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NOTODECTES IS THE FIRST ENDEMIC PACHYCORMIFORM GENUS (OSTEICHTHYES, ACTINOPTERYGII, PACHYCORMIFORMES) IN THE SOUTHERN HEMISPHERE

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ABSTRACT—Jurassic fishes from the Southern Hemisphere are poorly known in comparison with those of the Northern Hemisphere. The Tithonian (Late Jurassic) deposits of Argentina have yielded a rich and taxonomically diverse ichthyofauna. However, these fishes have been only partially described and need to be revised or studied. In this paper, the putative ichthyodectiform actinopterygian *Notodectes argentinus* is redescribed. The holotype comes from the Vaca Muerta Formation, in the southwestern part of Mendoza Province, Argentina. It consists of an incomplete, partially articulated skull in which some of the bones are preserved in three dimensions. The specimen has a unique character combination that allows us not only to diagnose the genus *Notodectes* but also confirm that it is a member of the actinopterygian order Pachycormiformes. At present, *Notodectes* represents the first endemic pachycormiform from the Southern Hemisphere and the first specimen found in Mendoza Province (northwestern region of the Neuquén Basin). Also, *Notodectes* is the first fast-swimming and clearly ichthyophagous pachycormid reported from the Jurassic of South America.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Jurassic marine fishes are well known in the Northern Hemisphere, especially in Europe. In contrast, the Jurassic marine ichthyofaunas of the Southern Hemisphere are far less well known. The Oxfordian (Late Jurassic) fishes from Chile are an important exception (e.g., Arratia, 2008). In Argentina, most of the marine Jurassic fishes have been found in the Vaca Muerta and Picún Leufú formations of Neuquén and Mendoza provinces, where they are the most abundant and diverse vertebrates (Arratia and Cione, 1996; Gouiric-Cavalli and Cione, 2009, 2011, 2013a, 2013b). Some of those specimens were studied by Dolgopol de Saez (1939, 1940a, 1940b, 1949) who identified a new genus and several new species based on fragmentary material. These identifications were later briefly discussed by Cione and Pereira (1990). Recently, these and many other undescribed materials were studied in detail within a Ph.D. dissertation (Gouiric-Cavalli, 2013). Several new taxa as well as new taxonomic interpretations and phylogenetic studies were the principal results of this research (Gouiric-Cavalli and Cione, 2009, 2011, 2013b; Gouiric-Cavalli, 2013).

One of the reviewed specimens was the holotype (and only known specimen) of *Notodectes argentinus* Dolgopol de Saez, 1949. The material was collected by Armando Leanza near the La Valenciana Mine, southern Mendoza Province, Argentina (Fig. 1). The fossil-bearing strata are currently considered to be Tithonian (Late Jurassic) beds of the Vaca Muerta Formation (Cione and Pereira, 1990).

Notodectes argentinus was originally described as an ichthyodectiform (Teleostei, Actinopterygii), mostly because of similarities in the shape and disposition of teeth. However, Cione and

Pereira (1990) revised the holotype and suggested that it was more likely to be a pachycormiform actinopterygian.

Pachycormiformes is an order of actinopterygian fishes that is restricted to the Mesozoic, ranging from the Lower Jurassic (e.g., *Pachycormus* Agassiz, 1833, and *Saurostomus* Agassiz, 1833, from the Toarcian of Holzmaden, southern Germany [Wenz, 1968]) to the uppermost Cretaceous (e.g., *Protosphyraena* Leidy, 1857, and *Bonnerichthys* Friedman et al., 2010, from Ciply-Malogne Phosphatic Chalk Formation at Ciply, Mons Basin, Belgium, and Tierra Loma Member of the Moreno Formation, Fresno County, California [Friedman et al., 2010, 2013; Friedman, 2012a]).

Pachycormiformes includes medium-sized species (from 40 to 111 cm total length) such as *Pachycormus* and *Orthocormus* Weitzel, 1930, to large fishes (from 500 to 1600 cm total length) such as *Bonnerichthys* and *Leedsichthys* Woodward, 1889. Many have been interpreted as fast-swimming, open-water fishes due to their hydrodynamic general body shape, well-developed temporal boss, lack of scales or tiny ones with reduced (or even absent) ganoin, powerful fins, especially the pectoral scythe-like fins, and by the presence of a large caudal fin with many rays oriented almost vertically and a very well-developed, hypural plate (Lambers, 1992). The medium-sized Pachycormiformes were ichthyophagous, which could have competed with some marine reptiles such as ichthyosaurs and small crocodyliforms (Gouiric-Cavalli, 2013). *Saurostomus* and *Pachycormus* have also been demonstrated to have fed on coleoids and ammonites (Wild, 1994; Prikryl et al., 2012; Thies and Hauff, 2012). The medium-sized pachycormiform *Ohmdenia* Hauff, 1953, was recently reviewed and ecologically reinterpreted (see Friedman, 2012b). In contrast, the large forms have been interpreted as suspension-feeders, probably being comparatively slower swimmers (Liston, 2008; Liston et al., 2013).

In this paper, we describe in detail the holotype of *Notodectes argentinus*, provide a generic diagnosis, and confirm that it corresponds to the order Pachycormiformes. We also report the first

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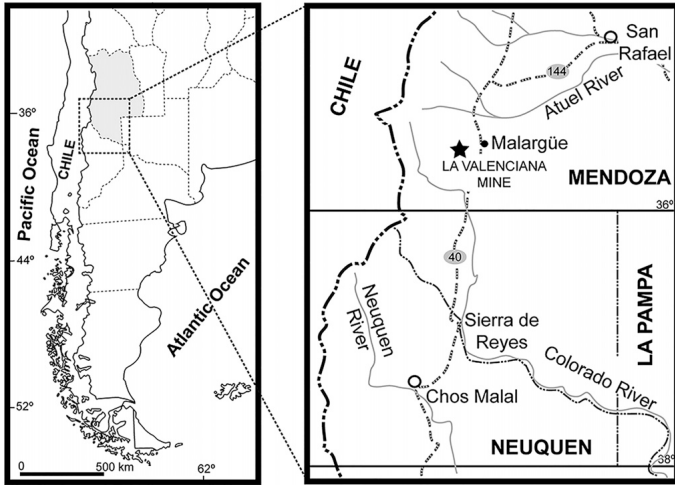


FIGURE 1. Map of La Valenciana Mine in Mendoza Province. The star indicates the fossil type locality.

endemic pachycormiform from the Southern Hemisphere, attributing its endemism to probable ecological constraints.

Institutional Abbreviations—**BSPG**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; **JM-E**, Jura Museum Eichstätt (SOS indicates that the fish was recovered in the Solnhofen Limestone), Eichstätt, Germany; **MB**, Museum für Naturkunde, Leibniz-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, Germany.

Anatomical Abbreviations—**a.c.**, acrodin cap; **ang.**, angular; **bi.**, bivalve; **ch.**, ceratohyal; **dpt.**, dermopterotic; **dsph.**, dermosphenotic; **ect.**, ectethmoid; **epb.**, epibranchial; **l.D.**, left dentary; **l.hyo.**, left hyomandibula; **l.Mx.**, left maxilla; **mpt.**, metapterygoid; **m.sc.**, mandibular sensory canal; **opp.**, opercular process; **P.**, parietal (= frontal of the traditional terminology [see Schultze, 2008]); **pmx.**, premaxilla; **Pp.**, postparietal (= parietal of the traditional terminology [see Schultze, 2008]); **r.D.**, right dentary; **rdem.**, rostrodermethmoid; **r.hyo.**, right hyomandibula; **r.Mx.**, right maxilla; **sang.**, surangular; **sc.**, sensory canal; **scl.**, sclerotic ring.



FIGURE 2. Photograph of the holotype of *Notodectes argentinus* Dolgopod de Saez, 1949 (MLP 48-1-1-1) in left lateral view. Scale bar equals 20 mm.

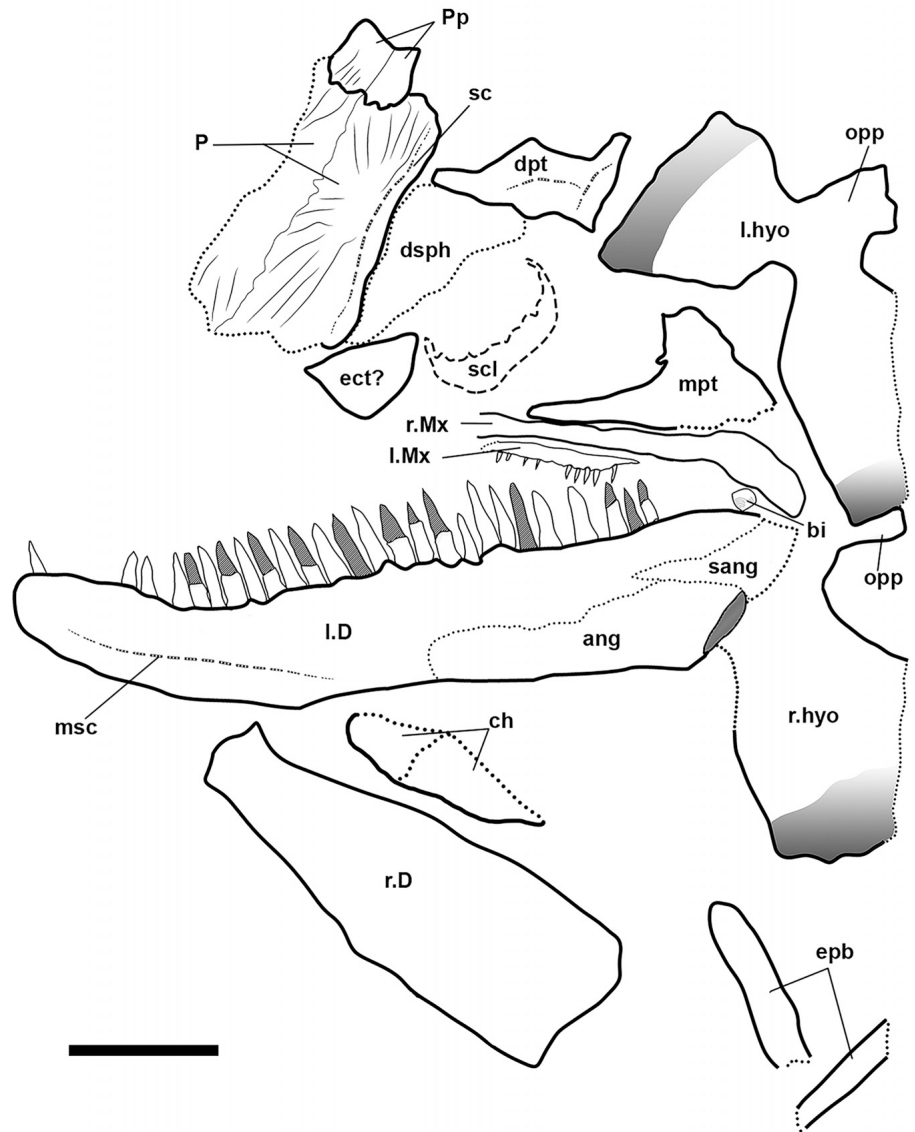


FIGURE 3. Interpretative drawing of *Notodectes argentinus* Dolgopol de Saez (MLP 48-1-1-1) in left lateral view. **Abbreviations:** ang, angular; bi, bivalve; ch, ceratohyal; dpt, dermopterotic; dsph, dermosphenotic; ect?, ectethmoid? epb, epibranchial; l.D, left dentary; l.hyo, left hyomandibula; l.Mx, left maxilla; mpt, metapterygoid; msc, mandibular sensory canal; opp, opercular process; P, parietal; Pp, postparietal; r.D, right dentary; r.hyo, right hyomandibula; r.Mx, right maxilla; sang, surangular; sc, supraorbital sensory canal; scl, sclerotic ring. Scale bar equals 20 mm.

COMPARATIVE MATERIAL AND METHODS

Methods

The type material of *Notodectes argentinus* (MLP 48-1-1-1) was prepared specifically for this study. The tool used was a Microjack no. 5, and the specimen was studied under hand lenses and using a Zeiss Stemi 2000-C stereomicroscope. The drawings were made under the Leica Wild M28 stereomicroscope with attached camera lucida and based on photographs, but each feature was checked under hand lens and stereomicroscope (where possible) to avoid the possibility of misinterpretations arising from the photographs.

Comparative Material

For a list of studied pachycormiforms, see Supplementary Data 1. For a complete list of the material used in comparative studies, see Gouiric-Cavalli (2013). Due to the large size of some of the pachycormiforms used in comparisons, these specimens were studied using high-magnification hand lenses and photographs of each complete specimen and of its particular bones.

Specimens mentioned in the text and figures are identified by their catalog numbers.

In Figure 6 we do not include '*Hypsocormus*' *macrodon* (Wagner, 1858) given the controversy of this species (see the discussion in Lambers, 1992). Similarly, we do not include *Prosauropsis* Sauvage, 1894, because no holotype is known (see Wenz, 1968, and Lambers, 1992, for discussion).

Terminology

The terminology of specialized structures in pachycormiforms, for example, rostrodermethmoid and temporal boss, follows Lambers (1992). The skull roof bones are named according to the terminology based on homology of the bones (e.g., Westoll, 1943; Schultze, 2008). When referring to the tooth caps (or tooth tips) present in *Notodectes*, we use the term acrodin following other morphologists (Ørvig, 1978; Patterson, 1982; Schultze, 1993). However, the interpretation and distinction between enamel and enameloid remains unclear (see Grande and Bemis, 1998; Sire et al., 2009).

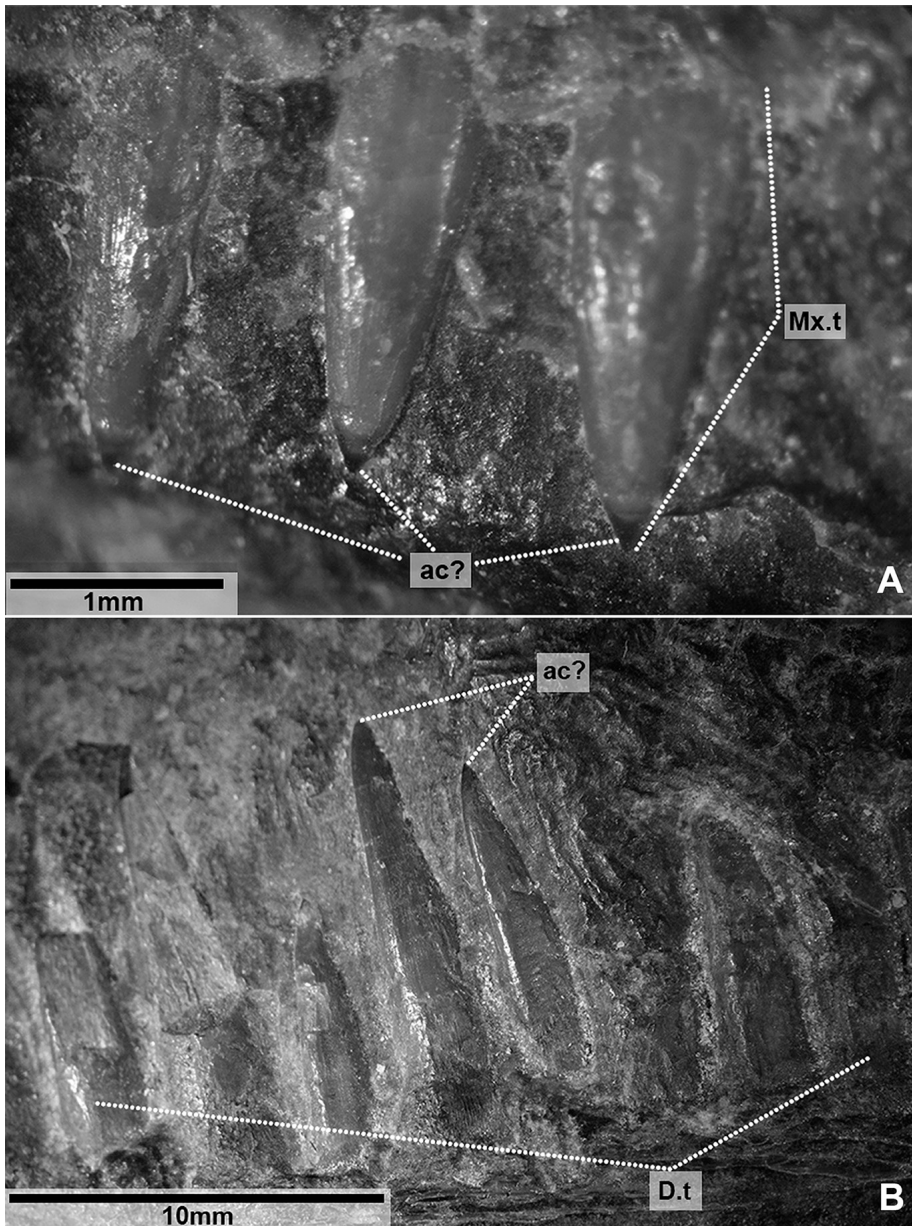


FIGURE 4. Holotype of *Notodectes argentinus* Dolgopol de Saez (MLP 48-1-1-1), details of the teeth in upper and lower jaws. **A**, upper jaw and maxillary teeth; **B**, lower jaw and dentary teeth. **Abbreviations:** **ac?**, acrodin cap?; **D.t**, dentary tooth; **Mx.t**, maxillary tooth.

GEOLOGIC SETTING

The holotype was collected in the “margas negras del Tithoniano, mina La Valenciana al Oeste de Malargüe, Provincia de Mendoza, Argentina” (Tithonian black marls, La Valenciana Mine, West of Malargüe, Mendoza Province [Dolgopol de Saez, 1949:450]; Fig. 1). However, in the original publication, there is an inconsistency relating to the stratigraphic provenance. Dolgopol de Saez (1949:449) wrote, “el holotipo fue colectado en la mina La Valenciana, la cual está ubicada estratigráficamente en un horizonte inmediatamente inferior al neocomiano” (the holotype was collected in La Valenciana Mine, which is stratigraphically located in a horizon immediately below the Neocomian). Nevertheless, the title of the publication, “Peces Cretácicos de Mendoza y Chubut” (Cretaceous fishes from Mendoza and Chubut), could be interpreted as the author believing that the fossil-bearing rocks were Cretaceous, and not Jurassic in age.

For this reason, the stratigraphic and geographic occurrence is emended as follows: Vaca Muerta Formation, Mendoza Group, Tithonian (Late Jurassic). Casa Pincheira (35°54'S, 69°90'W), near to the La Valenciana Mine in the middle part of the Malargüe River Basin, Mendoza, Argentina (Parent, 2003).

SYSTEMATIC PALEONTOLOGY

ACTINOPTERYGII Cope, 1887

NEOPTERYGII Regan, 1923

PACHYCORMIFORMES Berg, 1937

PACHYCORMIDAE Woodward, 1895

NOTODECTES Dolgopol de Saez, 1949

NOTODECTES ARGENTINUS Dolgopol de Saez, 1949
(Figs. 2–5A)

Type Species—*Notodectes argentinus* Dolgopol de Saez, 1949.

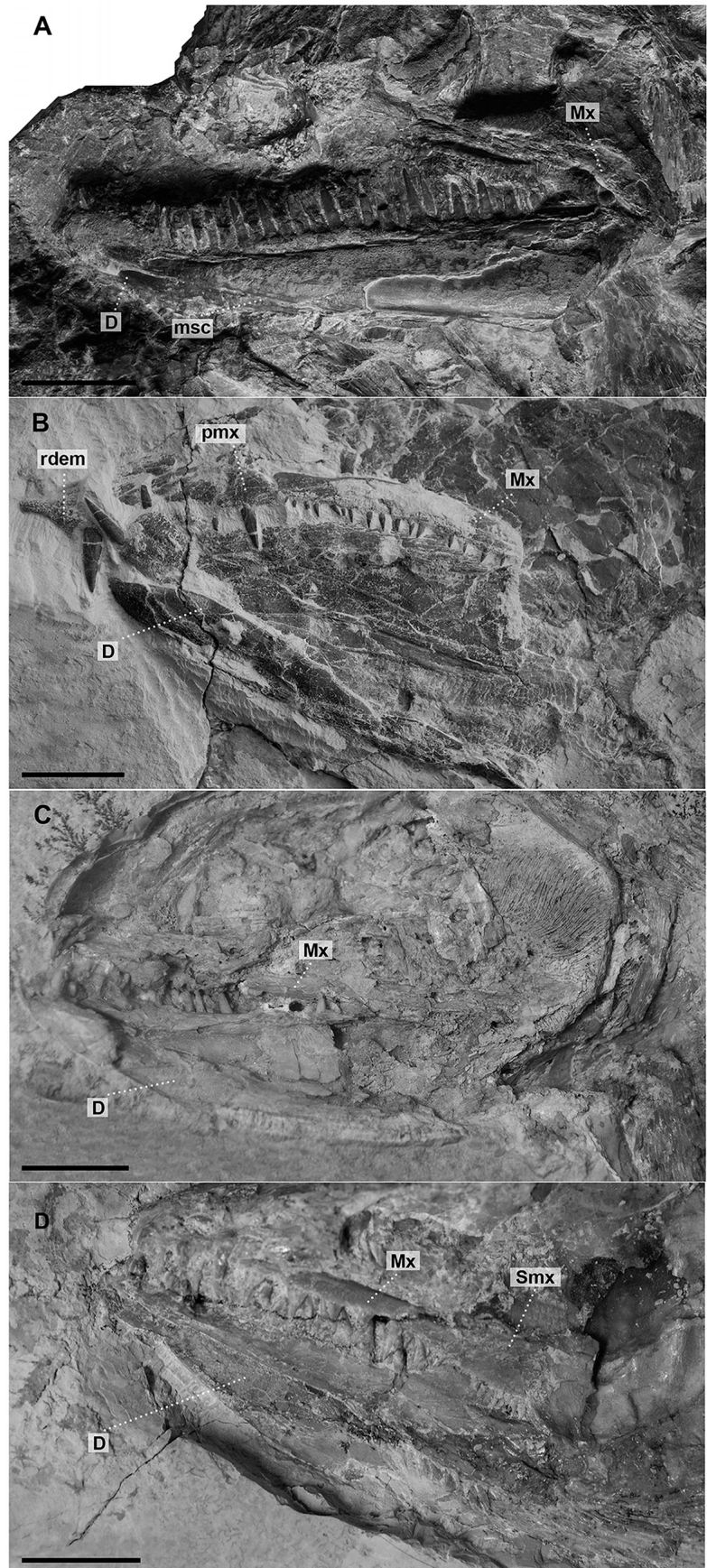


FIGURE 5. Bones of the head in four different pachycormiforms. **A**, *Notodectes argentinus* Dolgopol de Saez, 1949 (MLP 48-1-1-1); **B**, *Orthocormus* sp. (JMScha 2418); **C**, *Hypsacormus insignis* Wagner, 1860 (holotype BSPG ASVI 4b, reversed image); **D**, *Hypsacormus* sp. (BSPG 1964 XXIII 542). **Abbreviations:** **D**, dentary; **msc**, mandibular sensory canal; **Mx**, maxilla; **pmx**, premaxilla; **rdem**, rostrodermethmoid; **Smx**, supramaxilla. All scales bar equal 20 mm.

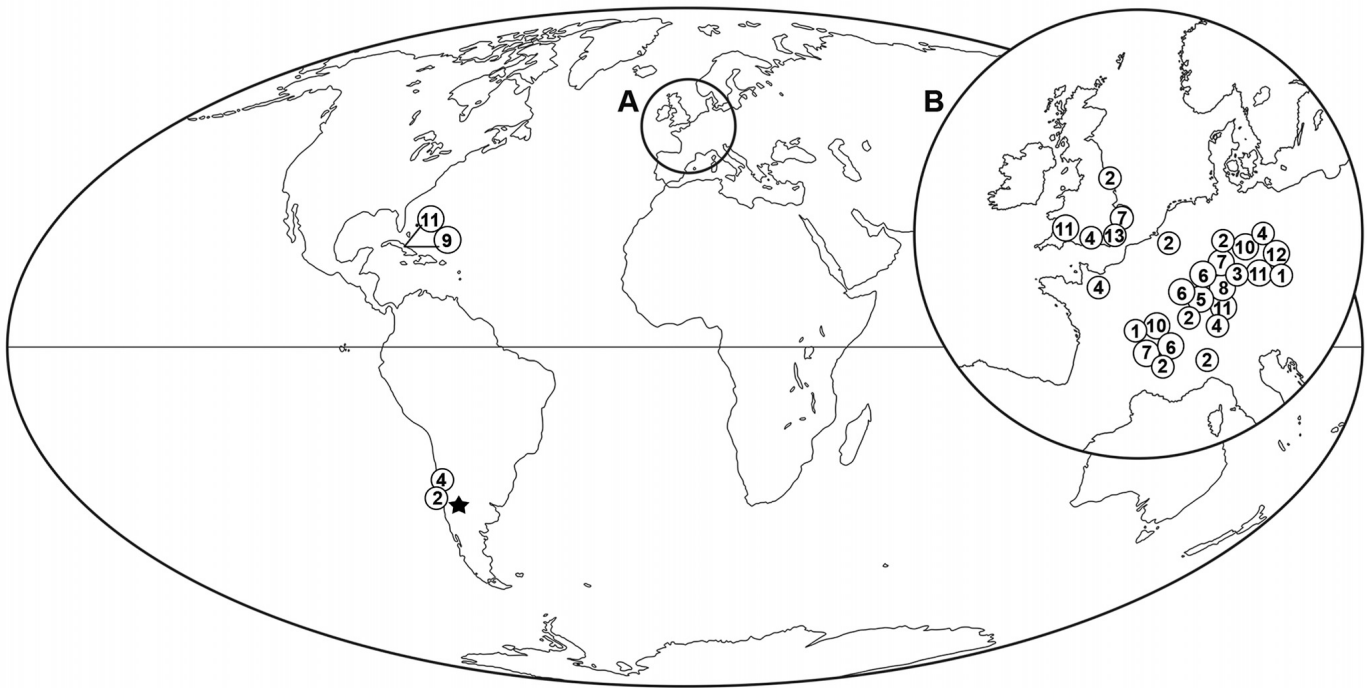


FIGURE 6. Distribution of Jurassic pachycormid genera. **B** is a detail of **A**. Numbers indicate pachycormid genera: **1**, *Orthocormus*, Upper Jurassic of France and Germany; **2**, *Pachycormus*, Lower Jurassic of France, Luxembourg, England, Belgium, Italy, and Germany and Upper Jurassic of Chile; **3**, *Ohmdenia*, Lower Jurassic of Germany; **4**, *Leedsichthys*, Middle to Upper Jurassic of England, France, Germany, and Chile; **5**, *Haasichthys*, Lower Jurassic of Luxembourg; **6**, *Euthynotus*, Lower Jurassic of France, Luxembourg, and Germany; **7**, *Saurostomus*, Lower Jurassic of France, England, and Germany; **8**, *Pseudoasthenocormus*, Upper Jurassic of Germany; **9**, *Eugnathides*, Upper Jurassic of Cuba; **10**, *Hypsocormus*, Upper Jurassic of France and Germany; **11**, *Sauropsis*, Lower Jurassic of Luxembourg, Lower and Upper Jurassic of Germany; Middle Jurassic of England; Upper Jurassic of Cuba; **12**, *Asthenocormus*, Upper Jurassic of Germany; **13**, *Martillichthys*, Middle Jurassic of England. For information about the precise localities of each genus, see Delsate, 1999a, 1999b; Lambers, 1992; Liston, 2010; Friedman, 2012b, and the literature cited therein. The black star indicates the approximate area of the type locality of *Notodectes*.

Holotype—MLP 48-1-1-1 (Fig. 2); an incomplete partially articulated skull, and fragments of the branchial apparatus. Some bones are three-dimensionally preserved.

Diagnosis—(Based on a unique combination of characters.) Pachycormidae without a clear or very well-developed (= protruded) temporal boss; small postparietals contacting in midline; parietals strongly ornamented with both wide and thin ridges radiating from the ossification center and with scattered, delicate tubercles; strong hyomandibulae with a very well-developed opercular process; posterior portion of the maxilla with conical and small teeth uniformly distributed; maxillary teeth ornamented with delicate ribs and with a cap, probably of acrodin; preserved maxillary teeth representing about 22% of the total length of dentary ones [*]; dentary with a well-developed anterior curvature; single row of very large teeth in the lower jaw; the length of each dentary tooth representing about 8–11% of the total length of the dentary; almost all dentary teeth with the same size and proportions (height/width); some dentary teeth perpendicularly directed, but most of them inclined forward (between 75° and 83°) [*]; closely arranged dentary teeth [*]; some dentary teeth lingually curved [*]; crown of dentary teeth with a circular base and mesiodistal oval section [*]; some dentary teeth with a depression in the medial region of the crown [*]; dentary with at least one small, conical, and slightly procumbent tooth. Characters identified with an asterisk [*] are unique among pachycormids.

Preservation—The holotype of *Notodectes argentinus* (Fig. 2) is partially preserved in a hard, black concretion. Some bones are articulated and preserved in three dimensions. Due to

postmortem deformation, the skull roof bones are displaced and exposed in dorsal view. Some bones of the skull roof are lost (i.e., rostrodermethmoid, supratemporal, and associated bones). The anterior portion of the maxilla is missing; the lower jaws are relatively well preserved, the left dentary only lacking its posterior-most part. The right dentary is partially preserved and in ventral view. No opercular bones are preserved. The suspensorium is represented by the right and left hyomandibulae and the left metapterygoid. The hyoid and branchial arches are represented by a ceratohyal and at least two epibranchials. The orbital series is represented by the impression of the left dermosphenotic. The other side of the fossil has several impressions of bivalves, ammonites, and isolated trace fossils (cylindrical smooth-walled burrows without branching that in some cases are distally curved).

DESCRIPTION

Skull Roof

The paired parietals are long and wide, forming a great part of the skull roof. Both bones are displaced from their original position and exposed in dorsal view (Figs. 2, 3). The rostrodermethmoid is missing. The right parietal is poorly preserved, whereas the left one only lacks its anterior-most part. The suture between parietals is smooth. Parietals are ornamented, with both wide and thin ridges, as well as scattered, delicate tubercles. Laterally, the left parietal meets the dermosphenotic in a long, almost straight suture.

The left dermosphenotic is preserved as an impression on the matrix (Fig. 2). As in most pachycormids, it is roughly triangular and borders the orbit dorsally. However, the shape of the pachycormid dermosphenotic is variable between genera and species. For instance, the dermosphenotics of both *Pachycormus* and *Euthynotus* Wagner, 1860, have a long anterior process that borders the dorsal margin of the orbit (this bone arrangement was named pattern 1b in Poplin, 2004). In other pachycormids, the dermosphenotic extends anteriorly and posteriorly over the orbit (this bone arrangement was named pattern 1d by Poplin, 2004). Recently, Arratia and Schultze (2013) described another morphotype for *Orthocormus roeperi*, where the dermosphenotic is more or less 'T'-shaped and has a short anterior process. The morphology of the dermosphenotic of MLP 48-1-1-1 appears to be intermediate between morphotype 1b (= extended more or less over the orbit) and 1d (= single dermosphenotic extended anteriorly and posteriorly) of Poplin (2004).

The supraorbital sensory canal extends parallel to the suture between parietal and dermosphenotic. No sensory canal is observed in postparietals. This condition is slightly different to that observed in other pachycormiforms; for instance, in *Pachycormus macropterus* (Blainville, 1818), "each canal enters the frontal [sic.] from the nasal and extends postero medially until it reaches the anterior end of the longitudinal cranial groove. Here it turns posteriorly and enters the parietals [sic.] without meeting the infraorbital sensory canal" (Mainwaring, 1978:14, fig. 1).

Supraorbitals are absent in pachycormiforms (Lambers, 1992); this bone was not observed in MLP 48-1-1-1. The paired postparietals are small and quadrangular. The suture between them is straight. Each postparietal meets the parietal through an 'M' suture.

The temporal boss (= frontoparietal boss) is unique to pachycormiforms, and the skull roof bones that form it appear to be variable between members of the group (see Lambers, 1992). Some species have a very well-developed temporal boss that projects anteriorly (*Orthocormus cornutus* Lambers, 1988). However, a clear boss is usually missing in several species, for instance, *P. macropterus* (Mainwaring, 1978, fig. 1) and *Orthocormus roeperi* (Arratia and Schultze, 2013, fig. 4), and it seems to be lost in others (e.g., *Euthynotus*). In species with a well-developed temporal boss, the boss usually projects anteriorly and the postparietals became separate. In MLP 48-1-1-1, the postparietals are joined in the midline (Figs. 2, 3), thereby we assume that a clear temporal boss was absent.

Upper Jaw

The posterior part of the left maxilla is well preserved (Fig. 2). The right maxilla is partially preserved. From the two maxillae it can be deduced that the bone is thin and elongate and posteriorly curves down slightly (Fig. 3). Because of the poor preservation, we cannot estimate its total length. There is a single row of conical teeth. The preserved maxillary teeth are smaller than those present in the lower jaw (ca. 22% of the total length of the bigger dentary teeth). Teeth are uniformly distributed and almost perpendicularly directed, but some are slightly inclined forward (between 80° and 85°). Each tooth is ornamented with faint basoapical ribs and has a dark apex that may represent an acrodin cap (Fig. 4A). No histological studies were conducted here, but it is noteworthy that an acrodin cap was not observed in other pachycormids examined by us. However, Thies and Mudroch (1996) described a smooth and slightly flattened enamel cap in *Sauropsis* teeth. Also, these authors mentioned that the tooth morphotype (with an enamel cap and strong, sharp, and vertical ribs in its tooth crown) is widespread among pachycormids.

Lower Jaw

The dentary is a large and robust bone that gradually becomes deeper posteriorly. The coronoid process is low. Measurements were taken from the left dentary, in which its anterior portion reached about 16 mm depth and the posterior one about 40 mm depth. The dorsal edge of the dentary is straight except for its anterior third that gently curves upward (the depth of the curvature is about 20% of the total length of the bone). This curvature is commonly present in other pachycormiforms and has been interpreted as due to the occurrence of a coronoid plate of a particular shape (Lambers, 1992). For instance, the anterior portion of the dentary is curved in *Hypsocormus insignis* Wagner, 1860, and this species has a large, swollen coronoid plate with at least eight teeth on its surface (Gouiric-Cavalli, pers. observ. of JM-E SOS 3554). Other pachycormids such as *Pachycormus macropterus*, with at least eight small coronoid plates, do not exhibit the anterior curvature of the dentary bone (see Mainwaring, 1978). Therefore, the presence of coronoid plates is not always related to an anterior curvature of the dentary bone, but if there is an anterior curvature in the dentary, we can assume the presence of at least one coronoid plate of particular (inflated) morphology. Consequently, because the dentary in MLP 48-1-1-1 is curved anteriorly, we assume that at least one coronoid plate was present. The lateral surface of the dentary is crossed in its ventral portion by the mandibular sensory canal. Only a few scattered tubercles and some weak ridges are seen on most of the surface of the dentary. However, in its rostral region, just in front of the anterior curvature, the ornamentation is more evident and consists of small, densely clustered tubercles.

The morphology and disposition of the dentary teeth in MLP 48-1-1-1 is unusual. All teeth have a circular base, are laterally compressed in their mesiodistal portion, and are very large with the exception of some anterior teeth and the 19th tooth, which are rather small (Fig. 4B). Some anterior and middle teeth are lingually curved and have an oval depression on the labial surface of the crown. Each tooth has delicate basoapical ribs on its surface. Similar ribs have been noted in other pachycormids examined here (e.g., *Hypsocormus insignis* BSPG ASVI 4a, b; JM-E SOS 539a). Some of the dentary teeth of MLP 48-1-1-1 are perpendicularly directed, but most of them are inclined forward at an angle ranging from 75° to 83°. A similar condition was observed in *Orthocormus teyleri* Lambers, 1988, but in this species the teeth are inclined at an angle of about 60°. In actinopterygians, typical enameloid is usually found at the tip of the tooth and is called 'cap enameloid' or 'acrodin cap' (Sasagawa et al., 2009). The 'acrodin cap' has the highest degree of mineralization and lacks organic matter (Sasagawa and Ishiyama, 1988; Sasagawa, 1997). Because the ornamentation of the teeth is interrupted in the distal portion and the tip is dark colored, showing an apparent compositional difference between the cap and the rest of the tooth, we favor the interpretation of this as indicating the presence of an acrodin cap (Fig. 4B).

The dentary of MLP 48-1-1-1 has a single, closely arranged row of teeth. This condition was not observed in other pachycormids examined by us. Up to now, *N. argentinus* is the only Late Jurassic pachycormid with this arrangement. The anterior dentary tooth of MLP 48-1-1-1 (Figs. 2, 3) is stout and slightly inclined forward (slightly procumbent), a condition similar to that observed in *Sauropsis longimanus* Agassiz, 1833 (see Lambers, 1992). A different situation is observed in, for example, *Orthocormus*, in which the anterior tooth is strongly inclined forward (highly procumbent); compare the specimens illustrated in Figure 5.

Other bones of the lower jaw, as in other pachycormids, are difficult to identify: the surangular is probably preserved as an impression (as with *Pachycormus macropterus*, it is a roughly triangular plate), and the angular, partially preserved as an

impression, is a large plate without traces of the mandibular sensory canal. Commonly, pachycormiforms have a single gular plate, but none is preserved in MLP 48-1-1-1.

Suspensorium

The hyomandibula is similar to that of all pachycormiform genera examined by us: robust, hourglass-shaped, inclined backward, and with a very well-developed opercular process (Lambers, 1992). The right hyomandibula is almost completely exposed, whereas the left one shows only its ventral portion (Figs. 2, 3). The total length of the left hyomandibula (measured longitudinally) is ca. 111 mm; its ventral portion is larger than the dorsal one. The distal end of both portions could have been cartilaginous. Neither symplectic nor quadrate was identified.

The metapterygoid, as in *Pachycormus macropterus* (see Mainwaring, 1978), has two more or less triangular (fan-shaped) portions. The dorsal portion is less developed than the ventral one.

Elements of the Hyoid and Branchial Arches

Only a fragmentary and partially exposed ceratohyal could be identified (Figs. 2, 3). The elements of the branchial arches are represented by at least two isolated epibranchials (Figs. 2, 3).

DISCUSSION

Dolgopol de Saez (1949) briefly described the new genus and species *Notodectes argentinus* and assigned it to the teleostean order Ichthyodectiformes on the basis of similarities in dentition. The characters discussed by Dolgopol de Saez (1949:452) were the presence of a preopercle similar to that of the Cenozoic osteoglossomorph *Brychaetus* Agassiz, 1845, described as a “preopérculo muy extendido” (very extended preopercle), and a wide pectoral fin located below the lower jaw. However, the study of the holotype revealed that no preopercle is preserved in MLP 48-1-1-1. Moreover, we believe that Dolgopol de Saez confused the left hyomandibula with the preopercle and the ventral portion of the right hyomandibula (or the ceratohyal) with the pectoral fin. Dolgopol de Saez (1949) also mentioned the presence of an otolith. Examination of this structure under binocular microscope showed the presence of concentric lines and delicate keels. We concluded that this element actually is a bivalve (Figs. 2, 3). Several identical impressions are present on the reverse side of the specimen.

In 1990, the holotype of *Notodectes argentinus* was briefly restudied by Cione and Pereira, who suggested that it was a pachycormid because of the morphology and position of the lower jaw, the hyomandibula, and the sclerotic ring. Those authors also mentioned that the anterior curvature of the dentary could be caused by a taphonomic distortion. However, as was mentioned above, this feature is common and actually distinctive for some pachycormids and is related to the presence of a coronoid plate of a particular morphology.

We conclude that the specimen MLP 48-1-1-1 clearly cannot be a member of the Ichthyodectiformes because it has a dentary that widens posteriorly, while the anterior portion curves upwards (in Jurassic ichthyodectiforms the lower jaw is triangular; see Alvarado Ortega, 2004); no supraorbital bones are identifiable (ichthyodectiforms have one); large conical teeth uniformly distributed and closely arranged over the lower jaw (Jurassic ichthyodectiforms have small teeth and in Cretaceous genera they alternate in size along the length of the lower jaw); parietals ornamented with wide and narrow ridges as well as delicate tubercles (ichthyodectiforms have smooth parietals); low coronoid process (ichthyodectiforms have a high coronoid process); and shape of the hyomandibula (robust, hourglass-shaped, both portions almost equal in size, and with a well-developed

opercular process) closely resembling that present in pachycormiforms (ichthyodectiforms have a hyomandibula with a well-developed dorsal portion and a narrow ventral one according to Berrell et al., 2014). Notwithstanding that MLP 48-1-1-1 shares with ichthyodectiforms the presence of a single row of almost vertical dentary teeth (see Patterson and Rosen, 1977), some pachycormids lack the ‘characteristic’ lateral row of teeth in the lower jaw (e.g., *Orthocormus roeperi*).

Here, we confirm the previous assignment to Pachycormiformes (Cione and Pereira, 1990) because the holotype (MLP 48-1-1-1) has the following character combination: dermosphenotic closing the dorsal margin of the orbit; small postparietals; a very well-developed, hourglass-shaped, backward inclined hyomandibula with a robust opercular process; posterior section of the maxilla curved downward; anterior portion of the dentary curved upward; and large dentary teeth uniformly distributed.

Notodectes is considered a valid genus on the basis of a unique character combination that includes some unique characters (marked with an asterisk [*]): dentary teeth in a single row that are perpendicular or slightly inclined forward; most teeth have a similar size and are very large, representing 8–11% of the total length of the dentary; dentary teeth closely arranged over the bone in such a way that there is no space between each tooth, as with other members of the family; dentary teeth with circular crown and laterally compressed in their mesiodistal portion; some teeth lingually curved [*]; dentary teeth with an oval depression on their crown [*]; slightly procumbent teeth in the lower jaw; anterior portion of the dentary curved upward due to the inferred presence of a coronoid tooth plate; preserved portion of the maxilla with relatively small conical teeth (representing 22% of the total length of a dentary tooth), ornamented with delicate ribs and having a dark tip; no clear and/or very well-developed temporal boss; parietals ornamented with wide and narrow ridges and scattered delicate tubercles; shape of dermosphenotic appearing to be intermediate between patterns 1b and 1d sensu Poplin, 2004; and supraorbital sensory canal running parallel to the suture between parietal and dermosphenotic.

COMMENTS ON PALEOBIOGEOGRAPHY

Jurassic pachycormiforms are mainly represented in Europe (England, France, Germany, and Luxembourg) (Lambers, 1992; Delsate, 1999a, 1999b; Friedman, 2012b). At present, there are two records from Cuba (see Gregory, 1923) and there are no records of Jurassic pachycormiforms from North America (Lambers, 1992; Liston, 2004). The group is poorly represented in the Jurassic of South America (Chile and Argentina; see Fig. 6). In the Oxfordian of Chile, the suspension-feeder *Leedsichthys* was reported from two localities in the Atacama Desert (Arratia and Schultze, 1999; Martill et al., 1999; Liston, 2010). Biese (1961) mentions the presence of the predator *Pachycormus* in the Oxfordian of Cerritos Bayos, Antofagasta, Chile. Later, Arratia (1985) identified the genus *Pachycormus* in the lower Callovian of Quebrada del Profeta in Antofagasta, Chile. In the Tithonian of Argentina, several pachycormid specimens were found; this material is currently under description (Cione et al., 1987; Cione in Leanza and Zeiss, 1990; Gouiric-Cavalli, 2013; this contribution).

As mentioned above, the best known Jurassic marine fishes occur in the Tethys area mainly in Europe. All the groups occurring in the marine Jurassic sediments of the Neuquén Basin are also common members of the Tethyan ichthyofaunas: Hybodontiformes, Batomorphii, Semionotiformes, Aspidorhynchiformes, Caturidae, Pachycormiformes, and others (Arratia and Cione, 1996; Cione, 1999; Gouiric-Cavalli and Cione, 2009, 2011, 2013a, 2013b; Gouiric-Cavalli, 2013).

The depositional environment of the Vaca Muerta Formation corresponds to a rapid and widespread marine transgression

originating from the Pacific Ocean as a consequence of a tectonic phase of compressional relaxation (Legarreta and Uliana, 1991; Parent, 2003). The Vaca Muerta Formation represents the distal facies of a series of carbonate and/or mixed systems that settled in the Neuquén Basin between the early Tithonian and early Valanginian (Legarreta and Uliana, 1991; Legarreta et al., 1993).

Several authors stressed that the close similarities in marine ichthyosaur, metriorhynchid, and plesiosaur faunas between Jurassic Eastern Pacific and Western Tethyan faunas (i.e., the presence of crocodyliforms such as metriorhynchids and *Cricosaurus* Wagner, 1858, as well as the ichthyosaur *Stenopterygius* Jaekel, 1904, in both faunas), which was explained in terms of a marine connection between the two areas through a Caribbean seaway named the Hispanic Corridor (Gasparini, 1985, 1992, 1996; Gasparini and Fernández, 1996, 1997, 2006). Furthermore, a proto North Atlanto-Pacific marine faunal province was proposed for the Jurassic, taking into account the reptiles as well as the fishes (Martill et al., 1999). This was also noted as an explanation for the observed molluscan paleobiogeography (Damborenea et al., 2013).

Pachycormids were either medium- to large-sized pelagic predators convergent with marine fishes of the Cenozoic and Recent Scombridae and Istiophoridae families (Lambers, 1992) or very large suspension-feeders with no actinopterygian recent analogues (Friedman et al., 2010). Many scombrids are circum-global in tropical and subtropical seas, including oceanic islands. For example, *Thunnus albacares* (Bonnaterre, 1788) and *Thunnus alalunga* (Bonnaterre, 1788) have a wide distribution across the Pacific Ocean (Eschmeyer, 2013). For these efficient swimmers, long trans-oceanic distances are not a barrier. Accordingly, some pachycormid genera, such as the Cretaceous genus *Protosphyraena*, were cosmopolitan (Lambers, 1992; Friedman, 2012a), and the giant Jurassic planktivorous fish *Leedsichthys* would not be limited by an open ocean (for a discussion see Liston, 2007). Nevertheless, in the ocean, the density of plankton is not uniform and the plankton blooms are located in restricted areas or patches (Cavendish, 2001). However, fishes and marine mammals—feeding on plankton—can relatively easily adjust to changes in their fluid environments and travel between blooms (Liston, 2007; McManus and Woodson, 2012).

The spatial distribution of organisms in the ocean is determined by interactions between an organism's behavior and physical oceanographic structure and process (McManus and Woodson, 2012). It is noteworthy that during the Jurassic, the Earth's climate was warmer than today, due to the presence of a broad tropical belt (Hallam, 1993).

Notodectes represents the only endemic pachycormiform genus known from the Southern Hemisphere because another putative endemic genus (*Australopachycormus* Kear, 2007) was found to be a junior synonym of the wide-ranging Cretaceous genus *Protosphyraena* (see Friedman, 2012a; Friedman et al., 2013). The wide-ranging distribution of pachycormids and tuna fishes appears to contrast with the occurrence of an endemic pachycormid genus of the Neuquén Basin. However, several tuna fish species do not present a cosmopolitan distribution. For instance, *Thunnus atlanticus* (Lesson, 1831) lives in the eastern Atlantic and *Thunnus maccoyii* (Castelnau, 1872) in the Southern Ocean south of 30°S, except when moving to the coast off northwestern Australia for spawning (Eschmeyer, 2013). Moreover, some scombrid genera also present a restricted distribution: for example, the two species of genus *Grammatocygnus*, *G. bilineatus* (Rüppell, 1836) (Red Sea, Indo-West Pacific, Marshall Islands, Tonga, and Samoa, reaching south to Australia and New Caledonia) and *G. bicarinatus* (Quoy and Gaimard, 1825) (Eastern Indian Ocean, western Pacific, northern Australia, and New Caledonia). Another example of restricted distribution is given by the monospecific genus *Orcynopsis* Gill, 1862, that inhabits the Western Baltic Sea, North Sea, Mediterranean Sea, and

eastern Atlantic (Eschmeyer, 2013). Notably, all these fishes are not small and their standard length exceeds 1 m. The relatively reduced distribution of these species could have been caused by ecological constraints: *Orcynopsis unicolor* (Geoffroy, 1817) is a neritic species; *Grammatocygnus bilineatus* inhabits open waters, but often it is seen swimming near outer reef walls or deep clear-water slopes; and *G. bicarinatus* forms schools near individual bays and reefs in barrier reef waters (Froese and Pauly, 2013). By analogy, the occurrence of an endemic genus such as *Notodectes* in the marine gulf that developed in the Neuquén Basin could be attributed to ecological constraints. Another example of endemism in the area is the teleost family Varasichthyidae, only known from the Late Jurassic of Chile and Cuba (see Arratia, 2008).

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