

Description of a new aspidorhynchid fish, *Belonostomus lamarquensis* sp. nov. (Halecostomi, Aspidorhynchiformes), from the continental Upper Cretaceous of Patagonia, Argentina

by Sergio BOGAN, Louis TAVERNE & Federico L. AGNOLIN

BOGAN, S., TAVERNE, L. & AGNOLIN, F.L., 2011 – Description of a new aspidorhynchid fish, *Belonostomus lamarquensis* sp. nov. (Halecostomi, Aspidorhynchiformes), from the continental Upper Cretaceous of Patagonia, Argentina. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **81**: 235-245, 13 figs, Brussels, November 30, 2011– ISSN 0374-6291.

Abstract

Some braincases, a predentary, a few vertebrae and scales of a new aspidorhynchid species, *Belonostomus lamarquensis* sp. nov., are described from the Upper Cretaceous (Campanian-Maastrichtian) Allen Formation of Patagonia, Argentina. The new species differs from the other *Belonostomus* species by its flank scales having an anterior smooth region separated by a vertical groove from a posterior region bearing a series of numerous and closely spaced subparallel ridges that end in a deeply crenulated posterior margin. The dermal bones are ornamented with ridges and tubercles, a rare character in *Belonostomus*. The endocranial bones are completely fused together, except the basisphenoid. Within the *Belonostomus* species, *B. lamarquensis* seems closely related to *B. hooleyi* from the English Lower Cretaceous, which also exhibits dermal bones with ridges and tubercles, and scales morphologically somewhat similar to those of *B. lamarquensis*.

Keywords: Actinopterygii, Aspidorhynchidae, *Belonostomus lamarquensis* sp. nov., braincase, predentary, Allen Formation, Upper Cretaceous, Patagonia, Argentina.

Résumé

Quelques neurocrânes, un prédentaire, des vertèbres et des écailles d'une nouvelle espèce d'aspidorhynchidé, *Belonostomus lamarquensis* sp. nov., sont décrits provenant de la Formation Allen d'âge Crétacé supérieur (Campanien-Maastrichtien) en Patagonie, Argentine. La nouvelle espèce diffère des autres espèces de *Belonostomus* par ses écailles des flancs avec une région antérieure lisse séparée par une gouttière verticale d'une région postérieure qui porte de nombreuses crêtes subparallèles pressées les unes contre les autres et qui se terminent au bord postérieur qui est profondément crenelé. Les os dermiques sont ornés de crêtes et de tubercules, un caractère rare chez *Belonostomus*. Les os endocrâniens sont complètement fusionnés entre eux, à l'exception

du basisphénoïde. Au sein des espèces de *Belonostomus*, *B. lamarquensis* semble plus particulièrement apparenté avec *B. hooleyi* du Crétacé inférieur d'Angleterre qui montre également des os dermiques avec des crêtes et des tubercules et dont les écailles sont morphologiquement proches de celles de *B. lamarquensis* mais sans être similaires.

Mots-clefs: Actinopterygii, Aspidorhynchidae, *Belonostomus lamarquensis* sp. nov., neurocrâne, prédentaire, Formation Allen, Crétacé supérieur, Patagonie, Argentine.

Introduction

Aspidorhynchiformes are an order of extinct marine neopterygian fishes characterized by an elongate and low body, a posteriorly displaced dorsal fin opposite to the anal, a long rostrum essentially formed by the dermethmoid (= rostral), and the premaxillae, and a median predentary (DE SAINT-SEINE, 1949: fig. 114; TAVERNE & ROSS, 1973: fig. 2; MAISEY, 1991: fig. p. 175; BRITO, 1997: figs 6, 31, 43, 51; among others). The flanks of their body are covered by very deep and antero-posteriorly narrowed lateral scales whose external surfaces are covered by a thick ganoine layer (WOODWARD, 1908: pl. 30, figs 6, 8; SCHULTZE & STÖHR, 1996: fig. 4; BRITO & MEUNIER, 2000: fig. 1; BARTHOLOMAI, 2004: fig. 10; among others) except in *Aspidorhynchus*, which lacks ganoine on its scales (BRITO & MEUNIER, 2000).

The members of this order have a nearly cosmopolitan geographic distribution with Asia as the only exception (BRITO, 1997: fig. 1), and a biochron extending from the Middle Jurassic to the Late Cretaceous (BRITO, 1997: fig. 2). There is also a mention of an aspidorhynchid predentary in the Early Palaeocene of North America (BRYANT, 1987) but this could be the result of a reworking from Upper Cretaceous layers.

This monophyletic clade contains a single family,

the Aspidorhynchidae, and includes four genera: *Aspidorhynchus* AGASSIZ, 1833, *Belonostomus* AGASSIZ, 1834, *Vinctifer* JORDAN, 1919 and *Richmondichthys* BARTHOLOMAI, 2004. Current phylogenetic hypotheses place *Aspidorhynchus* as the most plesiomorphic taxon within the family but there is some disagreement about which genus is the most apomorphic. MAISEY (1991: fig. p. 189) considers *Belonostomus* as the more specialized genus on the basis of its elongate prementary, whereas TAVERNE (1998) and BRITO (1997, 1999) give that role to *Vinctifer* because of its advanced caudal characters. *Richmondichthys* shares with *Vinctifer* some specialized features of the upper jaw (e.g. the very peculiar shape of the maxilla and the loss of the supramaxilla) but differs from it by the important feature of the shortening of its rostrum (BARTHOLOMAI, 2004).

Aspidorhynchiformes often are considered as evolved halecostomes closely related to Pycnodontiformes, Pachycormiformes, Pholidophoriformes and true teleosts (TAVERNE, 1998: 287; ARRATIA, 2000: figs 20, 21; among others), whereas some researchers place them within teleosts (PATTERSON, 1973: 298; BRITO, 1999b: 262; among others) but this choice essentially depends on the various definitions given by ichthyologists to the taxon Teleostei.

The fossil record of Aspidorhynchiformes in South America is rather rich but restricted to the genera *Vinctifer* and *Belonostomus*.

At least three species of *Vinctifer* are present in the Aptian-Albian deposits of Brazil: *Vinctifer comptoni* (AGASSIZ, 1841) [= *Vinctifer punctatus* DA SILVA SANTOS, 1985, cfr. BRITO, 1997: 710], *Vinctifer longirostris* DA SILVA SANTOS, 1990 and *Vinctifer araripensis* DA SILVA SANTOS, 1994. Scales of a *Vinctifer* sp. are known from the Barremian of Brazil (BRITO *et al.*, 1994). Remains of *Vinctifer* sp. are reported also from the Aptian-Albian of Venezuela (MOODY & MAISEY, 1994) and from the Aptian of Colombia (SCHULTZE & STÖHR, 1996). Finally, a partial braincase of *Vinctifer* sp. is briefly mentioned and poorly illustrated from the Campanian of Patagonia (BRITO, 1997: 714, fig. 29), but BARTHOLOMAI (2004: 535) pointed out that this material does not show enough characters in order to refer it to a peculiar aspidorhynchid genus.

It is to be noted that what we herein re-identify as *Vinctifer* sp. (called *Belonostomus* in TAVERNE, 1969) is also known from the Aptian-Albian Cocobeach Formation of Equatorial Guinea, an African geological formation, which at that time, when South America and Africa began to separate from each other, was geographically close to those of Brazil.

Regarding *Belonostomus*, there are several

records of isolated jaw bones in some Maastrichtian fossiliferous localities from Patagonia (Argentina) and Chile (CASAMIQUELA, 1992; BRITO & SUÁREZ, 2003). All these specimens were referred to the North American Late Cretaceous species *Belonostomus longirostris* LAMBE, 1902, based on the morphology of those bones. Some fragments of a *Belonostomus* sp. have been described from the Kimmeridgian of Argentina (LEANZA & ZEISS, 1990) but BRITO (1997: 745) referred them to *Vinctifer* for paleobiogeographic reasons. "*Belonostomus*" *carinatus* MAWSON & WOODWARD, 1907 from the Barremian of Brazil has been shown by BRITO (1997: 745-746) to be an undetermined holostean and not an aspidorhynchid.

Aspidorhynchus is not present in South America but one species, *Aspidorhynchus arawaki* BRITO, 1997, is recorded in the Oxfordian of Cuba (BRITO, 1999a). *Richmondichthys*, the closest allied genus of *Vinctifer*, is confined to the Albian of Australia (BARTHOLOMAI, 2004).

The aim of the present paper is to describe the newly discovered material of a new *Belonostomus* species from the continental Campanian-Maastrichtian beds of the Allen Formation, in northern Patagonia, Argentina. We have re-examined the specimen MACN RN 1078 figured by BRITO (1997: fig. 29) and considered by him as a *Vinctifer* sp. Its proportions, its large size, the disposition of the endocranial foramina, as well as the extensive fusion of endocranial bones, are in all points identical to our own samples. Therefore, we reassign that specimen to the new Patagonian species described below.

Geographic and stratigraphic position (Fig. 1)

The specimens here described were collected in the fossiliferous locality of Cerro Tortuga at Santa Rosa Basin (see NOVAS *et al.*, 2008), Río Negro province, Patagonia, Argentina. This locality is located at 39°26'50"S, 67°19'20"W. It is characterized by the presence of extensive outcrops belonging to the Campanian-Maastrichtian (Upper Cretaceous) Allen Formation (APESTEGUIA, 2002; LEANZA *et al.*, 2004). The deposits of the Allen Formation comprise siltstones and sandstones showing evidence of a lacustrine and fluvial environment (CASADIO, 1994).

Cerro Tortuga yielded a large amount of fossil vertebrates, including dryolestoid and gondwanatherian mammals, basal birds, theropods, sauropods, and ornithischian dinosaurs, as well as leptodactylid and pipid frogs, chelid turtles, sphenodontid lizards,

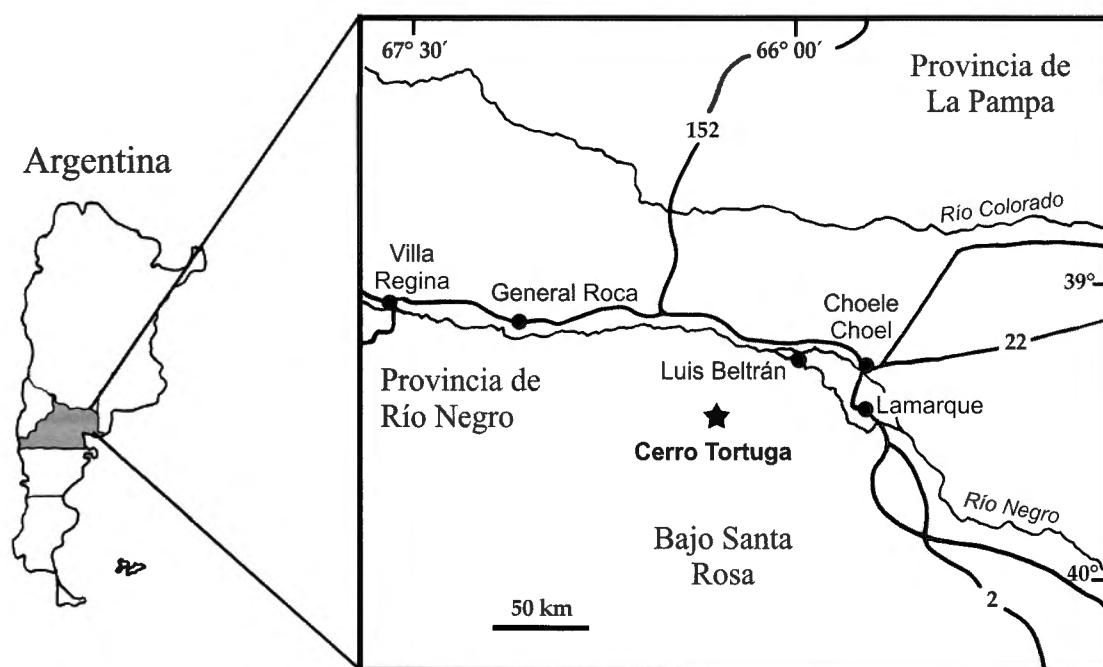


Fig. 1 – Map of Argentina with the region of Cerro Tortuga.

madtsoid snakes, and a wide variety of fresh-water fishes (BRITO, 1997; CORIA, 2001; CLARKE & CHIAPPE, 2001; HOPE, 2002; MARTINELLI & FORASIEPI, 2004; APESTEGUIA & ROUGIER, 2007; NOVAS *et al.*, 2008; ROUGIER *et al.*, 2009; BOGAN *et al.*, 2010), and freshwater mollusks (HUGO & LEANZA, 2001).

Systematic paleontology

Sub-class Actinopterygii KLEIN, 1885

Division Halecostomi REGAN, 1923

Order Aspidorhynchiformes BLEEKER, 1859

Family Aspidorhynchidae

NICHOLSON & LYDEKKER, 1889

Genus *Belonostomus* AGASSIZ, 1834

Type species: Belonostomus tenuirostris (AGASSIZ, 1833)

***Belonostomus lamarquensis* sp. nov.**

Figs 2-13

Derivatio nominis

From the city of Lamarque, Argentina.

Holotype

MML 454: an incomplete neurocranium.

Paratypes

MML 456: an incomplete neurocranium; MML 455: an incomplete skull roof; MML 450: an incomplete predentary; MML 464: an incomplete basioccipital bone; MML 524-69: vertebrae; MML 577: some articulated scales associated with a posttemporal; MML 578: a complete basioccipital with associated abdominal vertebrae; MML 841: a basioccipital region of a neurocranium; MML 844: more than one hundred scales; MACN RN 1078: an incomplete neurocranium.

Diagnosis

A large sized *Belonostomus* differing from the other species of the genus by having its flank scales divided in an anterior region with a smooth surface and a posterior region bearing a series of numerous and closely spaced subparallel ridges that end in a deeply crenulated posterior margin, the two regions being separated by a conspicuous vertical groove. Long predentary bearing large teeth in its median gutter and small teeth on its lateral margins. Ganoid layer of the dermal bones ornamented with ridges and tubercles. Frontal and parietal fused together. Deep irregular interdigitations between the two fronto-parietals. Dermopterotic and supratemporal fused together. Endocranial bones of the braincase completely fused, except the basisphenoid.

Description

The skull (Figs 2-10)

MML 450 is a fragment of an elongated, narrow and relatively large predentary. The piece measures 1.7 cm in length. Its outer face lacks the strong ganoine cover that is present in other *Belonostomus* species (see, e.g. TAVERNE & ROSS, 1973: fig. 2) but it is, however, feebly ornamented by some longitudinal ridges. There is a well-marked groove along the middle of its oral face. A series of four large conical teeth are preserved in that median gutter. The apexes of those teeth are missing and the wide pulpar cavity is visible. As usual in *Belonostomus*, each lateral margin of the bone bears a row of smaller teeth (FELIX, 1891: pl. 28, fig. 16; WOODWARD, 1908: pl. 30, figs 3, 4; BARDACK, 1968: fig. 1C, D; WHETSTONE, 1978: fig. 8; BRYANT, 1987: fig. 1) of which only the bases are preserved. Ventrally, the bone has a weak median keel, laterally delimited by shallow grooves. The suture for the articulation with the dentaries is narrow and shaped as an inverted “V”.

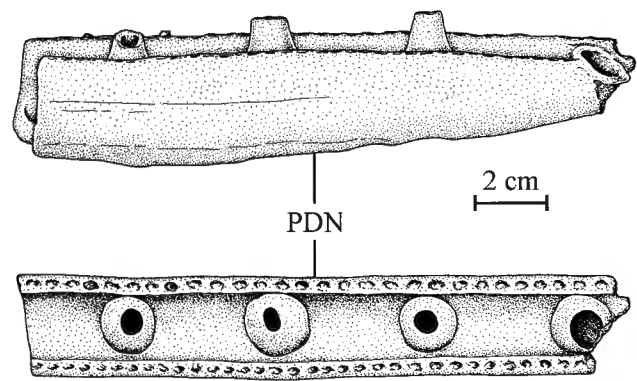


Fig. 2 – *Belonostomus lamarquensis* sp. nov. Fragment of the predentary MML 450 in lateral (above) and upper (below) views.

All five neurocrania have lost their rostrum and their orbital portion. Only the region between the sphenotic and occipital levels is preserved; i.e., the braincase itself.

The dermal bones of the skull roof are covered by a thick ganoine layer and have a conspicuous ornamentation composed by tubercles and well-developed ridges.

The frontal and the parietal of each side are fused in a compound fronto-parietal which covers with its antimeres most of the skull roof. Each fronto-parietal is strongly asymmetrical and has a complex median suture, which is displaced to the right half of the skull. This median suture is very sinuous and has irregular interdigitations. Laterally, the fronto-parietals end in a right lateral margin, like a step. The dermopterotic

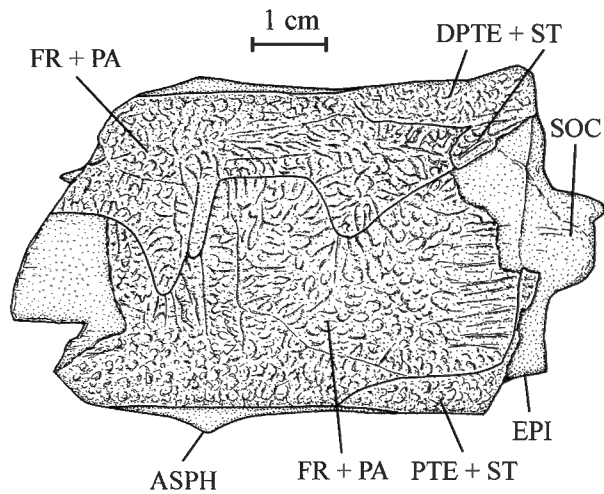


Fig. 3 – *Belonostomus lamarquensis* sp. nov. Holotype braincase MML 454 in dorsal view.

and the extrascapular of each side also are fused in a dermopterotic-extrascapular. These bones are poorly preserved in all the samples. They are asymmetrical, and the dermopterotic part of the compound bone is anteriorly projected.

In ventral and posterior view, all the braincases exhibit a notable fusion among the endocranial bones, which generally prevents distinguishing sutures between these bones. This condition was previously noted by BRITO (1997: 714) and BARTHOLOMAI (2004: 535) for the paratype specimen MACN RN 1078. However, on the right side of the skull of the holotype,

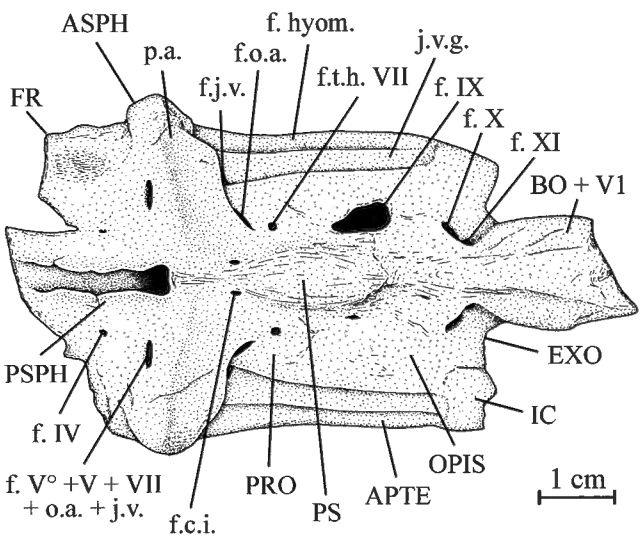


Fig. 4 – *Belonostomus lamarquensis* sp. nov. Holotype braincase MML 454 in ventral view.

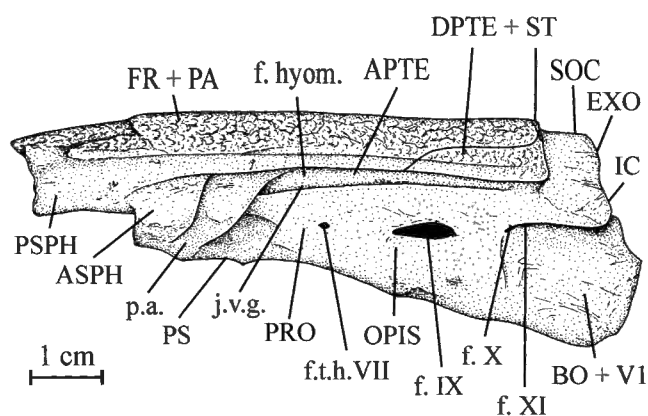


Fig. 5 — *Belonostomus lamarquensis* sp. nov. Holotype braincase MML 454 in lateral view.

traces of the sutures between the ascendant process of the parasphenoid and the autosphenotic, between the prootic and the opisthotic, and between the intercalar and the exoccipital are still discernible.

The orbitosphenoid is missing. The meningost of the basisphenoid is preserved on the braincase MACN RN 1078 and is not fused to the other endocranial bones of the braincase. The two pterosphenoids comprise the boundaries of a very large median opening for the two optical nerves (II), and more dorsally of a smaller median opening for the two olfactory nerves (I). Each pterosphenoid is pierced by at least three foramina. The foramen for the trochlear nerve (IV) is located on the dorsal robust wing of the bone. More ventrally, there is the trigemino-facial chamber with a broad foramen

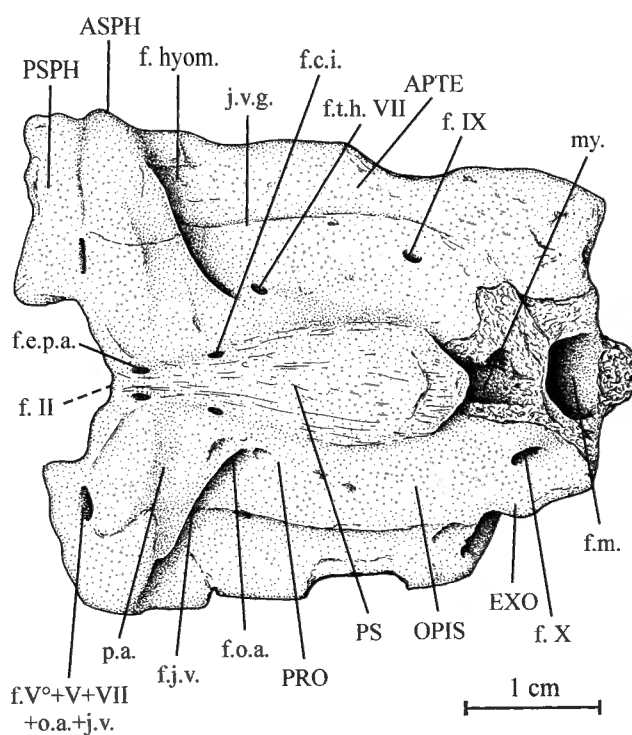


Fig. 7 — *Belonostomus lamarquensis* sp. nov. Paratype braincase MML 456 in ventral view.

for the exit of the *ramus profundus* (V°), the trigeminal nerve (V), the *rami ophthalmicus* and *buccalis* of the facial nerve (VII), the jugular vein and the orbital artery. Near this opening, but more medially, there is another smaller foramen for the common oculomotor nerve (III).

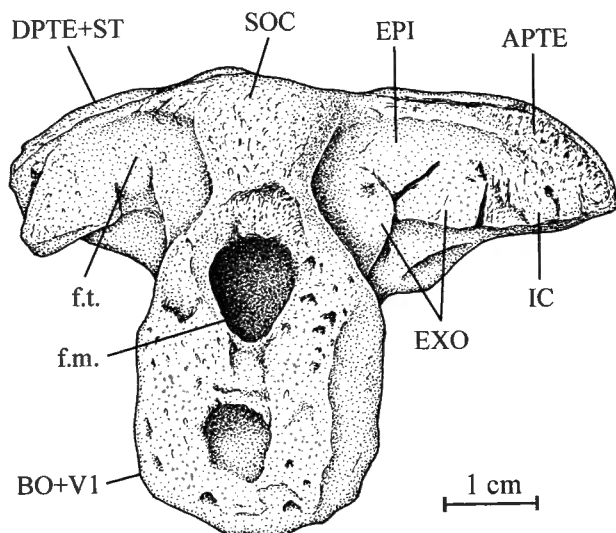


Fig. 6 — *Belonostomus lamarquensis* sp. nov. Holotype braincase MML 454 in posterior view.

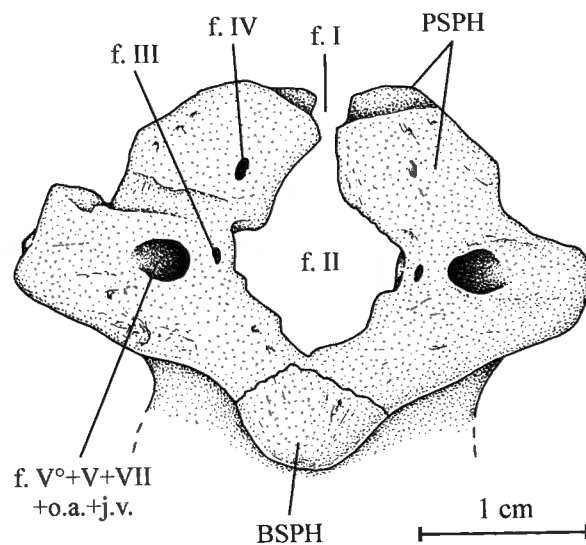


Fig. 8 — *Belonostomus lamarquensis* sp. nov. Paratype braincase MACN RN 1078 in antero-oblique view.

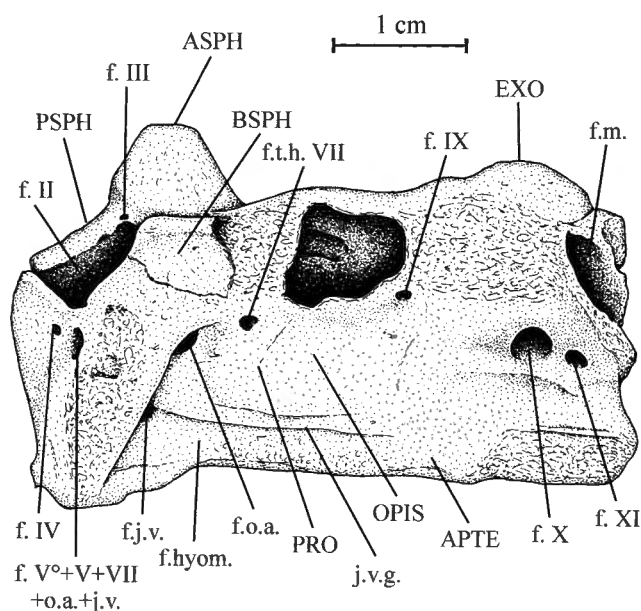


Fig. 9 – *Belonostomus lamarquensis* sp. nov. Paratype braincase MACN RN 1078 in right latero-ventral view.

The autosphenotics form a large protuberance on each side of the skull. The autopterotics seem to be fused with the dermopterotics. The prootics and opisthotics are ventrally grooved to form a deep and wide gutter, constituting the jugular depression together with that for the articulation with the hyomandibula. On its ventral surface, the prootic has two foramina, one anteriorly located for the *truncus hyoideomandibularis* of the facial nerve (VII), and one posteriorly, near the region of contact with the opisthotic, parasphenoid and basioccipital, for the exit of the glossopharyngeal nerve (IX). The opisthotics are large bones connected anteriorly with the prootics and posteriorly with the intercalars and exoccipitals but the sutures are generally not clearly visible. In all our samples, the posterior processes of the intercalars are broken away.

The parasphenoid is toothless and posteriorly fused to the basioccipital. The rear extremity of the parasphenoid is constricted at the level of a subvertical groove on each side of the basioccipital. Towards its anterior end, the bone becomes wider and forms a bulbous structure of ovoid contour until the level of the paired ascending processes of the parasphenoid. These ascending processes are robust, wide, laterally oriented and strongly bulging. They are continuous with the pterosphenotics and autosphenotics, all these bones being fused, constituting a single structure. The two small foramina for the internal carotid arteries are located at the basis of the ascending processes. A little forward on the middle of the parasphenoid, there is

another pair of small and closely spaced foramina for the efferent pseudobranchial arteries. This situation is similar to that present in *Vinctifer* (BRITO, 1992: fig. 2), whereas in *Richmondichthys*, these foramina are located on the ascending processes themselves, distant from the midline (BARTHOLOMAI, 2004: fig. 7C). The parasphenoid of the holotype is crushed in that region and the foramina for the efferent pseudobranchial arteries are not preserved. On both sides, at the region between the ascending process of the parasphenoid and the prootic and just before the foramen for the *truncus hyoideomandibularis* of the facial nerve (VII), there are two other foramina, one medially located through which the orbital artery enters in the trigemino-facial chamber, and one just above, at the anterior end of the jugular gutter on the prootic, allowing the penetration of the jugular vein in the trigemino-facial chamber.

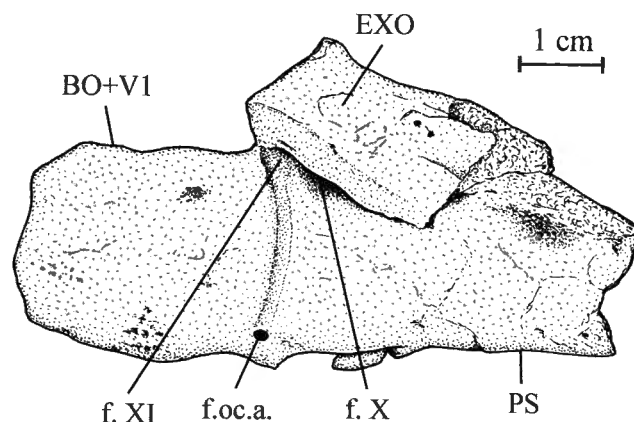


Fig. 10 – *Belonostomus lamarquensis* sp. nov. Paratype braincase (basioccipital region) MML 841 in right lateral view.

The basioccipital is subrectangular in shape, with a wide and flat ventral surface. The bone is fused with the first vertebra and, thus, strongly protrudes backwards, a condition known in all aspidorhynchid fishes, except in the Australian *Richmondichthys* in which the first vertebra is completely distinctive from the basioccipital (BARTHOLOMAI, 2004: fig. 7B, C). On its dorsal surface, the bone bears a wide and deep neural canal leading to the *foramen magnum* situated between the two exoccipitals. That is a diagnostic trait of the Aspidorhynchidae (MAISEY, 1991: fig. p. 179; BRITO, 1992: fig. 5). In lateral view, there exists a longitudinal and low osseous crest, ventrally bounded by shallow depressions. Also on its lateral surface, near the ventral margin of the basioccipital, there is on both sides an acute ridge that bifurcates distally, being here termed as “lateral basioccipital process”. This process is also observed in the genera *Vinctifer* and *Aspidorhynchus*.

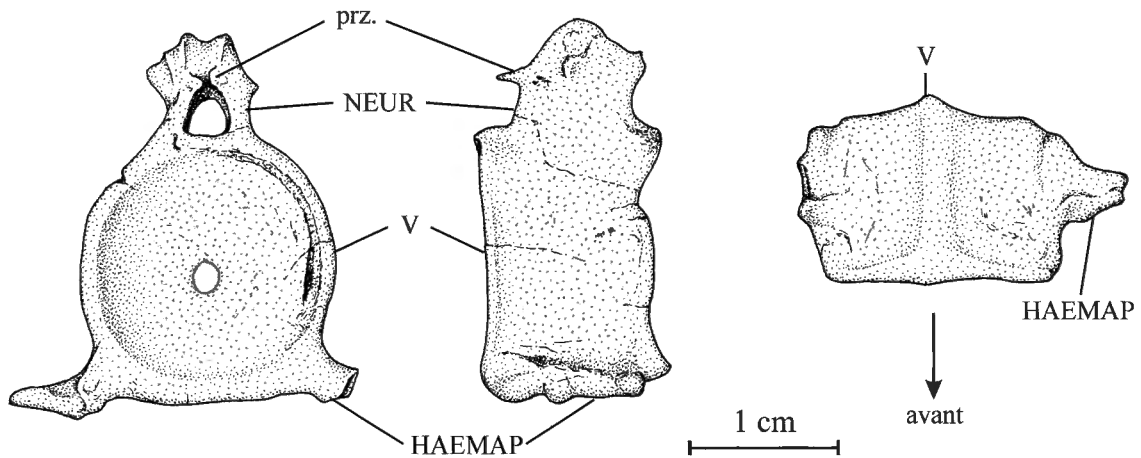


Fig. 11 – *Belonostomus lamarquensis* sp. nov. An abominal vertebra in anterior (on the left), left lateral (in the middle) and ventral (on the right) views (MML 524-69).

(see BRITO, 1997), but is absent or reduced in *Richmondichthys*. Anteriorly and dorsally to the lateral basioccipital process, there is a strong osseous bump, anteriorly delimited by a subvertical deep groove. At the basis of this groove, the basioccipital is on each side pierced by a small foramen for the occipital artery, a condition not mentioned in other aspidorhynchids but known in many actinopterygians. The sutures between the exoccipitals and the basioccipital are not clearly visible. However, it seems that the large foramen for the vagus nerve (X) on each side of the skull is open at the edges between these bones and just above and anterior to the subvertical groove. Immediately posterior to the vagus foramen, there is a smaller additional foramen for an occipito-spinal nerve (XI). Such a structure is also seen in *Richmondichthys* (BARTHOLOMAI, 2004; fig. 6B). On its internal surface, the anterior region of the basioccipital has wide articular surfaces for the parasphenoid. The paratype MML 456 has lost its basioccipital and the posterior end of the myodome cavity is visible behind the parasphenoid and just below the *foramen magnum*, indicating that the myodome enters in the basioccipital region.

The supraoccipital is evident as a well-developed median bony knob on the rear-face of the braincase. The sutures between the supraoccipital, the epiotics (= epioccipitals), the autopterotics, the intercalars and the exoccipitals are not clearly visible. However, on each side of the supraoccipital, in the region of the epiotic, autopterotic, intercalar and exoccipital, there is a large but not deep depression, the temporal (= posttemporal) fossa.

The girdles (Fig. 12)

An important part of a large right posttemporal is

preserved on sample MML 577. The bone is as deep as long, and much broader ventrally than dorsally. Its surface is strongly ornamented with ridges and tubercles. The anterior and ventral borders of the bone are straight and the posterior border convex.

The axial skeleton (Fig. 11)

The vertebrae are amphicoelous and holospondylous, with a wide opening in their centre for the passage of the notochord. Their ventral surface is nearly flat, but has a median longitudinal ridge, which is low and round. The neural arches are fused to the centra and contain a closed neural canal. Above this canal, there are two narrow and elongate neural spines. The neural

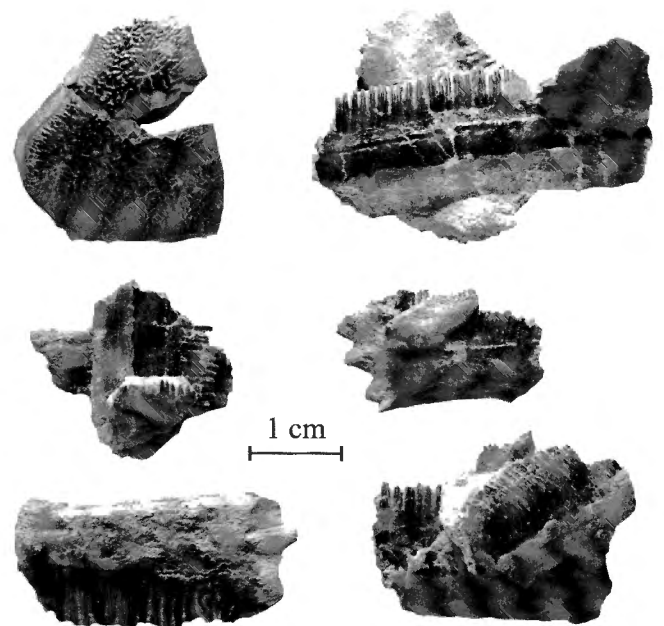


Fig. 12 – *Belonostomus lamarquensis* sp. nov. A right posttemporal and some scales (MML 577).

arches bear a pair of small pointed prezygapophyses. The haemapophyses (= parapophyses) are located near the ventral margin of the vertebral body and are fused with it. They are laminar, short and wide.

The squamation (Fig. 12)

In the same fossiliferous deposits, there are large numbers of lateral scales that are clearly referable to the Aspidorhynchidae. Among the materials, there are a row of associated scales with a fragment of strongly ornamented bone, probably a posttemporal or a fragment of opercle. The ornamentation of this bony fragment is in all points similar to that of the dermal bones of the four braincases, allowing us to refer all these scales to *B. lamarquensis* sp. nov.

The lateral scales are dorsoventrally elongate and subrectangular in shape. They are covered by a thick ganoine layer. On the best-preserved scales, there is a posterior region with a series of numerous and closely spaced subparallel ridges that end in a deeply crenulated posterior margin. In this way, the scale has a pectinate general shape. The posterior region with the ridges is separated by one conspicuous vertical groove from a deep but narrow anterior region with a smooth surface. On the internal surface, there is a poorly defined concave-convex articulation, representing the last trace of the actinopterygian peg and socket system and characteristic of aspidorhynchid scales.

Discussion

The presence of a long prementary undoubtedly attests that the Patagonian species belongs to the genus *Belonostomus* because the three other aspidorhynchid genera possess short prementaries (Fig. 13).

Its very peculiar scales are another argument to include the species from Argentina in the genus *Belonostomus*, because deepened lateral scales with a vertical groove between a smooth anterior zone and a posterior region with ridges ending in a crenulated border also exist in another species of this genus, *Belonostomus hooleyi* WOODWARD, 1916 from the Lower Cretaceous of England and the Isle of Wight (WOODWARD, 1916-1919: 100-101, pl. 21, figs 1, 3). However, the ridges in the English species are less numerous and the crenulation more coarse. Such flank scales are unknown in other aspidorhynchid species.

The ornamental condition of the skull roof in *B. lamarquensis*, with marked tubercles and broad ridges, resembles more that in *Aspidorhynchus* (WOODWARD, 1895: 419, 423, 426, 427, 1916-

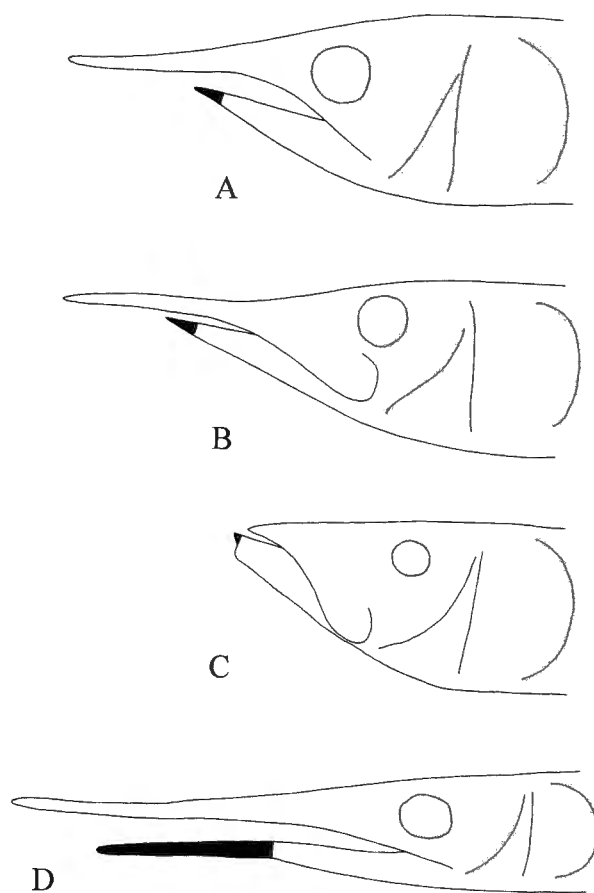


Fig. 13 – Schematic comparison of the head of the four aspidorhynchid genera with the prementary in black. (A) *Aspidorhynchus*, (B) *Vinctifer*, (C) *Richmondichthys* and (D) *Belonostomus*.

19: 97, fig. 33), *Vinctifer* (BRITO, 1997: 698) and *Richmondichthys* (BARTHOLOMAI, 2004: 529) than that of most *Belonostomus* species, in which the cranial roof is nearly smooth or ornamented with long and thin ridges (TAVERNE & ROSS, 1973: fig. 2). But there is one exception because the English *B. hooleyi* exhibits dermal skull bones “very coarsely ornamented with irregular rounded ridges and low elongated tubercles” (WOODWARD, 1916-1919: 100).

The deep interdigitations between the two frontoparietals are more like the situation in *Vinctifer* (MAISEY, 1991: fig. A on p. 175; BRITO, 1997: fig. 9) and *Richmondichthys* (BARTHOLOMAI, 2004: fig. 7A) than that in *Belonostomus* or *Aspidorhynchus*, in which the interdigitations are less pronounced (WOODWARD, 1916-1919: fig. 33).

B. lamarquensis sp. nov. has an extensive fusion of endocranial bones, as is normal in the genus *Belonostomus* (TAVERNE, 1981: fig. 5; BRITO, 1997: fig. 49). In *Vinctifer*, young specimens have clearly

visible sutures between the endocranial bones (BRITO, 1992: fig. 2) while those bones are fused in older specimens (MAISEY, 1991: fig. p. 178). *Aspidorhynchus* and *Richmondichthys* retain the unfused condition (WOODWARD, 1916-1919: fig. 33; BARTHOLOMAI, 2004: fig. 7B, C).

When referring specimen MACN RN 1078 to the genus *Vinctifer*, BRITO (1997) has expanded the biochron of the genus from the Early Cretaceous to the uppermost Cretaceous, indicating that it was not an exclusively Aptian-Albian genus as previously had been thought, and that the *Vinctifer* biozone, characteristic of such a time span, may be rejected. Our own observations do not corroborate BRITO's (1997) conclusions because the Late Cretaceous Patagonian aspidorhynchid is not a *Vinctifer* but a *Belonostomus*.

B. lamarquensis sp. nov. constitutes the southernmost species of the genus, and, on the basis of the available information, may be considered as a freshwater species, based on the evidence yielded by the geology of the fossiliferous outcrops. In the strata belonging to the Allen Formation, the new species appears to be abundantly represented by scales, vertebrae and isolated skull fragments, suggesting that it was a rather common inhabitant of this paleoenvironment during the Campanian-Maastrichtian interval.

The Patagonian Upper Cretaceous fragments of aspidorhynchid fish (CASAMIQUELA, 1992; BRITO & SUÁREZ, 2003) attributed until now to *Belonostomus longirostris*, a species known from the Cenomanian of North America, very probably belong to *B. lamarquensis*.

Conclusions

The highly specialized flank scales prove that *B. lamarquensis* sp. nov. deserves its peculiar specific status. Those scales, the ridges and tubercles on the dermal bones of the skull and the very large size of the fish denote a closer relationship of *B. lamarquensis* with *B. hooleyi* than with the other species of *Belonostomus*.

Acknowledgements

We thank Daniel Cabaza and Liliana López for their help during the revision of the collections of the MML, and Hugo De Potter from the Royal Institute of Natural Sciences of Belgium for his technical contribution. We are grateful to the Félix de Azara Foundation and to the Maimónides University for their constant support during our research. We also thank the society ANDESMAR for its help during

the development of the present paper. We specially thank Phil Hurst (NHM, Image Resources) and Zerina Johanson for sending us photographs of the *B. hooleyi* paratype specimen, and Dr. Jim Tyler (Washington) who has reviewed our manuscript.

List of institutional abbreviations

MML: Museo Municipal de Lamarque, Río Negro province, Argentina.

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.

NHM: Natural History Museum, London, England.

List of abbreviations used in figures

APTE: autopterotic

ASPH: autosphenotic

BO: basioccipital

BSPH: basisphenoid

DPTE: dermopterotic

EPI: epiotic (= epioccipital)

EXO: exoccipital

FR: frontal

HAEMAP: haemapophysis (= parapophysis)

IC: intercalary

NEUR: neural arch

NEUREP: neural spine

OPIS: opisthotic

PA: parietal

PDN: predentary

PRO: prootic

PS: parasphenoid

PSPH: pleurosphenoid (= pterosphenoid)

SOC: supraoccipital

ST: supratemporal (= extrascapular)

V: vertebral centrum

V1: first vertebra

f. I: foramen of the two olfactory nerves (I)

f. II: foramen of the two optic nerves (II)

f. III: foramen of the common oculomotor nerve (III)

f. IV: foramen of the trochlear nerve (IV)

f. V° + V + VII + o. a. + j. v.: foramen for the anterior exit from the trigemino-facial chamber of the *ramus profundus* (V°), the trigeminal nerve (V), the *rami ophthalmicus* and *buccalis* of the facial nerve (VII), the orbital artery and the jugular vein

f. IX: foramen of the glossopharyngeal nerve (IX)

f. X: foramen of the vagal nerve (X)

f. XI: foramen of the occipito-spinal nerve (XI)

f. e. p. a.: foramen for the efferent pseudobranchial artery

f. hyom.: fossa for the articulation with the hyomandibula

f. j. v.: foramen for the posterior entering of the jugular vein in the trigemino-facial chamber

f. o. a.: foramen for the posterior entering of the orbital artery in the trigemino-facial chamber

f. oc. a.: foramen of the occipital artery
 f. t. h. VII: foramen of the *truncus hyoideo-mandibularis* of the facial nerve (VII)
 j. v. g.: groove for the jugular vein
 my.: myodome
 p. a.: *processus ascendens* of the parasphenoid
 prz.: prezygapophysis
 t. f.: temporal (= posttemporal) fossa

References

- APESTEGUIA, S., 2002. Greater Gondwana and the Kaws Sea coastal tetrapod fauna (Campanian–Maastrichtian). In: Boletim do VI Simpósio Sobre o Cretáceo do Brasil. II Simposio Sobre el Cretácico de América del Sur, Sao Pedro, Brasil: 143–147.
- APESTEGUIA, S. & ROUGIER, G.W., 2007. A late Campanian sphenodontid maxilla from northern Patagonia. *American Museum Novitates*, **3581**: 1–11.
- ARRATIA, G., 2000. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the “pholidophoriforms”. *Paläontologische Zeitschrift*, **74** (1/2): 113–143.
- BARDACK, D., 1968. *Belonostomus* sp., the first holostean from the Austin Chalk (Cretaceous) of Texas. *Journal of Paleontology*, **42** (5) 1-2: 1307–1309.
- BARTHOLOMAI, A. 2004. The large aspidorhynchid fish *Richmondichthys sweeti* (Etheridge Jnr and Smith Woodward, 1891) from Albian marine deposits of Queensland, Australia. *Memoirs of the Queensland Museum*, **49** (2): 521–536.
- BOGAN, S., TAVERNE, L. & AGNOLIN, F.L., 2010. 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). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre*, **80**: 163–170.
- BRITO, P.M., 1992. L'endocrâne et le moulage endocrânien de *Vinctifer comptoni* (Actinopterygii, Aspidorhynchiformes) de Crétacé inférieur du Brésil. *Annales de Paléontologie (Vertébrés-Invertébrés)*, **78** (3): 129–157.
- BRITO, P.M., 1997. Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, données environnementales et biogéographiques. *Geodiversitas*, **19** (4): 681–772.
- BRITO, P.M., 1999a. Description of *Aspidorhynchus arawaki* from the Late Jurassic of Cuba (Actinopterygii: Halecostomi). In: ARRATIA, G. & SCHULTZE, H.-P. (editors), Mesozoic Fishes 2 – Systematics and Fossil Record. Verlag Dr. F. Pfeil, München: 239–248.
- BRITO, P.M., 1999b. The caudal skeleton of aspidorhynchids (Actinopterygii, Halecostomi): phylogenetic implications. In: ARRATIA, G. & SCHULTZE, H.-P. (editors), Mesozoic Fishes 2 – Systematics and Fossil Record. Verlag Dr. F. Pfeil, München: 249–264.
- BRITO, P.M., BERTINI, R.J., MARTILL, D.M. & SALLES, L.O., 1994. Vertebrate fauna from the Missão Velha Formation (Lower Cretaceous, N. E. Brazil). In: 3º Simpósio sobre as Bacias Cretácicas Brasileiras, UNESP, Rio Claro: 139–140.
- BRITO, P.M. & MEUNIER, F.J., 2000. The morphology and histology of the scales of Aspidorhynchidae (Actinopterygii, Halecostomi). *Geobios*, **33** (1): 105–111.
- BRITO, P.M. & SUÁREZ, M.E., 2003. Late Cretaceous *Belonostomus* (Pisces, Actinopterygii, Aspidorhynchidae) from Algarrobo, Chile, with comments on aspidorhynchid paleodistribution in South America. *Revista geológica de Chile*, **30** (1): 117–127.
- BRYANT, L.J., 1987. *Belonostomus* (Teleostei: Aspidorhynchidae) from the Late Paleocene of North Dakota. *Paleobios*, **43**: 1–3.
- CASADIO, S.A., 1994. Estratigrafía y paleontología del intervalo Maastrichtiano–Daniano en el Occidente de la Provincia de La Pampa, Argentina. Ph.D. thesis, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Córdoba, 353 pp.
- CASAMIQUELA, R.M., 1992. Notas sobre vertebrados de la frontera Cretácica-Terciaria II. La presencia del Aspidorhynchid “*Belonostomus*” (Osteichthyes, Aspidorhynchiformes) en la Formación Coli Toro (Maastrichtense), Ingeniero Jacobacci, Río Negro. *Mundo Ameghiniano*, **11**: 9–18.
- CORIA, R.A., 2001. New theropod from the Late Cretaceous of Patagonia. *Mesozoic Vertebrate Life*, **1**: 3–9.
- CLARKE, J.A. & CHIAPPE, L.M., 2001. A new carinate bird from the Late Cretaceous of Patagonia (Argentina). *American Museum Novitates*, **3323**: 1–23.
- FELIX, J., 1891. Versteinerungen aus der Mexicanischen Jura- und Kreide-Formation. *Palaeontographica*, **37**: 140–194.
- HOPE, S., 2002. The Mesozoic radiation of Neornithes. In: CHIAPPE, L.M. & WITMER, L.M. (editors), Mesozoic birds: above the heads of dinosaurs.: Berkeley University Press, Berkeley, U.S.A.: 168–218.
- HUGO, C.A. & LEANZA, H.A., 2001. Hoja Geológica 3966-III, Villa Regina, provincia Río Negro. *Instituto de Geología y Recursos Naturales, SEGEMAR, Boletín*, **309**: 1–53.
- LEANZA, H.A., APESTEGUIA, S., NOVAS, F. & DE LA FUENTE, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research*, **25** (1): 61–87.
- LEANZA, H.A. & ZEISS, A., 1990. Upper Jurassic limestones from Argentina (Neuquén Basin): stratigraphy and fossils. *Facies*, **22**: 169–186.

- MAISEY, J.G., 1991. *Vinctifer* Jordan, 1919. In: MAISEY, J.G. (editor), *Santana Fossils. An Illustrated Atlas*. T.F.H. Publications, Inc., Neptune City: 170-189.
- MARTINELLI, A.G. & FORASIEPI, A.M., 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales*, **6**: 257-305.
- MOODY, J.M. & MAISEY, J.G., 1994. New Cretaceous marine vertebrate assemblages from north-western Venezuela and their significance. *Journal of Vertebrate Paleontology*, **14** (1): 1-8.
- NOVAS, F.E., POL, D., CANALE, J.I., PORFIRI, J.D. & CALVO, J.O., 2008. A bizarre Cretaceous theropod dinosaur from Patagonia and the evolution of Gondwanan dromaeosaurids. *Proceedings of the Royal Society of London, B*, **276**: 1101-1107.
- PATTERSON, C., 1973. Interrelationships of holosteans. *Zoological Journal of the Linnean Society*, London, **53**, Supplement 1: 233-305.
- ROUGIER, G.W., CHORNOGUBSKY, L., CASADIO, S., ARANGO, N.P. & GIALLOMBARDO, A., 2009. Mammals from the Allen Formation, Late Cretaceous, Argentina, *Cretaceous Research*, **30** (1): 223-238.
- SCHULTZE, H.-P. & STÖHR, D., 1996. *Vinctifer* (Pisces, Aspidorhynchidae) aus der Unterkreide (oberes Aptium) von Kolumbien. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **199** (3): 395-415.
- TAVERNE, L., 1969. Sur la présence d'un Aspidorhynchidae (Pisces Holostéens, ordre des Aspidorhynchiformes) dans les terrains éocétaciques de la Guinée Équatoriale. *Revue de Zoologie et de Botanique Africaines*, **79** (3/4): 261-264.
- TAVERNE, L., 1981. Les Actinoptérygiens de l'Aptien inférieur (Töck) d'Helgoland. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **51**: 43-82.
- TAVERNE, L., 1998. Les poissons crétacés de Nardo. 6°. *Belonostomus* sp. (Aspidorhynchidae) et considérations sur les relations entre les Aspidorhynchiformes et les téléostéens (Pisces, Actinopterygii). *Bollettino del Museo Civico di Storia Naturale di Verona*, **22**: 275-290.
- TAVERNE, L. & ROSS, P.-H., 1973. Fischreste aus dem Töck (Unter-Aptien) von Helgoland. *Meyniana*, **23**: 99-111.
- WHETSTONE, K.N., 1978. *Belonostomus* sp. (Teleostei, Aspidorhynchidae) from the Upper Cretaceous Tombigbee Sand of Alabama. *The University of Kansas, Paleontological Contributions*, **89**: 17-19.
- WOODWARD, A.S., 1895. Catalogue of the fossil fishes in the British Museum (Natural History). Part III. Trustees of the British Museum (Natural History), London: I-XXXIX + 1-544.
- WOODWARD, A.S., 1908. The fossil fishes of the English Chalk. Part IV. Palaeontographical Society, London: 129-152.
- WOODWARD, A.S., 1916-1919. The fossil fishes of the English Wealden and Purbeck Formations. Palaeontographical Society, London: 1-148.
- S. BOGAN
Área Paleontología. Fundación de Historia Natural "Félix de Azara"
Departamento de Ciencias Naturales y Antropología
CEBBAD - Universidad Maimónides
Valentín Virasoro 732 (1405BDB)
Buenos Aires, Argentina
E-mail: sergiobogan@yahoo.com.ar
- L. TAVERNE
Résidence "Les Platanes"
Boulevard du Souverain, 142 (Box 8)
B-1170 Brussels, Belgium
E-mail: louis.taverne@gmail.com
- F. L. AGNOLIN
Área Paleontología. Fundación de Historia Natural "Félix de Azara"
Departamento de Ciencias Naturales y Antropología
CEBBAD - Universidad Maimónides
Valentín Virasoro 732 (1405BDB)
Buenos Aires, Argentina
and
Laboratorio de Anatomía Comparada y Evolución de los Vertebrados
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"
Av. Ángel Gallardo, 470 (1405)
Buenos Aires, Argentina
E-mail: fedeagnolin@yahoo.com.ar

Typescript submitted: April 26, 2011.

Revised typescript received: August 30, 2011

