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Jonoichthys challwa gen. et sp. nov., a new
Aspidorhynchiform (Osteichthyes, Neopterygii,
Teleosteoromorpha) from the marine Upper Jurassic sediments
of Argentina, with comments about paleobiogeography of
Jurassic aspidorhynchids

Jonoichthys challwa gen. et sp. nov., un nouvel Aspidorhynchiformes
(Osteichthyes, Neopterygii, Teleosteoromorpha) dans les sédiments marins
du Jurassique supérieur d'Argentine, avec des commentaires sur la
paléobiogéographie des aspidorhynchidés

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ABSTRACT

Aspidorhynchiformes as a whole are incompletely understood. Here, a new aspidorhynchiform, *Jonoichthys challwa* gen. et sp. nov., is described based on a single three-dimensionally preserved specimen recovered from Upper Jurassic marine rocks of the Vaca Muerta Formation, Neuquén, southern Argentina. The new taxon is based on a unique combination of characters (e.g., large skull roof plate composed by the fusion of certain bones; 'L'-shaped preoperculum with a single main preopercular sensory canal that lacks sensory tubules; three predentary tooth rows; an accessory cusp in the teeth of the median predentary tooth row, and a robust and deep body). It is expected that the morphological information provided here could be useful to further understanding of aspidorhynchiform phylogeny and Neuquén Basin biodiversity.

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RÉSUMÉ

Les Aspidorhynchiformes dans leur ensemble sont incomplètement connus. Ici, un nouvel aspidorhynchidé *Jonoichthys challwa* gen. et sp. nov., est décrit sur la base d'un unique spécimen conservé en trois dimensions, prélevé dans les roches marines du Jurassique supérieur de la Formation Vaca Muerta, Neuquén, en Argentine méridionale. Le nouveau taxon

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1. Introduction

Aspidorhynchiformes is a group of extinct neopterygians that have been traditionally considered typical marine forms with worldwide distribution – except Asia – (Brito, 1997). They range in age from the Middle Jurassic to the Late Cretaceous (Brito, 1997). At present, a unique family, Aspidorhynchidae, with four nominal genera (*Aspidorhynchus* Agassiz, 1833, *Belonostomus* Agassiz, 1843, *Vinctifer* Jordan, 1919, and *Richmondichthys* Bartholomai, 2004), comprises the group.

The phylogeny of the Aspidorhynchiformes has a complicated history and has been the subject of study by several authors. (e.g., Arratia, 1999, 2001, 2013; Brito, 1997). Although the monophyly of the group is not doubted, its taxonomy and consequently its content remain unclear. A great part of the anatomical descriptions as well as almost the entire information about the group is based mainly on incomplete specimens (Arratia, 2004).

The Aspidorhynchiformes were interpreted as ganoid holosteans (e.g., Danil'chenko, 1967), Halecostomi (e.g., Saint-Seine, 1949) or listed as an order without indicating a higher taxon (e.g., Berg, 1940; Lehman, 1966). At the beginning of the Hennigian era, they were included in Teleostei as basal forms (Patterson, 1973, 1977; Patterson and Rosen, 1977), an interpretation followed by several authors (e.g., Bartholomai, 2004; Brito, 1997; Brito and Ebert, 2009; de Pinna, 1996; Maisey, 1991). However, Arratia (1999) showed that the position of the group changes depending on the outgroup and in 2001 she interpreted them as a possible teleost stem-group, including it in the more inclusive clade, Teleostei (Arratia, 2001: f. 3). The most recent phylogenetic hypothesis suggests that Aspidorhynchiformes and Pachycormiformes are sister taxa (Arratia, 2013: f. 95).

The Jurassic genera *Aspidorhynchus* and *Belonostomus* have long been known (Agassiz, 1833–1844). However, to date, the best known species is *Vinctifer comp-toni* (Agassiz, 1841) from Brazil, whose morphological descriptions are based on numerous mechanical and acid-prepared specimens. *Richmondichthys sweeti* (Etheridge and Woodward, 1891) from Australia is relatively well known (see Bartholomai, 2004). Meanwhile, other *Vinctifer* species as well as most of the *Aspidorhynchus* and *Belonostomus* species are very incompletely known. Like pachycormiforms, the general morphology of most of the aspidorhynchiform species (including braincase, skull bones, caudal skeleton, paired and unpaired fins, and scales) is incompletely known. This partial knowledge of most of the members of Aspidorhynchiformes leads to

difficulties in the polarization of some characters, and also in differences in the interpretation of some structures (see Arratia, 2008a, 2009; Brito, 1999b).

The study of Jurassic aspidorhynchids is particularly complex mainly due to the poor and incomplete preservation of the specimens. New specimens recently recovered in Ettling, Germany, are an exception but at present they still remain incompletely known. Their braincase, caudal skeleton, vertebral column, scales, etc. remain unknown. There are only a few studies related to the anatomy of their unpaired fins (Arratia, 2008a, 2009). Cretaceous taxa have been more extensively studied, especially the genus *Vinctifer* (Brito, 1988, 1992, 1997; Maisey, 1991).

The greatest described diversity of aspidorhynchiformes comes from Jurassic and Cretaceous sediments of Europe (e.g., Agassiz, 1833–1844; Assman, 1906; Brito, 1997; Brito and Ebert, 2009; Eastman, 1914; López-Arbarello and Schröder, 2013; Maisey, 1991; Saint-Seine, 1949; Thiollière, 1848; Wagner, 1863) and lesser extend from South and Central America (e.g., Arratia and Schultze, 1999; Brito, 1997, 1999a; Brito and Suárez, 2003; Felix, 1891; González-Rodríguez et al., 2013; Jordan, 1919; Santos, 1985a,b, 1990; Schultze and Stöhr, 1996). In Argentina the group is poorly known and only few specimens were mentioned in the literature (e.g., Bogan et al., 2011; Cione et al., 1987; Leanza and Zeiss, 1990). Recently, the revision of *Pholidophorus argentinus* Dolgopolev de Saez, 1939 resulted in its reinterpretation as a member of Aspidorhynchiformes (Gouiric-Cavalli and Cione, 2013a). To date, the best-preserved Argentinian aspidorhynchiform material comes from Jurassic sediments of the Vaca Muerta Formation; however its diversity has been only briefly documented (Cione et al., 1987; Cione in Leanza and Zeiss, 1990; and Gouiric-Cavalli and Cione, 2009, 2011).

The present study is a starting point attempting to answer the statement made by several authors that 'Jurassic aspidorhynchids need an urgent revision' (see Arratia, 1999, 2004; Brito, 1997; López-Arbarello and Schröder, 2013). The anatomical description of a new endemic aspidorhynchiform, *Jonoichthys challwa* gen. et sp. nov., is presented here representing the first formal description of a Jurassic aspidorhynchiform from the Tithonian of Vaca Muerta Formation, Neuquén, Argentina. It is expected that the morphological information provided here could be useful to further understanding of aspidorhynchiform phylogeny and Neuquén Basin biodiversity. The information provided could be used for a better understanding of biogeographic distribution patterns of aspidorhynchids during Jurassic times as well as the routes used in its possible migrations/dispersion.

1.1. Comments on Neuquén Basin chondrichthyan and osteichthyan diversity

During the Late Jurassic the Neuquén Basin developed as part of a marine ingression from the North-East of the Tethys (Howell et al., 2005). The first studies on Jurassic marine osteichthyans in sediments of the Neuquén Basin were based on incomplete and poorly preserved specimens recovered from oil drilling in the area (Dolgopol de Saez, 1939, 1940a,b, 1949). Through the years materials were sporadically collected and for many of them the precise horizon remains unknown. In some parts of the basin the deposit shows high morphologic and taxonomic fish diversity. This is especially remarkable in the lithographic limestones of the Los Catutos Member, which correspond to the middle part of the Vaca Muerta Formation (Gouiric-Cavalli and Cione, 2009, 2011, 2013b; Gouiric-Cavalli et al., 2011).

The fossil chondrichthyans and osteichthyans material recovered through the years in the Neuquén Basin area were identified and reported but only briefly studied (e.g., Cione et al., 1987; Cione and Pereira, 1990). However some of the newly recovered specimens stand out for their good quality of preservation.

The diversity of taxa reported is represented by rare chondrichthyans: only a partially preserved bathomorph ray and a dorsal fin spine of a hybodontid shark have been reported (Cione, 1999; Cione et al., 2002) and a diversity of actinopterygians represented by halecomorphs, semionotiformes, aspidorhynchiformes, pachycormiformes, and teleosts (Cione et al., 1987; Cione and Pereira, 1990; Cione in Leanza and Zeiss, 1990; Gouiric-Cavalli and Cione, 2009, 2011, 2013a,b; Gouiric-Cavalli et al., 2011). At present, aspidorhynchiformes are one of the most abundant fish remains recovered in sediments of the Neuquén Basin and probably they were—together with pachycormiformes—the most abundant predatory fishes inhabiting the basin.

2. Material and methods

2.1. Institutional abbreviations

BSPG – Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Bavaria, Germany; JM-E – Jura Museum Eichstätt (SOS indicates that the fish was recovered in the Solnhofen Limestone, Bavaria; ETT indicates that the specimen was recovered in sediments of the quarry of Ettling, Bavaria), Germany; MB – Museum für Naturkunde, Leibnitz-Institut für Evolutions und Biodiversitätsforschung, Berlin, Germany; MLP – Museo de La Plata, División Paleontología Vertebrados, La Plata, Buenos Aires, Argentina; MOZ – Museo Provincial Dr. Prof. Juan Augusto Olsacher, Zapala, Neuquén, Argentina; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Alemania.

2.2. Preparation

The holotype of *Jonoichthys challwa* gen. et sp. nov. was mechanically prepared using pneumatic tools, needles, and widia tool tips. Chemical preparation using low

concentration (between 3 and 6%) of acetic acid was performed with the objective of observe sutures and ornamentation of bones. The specimen was studied under binocular microscope (Zeiss Stemi 2000-C) with different magnifications. Photographs were taken with digital cameras Canon PowerShot G10 (under microscope) and Canon Rebel T2i with a compact macro lens Canon EF 50 mm f/2.5. Drawings were done based on both, photographs (using a Wacom tablet over high-resolution photographs) and using stereomicroscopes Leica Wild M28 with attached camera lucida. Each feature was checked under hand lens and stereomicroscope to avoid misinterpretations of the photographs. Measures were taken with a digital Vernier caliper directly on the material as well as with the free software ImageJ using high-resolution photographs.

2.3. Measurements

Standard Length (SL) – distance from the anterior tip of the snout to the posterior tip of the hypurals – was calculated by comparison with complete preserved aspidorhynchids examined (note that in those specimens examined in which standard length cannot be taken with certainty, those which have squamation preserved in situ or hypural region partially preserved, I follow Arratia's (2013) proposal and designate the posterior border of the last scale bearing the lateral line as the end point of measurement). Also the data provided in Brito's (1997) paper were considered, from where the head length of *Vinctifer* and *Belonostomus* represents between the 25 to 30% of the standard length of the fish, and for *Aspidorhynchus* the head length represents about the 16 to 25% of its standard length.

Head length (HL) – distance between the most anterior tip of the snout to the posterior margin of the operculum – in the aspidorhynchids examined this measurement was calculated from the tip of the premaxilla to the end of the operculum.

Head depth (HD) – measured along the vertical axis in front of the anterior margin of the operculum – this measurement was taken only in those specimens with the head and opercular bones completely preserved and in lateral view. Also, data provided in Brito's (1997 p. 690) and Bartholomai's (2004 p. 542) papers were used for comparison.

Eye diameter is the greatest diameter of the orbit (measured from the anterior inner margin of the orbit to the posterior inner margin).

2.4. Terminology

I used terminology based on homology to describe bones of the skull roof following Westoll (1943) and Schultze (2008). To avoid confusion, the traditional terminology of a bone is given here, in this section, in square brackets: i.e., parietal [=frontal], postparietal [=parietal], suborbital [=postorbital]. Terminology and identification of cephalic sensory canals follow Northcutt (1989). Vertebral centra terminology follows Schultze and Arratia (1986, 1989, 2013) and Arratia et al. (2001).

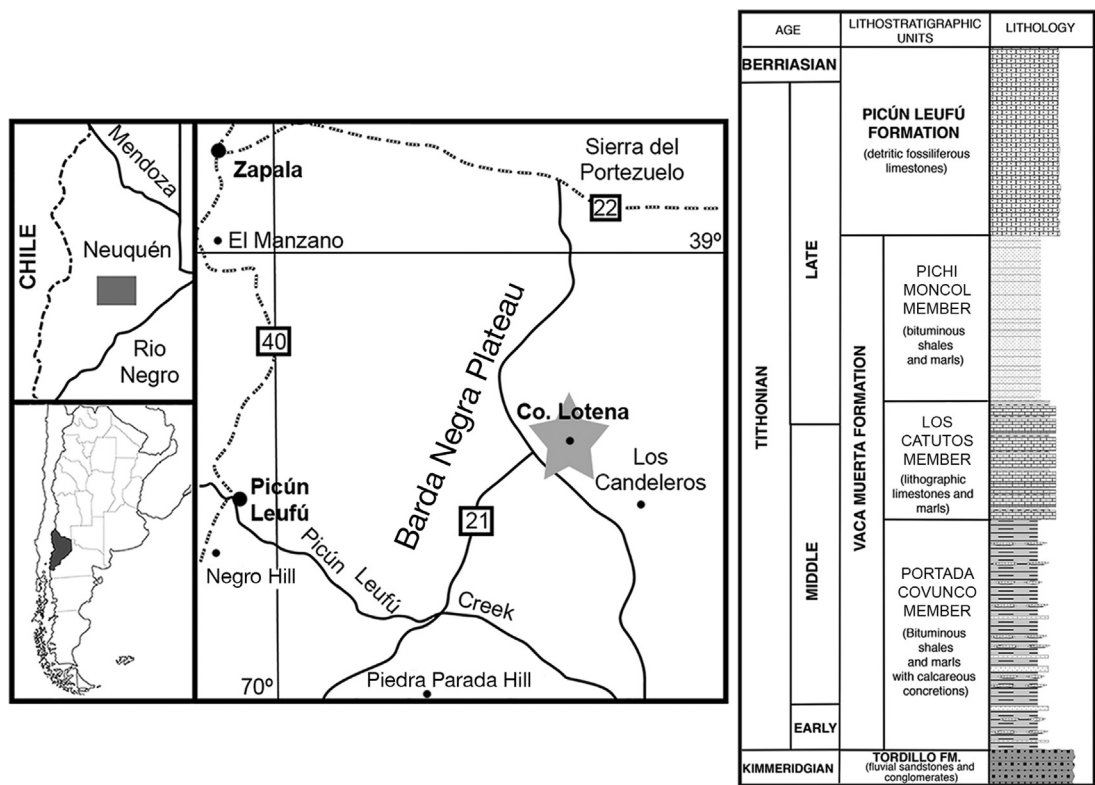


Fig. 1. A. Location map of the fossiliferous locality in Neuquén Province, Argentina. B. Generalized stratigraphic column of the Vaca Muerta Formation.
Fig. 1. A. Carte de situation de la localité fossilifère dans la province de Neuquén, Argentine. B. Colonne stratigraphique généralisée de la formation Vaca Muerta.

Anatomical abbreviations are given in each figure caption.

3. Age and geological background

The specimen MOZ-PV 1747 was recovered in sediments of the Vaca Muerta Formation in the proximities of Cerro Lotena, eastern part of Barda Negra Plateau; 70 km to the southeast of Zapala city, Neuquén, Argentina (Fig. 1A). People living near the type locality recovered the material in 1970, and no precise geographical coordinates are known for the material, but the approximate coordinates of the Cerro Lotena locality are 39° 16' S 69° 65' W.

The Vaca Muerta Formation represents the basal part of the Mendoza Group (Upper Jurassic to Early Cretaceous), and is characterized by the development of a thick succession of calcareous sandy shales and black shales with subordinate amounts of interbedded calcareous sandstones, siltstones and limestones (Leanza, 1973; Parent et al., 2011, 2013; Weaver, 1931). In Cerro Lotena the Vaca Muerta Formation reaches ca. 130 m thick and four ammonite zones have been recognized; *Pseudolissoceras zitteli* zone, *Aulacosphinctes proximus* zone, *Windhauseniaceras interspinosum* zone and *Virgatosphinctes mendozanus* zone (Leanza, 1980). Based on these ammonite zones the age of the Vaca Muerta Formation at this locality is considered to be uppermost Lower–Middle Tithonian (Leanza, 1980, 1993). The concretion in which the fish

was preserved has part of an ammonite near its ventral region. The preliminary identification of the ammonite allowed me to determinate a more accurate age for the fish, which is late Early to early Middle Tithonian, corresponding to the Portada Covunco Member (Parent et al., 2013). This unit is lithologically characterized by dark grey to dark brown of bituminous shales and marls with calcareous concretions and nodules with abundant fish remains and invertebrate shells (Leanza and Zeiss, 1990; Parent et al., 2013) (Fig. 1B). Paleoenvironmentally, this section of the Vaca Muerta Formation represents basinal sediments deposited from suspension under anoxic to dysoxic conditions (Spalletti et al., 2000).

4. Systematic paleontology

ACTINOPTERYGII (Cope, 1887)
 NEOPTERYGII Regan, 1923
 TELEOSTEOMORPHA Arratia, 2001
 ASPIDORHYNCHIFORMES Bleeker, 1859
 ASPIDORHYNCHIDAE Nicholson and Lydekker, 1889

Jonoichthys, gen. nov.
 (Fig. 2)

Diagnosis: based on a unique combination of characters. Characters marked with an asterisk (*) are autapomorphies. Massive and large aspidorhynchiform

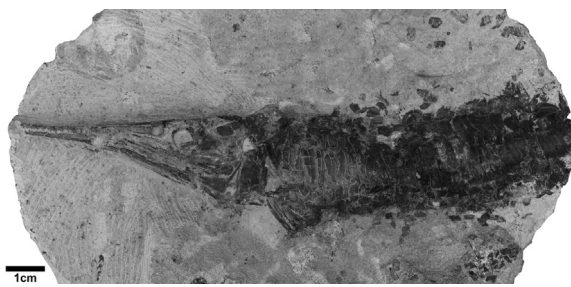


Fig. 2. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747.

Fig. 2. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747.

having a robust, highly compressed, and deep body. Skull bones heavily ossified. Large skull roof plate composed by the fusion of rostral, parietals, postparietals and dermopterotics (*). Cranial bones slightly ornamented with delicate ganoine ridges and striations. Massive head being its head depth of more than 30% of its head length (*). Long jaws extending posterior to the orbit. Presence of a relative

long, deep, and sharply pointed ‘rostrum’ formed mainly by the premaxillae. ‘Rostrum’ extending forward, at least 3% of the head length beyond the anterior tip of the predentary. Maxilla with a low and rounded antorbital lamina. Predentary at least ten times longer than deep and representing about 25% of the head length (*). Three rows of predentary teeth (*). Marginal predentary teeth ankylosed to predentary bone, a labial rounded accessory cusp in the teeth of the median predentary tooth row (*). Predentary with a straight ventral border. Major predentary and premaxillary teeth ornamented with longitudinal striations. Infraorbital sensory canal located in the lower third of the infraorbital bone. Large and caudally broad infraorbital 1. ‘L’-shaped preoperculum with a single and simple preopercular sensory canal (*) located near its posterior margin. Three flank scale rows, being the scales of the middle row the higher ones and carrying the lateral line, the remaining two flank scales rows with scales of similar size, representing 35% of the high of the scales of the middle scale row of flank scales. Lateral line of the middle row of flank scales located in the upper third of the scale. Flank scales with a smooth

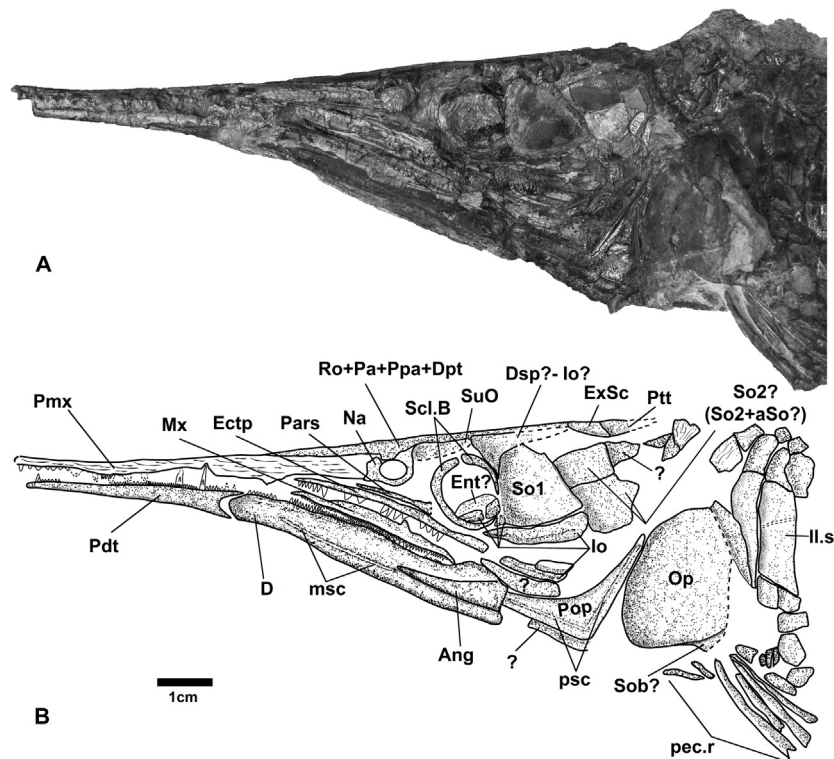


Fig. 3. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747. **A.** Original material in right lateral view. **B.** Interpretative drawing of the bones recognized in A. Ang: angular; D: dentary; Dsp?, dermosphenotic?; Ectp: ectopterygoid?; Ent?: entopterygoid?; ExSc: extrascapular; lo: infraorbitals; lo?: infraorbital?; ll.s: lateral line scale; Mx: maxilla; msc: mandibular sensory canal; Na: nasal; Op: operculum; Pars: parasphenoid; Pdt: predentary; pec.r: pectoral fin rays; Pmx: premaxilla; Pop: preoperculum; psc: preopercular sensory canal; Ptt: posttemporal; Ro + Pa + Ppa + Dpt: rostral + Parietal + Postparietal + Dermopterotic; Scl.r: sclerotic bones; SuO: supraorbital; So1: suborbital1; So2? (So2 + aSo): suborbital2? or suborbital 2 plus accessory suborbital bone; Sob?: suboperculum?;?: indeterminate bones.

Fig. 3. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747. **A.** Matériau original en vue latérale droite. **B.** Dessin interprétatif des os reconnus dans la figure A. Ang : angulaire ; D : dentaire ; Dsp? : dermosphénotique? ; Ectp : ectoptérygoïde ; Ent? : entoptérygoïde ; ExSc : extrascapulaire ; lo : infraorbitaire ; lo? : infraorbitaires? ; ll.s : écailles de la ligne latérale ; Mx : maxillaire ; msc : canal sensoriel mandibulaire ; Na : nasal ; Op : opercule ; Pars : parasphénoïde ; Pdt : prédentaire ; pec.r : rayons des nageoires pectorales ; Pmx : prémaxillaire ; Pop : préoperculaire ; Ptt : post-temporal ; Ro + Pa + Ppa + Dpt : rostral + pariétal + post-pariétal + dermoptérotique ; Scl.r : os sclérotiques ; SuO : supraorbitaire ; So1 : suborbitaire 1 ; So2? (So2 + aSo) : suborbitaire 2? ou suborbitaire 2 plus suborbitaire accessoire ; Sob? : sous-opercule? ;?: os indéterminés.

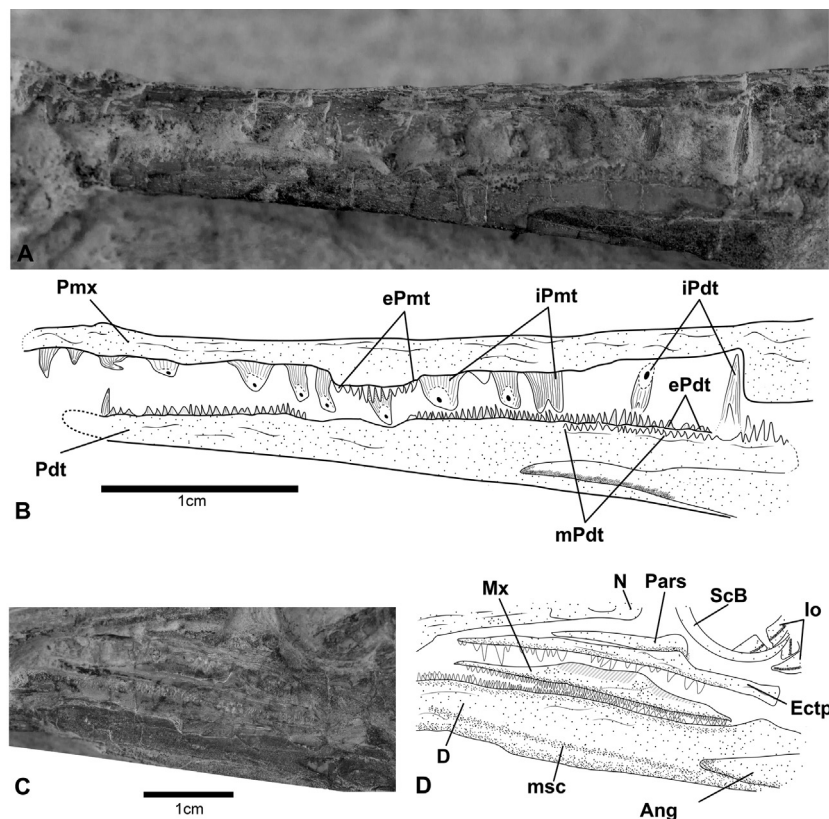


Fig. 4. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747. **A.** Detail of the 'rostrum' showing the teeth rows in premaxilla and prementary. **B.** Interpretative drawing of A. **C.** Detail of the teeth in maxilla, dentary, and ectopterygoid. **D.** Interpretative drawing of C. D: dentary; Ecpt: ectopterygoid; ePmt: external premaxillary tooth row; ePdt: external prementary tooth row; iPdt: internal prementary tooth row; iPmt: internal premaxillary tooth row; mPdt: marginal teeth of the prementary.

Fig. 4. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747. **A.** Détail du « rostre » montrant les rangées de dents dans le prémaxillaire et le prémentaire. **B.** Dessin interprétatif de la figure A. **C.** Détail des dents dans le maxillaire, le dentaire et l'ectoptérygoïde. **D.** Dessin interprétatif des os reconnus dans la figure C. D: dentaire; Ecpt: ectoptérygoïde; Epmt: rangée externe de dents du prémaxillaire; ePdt: rangée externe de dents du prémentaire; iPdt: rangée interne de dents du prémentaire; iPmt: rangée interne de dents du prémaxillaire; mPdt: dents marginales du prémentaire.

posterior margin and ornamented with delicate ganoine ridges disposed parallel to the major axis of the scale. Dorsal and ventral scales rows composed of both, quadrangular and pear-shaped scales and ornamented with few sinuous ganoine ridges and in some cases with a marked straight median ridge.

Type species: *Jonoichthys challwa*.

Content: type species only.

Jonoichthys challwa gen. et sp. nov.

(Figs. 2–5, 7)

cf. *Belonostomus* Leanza and Zeiss, 1990 p. 177.

Belonostomus nov. sp. A Gouiric-Cavalli, 2013 p. 166–189.

Diagnosis: as for the genus.

Holotype: MOZ-PV 1747, an incomplete, robust, highly compressed, and three-dimensionally preserved specimen. The skull has the bones of the opercular series slightly displaced. The left pectoral fin is almost complete. The flank scales are articulated and in its original position. The dorsal and ventral scales rows are disarticulated. The abdominal

cavity is filled with few small hourglass shaped vertebral centra of a teleost fish.

Etymology: Generic name derives from the native Tehuelche voice 'Jono' which means sea. Specific name derives from the native Mapuche voice 'challwa' which means fish.

Remarks: MOZ-PV 1747 preserves its head and anterior body part. Unpaired fins are not preserved. Due to preservation, morphological description and meristic data are restricted to the anterior part of the fish. Most of the vertebrae and ribs are obscured by the squamation.

4.1. Description

4.1.1. Overall morphology

Fusiform, highly compressed, massive, large, and robust aspidorhynchiform. The robust head is moderately large and triangular, tapering forwards (Figs. 2–3). The orbit represents about the 9% of the head length and is located dorsally in the lateral face of the head. The 'rostrum' is well developed, representing the 50% of the head length. The

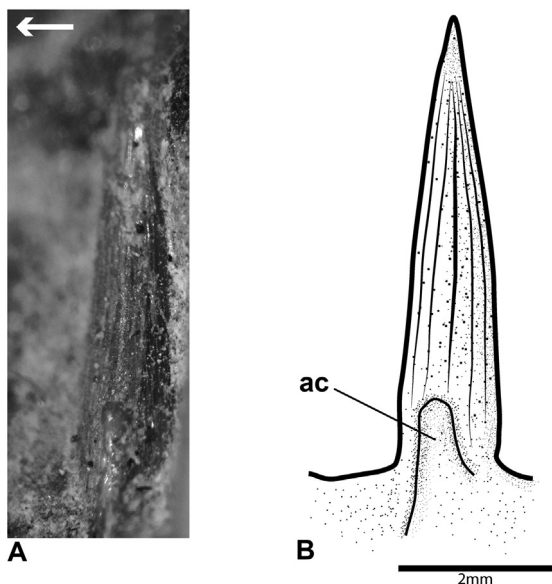


Fig. 5. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747. **A.** Detail of one middle tooth of the middle predentary tooth row. **B.** Interpretative drawing of figure A. ac: accessory cusp. The arrow point forward.

Fig. 5. *Jonoichthys challwa* gen. et sp. nov. holotype MOZ-PV 1747. **A.** Détail d'une dent de milieu de la rangée médiane de dents du prédentaire. **B.** Dessin interprétatif de la figure A. ac : cuspide accessoire. La flèche pointe vers l'avant.

suspensorium-lower jaw articulation is located posterior to the orbit. The upper jaw is slightly longer than the lower. There is a 'v' suture between predentary and dentary bones. The pectoral fins are incompletely preserved, placed close to the ventral margin of the body, and has few short and robust fin rays.

4.1.2. Braincase

The braincase is highly compressed and seems to be very well ossified. Except for the skull roof bones fused into a bony plate and part of the parasphenoid, no other bones of the braincase are observed.

4.1.3. Skull roof

The skull is highly compressed and its bones strongly ossified. Bones of the skull roof are covered by ganoine and weakly ornamented with ridges and scattered tubercles. Because of the lack of sutures between the rostral, parietals, postparietals, and dermopterotics, they are interpreted here as fused into a large skull roof bony plate (Fig. 3). Among aspidorhynchiforms the fusion of skull roof bones is widely distributed and different patterns of fusion are mentioned in the literature (Bartholomai, 2004; Brito, 1997; Maisey, 1991). However, in all the fusion patterns recognized, the rostral is never included together with the parietals, postparietals and dermopterotics. Due to the heavy ossification and thickness of the bones, no sensory canals have been recognized. The anterior-most part of the skull is composed of the 'rostrum', which is elongated and composed mainly of the fused tube-like premaxillae. Despite the bad preservation of the posterior region of

the skull roof the extrascapular (or supratemporal) commissure – separating the skull roof bony plate from the extrascapulars – is recognized and also the delicate suture between the extrascapulars. Each extrascapular is triangular and small. Posttemporals are partially preserved.

The right anterior nasal opening is delimited antero-ventrally by the nasal and by the compound skull roof bony plate dorsally. No supraorbital sensory canal is observed in the nasal bone.

4.1.4. Upper Jaw

Only the premaxilla and maxilla are preserved in the upper jaw. The premaxillae are fused into an acute 'rostrum', which slightly projects beyond the lower jaw. The total length of the premaxillae cannot be measured with certainty because its anterior portion is broken, although it seems not to extend much further. Each premaxilla is composed of two portions: a smooth internal part and a slightly ornamented external one. Premaxillary teeth are arranged in two rows: the external with tiny teeth that lack ornamentation and the internal row with comparative big conical teeth ornamented with longitudinal striations (Fig. 4A–B). Teeth of the internal row increase in size caudally. Premaxillary teeth are located over the entire oral surface of the bone.

MOZ-PV 1747 has an elongated, thin, and laterally compressed maxilla. It has a dorsal, low and rounded antorbital lamina. The maxillary teeth are thin, conical, tiny, and in some cases are curved forward (Fig. 4C–D). Teeth are evenly and spaced distributed over the maxillary bone. The maxilla extends to the middle portion of the orbit. Their anterior and posterior ends are slightly curved downward.

4.1.5. Lower Jaw

Predentary, dentary, and angular have been identified in the lower jaw. The anterior-most part of the lower jaw is represented by an unpaired predentary. This bone is long, triangular (widening backwards) in lateral view, toothed, and V shaped in cross section. It is linked with the dentary by a 'v' suture (with its apex pointing rostrally). The total length of the predentary is difficult to establish because its anterior-most distal portion is missing, but due to the sharpness of its front end, it probably did not extend much further. The predentary is shorter than the premaxilla and represents about 63% of the total dentary length. The predentary bears three tooth rows. The teeth of the marginal tooth row are ankylotized to the predentary; they are tiny, unornamented, closely arranged, and with a rounded apex (Fig. 4A–B). Lingual to that row, there are larger teeth, thinly ornamented with ridges and evenly spaced (Fig. 4A–B). Finally, there is a median predentary tooth row composed of comparatively large (ca. 5 mm) conical teeth that are evenly spaced over the predentary and having a conspicuous ornamentation consisting of vertical grooves (Fig. 4A–B). Each tooth of the median predentary tooth row is stout and, in labial position, bears a tiny rounded accessory cusp (Fig. 5). The teeth of the median tooth row increase in size posteriorly. The disposition of teeth and the number of tooth rows over the predentary bone seem to be unique to *Jonoichthys challwa* gen. et sp. nov.

The dentary is the major bone of the lower jaw. It is triangular, and low at the union with the prementary. Both dentary bones join anteriorly to form the knob that is recessed in the prementary. The mandibular sensory canal is located ventrally, and its trajectory is difficult to observe. The lateral surface of the dentary appears smooth and without visible ornamentation. The teeth are arranged in two rows over the dorsal (or dental) margin. The external (or marginal) tooth row is composed of small and thin teeth that considerably increase its width caudally. These teeth are closely arranged. Anterior teeth are unornamented but the posterior and bigger ones are delicately ornamented with longitudinal striations. Comparatively large teeth ornamented with vertical grooves compose the internal dentary tooth row; however, the teeth are difficult to observe because both maxilla and dentary are very close and also there is sediment covering it.

The angular forms the posteroventral and lateral wall of the lower jaw; it is located over the dentary and firmly sutured with it. The angular is triangular and without traces of mandibular sensory canal. A marked retroarticular process was not preserved.

The articulation between the lower jaw and suspensorium is placed posterior to the orbit.

4.1.6. Palatoquadrate and Suspensorium

Bones of the palatoquadrate are mostly hidden by bones of the cheek and upper jaw; however, because the maxilla is slightly out of place, the ectopterygoid is exposed. It is a laminated bone that bears conical and slightly posteriorly curved teeth larger than the maxillary ones. A relatively large bone located below the ventral part of the sclerotic ring is interpreted here as the entopterygoid (Fig. 3B).

4.1.7. Circumorbital bones

The circumorbital bone ring is represented by at least four infraorbitals, one partially preserved supraorbital, and an incomplete preserved dermosphenotic. Note that some degree of displacement of bones occurs in this area and it could be the case that infraorbitals of the right circumorbital ring are exposed (note, in Fig. 3B, the three elements below the large infraorbital 1). In addition, two (or three) suborbital plates and sclerotic bones are present.

Infraorbitals are rectangular and the infraorbital sensory canal is placed medio-ventrally. A different condition was observed in other aspidorhynchids examined in which the infraorbital sensory canal seems to run exactly through the middle part of the bone (e.g., SMNS 1957 339a, JM-ETT 49a). A bone interpreted here as the infraorbital 1 is elongated and large, has a thin anterior portion and an expanded posterior one; it is located ventral to the orbit and bears the infraorbital sensory canal. According to Brito (1997) among aspidorhynchids the first and last infraorbitals are the most developed; the infraorbital 1 the most elongated and the last one the highest (Fig. 3).

The supraorbital is partially preserved; it seems to be roughly rectangular. Its anterior margin is in contact with the nasal; the posterior one is in contact with the dermosphenotic, and dorsally it contact with the skull roof's bony plate.

Behind the eye there is an incompletely preserved, rather large bone that seems to be triangular; however its posterior portion is not preserved. No sensory canals could be recognized; however by position the bone could be a dermosphenotic or an infraorbital.

The suborbital 1 is large and roughly triangular. Posterior to it there are two complete (or one broken) plates. The ventral plate (or portion of a plate) is bigger than the dorsal. These bones could be interpreted as a broken suborbital 2 or as the suborbital 2 plus an accessory suborbital. Because that region of the skull is distorted due to preservation, borders between bones are difficult to establish with certainty. Note that depending on the specimens, the morphology and number of suborbitals can vary (Brito, 1997; Brito and Ebert, 2009). Suborbitals are ornamented with small ganoine tubercles.

Two, anterior and posterior, well-ossified sclerotic bones surrounding the eyeball form a complete sclerotic ring (Fig. 3). The internal sclerotic ring diameter is ca. 10 mm length and the external sclerotic ring diameter about 13 mm.

4.1.8. Opercular series

Opercular bones are placed posterior to the posterior margin of the skull roof plate. Bones of the opercular series shows some degree of displacement, distortion, and some of them are broken.

The operculum is well developed, having a straight anterior margin and a convex posterior one. This bone is raised probably due to escaping of gases during decay. Its posterior margin is damaged. The surface of the operculum is ornamented with delicate and thin striations and several tubercles. In the ventral-posterior portion of the operculum there is a piece of bone interpreted here as probably belonging to a portion of the partially preserved suboperculum.

The preoperculum, preserved slightly out of its original position, is 'L'-shaped; the ventral arm is relatively expanded and the dorsal one is narrow (Figs. 3, 6). The preopercular sensory canal is located close to the ventro-posterior border of the preoperculum; it is a single main canal without ventral sensory tubules branching from it. The dorsal and ventral portions of the preopercular sensory canal describe an angle slightly greater than 90°. Some aspidorhynchids e.g., *Aspidorhynchus sanzenbacheri* (e.g., JME-ETT 102), *Belonostomus* sp. (e.g., BSPG 1964-XXIII-518, JME-ETT 117, JME-ETT 118), *B. tenuirostris* (e.g., JM SOS 2846), and *B. muensteri* (e.g., Mbf. 1595 1-2) have a small, inverted 'U'-shaped dorsal branch just in front of the vertex formed by the dorsal and ventral arms of the main preopercular sensory canal. This branch is absent in MOZ-PV 1747.

4.1.9. Vertebral column

The vertebral column is located in the upper half of the body and the flank scales significantly cover it. However, in the abdominal region the flank scales are displaced, leaving visible two strongly compressed and smooth centra.

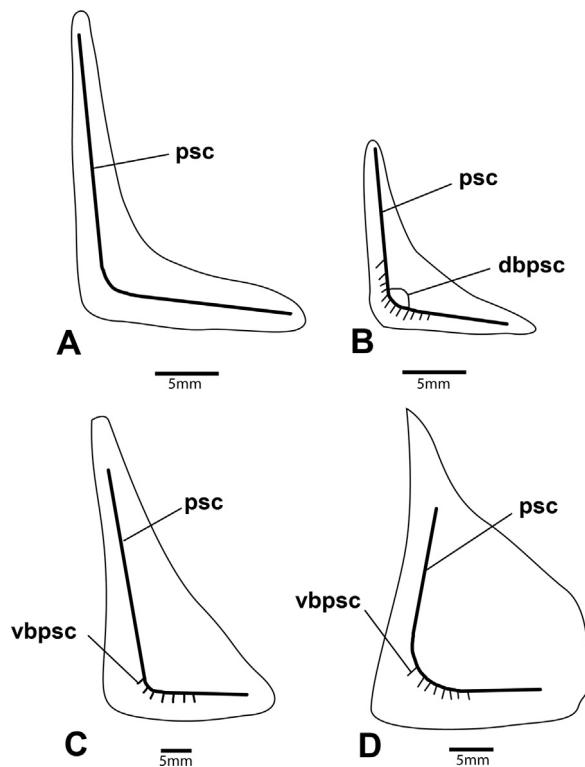


Fig. 6. Diagrammatic reconstruction of the preoperculum and preopercular sensory canals in Aspidorhynchiformes. **A.** *Jonoichthys challwa* gen. et sp. nov. **B.** *Belonostomus*. **C.** *Aspidorhynchus*. **D.** *Richmondichthys* and *Vincitifer*. dbpsc: dorsal branch of the preopercular sensory canal; psc: main preopercular sensory canal; vbpsc: ventral sensory tubules of the main preopercular sensory canal.

Fig. 6. Reconstruction schématique du préopercule et des canaux sensoriels préoperculaires chez les Aspidorhynchiformes. **A.** *Jonoichthys challwa* gen. et sp. nov. **B.** *Belonostomus*. **C.** *Aspidorhynchus*. **D.** *Richmondichthys* et *Vincitifer*. dbpsc: branche dorsale du canal sensoriel préoperculaire; psc: canal sensoriel préoperculaire principal; vbpsc: tubules sensoriels ventraux du canal sensoriel préoperculaire principal.

4.1.10. Scales

Typically, aspidorhynchiform scales are ganoid-type, specifically lepisosteoid-type (Brito and Meunier, 2000; Schultze, 1996), in which the basal bone is covered by ganoin lacking elasmodine and dentine (Sire et al., 2009). However, most *Aspidorhynchus* species lack ganoin and others have a variable number of ganoin layers over its scales (Brito, 1997; Schultze, 1966).

The ornamentation of the scales may vary among genera and even among species of the same genus. Ganoin tubercles are well developed in *Vincitifer* and absent in aspidorhynchids, with a thin layer of ganoin covering the scales, and in juvenile specimens (Brito and Meunier, 2000). Also, the width and density of ganoin tubercles over the scales seem to have importance at the generic level. To date, odontodes are only present in some scales of *Vincitifer* (Brito, 1997; Brito and Meunier, 2000). Also the posterior margin of the flank scales can be smooth (*Belonostomus*, *Aspidorhynchus*) or serrated (*Vincitifer* and *Richmondichthys*).



Fig. 7. *Jonoichthys challwa* gen. et sp. nov. MOZ-PV 1747. Magnification of the lateral section of the fish to show the flank scale rows and its ornamentation.

Fig. 7. *Jonoichthys challwa* gen. et sp. nov. MOZ-PV 1747. Agrandissement de la section latérale du poisson pour montrer les rangées d'écailles de flanc et leur ornementation.

The scales of MOZ-PV 1747 are ganoid-type. They are arranged in three series of flank scale rows. It seems that the dorsal scales are arranged in 2 or 3 rows and the ventral scales in at least 4 or 5 rows. The bulk of preserved scales in dorsal and ventral rows are highly disarticulated. Scales of the dorsal row are more or less quadrangular; also at least 4 pear-shaped scales are preserved. Ventral scale rows are composed of quadrangular scales.

The flank scales (Fig. 7) are rectangular, higher than wide, and have a peg and socket articulation. Flank scales are arranged in three longitudinal rows; the scales of the middle row are higher (three and a half times) than those immediately above and below. Scales of the middle row include the lateral line. Ganoin is preserved in all dorsal and ventral scales and in a few flank scales. Ventral and dorsal scales are strongly ornamented with sinuous ganoin ridges, and the pear-shaped scales have a median keel. Flank scales are smooth or softly ornamented with delicate and parallel ridges, also having one medium (or slightly offset) keel. The free posterior margin of the flank scales is smooth.

The arrangement of flank scale rows in *Jonoichthys challwa* gen. et sp. nov., seems to have similarity with the present in *Vincitifer*, *Richmondichthys* and *Belonostomus*, in which the middle row of flank scales is higher than those immediately above and below (Fig. 8). However, depending on the species, in *Vincitifer* and *Belonostomus*, scales of the middle flank scale row are between two to five times higher than the immediately upper and lower ones (Brito, 1997; Schultze and Stöhr, 1996). In *Richmondichthys* scales of the middle scale row of flank scales are five times higher than scales of the lower flank scale (Bartholomai, 2004).

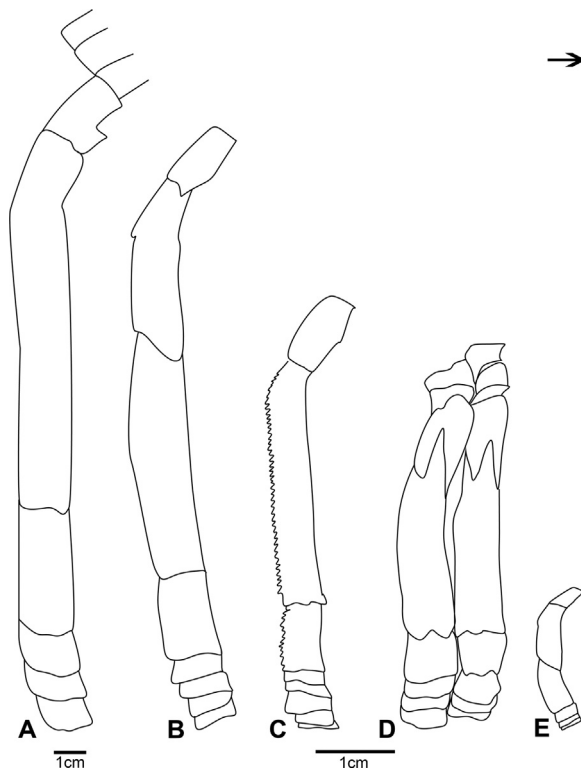


Fig. 8. *Jonoichthys challwa* gen. et sp. nov. MOZ-PV 1747. Diagrammatic drawing of scales to show the disposition and relation between the scales in Aspidorhynchiformes. **A.** *Richmondichthys* (modified from Bartholomai, 2004). **B.** *Aspidorhynchus* (modified from Schultze and Stöhr, 1996). **C.** *Vinctifer* (modified from Schultze and Stöhr, 1996). **D.** *Jonoichthys* n. gen. **E.** *Belonostomus* (modified from Schultze and Stöhr, 1996).
Fig. 8. *Jonoichthys challwa* gen. et sp. nov. MOZ-PV 1747. Dessin schématique d'écaillles pour montrer la disposition et la relation entre les écaillles chez les Aspidorhynchiformes. **A.** *Richmondichthys* (modifié d'après Bartholomai, 2004). **B.** *Aspidorhynchus* (modifié d'après Schultze et Stöhr, 1996). **C.** *Vinctifer* (modifié d'après Schultze et Stöhr, 1996). **D.** *Jonoichthys* n. gen. **E.** *Belonostomus* (modifié d'après Schultze et Stöhr, 1996).

5. Gondwanan aspidorhynchid diversity

The understanding of the aspidorhynchiformes as a whole is still incomplete. The study of the Gondwanan aspidorhynchids was mainly associated with the quality of preservation of their members and, to date the better-preserved and consequently known material comes from the Cretaceous of Brazil (e.g., Brito, 1997; Maisey, 1991).

Aspidorhynchus and *Belonostomus* are mainly known from the Northern Hemisphere. However, *Aspidorhynchus* was reported in the Upper Jurassic of Cuba and Antarctica (Brito, 1997; Richter and Thomson, 1989), the last one is a partially preserved specimen with controversial characteristics. It was considered as *Vinctifer* by Schultze and Stöhr (1996) and as *Aspidorhynchus* by Brito (1997), so it would require a revision of the assignation when more specimens become available for study. The Gondwanan record of *Belonostomus* is limited to marine Upper Jurassic and continental Upper Cretaceous sediments of Argentina (Bogan et al., 2011; Casamiquela, 1992; Cione et al., 1987; Gouiric-Cavalli, 2013; Leanza and Zeiss, 1990),

Upper Jurassic sediments of Chile (Brito and Suárez, 2003), Lower Cretaceous of Brazil (Brito and Yabumoto, 2011), Upper Cretaceous of Venezuela, Lebanon, and Morocco (Brito and Suárez, 2003; Costa, 1853, 1854–1856; Forey et al., 2003; Moody and Maisey, 1994). According to Arratia (2015) more findings are needed to support the assignation to *Belonostomus* of the Chilean material.

The continental Argentinian materials deserve attention: four fragments of jaw bones (two premaxillae and two predentaries) were reported from continental Upper Cretaceous sediments of the Coli-Toro Formation in Río Negro, Argentina by Casamiquela (1984, 1992). Casamiquela (1992) assigned that material to *Belonostomus longirostris* Lambe, 1902. Recently, isolated and fragmentary material from continental Upper Cretaceous (Campanian–Maastrichtian) deposits of the Allen Formation in northern Patagonia was assigned to a new species, *B. lamarquensis* Bogan, Taverne and Agnolin, 2011. Bogan et al. (2011) refer the Chilean material previously described by Brito and Suárez (2003) and Casamiquela's (1992) material as probably belonging to the new species. Also, the neurocranium (MACN 1078) previously described by Brito (1997) as belonging to *Vinctifer* sp. is referred to *B. lamarquensis*. However, the only diagnostic character exhibited by *B. lamarquensis* is the ornamentation of the isolated flank scales and there is no reason to refer the predentaries, premaxillae, and/or neurocranium to this new species. The authors mentioned that bones of the neurocranium in *B. lamarquensis* are strongly fused like in all *Belonostomus* species. However, this is the general condition showed by aspidorhynchids with the exception of *Aspidorhynchus* species and young *Vinctifer* specimens in which bones are unfused (Bartholomai, 2004; Brito, 1992, 1997). In this context, the new species *B. lamarquensis*, as well as the designation of other fragmentary material to that species, should be reviewed and supported with better materials.

Before this study, two unambiguous Gondwanan aspidorhynchiforms genera were reported: *Richmondichthys* from the Lower Cretaceous of Australia (Bartholomai, 2004) and *Vinctifer* from Lower Cretaceous of Brazil (e.g., Brito, 1988, 1997; Maisey, 1991). Some poorly preserved and/or fragmentary *Vinctifer* specimens were also reported from the Late Jurassic and Lower Cretaceous of Antarctica (Arratia et al., 2004; Schultze and Stöhr, 1996), Lower Cretaceous Venezuela and Colombia (Brito, 1997; Brito and Yabumoto, 2011; Schultze and Stöhr, 1996), and probably from the Lower Cretaceous of Africa (Taverne, 1969; Brito and Yabumoto, 2011).

To date, two new genera have been added: the new genus and species from the Upper Cretaceous of Chile, recently described by Arratia (2015) and previously reported and figured in Arratia and Schultze (1999) and *Jonoichthys* from the Upper Jurassic of the Neuquén Basin (this contribution).

As can be seen from preceding paragraphs, in the Mesozoic of Gondwana aspidorhynchids are diverse (Fig. 9). The Jurassic Gondwanan representatives are *Aspidorhynchus*, *Vinctifer*, *Belonostomus* and *Jonoichthys*. Meanwhile, the Cretaceous representatives are *Richmondichthys*, *Belonostomus*, *Vinctifer* and the new Chilean genus.

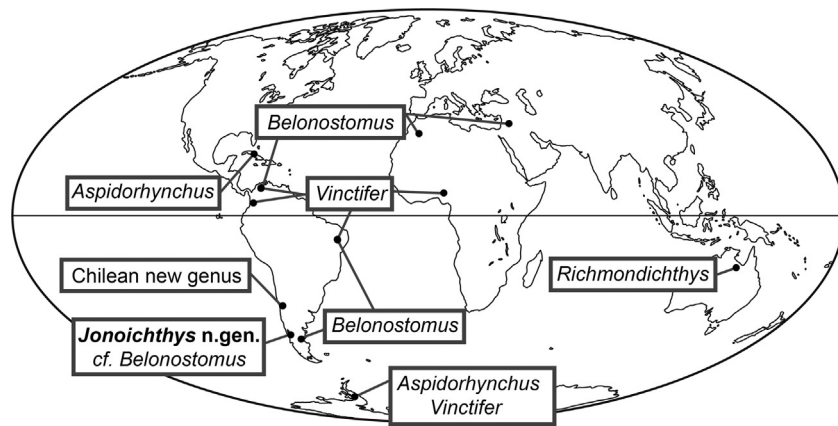


Fig. 9. Distribution of Aspidorhynchiformes in Gondwana.

Fig. 9. Répartition des Aspidorhynchiformes dans le Gondwana.

6. Discussion and final remarks

Jonoichthys challwa gen. et sp. nov. is assigned to Aspidorhynchiformes because it shows characters of the order like the presence of a 'rostrum' formed mainly by fused premaxillae; prementary as an accessory bone in the lower jaw; three rows of flank scales, etc. *Jonoichthys challwa* gen. et sp. nov. seems to share characters with *Belonostomus* and *Vinctifer*. For instance, it shares with *Belonostomus* the presence of a long rostrum formed mainly by fused premaxillae; presence of a long prementary; suture between dentary and prementary in 'v' (commonly widespread among Jurassic forms of *Belonostomus*). It shares with *Vinctifer* the presence of a massive, strongly ossified head and the robust and deep body. Some common characters to both, *Vinctifer* and *Belonostomus*, are present in *J. challwa* gen. et sp. nov. like the presence of three longitudinal rows of flank scales having one scale row with more developed, higher, scales. However, the patterns showed by these genera are slightly different (Schultze and Stöhr, 1996: f. 6).

Jonoichthys challwa gen. et sp. nov. is characterized by a unique character combination from where several characters are autapomorphies. *Jonoichthys* has a robust and deep body, a long prementary bone with three tooth rows (versus two tooth rows in *Belonostomus* and *Aspidorhynchus*, and lack of teeth in *Vinctifer*, *Richmondichthys*, and the new Chilean genus). *Jonoichthys* has a labial rounded accessory cusp in teeth of the median prementary row (versus sharpened pointed accessory cusp posteriorly located in some *Belonostomus* or the lack of an accessory cusp in *Aspidorhynchus* and other *Belonostomus* species). *Jonoichthys* has a marked 'L'-shaped preoperculum (versus triangular preopercle in *Vinctifer*, *Richmondichthys*, and *Aspidorhynchus* and slightly triangular in *Belonostomus*). *Jonoichthys* has a single and simple sensory preopercular canal (versus branched preopercular sensory canal in other aspidorhynchiforms). *Jonoichthys* has a skull roof plate in which the rostral is fused together with the parietals, postparietals and dermopterotics (versus rostral never participating of the skull roof plate in other aspidorhynchids).

The presence of a new endemic aspidorhynchid in the Late Jurassic of Argentina is interesting because supports the hypothesis that shows that the group was settled in both, Northern and Southern Hemispheres in Jurassic times. Also it shows that, although their study in the Southern Hemisphere is still embryonic, its diversity was greater (four genera in Gondwana vs. two in Laurasia) than previously expected.

The presence of aspidorhynchiformes in the Upper Jurassic of Argentina and Antarctica and in the Upper Jurassic of Europe supports the connection between Tethys and the Palaeopacific trough marine corridors like the Hispanic Corridor. This report plus data of previous western and eastern Palaeopacific discoveries show the relevance of this region as diversification zone showing a high morphological diversity in the West Palaeopacific area during the Mesozoic supporting previous hypothesis that shows that the area was probably a site of origin of some teleostean clades (see Arratia, 2004, 2008b).

A further detailed study of the Gondwanan aspidorhynchids could be very interesting and could bring important information related to biogeography, diversification, taxonomy and phylogeny of this group of actinopterygian. It will also help to clarify the relationships of this new genus with other members of the family.

The presence of *Jonoichthys challwa* gen. et sp. nov. together with the pachycormiform *Notodectes argentinus* Dolgopol de Saez, 1949 (Gouiric-Cavalli and Cione, in press) in the Late Jurassic of Argentina is noticeably because, as the Late Jurassic teleosts previously reported from the southern continents (see Arratia, 1994, 2008b), both teleosteomorphs are endemic to the Neuquén Basin, showing an increasing and until now poorly known morphological diversity of the area.

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