First Triassic and oldest record of a South American amiiform fish: *Caturus* sp. from the Los Menucos Group (lower Upper Triassic), Río Negro province, Argentina

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ABSTRACT. Some cranial fragments from the jaw region and the opercular series of the amiiform fish taxon *Caturus* sp. (Actinopterygii, Halecomorphi) are described from the continental Upper Trias of Los Menucos (Rio Negro province, Patagonia, Argentina). This find represents the first Triassic amiiform record and the first undoubted fossil caturid record from South America.

KEYWORDS: Amiiformes, Caturus sp., skull bones, continental Upper Trias, Patagonia, Argentina.

1. Introduction

The holostean fish order Amiiformes (Actinopterygii, Halecomorphi) is composed of four families, the Amiidae, Sinamiidae, Caturidae and Liodesmidae (Grande & Bemis, 1998). Amiidae are a long-living family, which appeared during the Late Jurassic and include about a dozen of genera (Gardiner, 1993; Grande & Bemis, 1998). The family is currently represented by a single species, the North American freshwater *Amia calva* Linnaeus, 1766 or bowfin. The three other families are entirely fossil and restricted to the Mesozoic.

Until now, the fossil record of Amiiformes in South America is rather patchy, being represented only by the family Amiidae and a doubtful record of the family Caturidae. A member of the subfamily Amiinae is reported from the Late Cretaceous of Patagonia, Argentina. This record was based on a dentary, probably belonging to the genus Amia Linnaeus, 1766 (Bogan et al., 2010) and on a cleithrum, initialy attributed to a large osteoglossomorph (Salgado et al., 2009: fig. 3A, B), but now attributed to Amia (Bogan et al., 2010: 167). Calamopleurus Agassiz, 1841 and Cratoamia Brito et al., 2008, both represented by complete skeletons, are two genera of the subfamily Vidalamiinae, occurring in the Lower Cretaceous of Brazil (Woodward, 1902; Maisey, 1991; Grande & Bemis, 1998; Brito et al., 2008). "Pappichthys" patagonica Ameghino, 1906, previously described from the Upper Tertiary of Argentina and identified as a fossil Amiidae (Ameghino, 1906), is now considered to be a member of the teleost family Osteoglossidae, close to Osteoglossum Cuvier, 1829 and Scleropages Günther, 1864 (Bogan et al., 2010). The identification of an incomplete skeleton of a putative halecomorph from the Upper Jurassic of the Neuquén Province (Argentina) as a caturid-like taxon by Cione (in Leanza & Zeiss, 1990) is refuted herein. A close inspection of its osteology suggests that the specimen may be better referred to the order Pachycormiformes.

The aim of the present paper is to describe an incomplete and disarticulated specimen of a caturid fish from the Los Menucos Group, which represents not only the first Triassic record for the family in Argentina, but also the first undoubted record for the Caturidae in South America.

2. The Los Menucos site and its temporal and spatial setting

Triassic fishes from South America are still poorly known (Arratia & Cione, 1996; López-Arbarello, 2004). Most continental taxa come from only three geological units: the Santa María Formation of southern Brazil, and units in the Cuyo (Mendoza province) and the Bermejo (San Juan-La Rioja provinces) basins of northwestern Argentina (Stipanicic, 1983, 2002; Stipanicic & Bonaparte, 1979; Gallego et al., 2004; López-Arbarello et al., 2006, 2008, 2010; López-Arbarello & Zavattieri, 2008). These three geological formations contain a rich actinopterygian

ichthyofauna, composed of Acrolepidae, Perleidiformes, Chondrosteans and several *incertae sedis* fishes (Gallego et al., 2004; López-Arbarello et al., 2006, 2008, 2010; López-Arbarello & Zavattieri, 2008). The fossil fish skeleton described here is the first vertebrate find from the Triassic beds of the Los Menucos Group, except for various tetrapod footprints. It was collected in the Los Menucos basin near the village of Los Menucos in the "25 de Mayo" Department, at the south corner of Río Negro province (Argentinia) (Fig. 1).

The fossiliferous levels of Los Menucos are part of the Los Menucos Group (Labudía et al., 1995; Labudía & Bjerg, 2001), which is composed of the Vera and Sierra Colorada Formations. The Vera Formation is exposed in the lower levels of the Los Menucos quarries, and can easily be correlated throughout the area on the basis of volcanic and sedimentary criteria. The Sierra



Figure 1. Map showing the fossiliferous locality of Los Menucos, in the Rio Negro province of Argentina.

Colorada Formation overlies the former and is composed of ignimbritic volcanic rocks, mainly riolites (Stipanicic et al., 1968; Pesce, 1974; Roseman, 1979; Labudía & Bjerg, 2001), dated as Norian (early Late Triassic; 222 ± 2 Ma, Rb/Sr isochron method; Rapela et al., 1996).

The Vera Formation, slightly older than the Sierra Colorada Formation, exhibits very rich fossiliferous levels, which yield an abundant paleoflora, termed the "*Dicroidium* Flora" (Stipanicic, 1967; Stipanicic & Methol, 1972; Pesce, 1974; Artabe, 1985a, b; Labudía et al., 1995; Labudía & Bjerg, 2001). Its fossil vertebrate fauna is composed of abundant, usually very well preserved vertebrate footprints, among which temnospondyl amphibians, crurotarsal archosaurians, lepidosauriforms and eutheriodont therapsidians (Casamiquela 1964, 1975, 1987; Leonardi, 1994; Leonardi & Henrique de Oliveira, 1990; Manera de Bianco & Calvo, 1999; Domnanovich, 2003; Domnanovich & Marsicano, 2006; Domnanovich et al., 2008) and the herein first discovery and description of skeletal material.

3. Systematic Paleontology

Subclass Actinopterygii Cope, 1887 Division Halecostomi Regan, 1923 Subdivision Halecomorphi Cope, 1872 Order Amiiformes Hay, 1929 Family Caturidae Owen, 1860

Genus Caturus Agassiz, 1834

Type-species: Caturus furcatus (Agassiz, 1833)

Caturus sp.

(Figs 2-6)

Material. MPCA 632, Cranial fragments, consisting of bones from the jaw region and from the opercular series, and of several indeterminate bony fragments (Fig. 2).

Description. The maxilla is very slender, with an elongate barlike shape (Fig. 3). It is of homogeneous depth along most of its length, with the exception of its posterior extremity which is slightly dorso-ventrally expanded. Its anterior end is sharp.



Figure 2. Specimen MPCA 632. A partial skull of a Caturidae from the Upper Triassic of Los Menucos (for legend see text).

The oral margin bears at least 23 or 24 large teeth, of which the posterior ones are anteriorly oriented, whereas those of the anterior portion of the bone are subvertically oriented. The teeth are very elongate and marked by a large cap of acrodin which is strongly labio-lingually compressed, with very sharp anterior and posterior keels. The tooth bases are wide and subcircular in contour, with a very large pulp cavity, as usually in Amiiformes (Grande & Bemis, 1998) and in other predator fishes. A small part of a narrow and probably long supramaxilla is present above the posterior part of the maxilla. Two fragments of a very long, thin and anteriorly sharp bone are also present above the maxilla. They probably are parts of a toothless ectopterygoid.



Figure 3. Specimen MPCA 632. The bones of the jaw region.



Figure 4. Specimen MPCA 632. The bones of the opercular series.

The dentaries are poorly preserved. They are subtriangular in contour, very elongated and narrow at the symphyseal level. The dorsal toothed margin is rectilinear and the ventral margin slightly concave. Posteriorly, the coronoid process is well marked. The precise total tooth count cannot be properly assessed. However, around 20 teeth have been recognized on each dentary. The teeth are indistinguishable in morphology from these of the maxilla. The posterior teeth are highly recurved anteriorly, whereas the teeth of the anterior half and symphyseal region are nearly subvertically oriented.

A large bone is partly covered by the anterior extremity of one of the dentaries. It is probably a lateral ethmoid. One of the two vomers is preserved above and before the maxilla. It is composed of a short enlarged anterior part and a long but narrower posterior part. Some very light marks below the anterior portion of the bone could be the traces of large teeth. A wide nasal is present before the maxilla. It bears the anterior portion of the supraorbital sensory canal. One antorbital is preserved. The bone is more or less oval with a long and thin anterior process. A large and broad sclerotic plate also is present. Two bones are present between the antorbital and the vomer. The dorsal one is larger and the ventral one thinner. They could perhaps be respectively an autopalatine and a dermopalatine. Two other smaller and indeterminate bones rest just before the two former.

Several plate-like bones belonging to the opercular series are visible but poorly preserved (Fig. 4). The preopercle has a very broad dorsal branch and a short ventral branch. The dorsal branch is broader at its base than at its top. The ventral part of the bone has an external ornamentation consisting of many thin and deep dichotomizing grooves radiating from a central point. The interopercle, a small fragment of the subopercle and two fragment of both opercles also are present. One of these two fragments indicates that the opercle is a large bone.

4. Discussion and conclusions

A long, slender and rod-like maxilla, bearing large teeth, such as that of the herein described specimen MPCA 632, is rather uncommon within primitive Neopterygii. These fishes generally possess a maxilla that is much deepened at its posterior extremity. However, a slender maxilla is known to occur in a single taxon of Furidae (= Eugnathidae) and in the Liodesmidae and Caturidae (Fig. 5B-E).

The long-snouted fossil fish family Furidae is present in several European countries from the Middle Trias to the Upper Jurassic. The genus *Furo* Gistl, 1848 (= *Eugnathus* Agassiz, 1844, not *Eugnathus* Schoenherr, 1833) contains many species and is probably heterogenous (Lambers, 1998). One of those species, *Furo microlepidotes* (Agassiz, 1833) from the Upper Jurassic of Germany, presents a thin rod-like maxilla with large teeth. However, this bone bears less than twenty teeth and they are proportionally larger than those of the Argentinian specimen MPCA 632 (Fig. 5B). The dentary has no more than about fifteen teeth (Lambers, 1998: fig. 4, 5). Moreover, the coronoid process is weakly developed (ibid. 1998: fig. 5) and there is a constriction between the upper and the lower parts of the preopercle, the lower branch not being broader than the upper (Fig. 6B). Thus, these characters differ from those present in the Argentinian specimen.

Liodesmus Wagner, 1859 from the Upper Jurassic of Germany is the unique genus within the family Liodesmidae. It is a small fish. Its total length does not exceed 12 cm, a much smaller size than that of specimen MPCA 632. *Liodesmus* has an antorbital with a very short anterior process (Grande & Bemis, 1998: fig. 406C). Its rod-like maxilla has a slightly enlarged and concave posterior border (Fig. 5C) as in many Amiidae and its preopercle is narrow and crescent-shaped (Fig. 6C). That is, once again, quite different from that in the Argentinian specimen.

Within the Caturidae, the genera *Caturus* Agassiz, 1834 and *Amblysemius* Agassiz, 1844 share the following two synapomorphies: a slender rod-like maxilla lacking a posterior



Figure 5. Schematic comparisons between the maxillae of (A) *Caturus* sp., specimen MPCA 632, (B) *Furo microlepidotes* (Agassiz, 1843) [modified from Lambers, 1998: fig. 4], (C) *Liodesmus gracilis* (Agassiz, 1843), without the teeth [modified from Grande & Bemis, 1998: fig. 243], (D) *Caturus furcatus* (Agassiz, 1833) [modified from Lambers, 1992, chapter 5: fig. 7] and (E) *Amblysemius pachyurus* (Agassiz, 1843) [modified from Lambers, 1994: fig. 3] (not to scale).



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Schematic Figure 6. comparisons between the preopercles of (A) Caturus sp., specimen MPCA 632, (B) Furo microlepidotes (Agassiz, 1843) [modified from Lambers, 1998: fig. 4], (C) Liodesmus gracilis (Agassiz, 1843) [modified from Grande & Bemis, 1998: fig. 406B], (D) Caturus furcatus (Agassiz, 1833) [modified from Grande & Bemis, 1998: fig. 401A] and (E) Amblysemius pachyurus (Agassiz, 1843) [modified from Lambers, 1994: fig. 3] (not to scale).

dorsal expansion, and elongate teeth showing acrodin caps sharply carinated and labiolingually compressed (Lambers, 1992, 1994, 1998; Grande and Bemis, 1998). These two conditions are also present in specimen MPCA 632. However, *Amblysemius* has very strong teeth, a maxilla bearing less than twenty teeth and with a ventrally curved posterior extremity (Fig. 5E), a dentary also with less than twenty teeth (Lambers, 1994: fig. 3) and a crescent-shaped preopercle (Fig. 6E). This situation is also quite different from that of the Argentinian specimen. Contrastingly, most *Caturus* species possess long but thin teeth on the jaws, often more than twenty teeth on the maxilla and the dentary, a maxilla with a posterior end that is slightly dorso-ventrally expanded but not ventrally curved (Fig. 5D), and a large preopercle with a broad dorsal branch, an enlarged base and a short ventral branch (Fig. 6D), in the same way as in specimen MPCA 632.

From the foregoing, we can confidently conclude that the Argentinian material studied herein belongs to the caturid genus *Caturus*. This genus contains many species. Most of them belong to the European realm. One species, *Caturus dartoni* (Eastman, 1899), is known in the Bathonian of Wyoming (Schaeffer & Patterson, 1984). Another species, *Caturus deani* Gregory, 1923, is reported from the Oxfordian of Cuba (Gregory, 1923). *Caturus* is herein recorded for the first time in South America.

It is to be noted that *Caturus* is considered as a marine amiiform fish. However, the genus is present in the Wealden and Purbeck Formations of England (Woodward, 1918), strata largely from continental origin (Allen, 1959), and in the Middle Jurassic Songa Limestones of the Democratic Republic of Congo (De Saint-Seine & Casier, 1962) now regarded as lacustrine (Taverne, 2011). The Argentinian *Caturus* is thus a third occurrence of the genus in beds from freshwater origin.

5. Institutional and Anatomical abbreviations

MPCA: Museo Provincial "Carlos Ameghino", Cipolletti city, Río Negro province, Argentina.

ANT: antorbital; APAL: autopalatine; DN: dentary; DPAL: dermopalatine; ECPT: ectopterygoid; IOP: interopercle; LETH: lateral ethmoïd; MX: maxilla; NA: nasal; OP: opercle; POP: preopercle; SCL: sclerotic plate; SMX: supramaxilla; SOP: subopercle; VO: vomer; c. pr.: coronoid process; c. sorb.: supraorbital sensory canal.

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