

# **“*Pholidophorus argentinus*” DOLGOPOL DE SAEZ, 1939 from Upper Jurassic beds of the Neuquén Province of Argentina is not a pholidophoriform but an aspidorhynchid (Actinopterygii, Aspidorhynchiformes)**

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## **Abstract**

The Late Jurassic marine deposits of Argentina host a diverse fish fauna that is currently under study. One of the species is *Pholidophorus argentinus* DOLGOPOL DE SAEZ, 1939, which is based on the caudal region of a single specimen collected in the Neuquén Basin. Here we propose that the material comes from the Picún Leufú Formation of the Neuquén Basin. DOLGOPOL DE SAEZ assigned the fish to *Pholidophorus* AGASSIZ on the basis of a combination of characters that were preliminarily revised by one of us (AC) several years ago. It was concluded that the type specimen did not present any diagnostic character to justify erection of a different species or to allow an assignment to the genus *Pholidophorus* s. str. Consequently, the specimen was referred to as *Halecomorphi* indet. A detailed anatomical study of the holotype permits us now to assign it to the Family Aspidorhynchidae. It is remarkable that the caudal anatomy, especially the fin rays, of this family is scarcely known. In fact, this is the first description of the caudal fin of a Jurassic aspidorhynchid from the Southern Hemisphere.

## **Introduction**

Numerous marine fish specimens were recovered from the Jurassic deposits of the Vaca Muerta and Picún Leufú Formations in the Neuquén Basin in Mendoza and Neuquén provinces of Argentina. However, the ichthyofauna is still poorly known. The first descriptions were made by DOLGOPOL DE SAEZ (1939, 1940, 1949). Thereafter, brief revisions of these papers and descriptions of new materials were done in the 80's (see CIONE et al. 1987; CIONE & PEREIRA 1987, 1990). At present, one of us (SGC) is studying the Late Jurassic fishes of the Neuquén Basin.

Among the materials studied by DOLGOPOL DE SAEZ (1939), an isolated caudal fin and caudal peduncle was considered by her as the type of the new species *Pholidophorus argentinus* of the Family Pholidophoridae, Order Pholidophoriformes. However, the material appears to pertain to a different group as we will demonstrate below.

The genus *Pholidophorus* AGASSIZ, 1832, was created to include two species (*Pholidophorus latiusculus* and *Ph. pusillus*) from the Triassic of Seefeld in Austria. Characters used to define the genus were primitive or widely distributed among neopterygians (ARRATIA 2000). After the original diagnosis of AGASSIZ, subsequent emended diagnoses for the genus *Pholidophorus* were published by WOODWARD (1895), LEHMAN (1966), NYBELIN (1966), and ZAMBELLI (1986). All these diagnoses used characters that actually are broadly distributed among neopterygians (ARRATIA 2000).

The order Pholidophoriformes was created by BERG (1937) to include several genera in addition to *Pholidophorus*, but the characters used in the diagnosis of the group were primitive or even incorrect (see ARRATIA 2000). Later, LEHMAN (1966) presented a slightly modified diagnosis for the order, but in his diagnosis all the characters used are primitive. Despite this, the Order Pholidophoriformes was widely

accepted (e. g., ROMER 1996, NELSON 1994). Recent studies of the group do not support the monophyly of the Order Pholidophoriformes as previously known (ARRATIA 2000).

Currently, the genus *Pholidophorus* AGASSIZ, 1832, as well as the Family Pholidophoridae and Order Pholidophoriformes are considered valid only for the species *Ph. latiusculus* AGASSIZ, 1832 and *Ph. bechei* AGASSIZ, 1837[1833–43] (see ZAMBELLI 1986 and ARRATIA 2000). The phylogenetic relationships of certain species previously assigned to Pholidophoriformes, as well as the definition of the genus *Pholidophorus*, were recently studied by ARRATIA (2000). In her work, among other characters, she analyzed the structure of the scales of several Late Jurassic “pholidophorids” from Germany, finding some important differences in the type (lepisosteid, amioïd, cycloid), ornamentation, and structure. ARRATIA (2001) proposed that at least four apomorphic characters support the monophyly of *Pholidophorus* sensu stricto.

Besides *Pholidophorus argentinus*, other putative Pholidophoriformes were also reported from Argentina: ?*Ph. dentatus* RUSCONI, 1946, and “*Ph.*” *vallejensis* RUSCONI, 1947, from the Triassic continental deposits of the Potrerillos Formation in Mendoza Province. These species were reviewed and studied later by LÓPEZ-ARBARELLO et al. (2010), who concluded that both *Ph. vallejenis* and ?*Ph. dentatus* are Actinopterygii incertae ordinis. Moreover, ?*Ph. dentatus* was regarded as a nomen dubium. Other records of “pholidophorids” indet. were reported from the Cretaceous continental sediments of La Cantera Formation in San Luis Province (FLORES 1969). These and new material are currently under study (GIORDANO 2010, GIORDANO & ARRATIA 2011).

On the other hand, Aspidorhynchidae NICHOLSON & LYDEKKER, 1889, is a monophyletic Mesozoic family that ranged in age from the Middle Jurassic to the Late Cretaceous. It had a worldwide distribution and currently includes four recognized genera: *Aspidorhynchus* AGASSIZ, *Belonostomus* AGASSIZ, *Vinctifer* JORDAN, and *Richmondichthys* BARTHOLOMAI. The family Aspidorhynchidae was the focus of studies for several authors (e. g., AGASSIZ 1833–1843; BRITO 1997, 1999; BRITO & MEUNIER 2000). However, the phylogenetic relationships of the Aspidorhynchidae within the neopterygians are still under debate (for different hypotheses concerning the phylogenetic position of the family see BRITO (1997) and ARRATIA (1999). This disagreement is mainly due to the incomplete understanding of the Jurassic forms, to different interpretations of several structures, and different taxa sets used in the studies.

The members of the family Aspidorhynchidae can be recognized easily because all present a long rostrum, consisting of an elongated premaxilla, a lower jaw with a supplementary bone, the prementary (short in *Vinctifer*, *Richmondichthys*, and *Aspidorhynchus*, and long in *Belonostomus*), rectangular (higher than wide) scales on the flanks of the body, and a retracted or posterior position of the anal and dorsal fins (for details see BRITO 1997).

In South America, the family Aspidorhynchidae is represented by two genera (*Vinctifer* and *Belonostomus*) and one problematic member from Chile (see ARRATIA & SCHULTZE 1999). The genus *Vinctifer* is found in several Early Cretaceous localities of Brazil (BRITO 1997), Venezuela (MOODY & MAISEY 1994), Colombia (SCHULTZE & STÖHR 1996) and Argentina (BRITO 1997). The genus *Belonostomus* was reported from the Upper Cretaceous of Chile (BRITO & SUÁREZ 2003) and Argentina (CASAMIQUELA 1992) and by some disarticulated but almost complete specimens found in some Late Jurassic (Tithonian) localities of Argentina (CIONE in LEANZA & ZEISS 1990; GOIRIC-CAVALLI & CIONE 2009, 2011a; GOIRIC-CAVALLI 2013). Recently, BOGAN et al. (2011) described several incomplete specimens from continental deposits of the Upper Cretaceous of Argentina. The fossils were assigned to a new species, *Belonostomus lamarquensis* BOGAN, TAVERNE & AGNOLIN. In the same paper, the authors assigned the neurocranium previously determined by BRITO (1997) as *Vinctifer* to their new species (see BOGAN et al. 2011: 237, figs. 8 and 9).

Concerning caudal fin structures of primitive neopterygians, the elements of the caudal skeleton (e. g., ural centra, preural centra, hypurals, epurals, uroneurals) as well as those of the caudal fin (e. g., principal rays, fulcra, fringing fulcra, scutes) deserve particular attention, because the caudal skeleton is one of the most important structural systems in fishes, bringing several characters that are of systematic and phylogenetic significance (see PATTERSON 1968, 1973; SCHULTZE & ARRATIA 1989; ARRATIA 1991, 2008; ARRATIA & SCHULTZE 1992, among others). The first studies on caudal skeleton of Jurassic fishes were made mainly by PATTERSON (1968), NYBELIN (1974), and PATTERSON & ROSEN (1977). Subsequent important and detailed revisions of the previous works as well as new studies were made by, among others, ARRATIA (1991), ARRATIA & LAMBERS (1996), BRITO (1997, 1999), ARRATIA & TINTORI (2004) and ARRATIA (2008). ARRATIA (2008: 78, figs. 19 and 21), in an important and illuminating study, describes very well-preserved caudal fins and caudal skeletons of Late Jurassic aspidorhynchiforms from Germany, highlighting structures that had been poorly or never described before for these fishes.

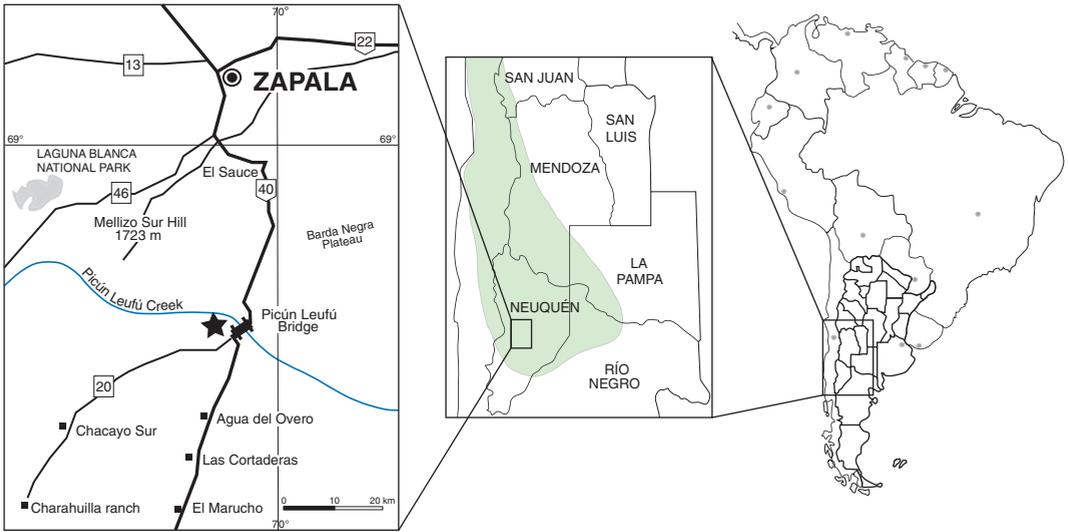


Fig. 1.

Location map (slightly modified from ARMELLA et al. 2007). Star indicates the type locality of *Aspidorhynchidae* indet. (= "*Pholidophorus argentinus*" DOLGOPOL DE SAEZ).

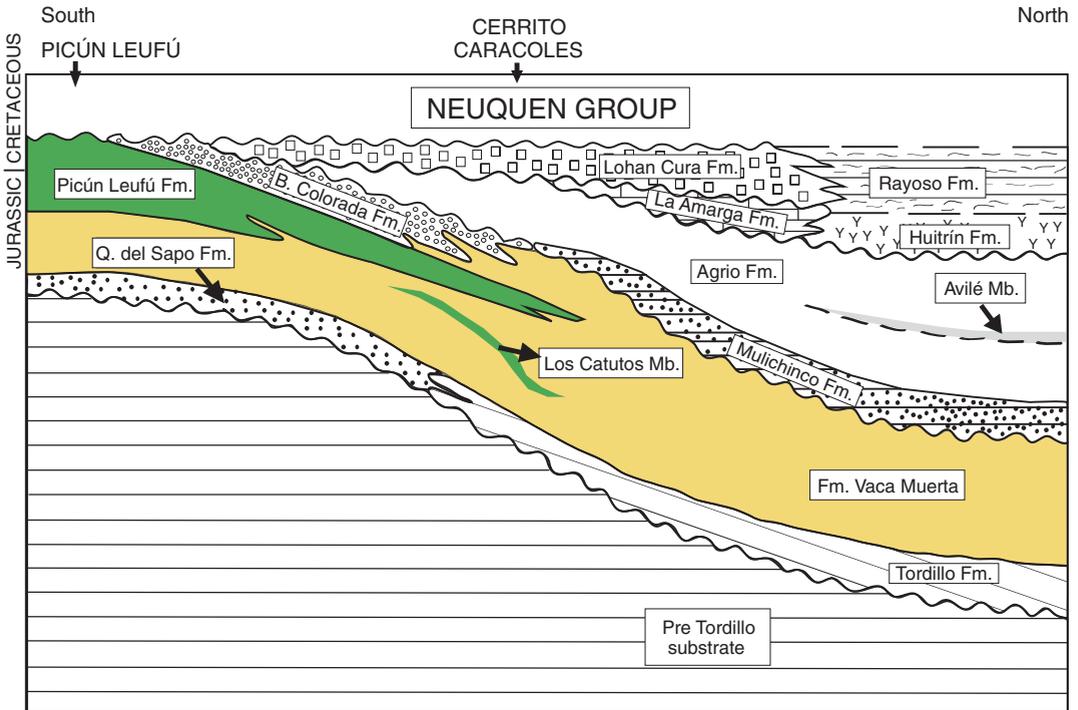


Fig. 2.

Geological map of the Picún Leufú Creek area (slightly modified from ARMELLA et al. 2007), showing the Tithonian–Berriasian interval represented by two marine lithostratigraphic units of the Mendoza Group (Vaca Muerta and Picún Leufú formations).

The goal of this paper is the detailed description of the holotype of "*Pholidophorus argentinus*" DOLGOPOL DE SAEZ to provide a sound basis for discussing its systematic re-assignment.

### Material and methods

A survey of young and adult actinopterygians, especially "pholidophorids" and aspidorhynchids, was made. The survey includes Jurassic neopterygians that are previously described in the literature as well as personal observations made by the first author. A special effort was dedicated to the Jurassic fishes from the Vaca Muerta and Picún Leufú Formations, Argentina, and those of the Bavaria area, Germany. Some of the best preserved specimens of Jurassic aspidorhynchiforms are housed in the Jura Museum in Eichstätt, Germany.

The type material described herein is deposited in the División Paleontología de Vertebrados at the Museo de La Plata, La Plata, Argentina under the number MLP 39-VI-30-4. The holotype is mainly preserved as an impression in a clear limestone. The description was based on both a latex peel and fossil impression. The examination was under a binocular microscope (Zeiss Stemi C2000). The drawings were made by the first author under a binocular Leica MS5 microscope with a camera lucida attached. The first author took the pictures with a Canon G10 camera attached to the binocular microscope. The nomenclature is according to ARRATIA (2000, 2008, 2009).

The material examined belongs to the following institutions: **MLP**, Museo de La Plata, Buenos Aires, Argentina; **MOZ**, Museo Prof. Dr. Juan Olsacher, Zapala, Argentina; **MACN**, Museo Argentino de Ciencias Naturales, Bernardino Rivadavia, Buenos Aires, Argentina; **JME**, Jura-Museum, Naturwissenschaftliche Sammlungen, Eichstätt [SOS Lithographic Limestones of Solnhofen, ETT Lithographic Limestones of Ettling], Germany; **MB**, Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **BSPG**, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany.

### Systematic paleontology

Class Actinopterygii COPE, 1887  
Subclass Neopterygii REGAN, 1923  
Order Aspidorhynchiformes BLEEKER, 1859

### Family Aspidorhynchidae NICHOLSON & LYDEKKER, 1889

**Diagnosis modified from BRITO (1997).** Fishes characterized by four synapomorphies: presence of elongated premaxillaries forming rostral tube embedded in ethmoid region; accessory bone in lower jaw, the prementary; occipital process of neurocranium formed by intercalar and autopterotic, and posterior position of preopercular sensory canal. Other characters are: triangular preopercle; posterior position of dorsal and anal fins; presence of four hypurals commonly; variable occurrence of supramaxilla; cranial bones covered with or without ganoin; three lateral rows of hypertrophied scales, higher than wide; and scales with or without ganoin.

### Aspidorhynchidae indet.

*Pholidophorus argentinus* DOLGOPOL DE SAEZ, 1939: 430, fig. 4.

"*Pholidophorus argentinus*" DOLGOPOL DE SAEZ in CIONE & PEREIRA (1990: 386, pl. 1 fig. A).

"*Pholidophorus*" *argentinus* DOLGOPOL DE SAEZ in ARRATIA & CIONE (1996: 63).

*Pholidophorus argentinus* DOLGOPOL DE SAEZ in LÓPEZ-ARBARELLO et al. (2008: 599).

**Holotype:** "*Pholidophorus argentinus*" (= Aspidorhynchidae indet.), MLP 39-VI-30-4, a partially preserved caudal fin and part of the caudal peduncle. There are scales covering the caudal peduncle. Some deep (higher than wide) disarticulated scales are associated.

**Original geographic provenance:** Plaza Huincul, "Arroyo Picún Leufú junto al camino que une Zapala con San Martín de los Andes, Neuquén" (DOLGOPOL DE SAEZ 1939: 428).

**Corrected geographic provenance:** National Road 40 where it crosses the Picún Leufú Creek (39°12'S 70°03'W) (Fig. 1).

**Original stratigraphic provenance:** DOLGOPOL DE SAEZ (1939: 428: “areniscas feldespáticas titónicas de Plaza Huincul”) considered by CIONE & PEREIRA (1990: 386) as Vaca Muerta Formation (Tithonian, Upper Jurassic).

**Corrected stratigraphic provenance:** In the Picún Leufú Creek area (Fig. 2), the Tithonian-Berriasian interval is represented by two marine lithostratigraphic units of the Mendoza Group (STIPANICIC et al. 1968), known as the Vaca Muerta (WEAVER 1931) and Picún Leufú (LEANZA 1973) formations. In this area, the Vaca Muerta Formation is Early to early Middle Tithonian in age (LEANZA 1973, ARMELLA et al. 2007). It is widely exposed throughout the Neuquén Basin, and consists of a thick unit of dark bituminous shales and marlstones deposited in an offshore marine environment (LEGARRETA & ULIANA 1991).

The Picún Leufú Formation is late Middle Tithonian to Early Berriasian in age (LEANZA 1973, ARMELLA et al. 2007). It is well developed along the entire southeastern margin of the basin (carbonate shelf of LEGARRETA & ULIANA 1991) and has been referred to a highstand systems tract (LEANZA & HUGO 1997, ARMELLA et al. 1999, SPALLETTI et al. 2000). It is composed of shallow marine carbonates and siliciclastic sediments that are yellowish and greenish in colour. The contact between the Vaca Muerta and Picún Leufú formations is diachronous and progradational (ARMELLA et al. 2007 and references cited therein) becoming younger in the central area of the basin, where the Picún Leufú Formation is laterally replaced by dark shales of the Vaca Muerta Formation. The dating was based on the ammonite fauna (LEANZA 1973, 1981).

The type section at Picún Leufú Creek is dominated by inner shelf facies representing prograding bars dissected by channels, and well-developed lagoonal facies with shoals (ARMELLA et al. 2007).

According to the lithology and area of collection, the material comes from the lower part of Picún Leufú Formation (also Tithonian in age; A. GARRIDO pers. comm. 2011).

## Description

The specimen is not very well preserved. However, using the holotype material, its latex peel, and comparisons with the German specimens, we were able to analyse and describe, in the greatest possible detail, the number, disposition, and variability of the elements of the caudal fin.

The caudal fin is, as was mentioned by CIONE & PEREIRA (1990: 388), abbreviated heterocercal and comprises 17 principal caudal fin rays. The distal part of the principal caudal fin rays is broken or absent and some of the rays are displaced from their original position. The segmentation pattern is straight. In the rays that are bifurcated, the bifurcation is slightly asymmetric. The first principal ray is shorter than the second one.

We could identify one dorsal procurrent ray. The basal fulcra cover part of the first and second segment of the first procurrent ray (interpreted here as a procurrent, not a rudimentary ray because of its long base and segmentation). The ventral lobe of the caudal fin includes at least three procurrent rays. These rays less developed caudad to rostrad.

The dorsal lobe has at least seven basal fulcra (Fig. 3). Because of the preservation we cannot determine if the basal fulcra are paired or not. Each fulcrum overlaps widely the following one. The distal tips of each fulcrum are arrow-shaped.

The ventral lobe presents three ventral basal fulcra; each fulcrum largely overlaps dorsally and laterally the posterior one. The first fulcrum is a paired element but the condition is unknown for the other elements. All fulcra are arrow-shaped and covered with a thin layer of ganoin delicately ornamented with tiny ridges.

In the dorsal lobe, one fusiform and delicate fringing fulcrum can be recognized. The fringing fulcrum is placed between the first principal ray and the second one (Fig. 3).

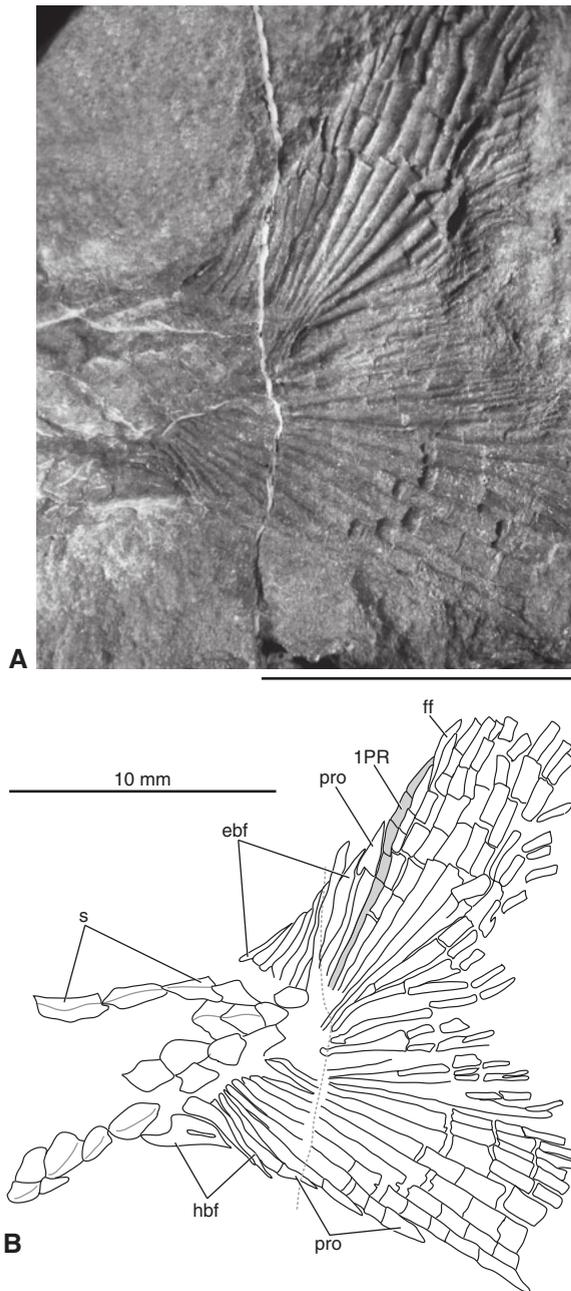
The scales associated with the caudal fin are located over the caudal peduncle, covering the bases of the caudal fin rays of both dorsal and ventral lobes and being more evident in the dorsal lobe. These scales are rhombic in shape, unornamented, mostly smooth, although some present one or two well-developed keels. The scales decrease in size rostrad to caudad. Dorsal and ventral sides of the caudal peduncle present a few rows of small rhombic scales with at least two longitudinal keels. Because of the incomplete preservation of the type material, we cannot determine the exact number of scale rows on the dorsal and ventral margin of the caudal peduncle.

There are some disarticulated, rectangular (higher than broad) scales associated with the caudal fin. These scales resemble the lateral scales present in all aspidorhynchids and are interpreted herein as lateral body scales.

## Discussion and comparison

DOLGOPOL DE SAEZ (1939) established this species based on an impression of a caudal region of a “ganoid” fish. The author assigned the material to the genus *Pholidophorus* based on the following character combination: homocercal caudal fin with 31 caudal fin rays, distance between both lobes of 24.4 mm, and presence of segmented caudal fin rays. Later, CIONE & PEREIRA (1990) suggested that the caudal fin is not “francamente homocerca” (= “really homocercal”) (as mentioned by DOLGOPOL DE SAEZ 1939: 430) but abbreviated heterocercal (see above). Besides, the authors noticed that DOLGOPOL DE SAEZ confused scale impressions with vertebrae and that the scales that are covering the caudal peduncle are not “rectangular” but rhombic. Finally, CIONE & PEREIRA (1990) concluded that the type specimen does not exhibit diagnostic characters and it cannot be recognized as a different species or even as a member of *Pholidophorus*; consequently, they designated the species as a nomen vanum (CIONE & PEREIRA 1990: 388, following the nomenclature of MONES 1989). However, the proposal of MONES was not accepted and, according to the International Code of Zoological Nomenclature, the species should be designated a nomen dubium.

Concerning the different caudal structures, basal and fringing fulcra are commonly present in basal actinopterygians but they have an irregular occurrence. Basal fulcra are present on the unpaired fins of basal teleostomorphs and are absent in actinopterygians such as recent polypteriforms, amiiforms, and teleosts (see ARRATIA 2009). As was mentioned above, at least the ventral or hypaxial basal fulcra observed in *Aspidorhynchidae* indet. (= “*Ph. argentinus*”) are paired structures covered with a thin layer of ganoin and delicately ornamented with tiny ridges. The fringing fulcra, as defined by ARRATIA (2009), are unpaired or paired structures associated with the leading margins of all fins. Within aspidorhynchids, fringing fulcra are present in *Aspidorhynchus* and *Belonostomus*. This morphology was described in detail for the Kimmeridgian–Tithonian *A. sanzenbacheri* (BRITO & EBERT 2009) from the lithographic limestones of Ettling, Germany (see: ARRATIA 2008, 2009) and was recently observed in several undescribed specimens tentatively assigned to the genus *Belonostomus* (GOURIC-CAVALLI pers. observ.: Fig. 4). The specimen described herein has spine-like



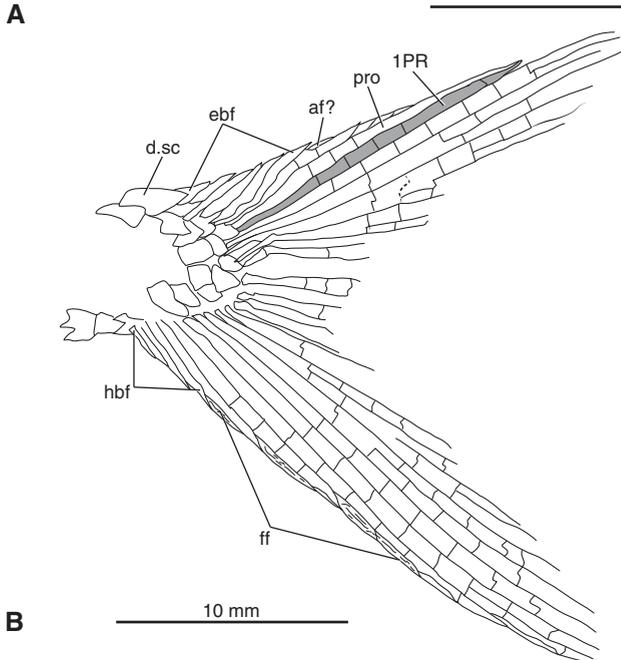
**Fig. 3.** Caudal fin and caudal peduncle of *Aspidorhynchidae* indet. Photograph (A) and drawing (B) of the holotype of “*Pholidophorus argentinus*”; MLP 39-VI-30-4. Abbreviations: **s**, scales; **ebf**, epaxial basal fulcra; **hbf**, hypaxial basal fulcra; **pro**, procurrent ray; **1PR**, first principal ray; **ff**, fringing fulcra. Scale bars = 1 cm.

fringing fulcra (C Pattern of ARRATIA 2009) in the dorsal lobe of the caudal fin. A similar condition was observed in *A. sanzenbacheri* and in several undescribed specimens of *Belonostomus* sp. (GOUIRIC-CAVALLI pers. observ.: Fig. 4).

The caudal fin of the aspidorhynchids is not well known because most of them are poorly preserved or incomplete. Recently, ARRATIA (2008: 78, fig. 19) described one exquisitely preserved caudal fin of a Jurassic indeterminate aspidorhynchiform from the lithographic limestones of Ettling, Germany. This material was later assigned to *Aspidorhynchus sanzenbacheri* (BRITO & EBERT 2009). In addition, ARRATIA (2008) described and figured the caudal fin and caudal skeleton of *Belonostomus tenuirostris* (ARRATIA 2008: 79, fig. 21), a specimen previously described and figured by BRITO (1999: 253, fig. 4).

In addition, the morphology of the scales over the caudal peduncle of Aspidorhynchidae indet. (= "*Ph. argentinus*"), rhombic in shape and with at least one longitudinal keel (mostly two), clearly resembles the scales present in most aspidorhynchids. Furthermore, disarticulated scales associated with the type species, rectangular (higher than wide) and having one longitudinal keel that divides the scale in two, clearly resemble the lateral scales present in all aspidorhynchid genera (GOUIRIC-CAVALLI & CIONE 2011b). Moreover, and agreeing with ARRATIA (2000), the members of the genus *Pholidophorus* have scales with a smooth posterior margin and with fine lines near the posterior margin (ARRATIA 2000: 118). This was not observed in the scales of the type material of "*Ph. argentinus*" (Fig. 3).

We conclude that the specimen is not assignable to the genus *Pholidophorus* sensu stricto based on the following character combination: rhombic and ornamented scales over the caudal peduncle vs. unornamented ones; ornamented rectangular (higher than wide) scales, interpreted



**Fig. 4.**

Caudal fin and caudal peduncle of *Belonostomus* sp. Reversed photograph (A) and drawing (B) of specimen JME ETT 117. Abbreviations: ff, fringing fulcra; 1PR, first principal ray; pro, procurrent ray; d.sc, dorsal scute; a.f?, accessory fulcra?; ebf, epaxial basal fulcra; hbf, hypaxial basal fulcra. Scale bars = 1 cm.

herein as lateral scales; spine-like fringing fulcra in the dorsal lobes of the caudal fin vs. proportionally longer ones; dorsal and ventral series of ornamented scales vs. unornamented ones; leading edge of dorsal and ventral lobe of caudal fin formed by one or more procurrent rays + one principal ray vs. leading edge formed only by principal ray. Based on these characters, we propose that the specimen pertains to the Family Aspidorhynchidae.

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### References

- AGASSIZ, L. (1832): Untersuchungen über die fossilen Fische der Lias-Formation. – *Jb. Mineral., Geol., Geogn. Petrefaktenkd.* **1832**: 139–149.
- (1833–1843): Recherches sur les poissons fossiles. 5 vols. – CVII+1798 pp.; Neuchâtel et Soleure (Petitpierre).
- ARMELLA, C., CABALERI, N. & LEANZA, H. A. (1999): Paleoambientes de la Formación Picún Leufú (límite Jurásico–Cretácico) en su localidad tipo, Cuenca Neuquina, Argentina. – *5 Simp. Cretáceo Brasil, 1er Simp. Cretácico América del Sur, Serra Negra, Brasil, Bol.*: 357–358.
- ARAMELLA, C., CABALERI, N. & LEANZA, H. A. (2007): Tidally dominated, rimmed shelf facies of the Picún Leufú Formation (Jurassic/Cretaceous boundary) in southwest Gondwana, Neuquén Basin, Argentina. – *Cretaceous Res.* **28**: 961–979.
- ARRATIA, G. (1991): The caudal skeleton of Jurassic teleosts; a phylogenetic analysis. – In: CHANG, M.-M., LIU, Y.-H. & ZHANG, G.-R. (eds.): *Early Vertebrates and Related Problems in Evolutionary Biology*: 249–340; Beijing (Science Press).
- (1999): The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. – In: ARRATIA, G. & SCHULTZE, H.-P. (eds.): *Mesozoic Fishes 2 – Systematics and Fossil Record*: 265–334; München (Pfeil).
- (2000): New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the “pholidophoriforms”. – *Paläontol. Z.* **74**: 113–143.
- (2001): Systematics problems concerning “pholidophoriforms” fishes. – 61st ann. Mtg. Soc. Vert. Paleontol., Montana October 2001, *J. Vert. Paleontol.* **21** (suppl. to 3), Progr. abstr.: 29A.
- (2008): Actinopterygian postcranial skeleton with special reference to the diversity of fin ray elements, and the problem of identifying homologies. – In: ARRATIA, G., SCHULTZE, H.-P. & WILSON, M. V. H. (eds.): *Mesozoic Fishes 4 – Homology and Phylogeny*: 49–101; München (Pfeil).
- (2009): Identifying patterns of diversity of the actinopterygian fulcra. – *Acta Zoologica, spec. issue suppl. to 90*: 220–235.
- ARRATIA, G. & CIONE, A. L. (1996): The record of fossil fishes of southern South America. – *Münchner Geowiss. Abh.* **30**: 9–72.
- ARRATIA, G. & LAMBERS, P. (1996): The caudal skeleton of pachycormiforms: parallel evolution? In: ARRATIA, G. & SCHULTZE, H.-P. (eds.): *Mesozoic Fishes 2 – Systematics and Fossil Record*, 191–218; München (Pfeil).
- ARRATIA, G. & SCHULTZE, H.-P. (1992): Reevaluation of the caudal skeleton of certain actinopterygian fishes. III. Salmonidae. Homologization of caudal skeletal structures. – *J. Morphol.* **214**: 1–63.
- (1999): Mesozoic fishes from Chile. – In: ARRATIA, G. & SCHULTZE, H.-P. (eds.): *Mesozoic Fishes 2 – Systematics and Fossil Record*: 565–593; München (Pfeil).

- ARRATIA, G. & TINTORI, A. (2004): A. The caudal skeleton of the Triassic actinopterygian *Prohalecites* and its phylogenetic relationships. – In: ARRATIA, G. & SCHULTZE, H.-P. (eds.): *Mesozoic Fishes – Systematics and Fossil Record*: 121–142; München (Pfeil).
- BERG, L. S. (1937). A classification of fish-like vertebrates. – *Bull. Acad. Sci. URSS, Cl. sci. math. natur., sér. Biol.* 1937 (4): 1277–1280. [Engl. with Russ.]
- BLAINVILLE, H. D. (1818): Poissons fossiles. – *Nouveau Dictionnaire d'Histoire Naturelle* 27: 332; Paris (Deterville).
- BLEEKER, P. (1859): Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebùs Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. – *Acta Soc. Regiae Scient. Indo-Neerlandicae* 6: XXXVI+276 pp.
- 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. – *Bull. Inst. Roy. Sci. Natur. Belg.* 81: 235–245.
- BRITO, P. M. (1997): Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, données environnementales et biogéographiques. – *Geodiversitas* 19: 681–772.
- (1999): The caudal skeleton of aspidorhynchids (Actinopterygii, Halecostomi): Phylogenetic implications. – In: ARRATIA, G. & SCHULTZE, H.-P. (eds.): *Mesozoic Fishes 2 – Systematics and Fossil Record*: 249–264; München (Pfeil).
- BRITO, P. M. & EBERT, M. (2009): A new aspidorhynchid fish (Teleostei: Aspidorhynchiformes) from the Upper Jurassic of Ettling, Solnhofen, Bavaria, Germany. – *C. R. Paleovol* 8: 395–402.
- BRITO, P. M. & MEUNIER, F. J. (2000): The morphology and histology of the scales of Aspidorhynchids (Actinopterygii, Halecostomi) and its phylogenetical implications. – *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. – *Rev. Geol. Chile* 30: 117–127.
- CASAMIQUELA, R. M. 1992: Notas sobre vertebrados de la frontera Cretácica-Terciaria II. La presencia del aspidorhynchido *Belonostomus* (Osteichthyes, Aspidorhynchiformes) en la Formación Coli Toro (Maastrichtense), Ingeniero Jacobacci, Río Negro. – *M. Ameghiniano* 11: 9–18.
- CIONE, A. L. & PEREIRA, S. M. (1987): Los peces del Jurásico de Argentina. El Jurásico anterior a los movimientos intermálmicos. – In: VOLKHEIMER, W. (ed.): *Bioestratigrafía de los Sistemas Regionales del Jurásico y Cretácico de América del Sur* 1: 287–298; Mendoza, Argentina (Comité Sudamericano del Jurásico y Cretácico).
- (1990): Los peces del Jurásico posterior a los movimientos intermálmicos y del Cretácico Inferior de Argentina. – In: VOLKHEIMER, W. (ed.): *Bioestratigrafía de los Sistemas Regionales del Jurásico y Cretácico de América del Sur* 2: 385–395; Mendoza, Argentina (Comité Sudamericano del Jurásico y Cretácico).
- CIONE, A. L., GASPARINI, Z., LEANZA, H. & ZEISS, A. (1987): Marine oberjurassische Plattenkalke in Argentinien (Ein erster Forschungsbericht). – *Archaeopteryx* 5: 13–22.
- COPE, E. D. (1887): Zittel's manual of palaeontology. – *Amer. Naturalist*, 21, 1014–1019.
- DOLGOPOL DE SAEZ, M. (1939): Noticias sobre peces fósiles argentinos. – *Notas Mus. La Plata, Paleontol.* 4 (19): 425–432.
- (1940): Noticias sobre peces fósiles argentinos. Leptolepídidos del Titoniense de Plaza Huincul. – *Notas Mus. La Plata, Paleontol.* 5 (26): 299–305.
- (1949): Noticias sobre peces fósiles argentinos. – *Notas Mus. La Plata, Paleontol.* 14 (96): 443–461.
- FLORES, M. A. (1969): El Bolsón de las Salinas en la Provincia de San Luis. – *J. Geol. Argentinas* 4: 311–327.
- GIORDANO, G. (2010): “Pholidophoriforms” of La Cantera Formation, Lower Cretaceous, San Luis, Argentina. – In: GONZÁLEZ-RODRÍGUEZ, K. & ARRATIA, G. (compilers). *Fifth Internatl. Mtg. Mesozoic Fishes – Global Diversity and Evolution: abstr. book & field guides. Ciencia al Día* 19: 45; Pachuca, Mexico (Universidad Autónoma del Estado Hidalgo, Mexico).
- GIORDANO, G. & ARRATIA, G. (2010): Ganoid scales of “pholidophoriforms” (Actinopterygii) from La Cantera Formation, Lower Cretaceous, San Luis, Argentina. – *Ameghiniana* 48 (4): R232.
- GOURIC-CAVALLI, S. (2013): Sistemática y relaciones biogeográficas de los peces del Titoniano (Jurásico tardío) de la Cuenca Neuquina de Argentina. – Vol. 1: 403 pp. (text); Vol. 2: 108 pp. (figures); Unpublished Ph.D. thesis, Universidad Nacional de La Plata, Argentina.
- GOURIC-CAVALLI, S. & CIONE, A. L. (2009). La ictiofauna marina del Jurásico superior de la Cuenca Neuquina de Argentina. Estado actual del conocimiento. – *Ameghiniana* 46 (4): 82R.
- (2011a): The marine ichthyofauna from the Upper Jurassic (Tithonian) of Vaca Muerta Formation, Neuquen Basin, Argentina: A preliminary report. – 22nd Int. Coll. on Latin American Earth Scie, Abstracts and Programme. *GAEA heidelbergensis* 18: 77.
- (2011b): “*Pholidophorus*” *argentinus* Dolgopol de Saez, 1939, an Aspidorhynchidae (Actinopterygii, Aspidorhynchiformes) from the Vaca Muerta Formation (Upper Jurassic) of Neuquén Province, Argentina. – *Ameghiniana* 48 (4): R234.

- LEANZA, H. A. (1973): Estudio sobre los cambios facies de los estratos limítrofes Jurásico-Cretácicos entre Loncopué y Picún Leufú, provincia del Neuquén, República Argentina. – Rev. Asoc. Geol. Argentina **28**: 97–132.
- (1981): The Jurassic Cretaceous boundary beds in west central Argentina and their ammonite zones. – N. Jb. Geol. Paläontol. Abh. **161**: 62–92.
- LEANZA, H. A. & HUGO, C. A. (1997): Hoja Geológica 3969-III, Picún Leufú, provincias del Neuquén y Río Negro. Programa Nacional de Cartas Geológicas a escala 1:250000. – Inst. Geol. Recursos Mineral., SEGEMAR, Buenos Aires, Bol. **218**: 135 pp.
- LEANZA, H. A. & ZEISS, A. (1990): Upper Jurassic lithographic limestones from Argentina (Neuquén Basin): stratigraphy and fossils. – Facies **22**: 169–186.
- LEGARRETA, L. & ULIANA, M. A. (1991): Jurassic/Cretaceous marine oscillations and geometry of a back-arc basin fill, central Argentine Andes. – In: MCDONALD, D. I. M. (ed.): Sedimentation, Tectonics and Eustasy. Internatl. Assoc. Sedimentol., Spec. Publ. **12**: 429–450.
- LEHMAN, J.-P. (1966): Actinopterygii. – In: PIVETEAU, J. (ed.): Traité de Paléontologie **4**(3): 1–242; Paris (Masson & Cie.).
- LÓPEZ-ARBARELLO, A., RAUHUT, O. W. M. & MOSER, K. (2008): Jurassic fishes from Gondwana. – Rev. Asoc. Geol. Argentina **63**: 586–612.
- LÓPEZ-ARBARELLO, A., RAUHUT, O. W. N. & CERDEÑO E. (2010): The Triassic fish faunas of the Cuyana Basin, Western Argentina. – Palaeontology **53**: 249–276.
- MONES, A. (1989): *Nomen Dubium* vs. *Nomen Vanum*. – J. Vert. Paleontol. **9**: 232–234.
- MOODY, M. J. & MAISEY, J.G. (1994): New Cretaceous marine vertebrate assemblages from north-western Venezuela and their significance. – J. Vert. Paleontol. **14**: 1–8.
- NELSON, J. S. (1994): Fishes of the World. Fourth Ed. – XIX+601 pp.; Hoboken, NJ, U.S.A. (J. Wiley & Sons).
- NICHOLSON, H. A. & LYDEKKER, R. (1889): A Manual of Palaeontology – 2<sup>nd</sup> ed. – 1964 pp.; Edinburgh and London (W. Blackwood and Sons).
- NYBELIN, O. (1974): A revision of the leptolepid fishes. – Acta Reg. Soc. scient. Litt. Gothoburgensis, Zool. **9**: 1–202.
- (1966): On certain Triassic and Liassic representatives of the family Pholidophoridae s. str. – Bull. Brit. Mus. (Natur. Hist.), Geol. **11**: 351–432.
- PATTERSON, C. (1968): The caudal skeleton in Lower Liassic pholidophorid fishes. – Bull. Brit. Mus. (Natur. Hist.), Geol. **16**: 201–239.
- (1973): Interrelationships of holosteans. – In: GREENWOOD, P. M., MILES, R. S. & PATTERSON, C. (eds.): Interrelationships of Fishes. Zool. J. Linn. Soc. **53** Suppl. 1: 233–305; London (Academic Press).
- PATTERSON, C. & ROSEN, D. (1977): Review of ichthyodectiform and other Mesozoic teleost fishes and the theory of classifying fossils. – Bull. Amer. Mus. Natur. Hist. **158**: 81–72.
- REGAN, C. T. (1923): The skeleton of *Lepisosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. – Proc. Zool. Soc. London **1923**: 445–461.
- ROMER, A. S. (1966): Vertebrate Paleontology. – VIII+468 pp.; Chicago (University of Chicago Press).
- RUSCONI, C. (1946): Nuevos peces triásicos de El Challao, Mendoza. – Rev. Soc. Hist. Geogr. Cuyo **1**: 1–15.
- (1947): Más peces triásicos de Mendoza. – An. Soc. Cient. Argentina **143**: 21–24.
- SCHULTZE, H.-P. & ARRATIA, G. (1989): The composition of the caudal skeleton of teleosts (Actinopterygii: Osteichthyes). – Zool. J. Linn. Soc. **97**: 189–231.
- SCHULTZE, H.-P. & STÖHR, D. (1996): *Vinctifer* (Pisces, Aspidorhynchidae) aus der Unterkreide (oberes Aptium) von Kolumbien. – N. Jb. Geol. Paläontol. Abh. **199**: 395–415.
- SPALLETTI, L. A., FRANZESE, J. R., MATHEOS, S. D. & SCHWARZ, E. (2000): Sequence stratigraphy of a tidally dominated carbonate-siliciclastic ramp; the Tithonian–Early Berriasian of the southern Neuquén Basin, Argentina. – J. Geol. Soc. **157**: 433–446.
- STIPANICIC, P. N., RODRIGO, F., BAULÍES, O. L. & MARTÍNEZ, C. G. (1968): Las formaciones presenonianas del denominado Macizo Nordpatagónico y regiones adyacentes. – Rev. Asoc. Geol. Argentina **23**: 367–388.
- WEAVER, C., (1931): Paleontology of the Jurassic and Cretaceous of west central Argentina. – University of Washington, Seattle, Mem. **1**: XV + 469 pp.
- WOODWARD, A. S. (1895): Catalogue of the Fossil Fishes in the British Museum (Natural History). Vol. 3. – London (British Museum (Natural History)).
- ZAMBELLI, R. (1986): Note sui Pholidophoriformes. VI Contributo. Pholidophorinae subfamiglia nuova del Triassico Superiore. – Riv. Mus. Civico Sci. Natur. ‘E. Caffi’ **10**: 1–32.

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