

First fossil record of an amiid fish (Halecomorphi, Amiidae) from the Latest Cretaceous of Patagonia, Argentina, and comments on the status of *Pappichthys patagonica* AMEGHINO, 1906 (Teleostei, Osteoglossidae)

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Abstract

We describe the first authenticated fossil record for the family Amiidae in Argentina. The specimen consists on an isolated dentary coming from the Uppermost Cretaceous Allen Formation, from Rio Negro province, Patagonia, Argentina, and belonging probably to the genus *Amia*. This specimen spans the biochronology of the Amiidae in South America, which were up to now restricted to Lower Cretaceous outcrops of Brazil. We also review the only previously reported amiid fish from the Neogene of South America. This single specimen consists of a dentary and some postcranial bones. It was originally named *Pappichthys patagonica* by AMEGHINO (1906). The study of this material allowed us to refer this species to the family Osteoglossidae, thus constituting the first fossil or extant record for the clade in Argentina.

Keywords: Late Cretaceous Amiidae, Neogene Osteoglossidae, *Pappichthys patagonica*, Argentina.

Résumé

Nous décrivons le premier fossile avéré pour la famille des Amiidae en Argentine. Le spécimen consiste en un dentaire isolé provenant du Crétacé terminal de la Allen Formation, dans la province du Rio Negro, Patagonie, Argentine, et appartenant probablement au genre *Amia*. Ce spécimen étend la biochronologie des Amiidae en Amérique du Sud, qui était restreinte jusqu'à présent aux gisements du Crétacé inférieur du Brésil. Nous revoyons également le seul amiidé précédemment décrit dans le Néogène de l'Amérique du Sud. Cet unique spécimen fut nommé à l'origine *Pappichthys patagonica* par AMEGHINO (1906). L'étude de ce matériel nous a permis de rapporter cette espèce à la famille des Osteoglossidae, devenant ainsi le premier représentant fossile ou récent de ce clade en Argentine.

Mots-clefs: Amiidae du Crétacé supérieur, Osteoglossidae du Néogène, *Pappichthys patagonica*, Argentine.

Introduction

The Amiiformes are halecomorph fishes represented today by the single extant species *Amia calva* LINNAEUS, 1766, the bowfin, which is geographically distributed among freshwater lakes and rivers in Eastern North America (NELSON, 2006: 99). This large predaceous fish constitutes a relict of a taxonomic group widely distributed among most continents during the Mesozoic and the Cenozoic. The first record for the Amiiformes occurs in the Late Triassic (Norian), whereas the oldest record of the extant family Amiidae is Late Jurassic (Oxfordian, Kimmeridgian) (GARDINER, 1993: 619; GRANDE & BEMIS, 1998: 636-646).

In South America, Amiidae are represented by two Brazilian Early Cretaceous genera belonging to the extinct subfamily Vidalamiinae, *Calamopleurus* AGASSIZ, 1841 and *Cratoamia* BRITO *et al.*, 2008. *Calamopleurus* is known in South America by two species, the Aptian *C. cylindricus* AGASSIZ, 1841 from the Santana Formation, and the Barremian *C. mawsoni* (WOODWARD, 1902) from the Ilhas Formation (MAISEY, 1991; GRANDE & BEMIS, 1998). The genus also exists in the Aptian of West Africa (TAVERNE, 1997) and in the Cenomanian of Morocco (FOREY & GRANDE, 1998). *Cratoamia* is an Aptian monospecific genus from the Crato Formation (BRITO *et al.*, 2008).

Another South American fossil Amiidae, *Pappichthys patagonica* AMEGHINO (1906) from the Upper Tertiary of Central Patagonia, Argentina, was reported more than a century ago. Today the fossil genus *Pappichthys* COPE, 1873 is considered as a junior-synonym of *Amia* LINNAEUS, 1766 (BORESKE, 1974: 47; GRANDE & BEMIS, 1998: 32; among others). *Pappichthys patagonica* is based on an incomplete dentary and some vertebrae. AMEGHINO (1906: 183, pl. 2, fig. 29) figured

the jaw fragment and gave it its scientific name but he did not formally describe the material. *Pappichthys patagonica* is thus a *nomen nudum*. This material has not been re-studied since then. However, ROMER & FRYXELL (1928: 526) excluded it from the Amiidae on the basis of AMEGHINO's illustration but without themselves having seen the material. This opinion has been followed by GRANDE & BEMIS (1998: 619) who assign the specimen to an indeterminate Neopterygii. On the other hand, CIONE (1986) considered it as a probable Percichthyidae.

The aim of our paper is, on the one hand, to describe a newly discovered amiid lower jaw fragment from the Upper Cretaceous of Patagonia, and, on the other hand, to review and to discuss the phylogenetic position of the putative amiid "*Pappichthys*" *patagonica*.



Fig. 1 – Map showing fossiliferous localities mentioned in the text. 1: Cerro Tortuga, Bajo Santa Rosa, Rio Negro province, where the amiid dentary was collected. 2: Miocene outcrop of southern Colhué Huapi Lake, Chubut province, having yielded the remains of "*Pappichthys*" *patagonica*.

Systematic palaeontology

- Subclass Actinopterygii COPE, 1887
 - Division Halecostomi REGAN, 1923
 - Order Amiiformes HAY, 1929
 - Superfamily Amioidea BONAPARTE, 1838
 - Family Amiidae BONAPARTE, 1838
 - Genus *Amia* (?) LINNAEUS, 1766
- Fig. 2

Material

Specimen MML 449 (Museo Municipal de Lamarque, Rio Negro, Argentina), an incomplete anterior portion of right dentary.

Formation and locality (Fig. 1)

The material here described was found by members of the Museo Municipal de Lamarque, Río Negro province, Argentina, in Cerro Tortuga at Santa Rosa Basin (see NOVAS *et al.*, 2008), a fossiliferous locality with extensive outcrops belonging to the Campanian-Maastrichtian (Late Cretaceous) Allen Formation (APESTEGUIA, 2002; LEANZA *et al.*, 2004). This locality yielded numerous important fossil vertebrates including the basal bird *Limenavis patagonica* CLARKE & CHIAPPE, 2001 and a dubious charadriiform bird, the abelisaurid *Quilmesaurus curriei* CORIA, 2001, the titanosaurid *Bonatitan reigi* MARTINELLI & FORASIEPI, 2004, the giant dromaeosaurid *Austroraptor cabazai* NOVAS *et al.*, 2008, as well as hadrosaurid dinosaurs, leptodactylid and pipid frogs, chelid turtles, sphenodontid lizards, madtsoiid snakes (CLARKE & CHIAPPE, 2001; CORIA, 2001; HOPE, 2002; MARTINELLI & FORASIEPI, 2004; NOVAS *et al.*, 2008). There is also a wide variety of fresh-water fishes. Among them, the first report is the mention and brief description by BRITO (1997) of an aspidorhynchid which was referred to the genus *Vinctifer* JORDAN, 1919, a generic referral that was recently criticized by BARTHOLOMAI (2004), which considered it as an indeterminate Aspidorhynchidae. More recently, MARTINELLI & FORASIEPI (2004) described specimens belonging to Siluriformes similar to Diplomystidae, Lepisosteidae, indeterminate teleosteans, a possible percichthyid perciform, as well as indeterminate ceratodontiforms and batoids. *Ptychoceratodus cionei* APESTEGUIA *et al.*, 2007 and *P. wichmanni* APESTEGUIA *et al.*, 2007, two ceratodontid Dipnoi, are the most recently described Cretaceous fishes from the locality (APESTEGUIA *et al.*, 2007).

Osteological study (Fig. 2)

The dentary is a massive bone dorsally curved in lateral view. At the symphysis level, this dentary is very narrow, almost pointed, but the bone deepens progressively. In lateral view, its alveolar margin is crenulated. Its external surface is nearly smooth, with only a lateral furrow of pits for the mandibular sensory canal. Five of these pits or pores are located near the alveolar margin. In addition, in the posterior margin of the bone, there exits a sixth pore more ventrally located. The dentary symphysis is dorsoventrally low.

In occlusal view, there is a single antero-posteriorly disposed tooth row composed of twelve more-or-less circular sockets in some of which the tooth bases are still implanted. These teeth are acrodont. The bases of teeth are in contact with each other, and show irregular wrinkles.

The medial surface of the dentary shows a widely opened Meckelian groove, which extends along the dentary forward to the symphysis. This groove exhibits an elongate foramen at the level of the ninth alveolus.

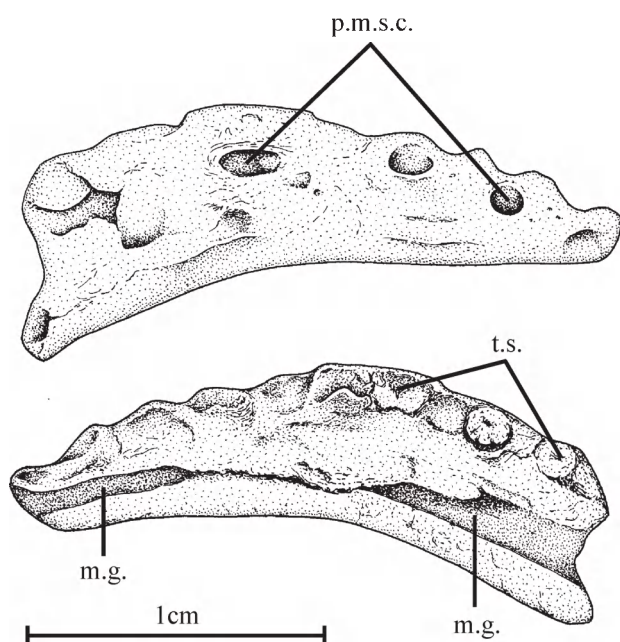


Fig. 2 – Right dentary of a Patagonian Amiidae, probably belonging to the genus *Amia* LINNAEUS, 1766 (MML 449). Above: external view. Below: inner view.

Division Teleostei MÜLLER, 1846
 Superorder Osteoglossomorpha
 GREENWOOD *et al.*, 1966
 Order Osteoglossiformes BERG, 1940
 Suborder Osteoglossoidae REGAN, 1909
 Family Osteoglossidae BONAPARTE, 1832
 Genus indeterminate

“*Pappichthys*” *patagonica* AMEGHINO, 1906
 (*nomen nudum et dubium*)

Figs 3-4

Material

MACN A-11263 (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina), anterior part of a left dentary (holotype).

MACN A-11592, abdominal and caudal centra, and an indeterminate bone scrap (referred specimen: AMEGHINO *in schedis*).

Formation and locality (Fig. 1)

Both samples MACN A-11263 and MACN A-11592, referred to *Pappichthys patagonica* by AMEGHINO (1906), where collected by his brother Carlos Ameghino in the expeditions to Argentine Patagonia during 1898 (AMEGHINO, 1900-1902, 1902). Regrettably, no exact record about the geographic location of the material collected during those fieldtrips is at present available, but the reference to its biostratigraphic position is almost certain. In this way, both MACN A-11263 and MACN A-11592 were collected from the “capas de *Colpodon*” or “*Colpodonense*” (AMEGHINO, 1906). Regarding its geographic location, the “*Colpodonense*” fossiliferous localities discovered and explored by Carlos Ameghino were restricted to two outcrops, placed at the south and northwest of the Colhué Huapi Lake, at the south of Chubut province (Argentina), and a locality at the valley of the Chubut River, at the north of the same province (AMEGHINO, 1906; BAEZ, 1977). BAEZ (1977) has described several anuran remains as coming from the same collections made by Carlos Ameghino, which yielded the materials referred to *P. patagonica*, currently deposited in the collections of the MACN. As pointed out by BAEZ (1977), all these materials belong to the “Gran Barranca” at the south of the Colhué Huapi Lake, as indicated by Carlos Ameghino (SIMPSON, 1935).

At present, the “*Colpodonense*” is attributed to the Colhuehuapian “Mammal-Age”, from the Lower Miocene Sarmiento Formation (SPALLETTI & MAZONNI, 1979; KAY *et al.*, 1999). The geochronological data obtained from the Colhuehuapian “Mammal Age” indicate an absolute age between 20 and 19 Ma (at Gran Barranca fossiliferous locality; KAY *et al.*, 1999).

In those stratigraphic levels, the remains of anurans are rather abundant, and suggest the presence of freshwater bodies (SCHAEFFER, 1949; LYNCH, 1971; BAEZ, 1977). The information provided by rodents and platyrrhine monkeys suggest the existence of a relatively wet and temperate climate, with abundant

wooded areas (GOIN *et al.*, 2007). Moreover, available data indicate that in those localities were surely near shore plains limited by the Atlantic Ocean (GOIN *et al.*, 2007).

Osteological study (Figs 3, 4)

The holotype MACN A-11263 consists of the anterior part of a left dentary. The bone is thick, elongate and low. The teeth are lost but eleven very large sockets arranged in a single row are present. Except for the first one, which is more or less circular, these alveoli are ovoid in transverse section, with their longer diameter forming a right angle with the length of the bone. The external surface of the dentary is nearly smooth, lacking pores of the lateral sensorial canal, but there is a conspicuous aperture at mid-height of the bone at the level of the seventh alveolus, probably accommodating a *ramus* of the trigeminal nerve (V) or a small blood vessel. Posteroventrally from this foramen, there is an elongate and conspicuous longitudinal bump. On the inner face, near the alveolar margin, there is a narrow longitudinal groove that delimitates the tooth row medially. Within this groove, at the level of the seventh socket, there exists a well marked pit, once again for a *ramus* of the trigeminal nerve (V) or a blood vessel. A groove for the

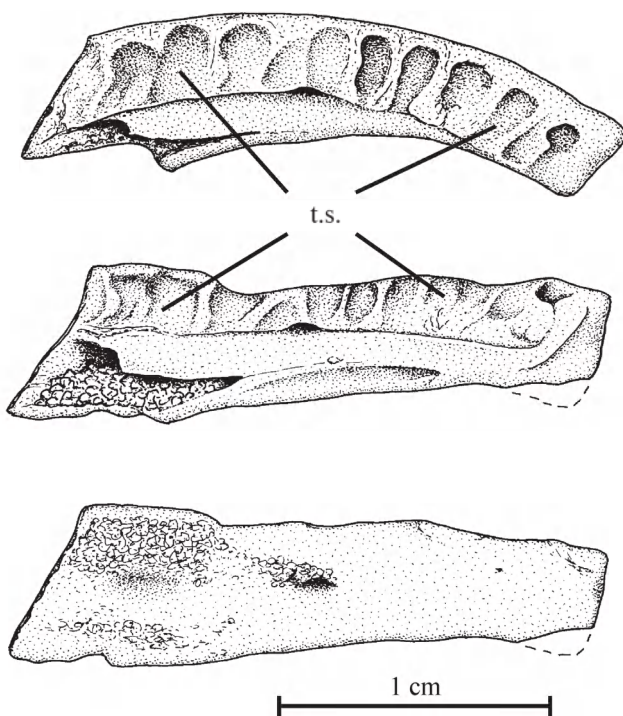


Fig. 3 – The osteoglossid “*Pappichthys*” *patagonica* AMEGHINO, 1906. A left dentary (holotype MACN A-11263). Above: dorsal view. Middle: inner view. Below: external view (reversed).

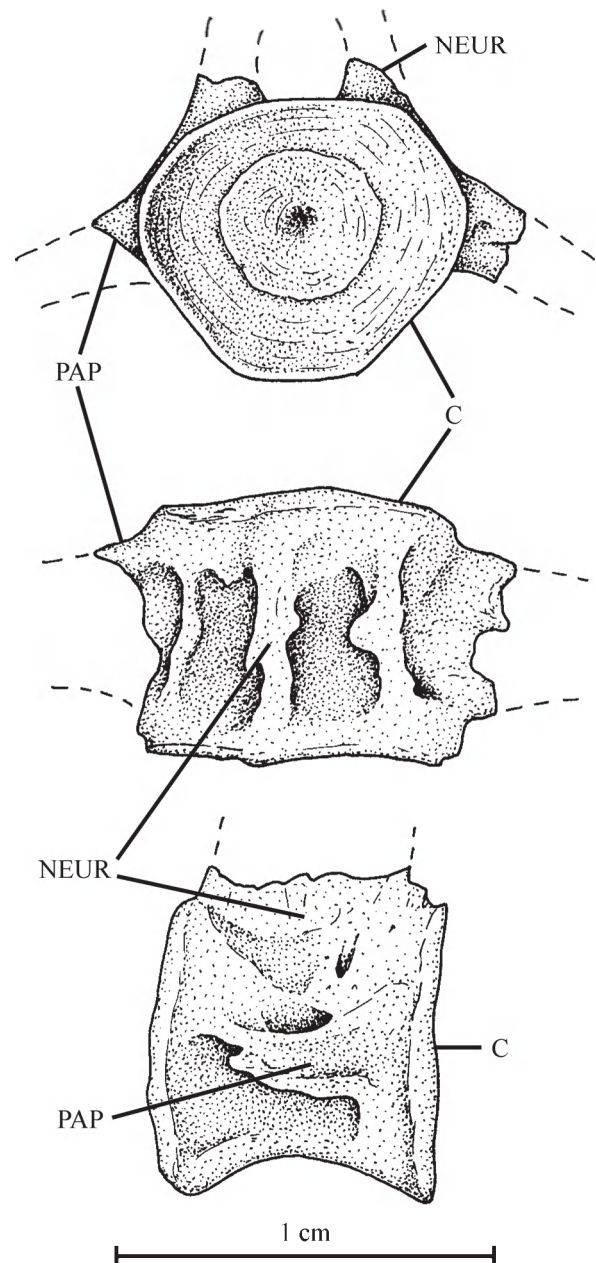


Fig. 4 – The osteoglossid “*Pappichthys*” *patagonica* AMEGHINO, 1906. An abdominal vertebra (MACN A-11592). Above: in anterior view. Middle: in dorsal view. Below: in left lateral view.

Meckelian cartilage is not present. The ventral margin of the bone is slightly convex. The symphysis is antero-posteriorly short and dorso-ventrally taller. In medial view, the symphysis exhibits a short, narrow and oblique groove which is dorsally oriented and which serves for the insertion of the intermandibular ligaments. The ventral corner of the symphysis is broken away. If complete, this symphyseal region would form a sort of small “chin”.

The axial skeleton remains consist of isolated centra

(MACN A-11592). The vertebrae are holospondylous, monospondylous and amphicoelous. There is a small opened notochordal canal.

The abdominal centra are slightly hexagonal in contour. The bases of the neural arches are antero-posteriorly elongate and are well fused to the centrum. The parapophyses (= haemapophyses) are also well developed, broad, fused to the centrum and located high on its lateral face.

The caudal vertebra possesses a centrum that is subcircular in contour and shows a well-developed constriction at mid-length. The arches are only partially preserved.

Discussion

The case of the Patagonian Amiidae

The presence on the inner face of the concerned dentary of a deep and widely opened groove for the Meckelian cartilage and of a foramen is a typical morphology of Amiiformes and other basal halecomorphs (ESTES, 1969; BORESKE, 1974; BRYANT, 1987; GRANDE & BEMIS, 1998; among others).

Moreover, wrinkled bases of teeth are also a condition widespread among Amiiformes (ESTES, 1969; BORESKE, 1974; BRYANT, 1987; GRANDE & BEMIS, 1998).

Within basal halecomorphs, the lower jaw morphology of Amiidae is clearly separable from other clades by the presence of a short, low and massive dentary bearing a single row of teeth with their bases in contact (ESTES, 1969; BORESKE, 1974; BRYANT, 1987; GRANDE & BEMIS, 1998).

The combination of these three characters allows us to refer MML 449 to the Amiidae.

One thing is certain. The Patagonian amiid does not belong to the South-American and African fossil genus *Calamopleurus* which exhibits a dentary not deepening very much from its anterior to its posterior part when seen in lateral view (GRANDE & BEMIS, 1998: fig. 302, 310, 311; BRITO *et al.*, 2008: fig. 4; among others). On the other hand, the shape of the Patagonian dentary corresponds rather well to that in the genus *Amia*, and, as in *Amia* also, some of the first sensory pores are located near the alveolar margin of the bone while the last pores are close to the ventral border of the dentary (JANOT, 1967: pl. 1, fig. 1; GRANDE & BEMIS, 1998: fig. 43, 44; among others).

That is why we refer this fossil Patagonian dentary to the genus *Amia* but, however, with a slight doubt because of the very partial preservation of the specimen.

Recently, SALGADO *et al.* (2009) have described some Upper Cretaceous vertebrate remains from Patagonia, including a cleithrum belonging to a large fish (*ibid.*, 2009: Fig. 3A, B). They assigned the bone to a big osteoglossomorph. However, the Osteoglossomorpha generally exhibit cleithra with a rather narrow ventral branch. The giant South-American *Arapaima* is the unique osteoglossid genus with a broad cleithral ventral branch but this branch is only slightly longer than the dorsal one (TAVERNE, 1977: fig. 137). The Patagonian cleithrum, with its very long and wide ventral branch bearing a strong crest on its inner face, is typically like an amiid cleithrum and especially that in the genus *Amia* (JANOT, 1967: pl. 5, fig. 4, pl. 9, fig. 1, pl. 10, fig. 3). It is quite possible that this cleithrum belongs to the same species as the dentary herein studied.

The case of "Pappichthys" patagonica

The dentary of "*P.*" *patagonica* does not exhibit a Meckelian groove on its inner face. Moreover, its vertebrae are typically teleostean and not "holostean". The conclusion is obvious: "*P.*" *patagonica* is a teleost and belongs to neither the genus *Pappichthys* (synonym of *Amia*) nor to another Amiidae or Amiiformes.

ROMER & FRYXELL (1928) reached the same conclusion but they did not try to assign the Patagonian fossil fish in any precise family.

On the other hand, CIONE (1986) thought that "*P.*" *patagonica* was a member of the Percichthyidae, a freshwater family of perciform fishes with ten Recent genera in Australia and two genera, one fossil and one Recent, in South-America. However, Percichthyidae possess a short and deep dentary, teeth of moderated size and not arranged in a single row, and a broad largely opened mandibular sensory canal (ARRATIA, 1982: fig. 16, 17). Such a dentary is totally different from that of "*P.*" *patagonica*, which certainly can not be included in the Percichthyidae.

"*P.*" *patagonica* is very partially known. However, we have seen that the fish presents at least two specialized characters. The dentary bears very large and antero-posteriorly compressed teeth arranged in a single row. The anterior abdominal vertebrae exhibit broad parapophyses (= haemapophyses) inserted high on the lateral faces of the centra and fused with them. Within teleosts, these two apomorphies are widely present in Osteoglossoidei (TAVERNE, 1977: fig. 53, 54, 63, 82, 83, 116, 141, 1978: fig. 9, 17, 19, 20, 28, 2009: fig. 1-3; among others), a suborder to which we refer the Patagonian fossil.

Within Osteoglossoidei, we can exclude a close relationship with the Pantodontidae. Indeed, those

small African freshwater fishes possess very peculiar alveolate parapophyses (TAVERNE, 1978: fig. 50-52) quite different from those in “*P.*” *patagonica*. In the Recent Arapaimidae and in all the known fossil osteoglossid genera (*Phareodus* LEIDY, 1873, *Brychaetus* WOODWARD, 1901, *Musperia* SANDERS, 1934, etc.), the dentary presents a quite different shape, shorter and deeper (TAVERNE, 1977: fig. 93, 107, 124, 134, 1978: fig. 2, 9, 15, 17, 28; among others) than in “*P.*” *patagonica*. By contrast, a low and long dentary with a small bony “chin” at the symphysis, like the Patagonian bone, is present in *Osteoglossum* CUVIER, 1829 and *Scleropages* GÜNTHER, 1864 (TAVERNE, 1977: fig. 42, 53, 54, 71, 82, 83; among others). “*Pappichthys*” *patagonica* seems to be closely related to those two Recent osteoglossid genera.

Someone could argue against an osteoglossid relationship for “*P.*” *patagonica* because its vertebrae bear fused and not autogenous neural arches. We know that the neural arches and parapophyses are primitively autogenous on abdominal vertebrae of most teleostean fishes (JOHNSON & PATTERSON, 1996: 278). On the contrary, BRINCKMAN & NEUMAN (2002: 44) state that the combination of autogenous neural arches together with fused parapophyses is diagnostic for Osteoglossiformes. That is often true but not always. In some cases, the neural arch of osteoglossiform fishes can be partially or totally fused with the centrum (TAVERNE, 1977: fig. 64, 65, 115-119, 141, 142, 1978: fig. 49-51). So, the fused neural arches of the vertebrae in “*P.*” *patagonica* are not a pertinent argument to exclude an osteoglossid relationship for this fish.

On the basis of the incomplete nature and the absence of autapomorphic features in the available specimens of “*P.*” *patagonica*, we consider it as a *nomen dubium*.

Conclusions

As is indicated in the preceding discussion, we report for the first time a fish of the family Amiidae from the Campanian-Maastrichtian (Late Cretaceous) of Patagonia, Argentina. This constitutes the first record for the clade Amiidae at the Southern Cone, which expands the biochronology for this fish group in South America. Previously on this continent, the Amiidae were restricted to Early Cretaceous times of Brazil. The only previously reported Amiidae described in Argentina belongs to “*Pappichthys*” *patagonica*, a fossil fish coming from Lower Miocene levels of Central Patagonia. This material is herein referred to the osteoglossiform family Osteoglossidae, which previously lacked any extant or fossil record in Argentina.

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Key to the abbreviations

C: vertebral centrum
 NEUR: neural arch
 PAP: parapophysis (= haemapophysis)
 m. g.: Meckelian groove
 p. m. s. c.: pores of the mandibular sensory canal
 t. s.: tooth socket

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