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Fish faunas from the Late Jurassic (Tithonian) Vaca Muerta Formation of Argentina: One of the most important Jurassic marine ichthyofaunas of Gondwana

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ABSTRACT

The marine deposits of the Vaca Muerta Formation (Tithonian–Berriasian) houses one of the most diverse Late Jurassic ichthyofaunas of Gondwana. However, most of the specimens remain undescribed. Jurassic fishes have been recovered from several localities at Neuquén Province (i.e., Picún Leufú, Plaza Huincul, Cerro Lotena, Portada Las Lajas, Los Catutos, and Arroyo Covunco) but also from Mendoza Province (i.e., La Valenciana, Los Molles, and Arroyo del Cajón Grande). Presently, the fish fauna of Los Catutos, near Zapala city (Neuquén Province), has yielded the highest number of specimens, which are taxonomically and morphologically diverse. At Los Catutos locality, the Vaca Muerta Formation is represented by the Los Catutos Member, which is considered the only lithographic limestones known in the Southern Hemisphere. Here, we review the Tithonian fish faunas from the Vaca Muerta Formation. During Late Jurassic times, the actual Argentinian territory could have been a morphological diversification center, at least for some actinopterygian groups. The apparently lower species diversity recorded in marine Jurassic ichthyofaunas of Argentina (and some Gondwanan countries) in comparison with Chilean and European fish faunas could be related to the fish paleontological research history in Gondwana and the low number of detailed studies of most of specimens recorded.

1. Introduction

Fishes comprise more than one-half of the total number of recognized extant vertebrate taxa. They are clustered in four major groups: agnathans (cyclostomes and ostracoderms), chondrichthyans (rays and sharks), actinopterygians (ray-finned fishes), and sarcopterygians (lobe-finned fishes or lungfishes and coelacanths). Agnathans and chondrichthyans appeared in the Late Ordovician (Sansom et al., 2001), actinopterygians and sarcopterygians in the Late Silurian (Cloutier and Arratia, 2004).

Throughout fish evolution many fish groups appeared, bloomed and went extinct. The Permo–Triassic extinction event set the stage for the evolution of modern fish faunas and both, neoselachians and teleosts, first appeared during the Triassic (Arratia, 2004, 2013; Maisey et al., 2004; Underwood, 2006). However, many of the groups that appeared or radiated in the Triassic became extinct in the Triassic/Jurassic boundary (Arratia, 2004; López-Arbarello et al., 2008).

The Jurassic was an important period in the evolution of Neoselachii and Teleostei (e.g., Arratia, 1997, 1999; Cione, 1999) representing a moment of origin, diversification, and early evolution of modern fish diversity. Several fish groups were present in the Jurassic for instance chondrichthyans (e.g., chimaeroids, hybodontiforms sharks, batoids, orectolobids, carcharinids), sarcopterygians (e.g., dipnoans, coelacanthiforms), chondrosteans, holosteans (e.g., amiids, semionotiforms, caturioids, ionoscopiforms, macrosemiforms, pycnodontiforms), teleosteomophs (i.e., pachycormiforms and aspidorhynchiforms), and teleosts *sensu stricto* (e.g., ichthyodectiforms, pleuropholids, leptolepids, elopomorphs).

Presently, our understanding of Jurassic chondrichthyans and actinopterygians is linked to the quality of preservation and completeness of the fossil record. European marine localities and their fishes have been studied for a long time (e.g., Wagner, 1860; Woodward, 1895; Weitzel, 1930; Saint-Seine, 1949; Leeds, 1956;

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Wenz, 1968; Hauff and Hauff, 1981; Lambers, 1992; Liston, 2010; Arratia, 1997; Arratia and Schultze, 2013). On the other hand, only few Jurassic marine fish-bearing units have been reported from the Americas [e.g., Viñales in Cuba (White, 1942), El Profeta, and Cerritos Bayos in Chile (Arratia and Schultze, 1999a)]. The Oxfordian ichthyofauna of the El Profeta is the most extensively studied of South America, the fishes recorded have an outstanding preservation, which includes soft tissues (Schultze, 1989; Arratia, 2015). These fishes have been shown to be important to understand the phylogenetic and evolutionary history of some teleostean taxa (Arratia, 1994, 2008). Also, these fishes have been useful to explain the paleobiogeographic relationships of some of their relatives (e.g., Arratia et al., 1975a,b; Arratia and Schultze, 1999a; Arratia, 2015).

In Argentina, Jurassic marine fishes have been recovered in Mendoza and Neuquén provinces, western region of the country. Most of the specimens comes from Tithonian levels of the Vaca Muerta Formation (e.g., Dolgopol de Sáez, 1940a, b; Cione, 1999; Cione and Pereira, 1990; Cione et al., 1987, 2002; Leanza and Zeiss, 1990; Arratia and Cione, 1996; Gouiric-Cavalli, 2013; Gouiric-Cavalli and Cione, 2011, 2013a; Gouiric-Cavalli et al., 2011). To date, only one specimen has been recovered in Tithonian levels of the Picún Leufú Formation (Dolgopol de Sáez, 1939; Gouiric-Cavalli and Cione, 2013b).

At Neuquén Province, the Vaca Muerta Formation crops out in several localities, most of which yielded fishes (i.e., Picún Leufú, Plaza Huincul, Cerro Lotena, Portada Las Lajas, Los Catutos, and Arroyo Covunco). At Mendoza Province the Vaca Muerta Formation crops out in few bearing-fish localites (i.e., Los Molles, La Valenciana, and Arroyo del Cajón Grande). Currently, the most fossiliferous localities are located at Neuquén Province being Los Catutos the richest in terms of number of specimens and the more taxonomically diverse. From Los Catutos several fish groups has been reported: halecomorph, lepisosteiforms, teleosteomorph, and teleosts (e.g., Cione et al., 1987; Gouiric-Cavalli, 2013). Nonetheless, great part of these specimens have not been studied in detail.

The Vaca Muerta and Picún Leufú formations are located in the embayment of the Neuquén Basin. The Neuquén Basin (Late Triassic–Early Cenozoic) is the most important hydrocarbon-producing province in southern South America (Howell et al., 2005). Most of the hydrocarbon fields are located in the Neuquén embayment where the Mesozoic sedimentary record is in the subsurface and the strata are relatively undeformed (Howell et al., 2005). During drilling and mining activities carried out by oil companies in levels of the Vaca Muerta and Picún Leufú formations, some poorly preserved fishes were recovered. These fishes were firstly studied by Dolgopol de Sáez who named several new taxa based on those fragmentary material: actinopterygians (*Pholidophorus argentinus* Dolgopol de Sáez, 1939, *Notodectes argentinus* Dolgopol de Sáez, 1949, *Leptolepis dubius* Dolgopol de Sáez, 1939, *Leptolepis patagonicus* Dolgopol de Sáez, 1939; *Leptolepis australis* Dolgopol de Sáez, 1939) and the sarcopterygian, *Bunoderma baini* Dolgopol de Sáez, 1940b. Later, Dolgopol de Sáez's assignations were revised and the taxa were considered as *nomen vanum* or reinterpreted as belonging to a different actinopterygian group (see Cione and Pereira, 1990 and Gouiric-Cavalli and Cione, 2013b).

During decades, sediments of the Vaca Muerta and Picún Leufú formation have been exploited looking for vertebrates (mainly reptiles) and invertebrates. Most of the fish material were recovered from Vaca Muerta Formation sediments at Los Catutos and Cerro Lotena localities. Some of these specimens were illustrated and briefly described by Cione (1999), Cione et al. (1987, 2002), and Leanza and Zeiss (1990). These authors reported chondrichthyans (an indeterminate batomorph and an indeterminate hybodontiform spine) and actinopterygians (caturid-like, semionotiforms, indeterminate pachycormiforms, cf. *Belonostomus*, indeterminate teleosts, and *Tharsis*-like).

During decades, staff of the "Prof. Dr. Juan Olsacher Museum" and researchers of La Plata Museum and San Luis University have been collecting and studying fossil specimens recovered at different Vaca Muerta Formation localities. The findings comprise vertebrates (e.g., actinopterygians, ichthyosaurs, pliosaurs, crocodyliforms, pterosaurs) and invertebrates (e.g., ammonites, gastropods, bivalves, echinoderms). Among vertebrates, some reptile groups have been extensively studied (i.e., ichthyosaurs, pliosaurs, crocodyliforms; see Gasparini and Fernández, 2005; Gasparini et al., 2015). Among invertebrates, ammonites and gastropods have been studied in detail (e.g., Leanza and Zeiss, 1990; Zeiss and Leanza, 2008; Parent et al., 2013). However, new specimens, taxonomic assignments, and redescriptions of previous published specimens are in constant appearance and the study of vertebrates and invertebrates of the Vaca Muerta Formation is in constant progress.

In South America, the Neuquén basin in western Argentina together with El Profeta in northern Chile have yielded the best-preserved marine Late Jurassic fishes of this continent (e.g., Schultze, 1989; Gouiric-Cavalli, 2013). Nonetheless, Argentinian fishes were practically forgotten in museum collections. A thorough study and review of Argentinian specimens housed at museums collections as well as new expeditions to the Vaca Muerta Formation localities are presently being carrying out.

Within the Neuquén basin, fishes from the Vaca Muerta Formation have been recovered mainly from two localities: Los Catutos and Cerro Lotena. Only few specimens have been studied in detail (Gouiric-Cavalli, 2013, in press; Gouiric-Cavalli and Cione, in press) and many have been mentioned in literature (e.g., Cione et al., 1987, 2002). At Los Catutos locality, sediments of the middle Los Catutos Member of the Vaca Muerta Formation crops out (Leanza and Zeiss, 1990). Los Catutos Member consists of lithographic limestones that range in age from middle to upper Tithonian (Leanza and Zeiss, 1990). On the other hand, at Cerro Lotena, the lower Portada Covunco Member of the Vaca Muerta Formation is cropping out (Parent et al., 2013). Based on ammonites, a middle Tithonian age was defined for the Portada Covunco Member (Parent et al., 2013).

Most of the fishes reported and reviewed here have been recovered from Los Catutos Member at Los Catutos locality. These specimens are mainly represented by middle-sized adults, ichthyophagous fishes. The osteichthyans have relatively good preservation quality, in two dimensions, and in some cases soft tissue is preserved. In addition to the Los Catutos fishes, few specimens has been recovered at Cerro Lotena locality. Preservation quality at Cerro Lotena is outstanding and the specimens are represented mainly by isolated skulls, three-dimensionally preserved, that preserves branchial lamellae.

Tithonian levels of Vaca Muerta Formation yielded several actinopterygians groups (e.g., semionotiforms, lepisosteiforms, teleosteomorphs, teleosts), which are also present in European and Chilean Late Jurassic localities. Presently, new teleosteomorphs have been described for the Tithonian of Argentina (Gouiric-Cavalli and Cione, in press; Gouiric-Cavalli, in press). However, most of the Tithonian material have not been studied or are under description process. The study of Tithonian marine fishes of the Vaca Muerta Formation of Argentina, together with other relative marine fishes of Gondwana, could change previous interpretation about the origin, diversification and paleobiogeography of Jurassic ichthyofaunas.

The main goal of this contribution is to give an actualized summary of the Tithonian fish faunas of the Vaca Muerta Formation. We hypothesize that, like Chile and Antarctica (e.g., Arratia, 1994, 2008; Arratia and Hikuroa, 2010), Argentina could have

been a morphological diversification center for some actinopterygian groups.

2. Geological setting

The Neuquén basin was a retro-arc basin developed in Mesozoic times in the Pacific margin of South America (Legarreta and Uliana, 1996) (Fig. 1.1). It houses a near-continuous Late Triassic–Early Cenozoic succession that was deposited on the eastern side of the evolving Andean mountain chain (Howell et al., 2005). Marine sequences developed throughout the basin during Late Jurassic–Early Cretaceous are included in the Mendoza Group (Stipanicic, 1969) or Mendoza Mesosequence (Legarreta and Gulisano, 1989).

The Neuquén basin is characterized by the presence of three marine organic-rich facies (i.e., Los Molles, Vaca Muerta and Agrio formations). Anoxic conditions were in tune with the Jurassic–Cretaceous ups and downs of eustasy (Legarreta and Villar, 2011). In Argentina the Neuquén basin is developed at the East of the Andes System, between the 32° and 40°S, mainly in the Neuquén Province and also covering part of Mendoza, Río Negro and La Pampa (Digregorio et al., 1984). It was in connection with the Chilean basins of Chañarcillo and Aconcagüa (Benedetto, 2010).

Paleontology of the Neuquén basin has global significance. Marine invertebrates stands out having one of the most complete Jurassic and Cretaceous record. Accurate biostratigraphic charts and the comparative correlation with faunas and successions from North America and the Tethys area were possible due to the completeness of this record (e.g., Aguirre-Urreta et al., 1999; Riccardi et al., 1999).

Late Jurassic Neuquén basin sediments are mainly represented by the Vaca Muerta Formation. The Vaca Muerta Formation was defined by Weaver (1931) to identify a succession of Tithonian dark calcareous shales characterized by the presence of Mendozanus, Zitteli and Internispinosum zones (Zeiss and Leanza, 2010). Along the Neuquén Basin, the Vaca Muerta Formation exhibits a strong facial variation (e.g., Groeber, 1929; Weaver, 1931; Leanza, 1973) showing deepest marine facies towards western active margins of the basin (black shales rich in ammonites [Leanza, 1973; Leanza and Hugo, 1977]) and a mixed carbonate-siliciclastic ramp toward its Eastern cratonic passive margin (Spalletti et al., 2000).

The Vaca Muerta Formation can be subdivided into three members (Fig. 1.2): the lower Portada Covunco Member (Parent et al., 2013), the middle Los Catutos Member (Leanza and Zeiss, 1990), and the upper Pichi Moncol Member (Parent et al., 2013). The fishes reported here comes from the Los Catutos and the Portada Covunco members.

The lower Portada Covunco Member, which is lower-middle Tithonian in age (Leanza and Zeiss, 1990) consists of a thick succession of sandy shales rich in organic matter with thin intercalations of calcareous sandstones, calcareous sandy siltstones, calcareous siltstones, wacky sandstones, and calcareous pelite. The Portada Covunco Member crops out in Cerro Lotena, Cerro Granito, and Sierra de la Vaca Muerta areas (Parent et al., 2013). Several fish

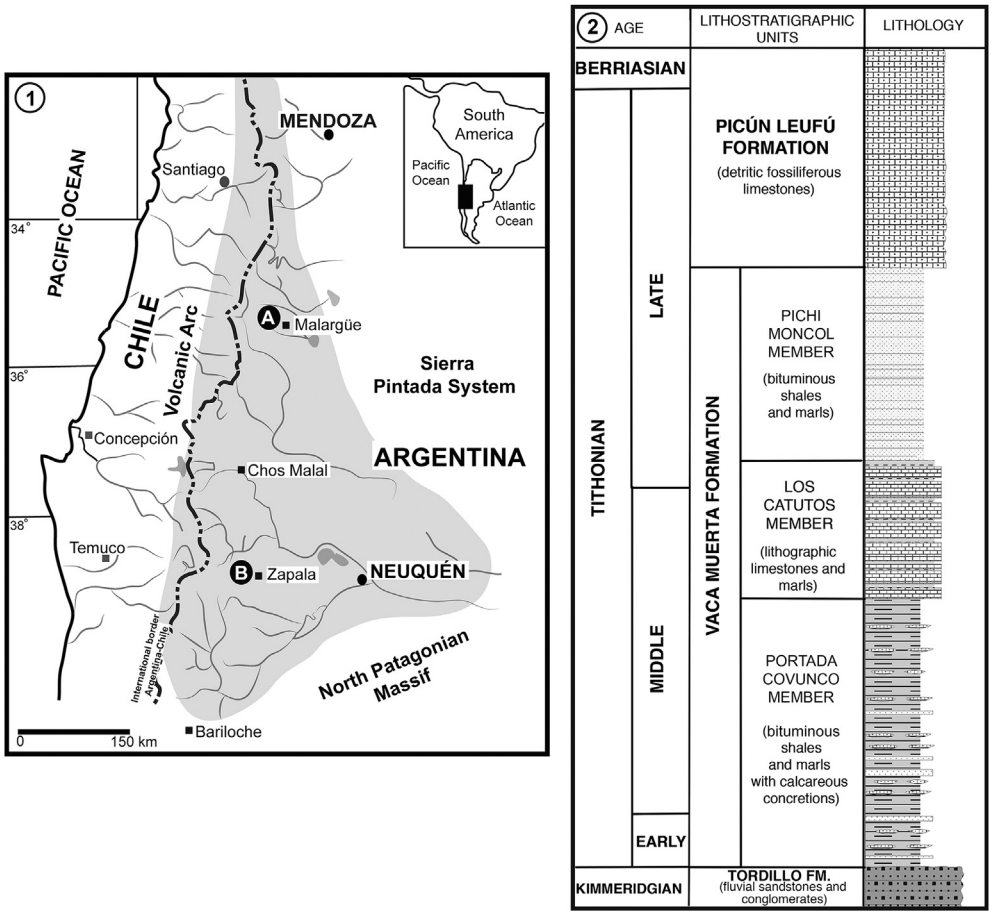

Fig. 1. **1**, Neuquén Basin map that shows the main areas in which fossil fishes were recovered. **A**, La Valenciana (=Casa Pincheira), Malargüe Department, Mendoza Province; **B**, Los Catutos, Zapala, Neuquén Province. In gray is represented the marine transgression from the Paleopacific Sea. Modified from Howell et al. (2005); **2**, Generalized stratigraphic column of the Vaca Muerta Formation. Modified from Zeiss and Leanza (2010).

remains and invertebrate shells were recovered from it (Parent et al., 2013; Gouiric-Cavalli, 2013).

The Pichi Moncol Member, which is upper Tithonian in age (Leanza and Zeiss, 1990) consists of a thick monotonous succession of thin laminated calcareous sandstones and sandy shales, with thin interbedded marls and scarce levels of fine-grained sandstones and silty sandstones (Parent et al., 2013). Like Portada Covunco Member, the Pichi Moncol Member crops out at Cerro Lotena, Cerro Granito, and Sierra de la Vaca Muerta areas (Parent et al., 2013). Invertebrates (ammonites and oysters) are scarce and poorly preserved (Parent et al., 2013).

The middle Los Catutos Member was defined by Leanza and Zeiss (1990) and correspond to the late middle Tithonian (Leanza and Zeiss, 1990, 1992; Parent et al., 2013) or late middle–early late Tithonian (Zeiss and Leanza, 2010), based on ammonites. At the type locality, Los Catutos Member reaches 116 m of maximum thickness (Parent et al., 2013). The sediments are immature, which means that they do not suffered a significant burial under a mild diagenetic process (Scasso et al., 2002).

Los Catutos Member consists of a rhythmic succession of lithographic limestones, marls, and shales. Lithological and chemical features of the Los Catutos Member are similar to those present in sequences of the Tethys area (Scasso et al., 2002). Los Catutos Member is highly fossiliferous. Although several vertebrates groups were recovered (e.g., actinopterygians, chondrichthyans, turtles, ichthyosaurs, plesiosaurs, pterosaurs; Cione et al., 1987; Gouiric-Cavalli, 2013; Gasparini et al., 2015), invertebrates are mainly represented by ammonites, which are taxonomically and morphologically diverse (Zeiss and Leanza, 2010).

2.1. Paleoenvironmental approach of the Vaca Muerta formation

The widespread condition of the sedimentary deposits of the Vaca Muerta Formation evidences a gradual decrease in depth and an increase of oxygenation of the ancient water masses (Gulisano et al., 1984). Thus, the three members of the Vaca Muerta Formation have been charaterized as follow:

The lower Portada Covunco Member consists of basinal deposits sedimented from suspension under anoxic to dysoxic conditions (Spalletti et al., 2000; Parent et al., 2013). The middle Los Catutos Member corresponds to an outer ramp system, deposited in shallow, dysaerobic, low energy open marine conditions, and without development of coral reefs (Leanza and Zeiss, 1990; Scasso et al., 2002). Finally, the upper Pichi Moncol Member corresponds to outer ramp facies in where water masses were well oxygenated (Spalletti et al., 2000).

Most of the Vaca Muerta Formation outcrops exhibit a great developed of black shales facies. These facies were interpreted as deposited in euxinic bottom waters without bioturbation, scavengers, and benthic organisms (Leanza, 1973). These stagnant bottom water conditions are the normal facies of the Vaca Muerta Formation and have been also observed in part of the Los Catutos Member (Leanza and Zeiss, 1990). Several authors suggest not only euxinic but also anoxic conditions in the seafloor (e.g., Gasparini et al., 1996). The recovered specimens (e.g., ammonites) at the Neuquén embayment suggested that superficial marine water was well oxygenated during late Jurassic times. Thus, a high diversity of fish taxa could have been lived in the Neuquén embayment of the Paleopacific sea. Meanwhile, bottom waters could be anoxic and toxic for organisms to live. The variation from well-oxygenated superficial water masses to anoxic/euxinic bottom waters could be related to a thermopycnoline, which is a zone with marked variation in temperature and density that cause a superficial, warm, and low density water mass and a cooler, denser, and oxygen poor bottom water mass (Gasparini et al., 1996). These paleoecological conditions are different from those of Late Jurassic Cerin (France) in where a coastal lagoon environment has been developed (Bernier et al., 1994), and/or the back reef archipelago at Solnhofen (Germany) (Viohl, 1996).

3. Institutional abbreviations

MCNM, Museo de Ciencias Naturales Juan Moyano, Mendoza, Argentina; **MLP**, Museo de La Plata, División Paleontología Vertebrados, La Plata, Buenos Aires, Argentina; **MOZ**, Museo Provincial Dr. Prof. Juan Augusto Olsacher, Zapala, Neuquén, Argentina; **UNS**, Universidad Nacional del Sur, Bahía Blanca, Buenos Aires, Argentina.

4. Vaca Muerta formation: Jurassic fish-bearing localities

Osteichthyans were commonly recovered from Jurassic marine levels of the Vaca Muerta Formation at Neuquén and Mendoza provinces (e.g., Weaver, 1931; Dolgopol de Sáez, 1940a, b; 1949; Rusconi, 1946, 1948; Aramayo, 1981; Cione et al., 1987; Cione and Pereira, 1990; Gouiric-Cavalli, 2013, in press). However, few chondrichthyans has been reported form the Jurassic of the Vaca Muerta Formation (Cione, 1999; Cione et al., 2002). Presently, some previously erected species are under review and the new osteichthyans material recovered in the Vaca Muerta Formation is under study. Below, the findings by locality are commented and briefly discussed.

4.1. Plaza Huincul, Neuquén Province (Fig. 2.3)

Although the material reported from Plaza Huincul (Tithonian) is poorly preserved and fragmentary, new taxa has been erected. The osteichthyan diversity reported consists of coelacanthids (*Bunoderma baini* Dolgopol de Sáez, 1940b) and teleosts (*Leptolepis argentinus* Dolgopol de Sáez, 1940a [Fig. 3.1] and *L. patagonicus* Dolgopol de Sáez, 1940a). The posterior revision of these specimens led to taxonomic reinterpretations. Thus, the putative coelacanthid, *Bunoderma baini* was reinterpreted as a teleost *incertae sedis* (Cione and Pereira, 1990) and the leptolepids as indeterminate teleosts considered as *nomina dubia* (Cione and Pereira, 1990).

4.2. Arroyo Picún Leufú, Neuquén Province (Fig. 2.3)

The ichthyofauna from Arroyo Picún Leufú (Tithonian) consists of poorly preserved material. The taxa reported includes teleosts (i.e., *Leptolepis australis* Dolgopol de Sáez, 1940a, *L. dubius* Dolgopol de Sáez, 1940a; and *L. patagonicus* Dolgopol de Sáez, 1940a [Fig. 3.2]), semionotids (i.e., isolated scales of *Lepidotes* cf. *maximus* Wagner, 1863; Weaver, 1931; Arratia and Cione, 1996), indeterminate coelacanthids (Dolgopol de Sáez, 1940b), and "pholidophorids" (*Pholidophorus argentinus* Dolgopol de Sáez, 1939 [Fig. 3.3]).

Further review of these specimens allowed the reinterpretation of the taxa. For instance, *Pholidophorus argentinus* was reinterpreted as an aspidorhynchiform and considered as coming from Tithonian levels of the Picún Leufú Formation instead of Vaca Muerta Formation (Gouiric-Cavalli and Cione, 2013b). Leptolepids were considered indeterminate teleosts (Cione and Pereira, 1990).

Note that currently the genus *Lepidotes* is considered as non-monophyletic (e.g., Cavin, 2010; Arratia, 2015), and all those species previously assigned under this name should be reviewed. The Argentinian material should be temporarily referred as "*Lepidotes*".

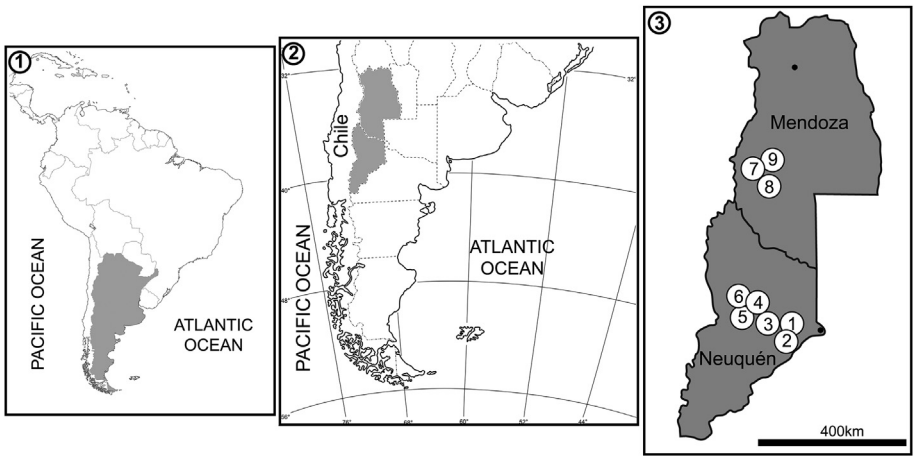

Fig. 2. Argentina map showing the main Jurassic fish-bearing localities at Neuquén and Mendoza provinces. **1**, Plaza Huincul, Neuquén; **2**, Picún Leufú, Neuquén; **3**, Cerro Lotena, Neuquén; **4**, Las Lajas, Neuquén; **5**, Los Catutos, Neuquén; **6**, Arroyo Covunco, Neuquén; **7**, La Valenciana (=Casa Pincheira), Mendoza; **8**, Los Molles, Mendoza; **9**, Cajón Grande, Mendoza.

4.3. Cerro Lotena, Neuquén Province (Fig. 2.3)

The fishes recovered at Cerro Lotena [late Early to early Middle Tithonian, Portada Covunco Member (Parent et al., 2013) of the Vaca Muerta Formation (Leanza, 1980, 1993)] comprise osteichthyans and chondrichthyans.

Among chondricthyans an isolated hybodontid dorsal fin spine has been described (Cione et al., 2002). Osteichthyans are represented by semionotid scales assigned to *Lepidotes maximus* (Weaver, 1931; Cione and Pereira,1990). However, this taxonomic designation should be considered following the explanations given above.

New and well-preserved osteichthyan material has been recently discovered at Cerro Lotena. These new material comprises pachycormiforms and aspidorhynchiforms (Gouiric-Cavalli, 2013, in press). Pachyormiforms are currently under study. Aspidorhynchiforms are represented by a new genera and species, *Jonoichthys challwa* Gouiric-Cavalli, in press (Fig. 4.1). Up to date, *Jonoichthys* is the oldest aspidorhynchid recovered at the Vaca Muerta Formation. Also, *Jonoichthys* is considered an endemic Gondwanan genus. This taxon is important because supports the hypothesis that Aspidorhynchidae was settled in both, Northern and Southern Hemispheres in Late Jurassic (Tithonian) times (Gouiric-Cavalli, in press).

4.4. Portada de Las Lajas, Neuquén Province (Fig. 2.3)

At Portada Las Lajas, the Vaca Muerta Formation is Middle Tithonian in age (Leanza, 1980). From Portada Las Lajas only a chondrichthyan has been reported (Cione, 1999). The specimen consists of a partially preserved skull, branquial arches, left pectoral fin, and pectoral girdle and was referred to Bathomorphii as a "rhinobatid" ray (Cione, 1999) (Fig. 5.1).

4.5. Los Catutos, Neuquén Province (Fig. 2.3)

Presently, Los Catutos is the most taxonomically rich and diverse fish-bearing locality of the Vaca Muerta Formation. Los Catutos lithographic limestones were firstly exploited at small scale by local people (Gasparini et al., 2015). In 1934 large-scale exploitations began, mainly in Covunco area (Gasparini et al., 2015). Fossils appeared sporadically during the mining activities. The quarries located in Los Catutos area yielded the best vertebrate fossils from these lithographic units. However, explorations looking for vertebrates in Los Catutos were never been authorized and the material housed in the MOZ's collection came from donations of people working at the quarries. Gasparini et al. (2015) noted that probably the vertebrate sample only have the best-preserved specimens or those that workers were authorized to donate.

At Los Catutos, the vertebrate and invertebrate faunas are strictly marine (with the exception of pterosaurs). Preliminary reports of the Los Catutos fish faunas shown a high morphological and taxonomical diversity including osteichthyans: Semionotidae, halecomorph caturid-like (Fig. 5.2), Aspidorhynchidae (Figs. 4.2–3 and 5.3), Pachycormidae (Figs. 4.1 and 5.4), and teleosts (Cione et al., 1987; Cione and Pereira, 1990; Cione in Leanza and Zeiss, 1990; Cione, 1999). However, the specimens were not studied in detail.

Presently, a new putative *Belonostomus* species (Figs. 4.2–3, 5.3) and two pachycormid morphotypes, a suspension-feeder (Fig. 5.4) and an ichthyophagous (Fig. 4.4), have been reported from this locality (Gouiric-Cavalli, 2013). Nowadays, the ichthyofauna from Los Catutos is under study.

4.6. Arroyo Covunco, Neuquén Province (Fig. 2.3)

The Vaca Muerta Formation at Arroyo Covunco range in age from the Tithonian to Berriasian (Kietzmann and Vennari, 2013). From Tithonian levels of the Vaca Muerta Formation, Aramayo (1981) reported an isolated vomerine dentition (Fig. 3.4) and assigned it to *L. maximus*. She argued that the Argentinian vomerine dentition has no differences with the European one. However, there is no soundest evidence to assign this material to *Lepidotes* (Arratia and Cione, 1996) or any European genera. This taxonomic designation has to be reviewed and the Argentinian specimen should be temporarily referred as "*Lepidotes*".

4.7. Casa Pincheira, Malargüe Department, Mendoza Province (Fig. 2.3)

At Casa Pincheira, the Vaca Muerta Formation is Tithonian–Berriasian in age. At this locality, fishes have been found at Tithonian levels. Dolgopol de Sáez (1949) described the new genus and species, *Notodectes argentinus* (Fig. 3.5) and assigned it to Ichthyodectiformes. Recently, the holotype and only specimen of *N. argentinus* was reviewed and considered a pachycormiform fish being the first endemic pachycormid genus in the Southern Hemisphere (Cione and Pereira, 1990; Gouiric-Cavalli and Cione, in press).

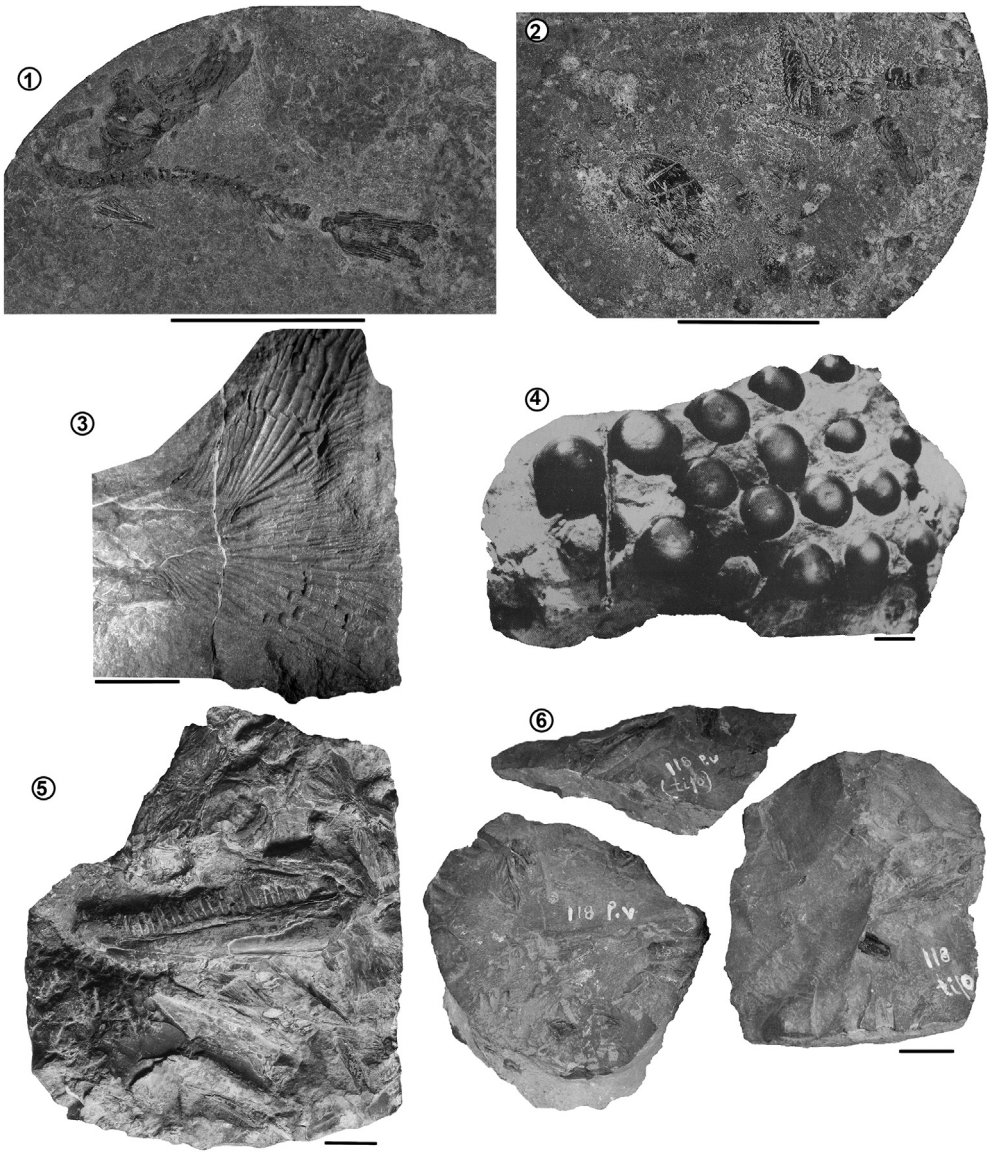

Fig. 3. Argentinian Late Jurassic fishes: **1**, MLP 40-XI-7-5, holotype of *Leptolepis argentinus* Dolgopol de Sáez, 1940a, Vaca Muerta Formation, Arroyo Picún Leufú, Neuquén; **2**, MLP 40-XI-7-1, holotype of *Leptolepis patagonicus* Dolgopol de Sáez, 1940a, Vaca Muerta Formation, Arroyo Picún Leufú, Neuquén; **3**, MLP 39-VI-30-4, holotype of *Pholidophorus argentinus* Dolgopol de Sáez, 1939, Picún Leufú Formation, National Road 40 where it crosses the Picún Leufú Creek, Neuquén; **4**, PV.UNS. 10010, scanned image of "*Lepidotes*" cf. *maximus* Wagner, 1863 from Cione and Pereira 1990: 397 fig. A, Vaca Muerta Formation, Arroyo Covunco, Neuquén; **5**, MLP 48-1-1-1, holotype of *Notodectes argentinus* Dolgopol de Sáez, 1949, Vaca Muerta Formation, La Valenciana (=Casa Pincheira), Malargüe, Mendoza; **6**, MCNAM-PV 118 holotype of ?*Platysomus pehuenchensis* Rusconi, 1946, Vaca Muerta Formation, Los Molles, Malargüe, Mendoza Scales = 2 cm (except in **4** in which is 0.5 cm).

4.8. Los Molles, Malargüe Department, Mendoza Province (Fig. 2.3)

At Los Molles the late Tithonian levels of the Vaca Muerta Formation has yielded a solely chondrostean fish, ?*Platysomus pehuenchensis* Rusconi, 1946 (Fig. 3.6). Cione and Pereira (1990) reviewed Rusconi's description and illustration considering that *? P. pehuenchensis* is an Halecostomi *incertae sedis*. Although the holotype was lost at the time that the paper by Cione and Pereira was published it was recently found at MCNM's collections and is currently under revision.

4.9. Arroyo del Cajón Grande, southwest of Malargüe Department, Mendoza Province (Fig. 2.3)

At Arroyo del Cajón Grande, the Vaca Muerta Formation is upper Tithonian–lower Berriasian in age (Vennari et al., 2014). From this locality Rusconi (1948) reported the chondrostean ?*Platysomus cajonensis*. The holotype of ?*P. cajonensis* consists of a ganoid scale patch (Rusconi, 1948). Cione and Pereira (1990) considered that these scales are not diagnostic and ?*P. cajonensis* was listed as *nomina dubia*. At the time of Cione and Pereira's publication and nowadays the holotype remains lost.

5. The record of Jurassic marine actinopterygians of Gondwana

The Jurassic marine actinopterygians diversity of the Gondwanan continents (South America, Africa, Australia, and Antarctica) is still incompletely known. Noteworthy, the thoroughly study of Oxfordian Chilean fishes has been important to understand the phylogeny and biogeography of some teleostean groups (e.g., Arratia, 1981, 1982, 1984, 1985, 1986, 1987, 1994, 2008; Arratia and

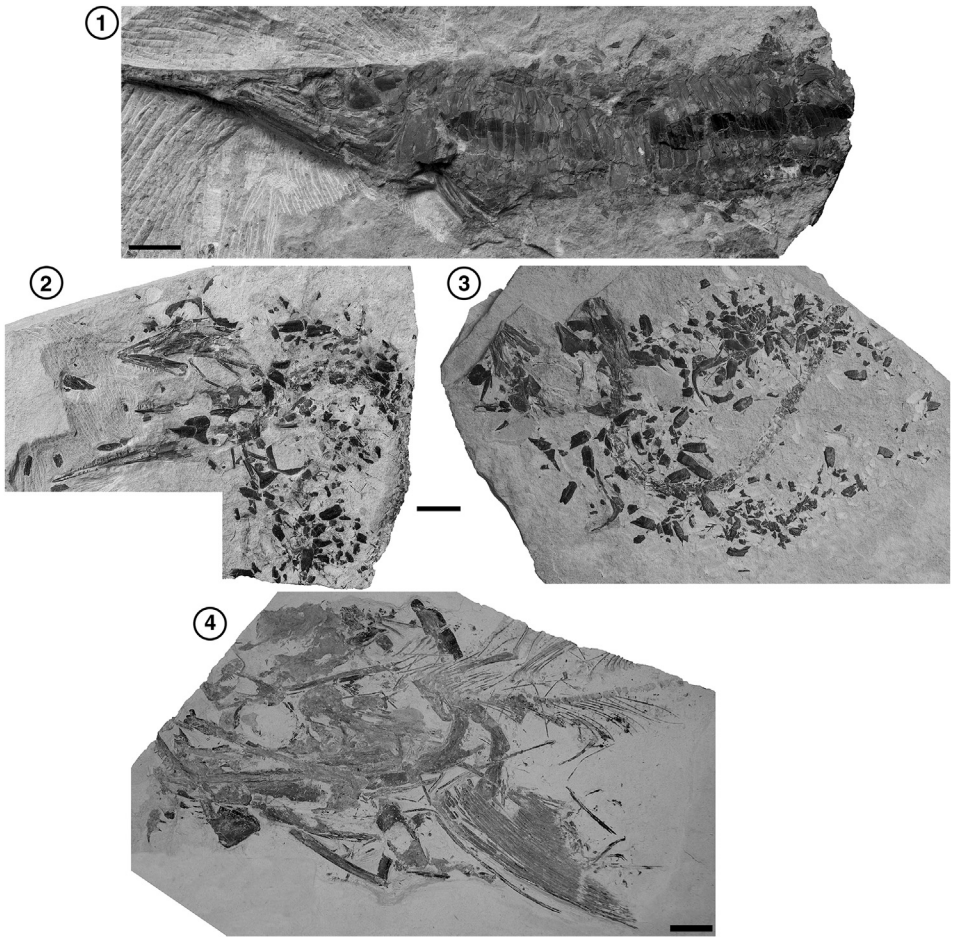

Fig. 4. Part of the recently described material from Tithonian levels of the Vaca Muerta Formation. **1**, *Jonoichthys challwa* Gouiric-Cavalli, in press, MOZ-Pv, 1747, Cerro Lotena, Neuquén; **2**–**3**, *Belonostomus* nov. sp. B Gouiric-Cavalli, 2013 (unpublished results), Los Catutos, Zapala, Neuquén; **4**, Pachycormiformes nov. gen et sp. A Gouiric-Cavalli, 2013 (unpublished results), Los Catutos, Zapala, Neuquén. Scales = 2 cm.

Schultze, 1985, 1999a; Arratia et al., 2004). This section summarizes the state of the art of the Jurassic marine actinopterygians fishes of Gondwana.

5.1. Halecomorphi

Few halecomorphs were reported from the Jurassic of Gondwana. Three genera and species of Amioidea have been reported from the marine Middle Jurassic Stanleyville beds (Saint-Seine, 1955). These taxa were located as halecostomes with uncertain relationships (Patterson, 1973). Later, Arratia (2004) listed those specimes as teleosts.

5.1.1. Caturidae

Caturids were recorded in marine levels of Stanleyville beds at Songa (Saint-Seine and Casier, 1962). A caturid-like specimen has been reported from Tithonian levels of the Vaca Muerta formation at Los Catutos locality, Argentina (Cione et al., 1987; Gouiric-Cavalli, 2013 see above, Section 4). This caturid-like specimen is presently under study by SGC.

5.1.2. Lepisosteiformes (sensu López-Arbarello, 2012)

The group is poorly represented in Gondwana. Isolated specimens of "*Lepidotes*" have been recorded from Cerro Sandón, Cerritos Bayos, and Cordillera de Domeyko in Chile (Biese, 1961; Arratia, 1987, 1994, 2015; Arratia and Schultze, 1999a). Also, *Lepidotes tendagurensis* Arratia and Schultze, 1999b has been recorded in Tithonian levels Tendaguru Formation, Tanzania. *Lepidotes* isolated scales has been recorded from Mugher, Stanleyville beds in Africa (Arratia et al., 2002). Teeth and scales of *Lepidotes* cf. *deccanensis* and an indeterminate Semionotidae have been recorded in the Middle-Upper Jurassic marine levels of Kota Formation, India (Prasad et al., 2004). Also, one teeth of ?*Ionoscopus*-type has been recorded in the same lavels of the Kota Formation, (Prasad et al., 2004). In Argentina, some putative lepisosteiforms were recovered form Tithonian levels of the Vaca Muerta Formation (see above Section 4). The Argentinian material is currently under study.

5.1.3. Semionotiformes (sensu López-Arbarello, 2012)

Ophipsiella, *Macrosemius*, and *Songanella* were recovered in Stanleyville beds, Africa (Saint-Seine and Casier, 1962; Murray, 2000). The African material assigned to Macrosemiidae should be reviewed to clarify its taxonomy (see Bartram, 1977; Murray and Wilson, 2009).

5.2. Pycnodontomorpha

In the Jurassic of Gondwana, pycnodontids are poorly represented. Chilean pycnodontids are represented by several specimens of *Gyrodus* sp. recovered from several Sinemurian–Oxfordian localities (Arratia and Schultze, 1999a; Kriwet, 2000; Arratia, 2015).

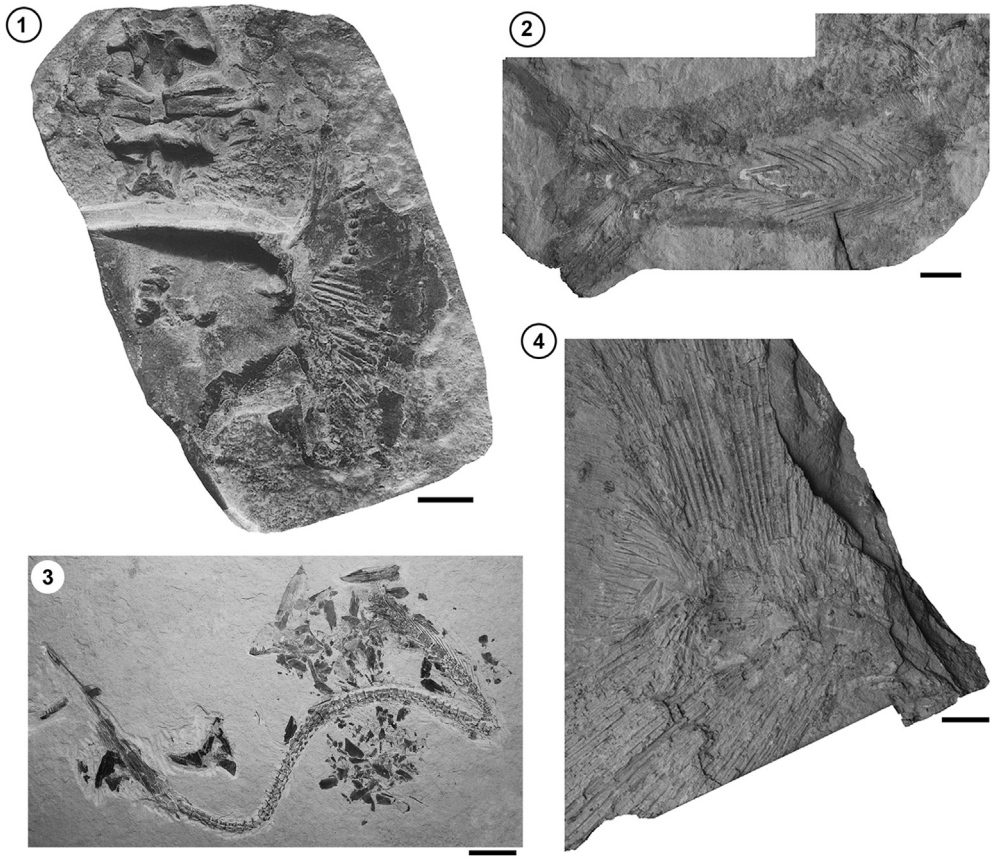

Fig. 5. Argentinian Jurassic fishes from Los Catutos Member of the Vaca Muerta Formation: **1**, MOZ-Pv 2564, Bathomorphii indet. Cione, 1999 [scanned image from Cione 1999: 25 Fig. 4], Las Lajas; **2**, MOZ-Pv 1645, caturid-like Cione in Leanza and Zeiss (1990), Los Catutos; **3**, Los Catutos MOZ-Pv 3642, cf. *Belonostomus* sp., Cione in Leanza and Zeiss (1990) and later assigned to *Belonostomus* sp. nov. B by Gouiric-Cavalli (2013), Los Catutos; **4**, MOZ-Pv 1533, Pachycormiformes indet. Cione in Leanza and Zeiss (1990), and later assigned as Pachycormiformes gen. et sp. nov. B by Gouiric-Cavalli (2013) Scales = 2 cm.

Also, a vomerine dentition has been recovered from marine levels of the Arcilita Mugher, Africa (see Arratia et al., 2002).

5.3. Teleosteomorpha (Teleostei and its posible stem–groups)

Atacamichthys has been described in the Oxfordian of Quebrada Corral, Chile (Arratia and Schultze, 1999a). *Pachycormiformes*: Pachycormids are very incompletely known in Gondwana. *Leedsichthys* isolated gill rakers have been recorded in the Oxfordian of Atacama Desert, Chile (Arratia and Schultze, 1999a; Liston, 2007; Friedman et al., 2010). *Pachycormus* has been reported in the Oxfordian of Cerritos Bayos and Quebrada del Profeta (Biese, 1961; Arratia, 1985). The Chilean specimens are fragmentary and poorly preserved. Presently, the Argentinian Tithonian pachycormids are the best-preserved of Gondwana. Also, Argentinian pachycormids could be the more diverse (taxonomic and morphological) pachycormids in Gondwana (Gouiric-Cavalli, 2013; Gouiric-Cavalli and Cione, in press; this contribution). *Aspidorhynchiformes*: Jurassic aspidorhynchids have been recovered in the Tithonian of Antarctica (Brito, 1997; Richter and Thomson, 1989; Arratia et al., 2004). However, the Antarctic material is partially preserved and some of the specimens has controversial characters (see Schultze and Stöhr, 1996; Brito, 1997; Gouiric-Cavalli, in press). In Argentina, aspidorhynchids are recovered in Tithonian levels of the Vaca Muerta Formation [i.e., *Belonostomus* (Gouiric-Cavalli, 2013) and *Jonoichthys* (Gouiric-Cavalli, in press). Currently, part of the aspidorhynchiform material is under study. *Teleostei*: Jurassic teleosts have been recorded in Australia, Chile, Antarctica, Africa, and Argentina. The main groups recovered are leptolepids, "pholidophoriforms", ichthyodectiforms, crossognathiforms, pleuropholids and also several indeterminate teleosts (Schaeffer, 1972; Arratia, 1994, 2013, 2015; Arratia and Schultze, 1985, 1999a,b; Arratia et al., 2002, 2004; Arratia and Hikuroa, 2010; Murray, 2000). The Chilean crossognathiforms are the oldest known members of the group (Arratia, 2015).

Presently, the best-known Jurassic marine fish faunas from South America come from Chile and Argentina. The studies in both countries are in progress.

6. Discussion

Gondwanan marine Jurassic ichthyofaunas seem to be taxonomically less diverse in comparison with European ones. However, Jurassic fish faunas from Chile showed to have a comparable richness and taxa diversity, including two endemic teleosts family (e.g., Schultze, 1989; Arratia, 1982, 1984, 1994, 2015; Arratia and Schultze, 1999a). Consequently, this bias may has not been such. Instead it could be related to a relatively younger paleontological research history in Gondwana and due to the scarceness of detailed morphological studies of most of the specimens recorded (except Chilean ones).

Potentially important Jurassic ichthyofaunas have been recorded in Gondwana (e.g., Lower Jurassic ichthyofauna from Kota Formation in India [e.g., Prasad et al., 2004]; Middle Jurassic fishes from Democratic Republic of Congo [e.g., Saint-Seine and Casier, 1962]; Late Jurassic fish fauna of Neuquén, Argentina [Gouiric-

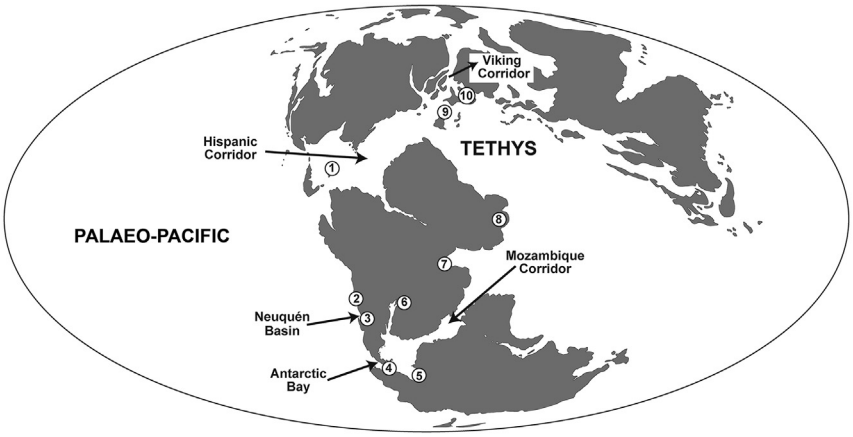

Fig. 6. Location of the main Jurassic Gondwana and Laurasia fish-assemblages and the marine pathways mentioned in the text. **1**, Viñales, Cuba; **2**, El Profeta, Chile; **3**, Los Catutos, Argentina; **4**, Tumbledown Cliff, Antarctica; **5**, Behrendt Mountains and Hauberg Mountains, Antarctica; **6**, Congo Basin, Africa; **7**, Songa beds, Africa; **8**, Mugher Mudstone, Ethiopia; **9**, Cerin, France; **10**, Solnhofen, Germany.

Cavalli, 2013; this contribution]). Currently, marine Late Jurassic ichthyofaunas of Gondwana are almost exclusively represented in the Oxfordian of the Antofagasta region in Chile (e.g., Arratia and Schultze, 1999a; Arratia, 2015 and paper cited therein) and in the Tithonian levels of the Vaca Muerta Formation in Argentina (e.g., this contribution). Chilean and Argentinian Late Jurassic fish faunas contributed to the knowledge of taxonomic diversity, evolution, and paleobiogeography of the Gondwanan fishes (e.g., Arratia, 1994, 2015; Gouiric-Cavalli, in press).

The Vaca Muerta Formation houses one of the most diverse Late Jurassic fish faunas of Gondwana hosting neoselachians (batoid and hybodontid) and osteichthyans (semionotids, halecomorphs, teleosts, teleosteomorphs, and several indeterminate actinopterygians). Most of the Argentinian specimens recorded correspond to middle-sized adult, that are ichthyophagous fishes. On the contrary, Chilean fishes correspond to small-sized adult fishes (except a giant suspension-feeder) (Arratia pers. comm. 2015).

Considering high level taxa (above order rank), a similar association has been recorded in the Late Jurassic of Chile and Europe. However, genera and species usually are not the same. Furthermore, some groups that have been recovered from Chilean (i.e., pycnodontids) and European localities (i.e., chimaeroids, pycnodontids, coelacanthids, and macrosemiids) have not been so far recorded in the Vaca Muerta Formation localities. Although Chilean Jurassic levels have not yielded aspidorhynchiforms, they has been recovered in Late Jurassic Argentinian localities and in Late and Upper Cretaceous Chilean localities (Brito and Suaréz, 2003; Arratia, 2015)

The opening of marine pathways [i.e., Hispanic Corridor (=Caribbean Seaways of Gasparini and Iturralde-Vinent, 2006) and Mozambique Corridor (=Trans-Erythraean Seaway of Arratia and Hikuroa, 2010)], impacts in the palaeobiogeographic distribution of the fishes reported here (see Fig. 6). These pathways certainly affected the ocean circulation and climate and could be used for the fishes as migration and/or dispersion routes between Paleopacific and Tethys oceans.

Some of the fish groups recorded in the Vaca Muerta Formation are interesting from an evolutionary point of view (i.e., teleosteomophs because are transitional between Holostei-Teleostei). Nevertheless, the anatomy, taxonomy, and systematic position of most of the taxa recorded in Vaca Muerta Formation is still unsolved.

At the present state of the art, some Jurassic actinopterygian families and genera are endemic to southern South America (i.e., Varasichthydae, *Notodectes*, and *Jonoichthys*). The fish diversity recorded in the Tithonian of the Vaca Muerta Formation plus the record of endemic aspidorhynchids and pachycormids shows that at the end of the Jurassic this region of South America could have been played a not negligible role in the morphological diversification of some taxa.

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