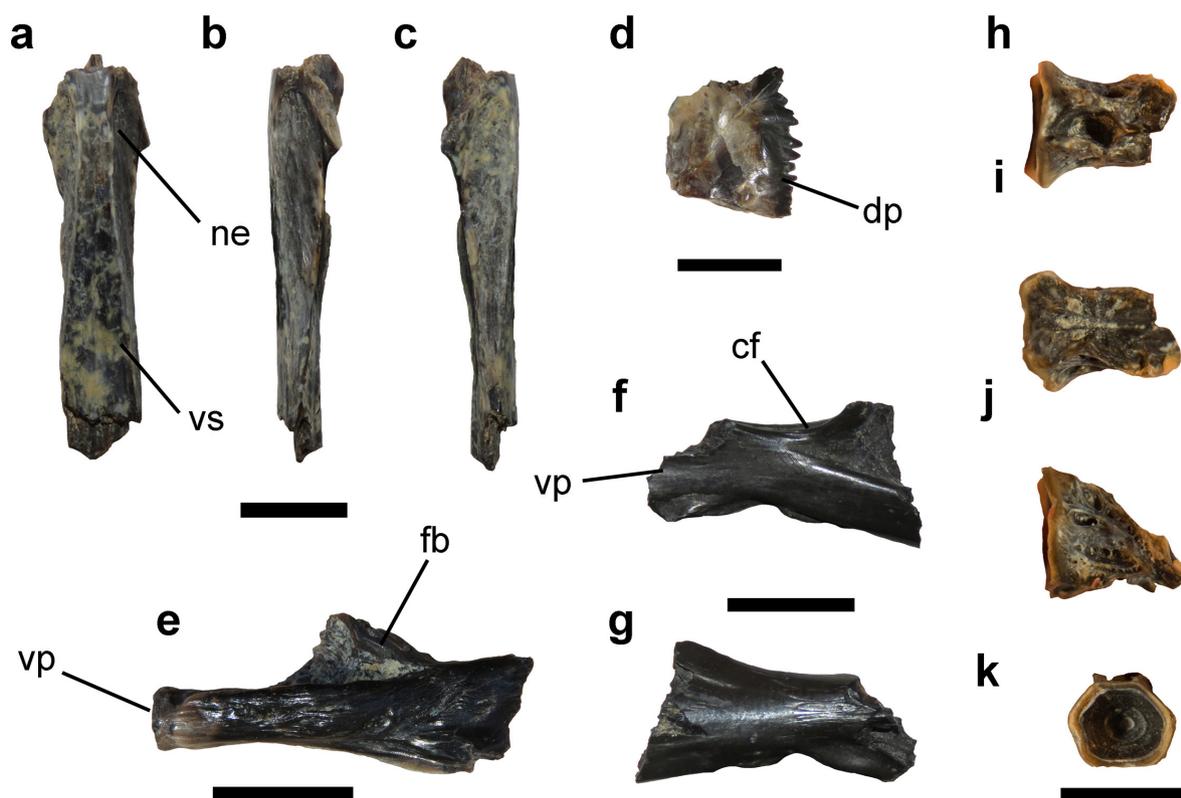


Figure 4. Percichthyidae genus and species indeterminate. a-c, parasphenoid (LIEB-PV 8002) in a, ventral; b, left lateral; and c, dorsal views. d, left preopercular (LIEB-PV 8002) in lateral view. e, ceratohyal (LIEB-PV 8002) in lateral view. f-g, incomplete ceratohyal (LIEB-PV 8005) in e, lateral; and f, medial views. References: cf, ceratohyal foramen; dp, dentate posterior margin; fb, flange of bone; ne, parasphenoid neck; vp, ventral process; vs, ventral surface. Scale bar: a-c, e, 1 cm; d, h-k, 0.5 cm.

Parasphenoid

It is an elongate bone (Figure 4a-c). The ventral surface is notably flat and straight, with sharply demarcated lateral margins. It shows a slight constriction near the posterior third of the bone. Dorsally it shows a well-developed longitudinal median crest.

Ceratohyal

It is an elongate element with a well-defined neck (Figure 4e-g). As occurs in *Percichthys* and *Macquaria* (MacDonald 1978) the ceratohyal foramen is represented by a shallow concavity, and is not dorsally closed by an osseous process, contrasting with *Percilia* and some

other basal Percomorphaceae (Arratia 1982, Otero 2004). The ventral process for articulation with the hypohyal is well-developed and rod-like, subcircular in cross-section. In medial view, the ventral process is dorsally excavated and this concavity is laterally delimited by a thin flange of bone.

Basioccipital

The basioccipital bears ventrally oriented surfaces for Baudelot's ligament (Figure 4h-k). In ventral view there is a very large concavity. The articular facet of the basioccipital for the first vertebra has an overall rounded shape with a small thickening on its dorsal part.

First precaudal vertebra

As occurs in all known percomorphaceans the first precaudal vertebra shows an autogenous neural arch, being not fused to the vertebral centrum (Gayet 1987)(Figure 5a-c). The centrum shows at its anterodorsal surface two large articular surfaces for the exoccipital bone, and are separated from each other by a small subtriangular-shaped process.

The vertebral centrum is strongly anteroposteriorly compressed at its base, a condition shared with *Plesiopercichthys* and differing from living percichthyids (Agnolín et al. 2014). The lateral surface of the centrum is straight and obliquely oriented, resulting in a transversely narrow base. The ventral surface is relatively flat, differing from the rounded condition shown by *Percichthys*.

In lateral view there are a large number of irregular concavities separated by osseous

trabeculae, that are mostly located near the dorsal half of the centrum. Remaining surface of the centrum is ornamented by longitudinal striations and grooves. The postzygapophyses are well-separated from each other, are relatively small and ellipsoidal in contour, whereas in *Plesiopercichthys* and *Percichthys* are subcircular in shape.

Precaudal vertebrae

The largest elements have a transverse width of 24 mm. (Figure 5d). In lateral view exhibit a striated bone texture, with some cases of a trabecular bone formed by wide pits and strong bone laminae. Anterior precaudal centra are strongly anteroposteriorly compressed and the lateral surface is not deeply trabeculate. In ventral view, they show a wide and deep concavity that is subrectangular in contour.

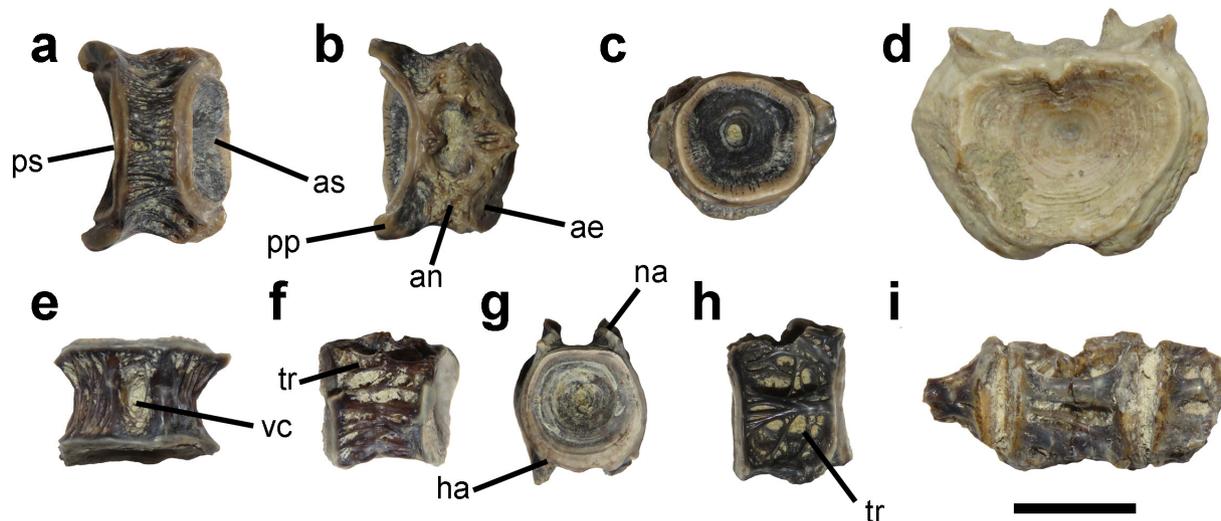


Figure 5. Percichthyidae genus and species indeterminate. Vertebrae. a-c, first precaudal vertebral centrum (LIEB-PV 8000) in a, ventral; b, dorsal; c, anterior; d, large-sized precaudal vertebral centrum (LIEB-PV 8001) in anterior view; e-f, precaudal vertebral centrum (LIEB-PV 8001) in e, ventral, and f, right lateral views. g-h, caudal vertebra (LIEB-PV 8001) in g, anterior; h, right lateral views. i, three articulated caudal vertebrae (LIEB-PV 8000) in lateral view. h-k, basioccipital (LIEB-PV 8009) in h, ventral; i, dorsal; j, left lateral; and k, posterior views. References: ae, articular surface for the exoccipital; an, articular surface for the neural arch; as, anterior articular surface; ha, haemal arch; na, neural arch; pp, posterior porcess; ps, posterior articular surface; tr, trabecular bone; vc, ventral concavity. Scale bar: 1 cm.

Caudal vertebrae

Caudal vertebrae show an elongate centrum (Figure 5g-i). The lateral, ventral and dorsal surfaces exhibit a prominent trabeculate bone texture. In lateral view the surface shows a longitudinal thick ridge at mid-height of the centrum. Ventral and dorsal concavities are deep and wide.

Pterygiophore

First large anal pterygiophore is represented by the fusion of two consecutive elements, that constitutes the contact with the first and second spines (Figure 6a-c). It is an elongate element with a blade-like proximal end.

Distally it shows two pairs of articular surfaces for the articulation with the first two spines of the anal fin. In posterior view, this compound bone shows a short central keel that extends at the basal quarter of the element. This keel proximally ends in a small flange of bone that shows a gently convex anterior surface that continues with the central keel. The central keel is surrounded by a pair of small longitudinal ridges that converge towards its base with the central keel. Laterally the pterygiophore shows two large laminae that extend toward the base of the bone. At the anterior surface, the base of the pterygiophore shows a small and complex articular surface that is gently concave and articulates with the distal radial element.

A single first pterygiophore from the dorsal fin was recovered (Figure 6d-f). It is identified as the first element because at the anterior surface lacks articulation surface for other pterygiophore, and because it shows an osseous platform, with a mostly flattened anterior surface that presents a single longitudinal midline groove.

The pterygiophore is hyperostosed and thickened. Its surface is decorated by a rugose texture. At its proximal end it shows two

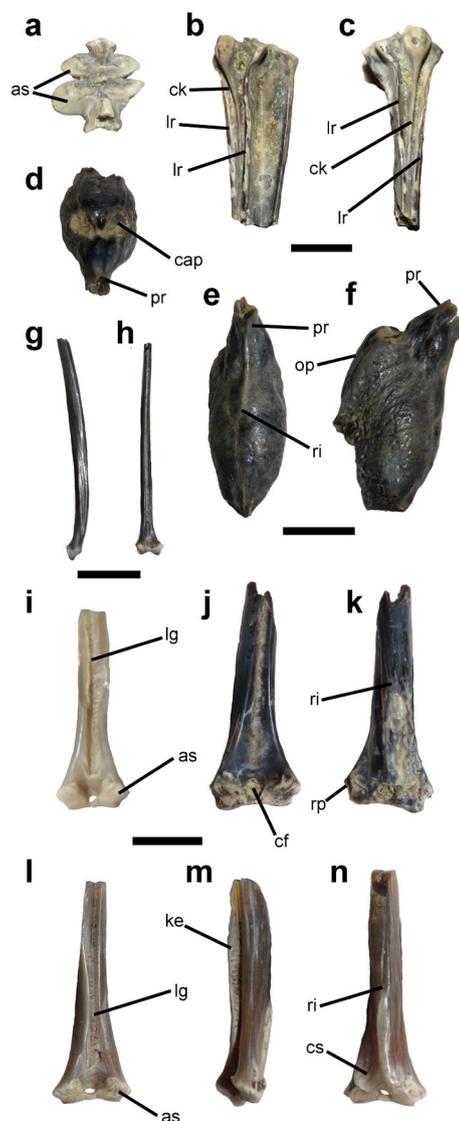


Figure 6. Percichthyidae genus and species indeterminate. Spines and pterygiophores. a-c, first anal pterygiophore (LIEB-PV 8004) in a, distal; b, right lateral; c, posterior views. d-f, first dorsal hyperostosed pterygiophore (LIEB-PV 8005) in d, proximal; e, posterior; and f, lateral views. g-h, fin spine (LIEB-PV 8004) in g, lateral; and h, posterior views. i, articular end of fin spine (LIEB-PV 8004) in posterior view. j-k, articular end of fin spine (LIEB-PV 8004) in j, posterior, and k, anterior views. l-m, articular end of fin spine (LIEB-PV 8004) in l, posterior; m, lateral; and n, anterior views. References: as, articular surface; cap, cup-shaped articular surface for spine; cf, central foramen; cs, concavity for preceding spine; ck, central keel; ke, longitudinal keel; lg, longitudinal groove; lr, lateral ridge; op, osseous platform; pr, proximal radial; ri, ridge; rp, rounded process. Scale bar: a-c, g-n, 0.5 cm; d-f, 1 cm.

cup-shaped surfaces for the articulation of the first dorsal spine. Posteriorly, the proximal radial is posterodorsally oriented and is tube-like.

Spines

The fin spines have a rounded, lobed base (Figure 6g-k). In anterior view these elements have a rounded ridge positioned at one side at the base and twists to a central position higher on the blade. This ridge is proximally delimited at the basal quarter of the spine by a well-defined groove that represents the contact with the preceding spine. In anterior view it shows two articular surfaces of subcircular contour that are located lateral to the central foramen. At the posterior surface there are two low and rounded projections (the locking processes of Gayet 1987) near the base of the element. Presence of combined spine rays, having a rounded anterior ridge, two articular surfaces anteriorly and two posterior projections posteriorly indicate that the spines belong to the percomorphacean clade (Murray & Thewissen 2008).

The pelvic fin spine is represented by a single proximal end. It shows a roughly subtriangular contour in cross-section. It is strongly asymmetrical, it exhibits a complex proximal articular surface as is typical of percomorphaceans (Otero 2004). The proximal heel is saddle-shaped and shows two articular facets that are separated by a notch. In anterior view there is a well-developed and rounded stop. In posterior view the proximal end shows a narrow rod-like posteroventral process. It exhibits a longitudinal groove that runs along the spine blade.

Comments

In spite of being represented mostly by a large number of isolated and fragmentary material we infer that the different specimens may belong to

a single fish species. At first sight, the elements are concordant in main anatomical characters, being reminiscent to percichthyids. Further, the overlapping material is congruent with the presence of a single species, or closely related species, at least.

The specimens here described share a combination of characters that are typical of the Percomorphacea clade, including presence of spinose rays in dorsal and anal fins, first precaudal vertebra with two articular surfaces indicating an autogenous neural arch, presence of wide trabeculae on lateral surface of vertebral centra, morphology of the ascending process of premaxilla, edentulous maxilla, and serrated posterior margin of the preopercle (see Johnson 1993, Gayet & Meunier 1998, Agnolín 2012). Percomorphaceans are a very diverse group that include a large number of “perch-like” fishes exhibiting a conservative osteology. Some features of the material here described may indicate that specimens may be related to the Percichthyidae. The presence of enlarged pits of the sensitive canal on the dentary, premaxilla and dentary with very small and conical teeth and ceratohyal with concave dorsal margin showing an opened ceratohyal foramen, is a combination of traits that is concordant with such proposal (Arratia 1982, MacDonald 1978, Johnson 1993).

When compared with South American percichthyids of the genera *Percichthys*, *Santosius* and *Plesiopercichthys* (see Arratia & Quezada-Romegialli 2019), the specimens here reported show some differences, including symphyseal region of the dentary composed by two bumps separated by a longitudinal groove, premaxilla with a wide and thickened ascending process, and hyperostotic and enlarged first pterygiophore of the dorsal fin. Such features are unknown in any known extinct

or extant percichthyid, precluding an accurate taxonomical referral of present material.

Anura Fischer, 1813

Neobatrachia Reig, 1958

Calyptocephalellidae (Reig, 1960)

Genus and species indeterminate

Referred material

LIEB-PV 8006, incomplete right maxilla; LIEB-PV 8007, incomplete right maxilla; LIEB-PV 8008, proximal end of urostyle.

Locality. Río Chico 2.

Description

The preserved maxillae are poorly preserved and show incomplete anterior and posterior ends, as well as the ascending ramus (Figure 7).

Most of the external surface of the bones is ornamented by pits and ridges, with the exception of the nearly smooth alveolar margin. The preserved base of the ascending ramus suggests that it was relatively tall and subvertically oriented.

The lateral surface of the bone is strongly convex and laterally prominent when compared with the alveolar margin, which is separated by a longitudinal step. The smooth alveolar margin is anteriorly tall and becomes lower towards the posterior end of the bone.

Medially, the ascending ramus is separated from the pterygoid process by a deep longitudinal groove. The preserved base of the pterygoid process indicates that it was medially oriented and was dorsolaterally curved. The palatine shelf is step-like, robust and prominent, well separated from the maxillary body.

The pars dentalis shows the preserved base of the teeth, which are subvertically oriented and subparallel to each other. The bases indicate that each tooth root was ankylosed to the maxilla, conforming typically pedicelate

dentition, as diagnostic of Neobatrachia (Reig 1958).

The preserved part of urostyle indicates a notably robust element (maximum transverse width 22.26 mm) that was relatively short, judging by the abrupt convergence of the margins of the bone (Figure 8). As in other neobatrachians the urostyle lacks transverse processes and a

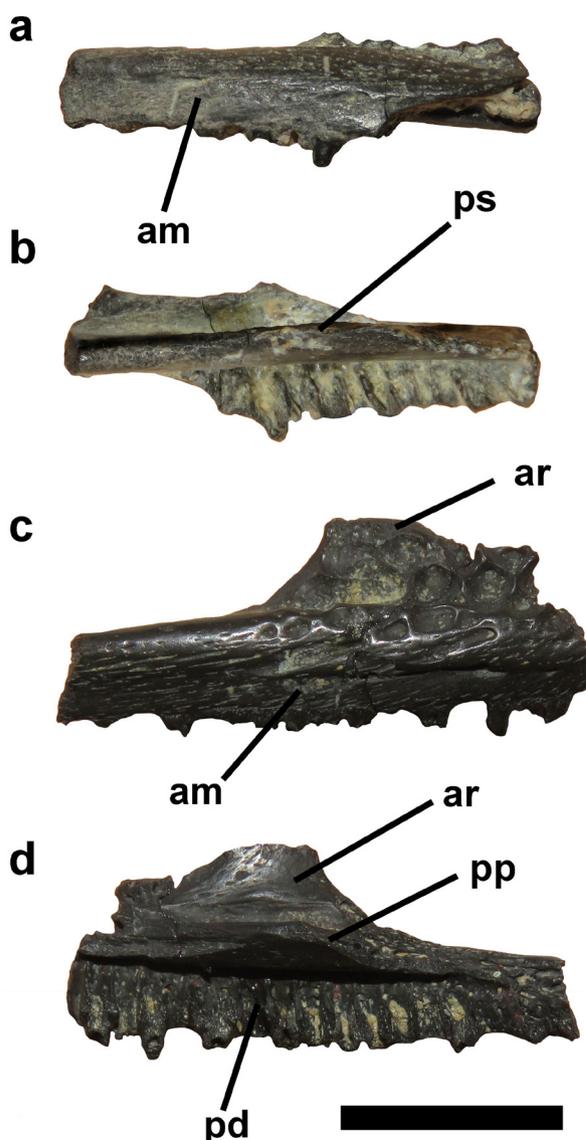


Figure 7. Indeterminate *Calyptocephalellidae*. a-d, LIEB-PV 8006-8007, right maxillae in a,c, lateral; b,d, medial views. References: am, alveolar margin; ap, ascending ramus; pp, pterygoid process; ps, palatine shelf. Scale bar: 1 cm.

bicondylar proximal articulation (Gómez et al. 2011). The proximal articular surfaces are dorsoventrally tall and suboval in contour. The right proximal articular surface is notably larger than the left one. The dorsal longitudinal crest of the urostyle is represented by a transversely thickened base. Ventrally, the urostyle shows a poorly defined longitudinal crest. Based on comparisons with the living species *Calyptocephalella gayi* (see Otero et al. 2014), the specimen here described may have reached a total body length of about 70 cm, being one of the largest known neobatrachians.

Comments

The maxillae LIEB-PV 8006 and LIEB-PV 8007 are referred to Calyptocephalellidae by having an external ornamentation composed by pits and ridges, dorsoventrally tall pars dentalis, well developed and laminar pterygoid process, alveolar margin and palatine shelf step-like, and ascending process subvertically oriented and laminar in cross-section (Casamiquela 1958, Baez 1977, Gómez et al. 2011, Agnolín 2012). Because of the incomplete nature of

specimens here described we refer the material as Calyptocephalellidae indet.

The fragmentary and isolated nature of LIEB-PV 8005, precludes a clear taxonomical referral. The robustness and the anteroposterior shortening of the specimen are features typical of Calyptocephalellidae (Reig 1960, Agnolín 2012). The large size of the specimen as well as the asymmetrical proximal articular surfaces, are typical of the genus *Gigantobatrachus* (Casamiquela 1963). Because of its fragmentary nature, the specimen is here considered as an indeterminate calyptocephalellid.

DISCUSSION

Sedimentological research in the fossil sites indicates the presence of low energy fluvial deposits and lagoons (González Ruiz et al. 2012). If we assume that fossil fishes described above are percichthyids, their presence, together with that of strictly freshwater calyptocephalellid frogs (Veloso et al. 2008, Stuart et al. 2008), are indicative of a permanent and important

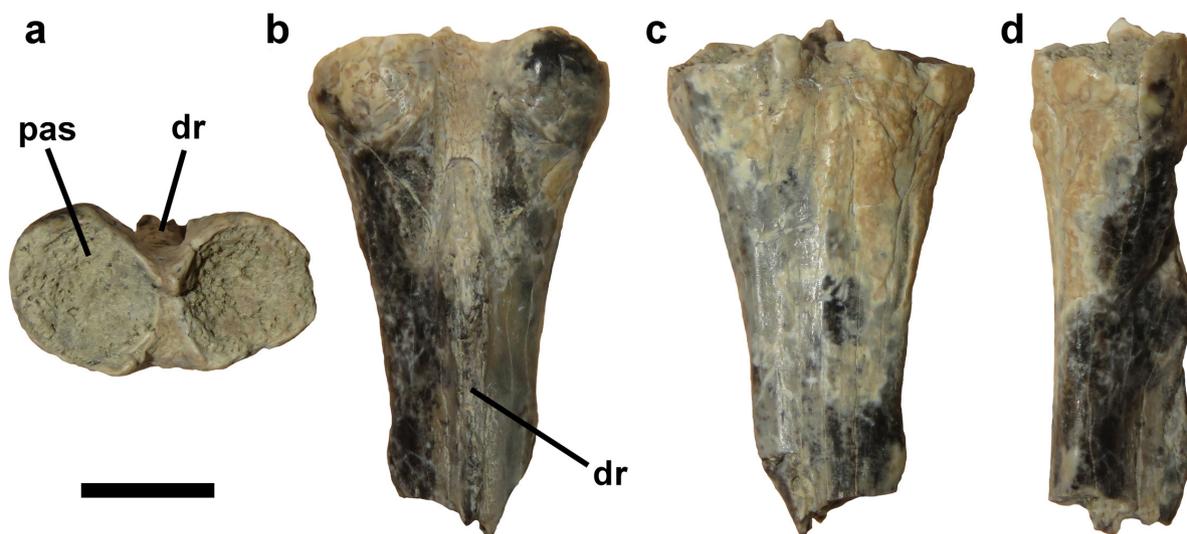


Figure 8. Indeterminate Calyptocephalellidae. a-d, LIEB-PV 8008, incomplete urostyle in a, anterior; b, dorsal; c, ventral; and d. right lateral views. References: dr, dorsal ridge; pas, proximal articular surface. Scale bar: 1 cm.

freshwater environment, in agreement with geological data.

In spite of being represented by a large number of bones, all remains of fishes and frogs here reported may be comfortably referred to a few taxa. This pattern is also observed in most fossiliferous sites of Paleogene and early Neogene (until middle Miocene times) in Patagonia, which show a very low diversity of fishes and frogs (see Arratia & Cione 1996, Baez 2000, Cione & Baez 2007). Percichthyid-like percomorphaceans and calyptocephalellids have a long history in freshwater basins in southern South America. Both were reported since late Cretaceous times (Cione 1987, Baez 1987, Gayet 1991, Gayet & Meunier 1998, Martinelli & Forasiepi 2004, Agnolín 2012) and today, both are still present in Patagonia (Cione 1986, Baez 2000).

Further, during the Tertiary, percichthyid-like taxa are the most abundant fishes recovered in Patagonian fossil sites (e.g., Cañadón Hondo, Puesto Galván, Cerro David), whereas other taxa as atheriniforms, siluriforms and osteoglossiforms are known from few fossiliferous sites (Bogan et al. 2010, Azpelicueta & Cione 2011). To this meagre diversification, by the late Miocene in northern Patagonia, Cione et al. (2005) added the occurrence of several Brazilian fish lineages that reached southern Pampas and northern Patagonia during the Miocene (Bogan & Agnolín 2019). This constitutes the only important change recovered in the fossil record on the fish assemblages at northern Patagonia during most of the Tertiary. In the same sense, calyptocephalellids and pipoids, are known from a large number of sites since the earliest Tertiary up to the Miocene, whereas other anurans are restricted to a few isolated findings (see Cione & Baez 2007, Nicoli 2017, Aranciaga Rolando et al. 2019).

In sum, in spite of the several climatic sways that occurred along the Tertiary, in Patagonia fossils fishes and frogs are represented by a few and widespread lineages with ancient roots in the continent (Cione 1978, see Ortiz-Jaureguizar & Cladera 2006). We are not certain if this low diversity reflects the the relative isolation of Patagonian freshwater basins with respect to the rest of the continent along the Cenozoic, and/or a bias in the fossil record. One of the possible bias is the still incomplete knowledge of lower vertebrate faunas from the Tertiary of Patagonia. This is evidenced by the fact that several fish taxa are known from single sites. The other bias, could be related to the possibility that only a few, specific depositional environments are represented in the geology of the sampled fossiliferous localities, and that the environments where other taxa lived are not preserved in the geological record.

CONCLUSIONS

Cenozoic freshwater fishes from Patagonia include abundant percichthyid-like taxa and scarce atheriniforms, siluriforms and osteoglossiforms (Bogan et al. 2010, Azpelicueta & Cione 2011), whereas anurans are mostly represented by calyptocephalellids and pipoids (Baez 2000). The fossil record of frogs and fishes in Patagonia reflects a poor diversity of few lineages that have a large evolutionary history that in some cases can be traced to the late Mesozoic.

As indicated above, a large number of fossil freshwater fishes and anurans remain undescribed, and were only briefly mentioned (e.g., Feruglio 1949, Casamiquela 1963, Dessanti 1972, Pascual et al. 1984, Bown & Larriestra 1990, Baez 2000). According to that, and considering that the fossil record of freshwater fishes and

frogs in the Miocene of Patagonia is patchy and biased, and rests on few remains coming from isolated localities (Arratia & Cione 1996, Baez 2000, Cione & Baez 2007), our present report constitutes an important addition to the poor knowledge of these faunas in Patagonia.

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