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First vertebrate body remains from the Permian of Argentina (Elasmobranchii and Actinopterygii)

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ABSTRACT

Isolated shark and actinopterygian teeth and scales were found in marine levels of the El Jarillal Formation (Early Permian), which crops out near the Cerro Vizcacha, Provincia de Mendoza, Argentina. Scarce previous Paleozoic vertebrate remains are known from Argentina and none was described from the Permian. Only tetrapod traces were reported before. However, vertebrates (especially fishes) are relatively abundant in other South American countries such as Brazil, Bolivia, Uruguay, Colombia, and Venezuela, from where "agnathan", placoderm, acanthodian, chondrichthyan, actinopterygian, dipnoan, crossopterygian, and tetrapod remains are known. In this paper we report the southernmost Paleozoic vertebrates body remains record and the first description of a hybodontid tooth from the Paleozoic of South America. Hybodontiforms were previously known in South America by fin spines, placoid scales and one putative undescribed tooth. We also give the first report South American shark dermal denticles traditionally ascribed to the form genus *Petrodus*, which probably belongs to a hybodontoid shark. Finally, several "basal actinopterygians" scales and teeth are assigned to morphotypes found in other South American Permian Formations. We did not found other fish taxa already known from late Paleozoic beds of the continent such as xenacanthiform sharks, lungfishes or coelacanthiforms. As an appendix, we summarize the Permian fish record of the continent.

1. Introduction

Spanish "Cronistas de Indias" from the 16th and 17th centuries reported the first South American fossil vertebrates as giant human remains (Cieza de León, 1553; de Acosta, 1590). Later voyagers mentioned large mammal fossil bones from northern South America and Argentina (Falkner, 1764; von Humboldt, 1814). Cuvier (1796) published the first scientific description of a South American vertebrate. Nevertheless, more detailed paleontological and stratigraphic studies began in South America with the publications of Spix and Martius (1823-1831), D'Orbigny (1842) and Darwin (1846). In Argentina, the first report (without description) of fossil fishes was the paper by Bravard (1858) mentioning Miocene sharks and teleostean species from Entre Ríos. However, it was not until the 20th century that the fossil fish fauna of Argentina, Bolivia, Chile, Peru, and Uruguay started to be thoroughly described (see Arratia and Cione, 1996; López-Arbarello et al., 2008 and Richter, 2000 for syntheses of the southern South American record).

Paleozoic fish records are much less abundant in the continent than Mesozoic and Cenozoic ones. "Agnathans," placoderms, chondrichthyans, acanthodians, actinopterygians, and sarcopterygians were described mostly in Bolivia and Brazil. Paleozoic fish reports from Argentina are very rare, mostly fragmentary, and restricted to the arandaspid *Sacabambaspis*, chondrichthyan scales, some "basal actinopterygians", and sarcopterygian scales (Tornquist, 1904; Manceñido, 1973; González, 1985; Riccardi and Sabattini, 1985; Albanesi et al., 1995; Díaz Saravia, 2001). However, none occurred in Permian beds.

During field work done for obtaining fossil material for the PhD dissertation by one of us (HF), isolated hybodontid shark and actinopterygian teeth and scales were found in beds of Permian age of western Argentina. In this paper we describe them as the first Permian vertebrate body fossil remains for Argentina and summarize the Permian fish record of South America.

Abbreviations: OM, optical microscope; SEM, scanning electronic microscope; MHNSR, Museo de Historia Natural de San Rafael.

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2. South American Permian fish record

A better knowledge of Permian fishes is relevant taking into account that at the end of this period the largest biotic turnover known occurred. Mesozoic fishes evolved from some lineages that survived from the Permian. During this period, chondrichthyans and actinopterygians were diverse, dipnoans and actinistians were represented by several genera, and the few remant "rhipidistian crossopterygians" and acanthodians became extinct (Mutter et al., 2008). Although many lineages went to extinction at the Permian-Triassic boundary others survived into the Triassic but became extinct before the Jurassic (among others, eugenodontiform, xenacanth, and phoebodontid condrictians; and perleidiform, dicelopygiid, elonichthyid, and acrolepid "basal actinopterygians" (Maisey et al., 2004; Mutter and Neuman, 2008; López-Arbarello et al., 2008). The term "basal actinopterygians" is informally used to refer to a non-monophyletic group of all non-neopterygian actinopterygians.

The Permian fish record of South America includes cartilaginous and bony fishes from several stratigraphic units and basins, mainly marine beds from Brazil, Uruguay, Bolivia, Chile, and Argentina. Most remains are fragmentary, but several "basal actinopterygians" are based on complete specimens and new genera and species were recognized (see Appendix A).

The elasmobranch orders Petalodontiformes, Sphenacanthiformes, Eugeneodontiformes, Orodontiformes and Symmoriformes are known from Brazil (Richter, 2004a,b, 2007; Chahud et al., in press). Other elasmobranchians such as ctenacantiforms and xenacanthiforms have been frequently reported from Brazil, including species of the genera *Ctenacanthus*, *Wurdingeria*, *Xenacanthus* and *Sphenacanthus* (e.g. Richter et al., 1985; Richter, 2004a, 2005; Chahud, 2007; Chahud and Fairchild, 2007; Chahud and Petri, 2008; Chahud et al., in press). Many of the nominal species of *Xenachanthus* from Brazil are actually *nomina nuda*, because they were not described (see Chahud and Fairchild, 2007).

Hybodontiform sharks were reported from the Permian to Cretaceous of South America. The most complete remains come from the Early Cretaceous Santana Formation of Brazil but some isolated teeth and spines are known from Jurassic beds of Uruguay and southern Argentina (Cione et al., 2002). The only previously known Permian record of hybodontiforms is represented by fragmentary spines and one undescribed tooth, which come from Brazilian and Chilean localities (Richter and Breitkreuz, 1997; Malabarba et al., 2003; Cisneros et al., 2004; Richter, 2004a).

In Bolivia, isolated teeth assignable to petalodontiforms and one eugeneodontiform species (*Parahelicoprion mariosuarezi*) were described by Janvier (1991; see also Merino-Rodo and Janvier, 1986) from the Copacabana Formation. Holocephali are represented by a sole indeterminated bradyodont remain (Merino-Rodo and Janvier, 1986; Janvier, 1991).

Acanthodians are known since the latest Ordovician. In South America, acanthodians scales and partial fin spines were reported from the Middle-Late Permian Teresina Formation (Mutter and Richter, 2007). This record is the youngest in the world. Previously one spine and one scale attributed to Acanthodii were reported from the Late Permian Estrada Nova Formation of Brazil (Würdig-Maciel, 1975). However, the scale resembles a chondrichthyan dermal denticle (Würdig-Maciel, 1975; her Table XII, Fig. 4).

In South America, many "basal actinopterygian" are known by isolated scales and teeth that were identified as indeterminate Actinopterygii or "Palaeonisciform". Most of these lineages are exclusively or mostly represented in the Palaeozoic or Triassic (López-Arbarello et al., 2008). They occur in Argentina (Manceñido, 1973; González, 1985), Bolivia (Beltan et al., 1987; Janvier, 1991), Brazil (Würdig-Maciel, 1975; Richter et al., 1985; Cox and Hutchinson, 1991; Klein et al., 1995; Dias, 1996; Richter and Langer, 1998; Malabarba et al., 2003; Cisneros et al., 2004; Chahud, 2007; Chahud and Fairchild, 2007; Chahud and Petri, 2008), and Uruguay (Mones, 1986; Piñeiro, 2006). Bryant *in* Ruedemann (1929) assigned fossil fish scales to the genera *Elonichthys* and *Acrolepis*. However, that identification is not reliable.

Fortunately, several articulated fossil fishes were described and assigned to different "basal actinopterygian" families. Beltan (1978, 1981) described many endemic new taxa from the San Gregorio Formation, Uruguay. She considered this unit to be Late Carboniferous in age. However, on the basis of palynological evidence, the San Gregorio Formation could have been deposited, at least in part, during the Early Permian (Mones, 1986; Piñeiro, 2006). Beltan (1978) described the species *Mesonichthys antipodeus*, *Gondwananichthys maximus*, and *Carbonilepis uruguayeensis*, which were assigned to the family Acrolepidae; *Elonichthys macropercularis* to Elonichthyidae; *Rhadinichthys rioniger* to Rhadinichthyidae; *Itararichthys microphtalmus* to Pygopteridae; and *Daphnaechelus formosus* to Amblypteridae. Later, Beltan (1989) assigned the species *Irajapintoseidon uruguayensis* and *Monesedeiphus depressus* to the order Cheirolepidiformes. In a recent review, Figueiredo and Gallo (2006) reassigned *Itararichthys microphtalmus* to the Acrolepidiidae and *Mesonichthys antipodeus* to the Cosmoptychiidae. All these endemic taxa are presently interpreted as non-neopterygian "basal actinopterygians" of widely distributed families. However, a former "basal actinopterygian," *Coccocephalichthys tessellatus* (Coccocephalichthyidae) from Uruguay (Beltan, 1981) is presently assignable to neopterygians according to Figueiredo and Gallo (2006).

Other well preserved bony fishes come from different units in Brazil: the elonichthyids *Elonichthys gondwanus* (Richter et al., 1985, 2000) and *Santosichthys mafrensis* (Malabarba, 1988; Richter et al., 2000), the amblypterids *Tholonosteon santacatarinae* (Beltan, 1978; Richter et al., 1985, 2000) and *Tholonotus brasiliensis* (Dunkle and Schaeffer, 1956; Richter et al., 1985, 2000), the brazilichthyid *Brazilichthys macrognathus* (Cox and Hutchinson, 1991; Richter et al., 2000), and the *incertae familia* species *Rubidus pascoalensis* (Richter, 2002) and *Angatubichthys mendesi* (Figueiredo and Carvalho, 2004).

Merino-Rodó and Janvier (1986, see also Janvier, 1991) described platysomid actinopterygians from the Copacabana Formation of Bolivia. The possible occurrence of *Birgeria* (a Triassic genus) was reported from Vitiacua Formation of Bolivia (?Late Permian-Triassic; Beltan et al., 1987).

Finally, few "basal sarcopterygians" were reported from the South American Permian. They include several lungfish plates from Brazil and Bolivia (Beltan et al., 1987; Cox and Hutchinson, 1991; Dias, 1996; Malabarba et al., 2003; Cisneros et al., 2004; Toledo and Bertini, 2005; Chahud and Fairchild, 2007), some indeterminate actinistians from Bolivia, Brazil, and Uruguay (e.g. Janvier, 1991; Piñeiro, 2006; Chahud, 2007) and the species *Coelacanthus* cf. *C. granulatus* from the Vitiacua Formation of Bolivia (?Late Permian-Triassic; Sempere et al., 1992).

3. Stratigraphic and geographic provenance

The material described here comes from the late Paleozoic deposits that crop out near the Cerro Vizcacha area, Provincia de Mendoza, Argentina (Fig. 1a). They are part of the Calingasta-Uspallata Basin along the western margin of the Precordillera Argentina. Structural and sedimentological descriptions of these deposits were provided by Keidel (1939), De Römer (1964), Frakes and Crowell (1969), Amos and López-Gamundí (1981), Buggisch et al. (1994), von Gosen (1995), among many others. Several studies pointed to the paleontological content (with especial reference to marine "invertebrates") of many parts of the sequence (Dessanti and Rossi, 1950; Amos and Rolleri, 1965; Archangelsky

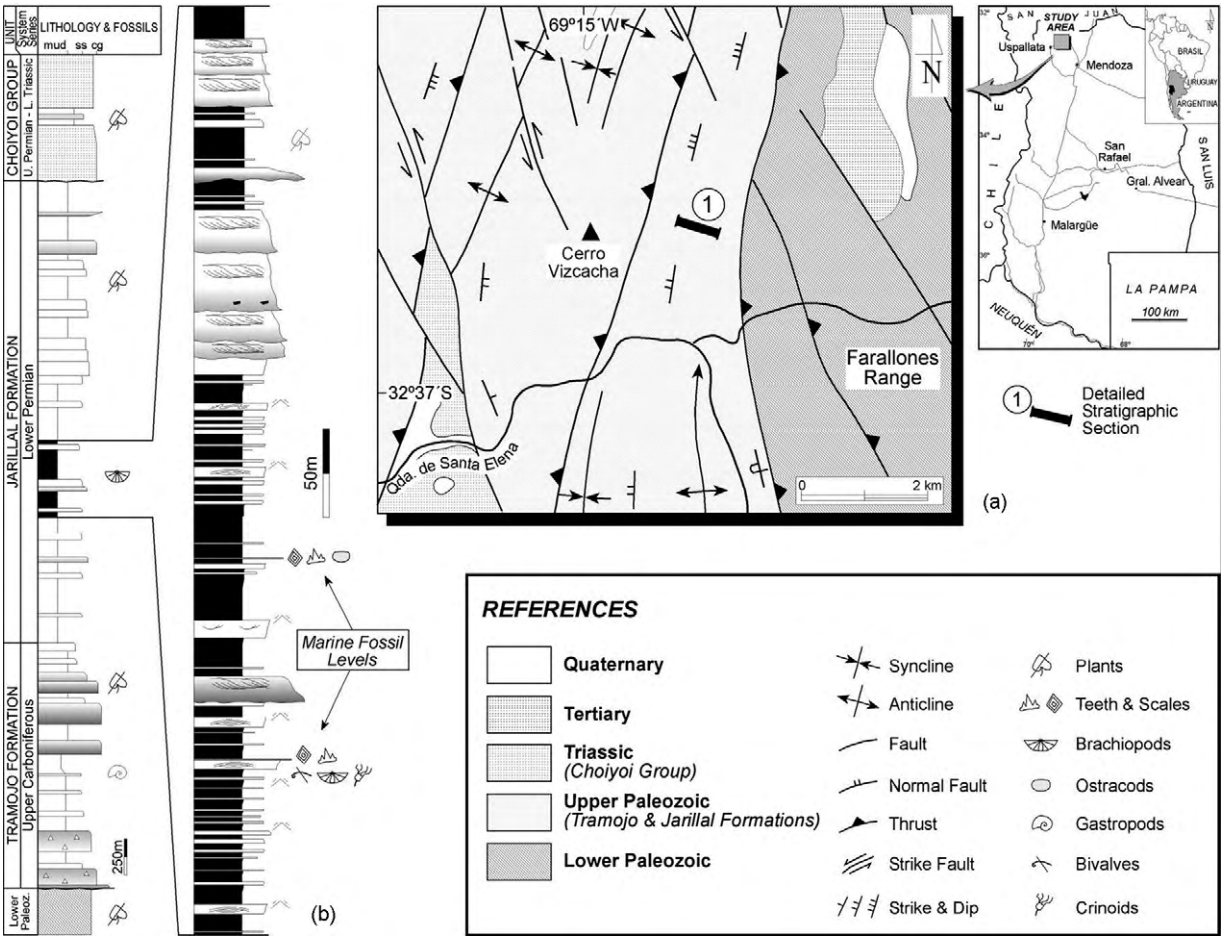

Fig. 1. Location map and section.

and Lech, 1986; Archangelsky and Archangelsky, 1987; Taboada, 1998).

In the study area, the Late Paleozoic units (referred here as Tramojo and Jarillal Formations) are made up of more than 2000 meters of marine and continental sediments, which were deposited during Late Carboniferous to Early Permian times (Fig. 1b). These sequences were affected by a large-scale folding event with north-south and north northeast-south southwest axes trend (von Gosen, 1995).

The Tramojo Formation overlies unconformably the lower Paleozoic basement (Fig. 1b), composed by low-grade metamorphic rocks (phyllites with intercalated quartzite levels). The lower part of the Tramojo Formation consists of glacially-influenced sequences related to different stages of the glacial retreat. These deposits contain an impoverished record of marine macrofossils and palynomorphs that suggest a Late Carboniferous age (Gutiérrez, 1999). In turn, the upper part of this unit is characterized by fluvio-deltaic and lacustrine deposits, containing fossil megafloras (*Nothorhacopteris-Botrychiopsis-Ginkgophyllum* Zone) and palynological assemblages of Late Carboniferous age (Fig. 1b).

The Jarillal Formation is composed by shales and sandstones accumulated in wave- and tide-dominated shallow marine environments corresponding to the largest Wesphalian-Asselian transgression in western Argentina. It presents a rich marine "invertebrate" fauna (*Costatumulus* Zone) of Early Permian age. The upper part of this formation shows a transgression-regression cycle, where shallow marine deposits (fluvio-deltaic systems modified by tides) are followed by brackish and continental facies (fluvio-lacustrine systems). Although in these upper levels no fossils were recorded, its position into the stratigraphic succession suggests as far as Early Permian age.

The Carboniferous to Permian deposits as well as the metamorphic sequences are partly overlain by a thick pile of volcanic rocks, which is built up of pyroclastics and rhyolite flows (Choiyoi Group, Fig. 1b). According to radiometric data these volcanic rocks are assigned to the Permo-Trias (Rocha Campos et al., 1971; Caminos et al., 1979).

The vertebrate remains described in this paper come from two different levels of the middle part of the Jarillal Formation (Fig. 1b), where they are associated with ostracods, brachiopods, gastropods, bivalves, and crinoids. A detailed stratigraphic section was measured (bed by bed) with a Jacob staff, covering a total thickness of 597 meters.

4. Materials and methods

The material is deposited in the Museo de Historia Natural de San Rafael, Parque Mariano Moreno, 5600 San Rafael, Provincia de Mendoza, Argentina.

Most specimens were obtained immersing the calcareous sandstone in a solution to 5% of acetic acid. Remains were washed, drained, and dried. Hybodontiform teeth were prepared by mechanical processing. The specimens were photographed with a Philips 505 scanning electron microscope and images were processed using soft imaging system ADDA II.

Thin cross sections of "basal actinopterygians" scales were made for histological porpouses and observed with Photo

Microscope Carl Zeiss Phomi III. The terminology is according to Richter (1981).

The "basal actinipterygian" teeth and scales were described according to the morphotypes of Richter (1981, 1983), Richter et al. (1985, 1999; see also Würdig-Maciel, 1975), and Trinajstic (1999). Elasmobranch terminology is according to Cappetta (1987) for the teeth and to Zangerl (1981) for the dermal denticles. In Appendix A, chondrichthyan systematics is according to Cappetta et al. (1993) and "basal actinopterygian" systematics according to Figueiredo and Gallo (2006).

5. Systematic paleontology

5.1. Chondrichthyes

ELASMOBRANCHII Bonaparte (1838).
EUSELACHII Hay (1902).
HYBODONTIFORMES Owen (1846).
HYBODONTIDAE Owen (1846).
HYBODONTINAE Owen (1846) *sensu* Maisey, 1989.
Hybodus Agassiz (1833-1843).
cf. Hybodus sp.
Fig. 2a and b.

Material: MHNSR-603-14, one tooth.

Description: The crown presents a strong high central cusp with well-developed cutting edges (Fig. 2a and b). It is lingually inclined and sub-circular in cross section. The tip is eroded. The crown is ornamented with four vertical coarse folds both on the labial and lingual faces. The folds are basally thickened. The crown base is mesio-distally expanded with a well-developed crown shoulder. There is one lateral cusplet base, which is not separated from the main cusp (Fig. 2b). The cusplet base is sub-circular in cross section. The other side is damaged.

The root is labiolingually wide and basally almost flat, with a shallow concavity. The lingual face shows several large foramina. The labial face presents a row of nine foramina (Fig. 2b).

Discussion: The tooth most closely resembles those of hybodontoids and, in part, those of the protacrodontid *Protracrodus* and differs from other Paleozoic chondrichthyans. Although hybodontiforms are primarily Mesozoic sharks, they are present in the Paleozoic. Zangerl (1981) suggested an origin as early as the Middle Devonian. Much of the systematics of hybodontoid and protacrodontoid sharks is based on isolated teeth.

The hybodontiform families Lonchidiidae, Polyacrodontidae, Hybodontidae, and Acrodontidae (*sensu* Rees and Underwood, 2002) were recognized in the Paleozoic. These families are known from the Carboniferous to the Cretaceous (Johnson, 1981; Schultze, 1985; Cisneros et al., 2004; Derycke-Khatir et al., 2004, 2005; Derycke-Khatir et al., 2004, 2005; Ivanov, 2004; Richter, 2004a).

The material described herein differs from Polyacrodontidae, Acrodontidae, and Lonchidiidae teeth because it presents the following character combination: strong and lingually inclined relatively high central cusp, sub-circular in cross section and ornamented with vertical coarse folds on both labial and lingual faces; crown base mesio-distally expanded with well developed crown shoulder; cusplets; slightly concave root base with labial and lingual foramina.

The material shows gross morphological similarities with the protacrodontid genus *Protacrodus* but especially with the hybodontiform genus *Hybodus*. *Protacrodus* teeth are labio-lingually compressed, the cusplets are connected by a distinct occlusal blade and the root is hemiaulacorhize (Zangerl, 1981; Derycke-Khatir, 1992; Ginter, 2001, 2002; Ginter et al., 2002; Ginter and Piechota, 2004). The tooth described herein differs from *Protracrodus* in having high and curved lingually crown, ornamented with basally thickened folds; the root is labio-lingually thick. Besides, *Protacrodus* is only known from the Devonian and Carboniferous (Cappetta et al., 1993). Although Mutter and Richter (2007) reported "isolated shark teeth suggestive of the Devonian genus *Protacrodus*" in the Teresina Formation, the presence of that genus in permian levels has not been confirmed.

The Paleozoic remains attributed to *Hybodus* are generally fragmentary. Teeth and spines were frequently referred to as *Hybodus*-like or "*Hybodus*" sp. (Simpson, 1974; Johnson, 1981; Schultze, 1985; May and Hall, 2002). However, there is one Paleozoic hybodontid that is based on complete specimens from the Upper Carboniferous of Kansas (*Hamiltonichthys mapesi* Maisey, 1989). *Hamiltonichthys* is a basal hybodontoid with tooth crown ornamented with very fine folds. It differs from the material described herein in having a lingually swollen crown and no cusplets.

In South America, Richter and Breitkreuz (1997) mentioned but not described or figured a tooth identified as *Hybodus* sp. that was found in the Lower to Middle Permian of northern Chile.

Hybodontiformes?
Family *incertae sedis*.
Petrodus sp. Mc Coy (1848).
Fig. 2c and d.

Material: MHNSR-603-16, one dermal denticle.

Description: The dermal denticle is conical, with an oval, almost flat base, which projects as a narrow flange. There is a single central foramen in the base. Seven vertical folds radiate from the apical central region to the base. Two of these folds bifurcate midway down the denticle base. The width of the folds increases towards the base.

Discussion: Dermal denticles belonging to the form genus *Petrodus* are common in Paleozoic (mainly of Late Carboniferous age) marine assemblages and have been found associated with different chondrichthyan remains (Case, 1970; Schultze, 1985; Goto, 1994; Itano et al., 2003; Elliot et al., 2004; Hamm et al., 2004).

Petrodus is a morphogenus that was linked with hybodont sharks and bradyodonts (Chorn and Reavis, 1978). Woodward (1889) noted that the dermal conical "granules" of the Mesozoic shark *Hybodus delabechei* were very suggestive of the small Carboniferous fossils named *Petrodus*. Chorn and Reavis (1978) proposed that dermal denticles called *Petrodus* and *Listracanthus* might have occurred in the same animal and suggested an association with the morphogenus *Edestus*. Mutter and Neuman (2006) described small and large dermal denticles of *Listracanthus pectenatus* from the Lower Triassic of British Columbia. However, they suggested that *L. pectenatus* small dermal denticles and *Petrodus patelliformis* were not synonyms. The hybodontoid *Moyacanthus thomasi* and *Petrodus* denticles have been also found together (Zangerl, 1981). Besides, Zangerl (1981) mentioned that the association between the teeth genera *Carcharopsis* and *Petrodus* could indicate that *Petrodus* is an animal whose skin is armored with petrodi denticles and *Carcharopsis* dentition. Consequently, its taxonomic assignation is still doubtful (Elliot et al., 2004).

Hybodontiformes indet.
Fig. 2e.

Material: MHNSR-603-15 (figured), MHNSR-603-17, two dermal denticles.

Description: The material corresponds to compound scales. The surface is ornamented with vertical folds which extend from tip to base. The odontodes are nearly circular in cross section, and the flat bases present a nutritious foramen.

Discussion: The scales appear to be of the hybodontid scale type (e.g. the Jurassic *Hybodus delabechei*; Reif, 1978a). They also resemble the "high complex scales" found in association with hybodonts and other fishes in the Permian of Kansas (Schultze, 1985 his Fig. 3.6). Both compound and single scales

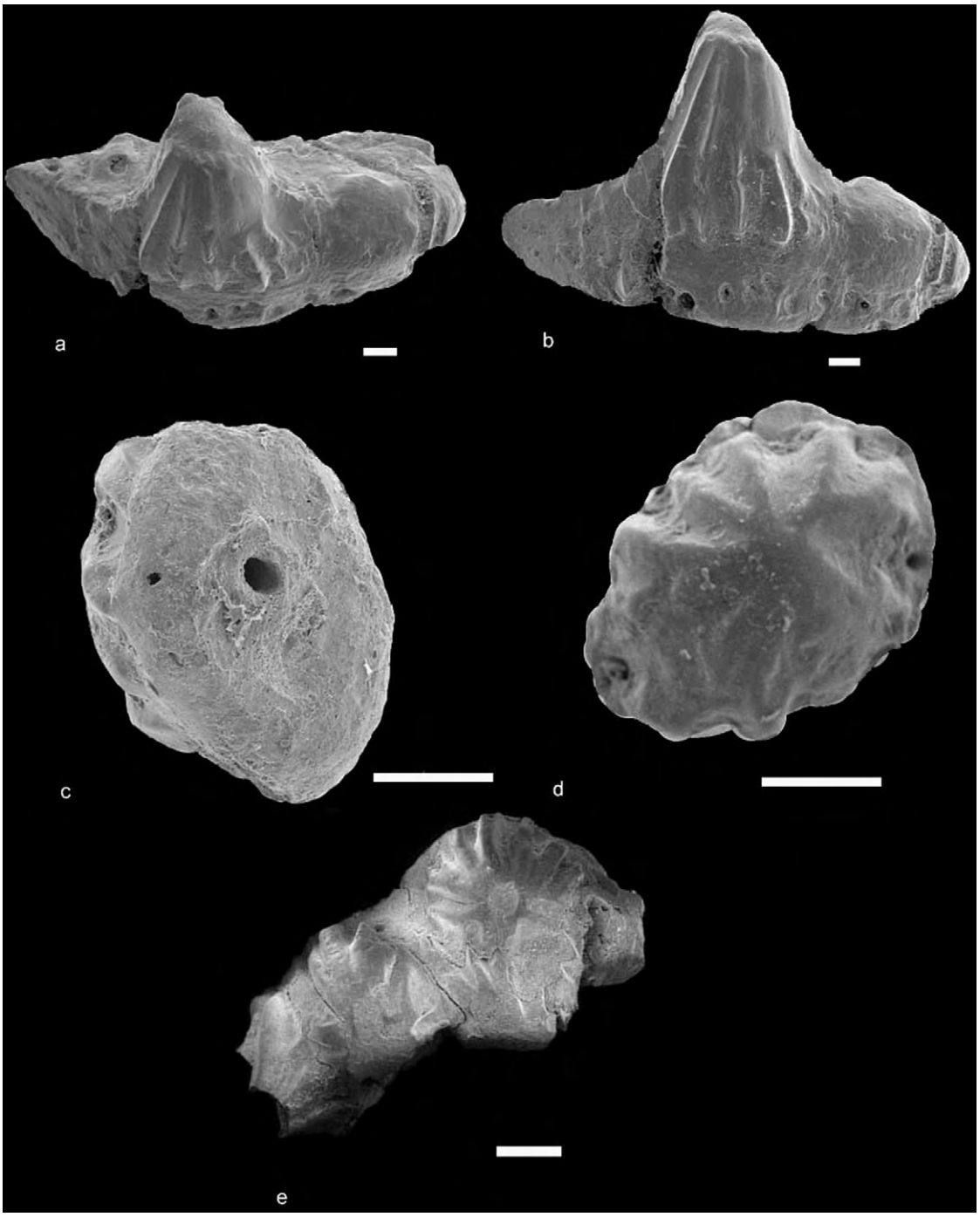

Fig. 2. El Jarillal formation. Hybodontiform tooth and scales. (a) MHNSR 603-14 cf. *Hybodus* sp. tooth almost occlusal view. (b) MHNSR 603-14 cf. *Hybodus* sp. tooth labial view. (c) MHNSR 603-16 *Petrodus* sp. basal view. (d) MHNSR 603-16 *Petrodus* sp. dorsal view. (e) MHNSR 603-15 Hybodontiform indet. Compound scale dorsal view. Bar-scale = 250 μm.

(e.g. *Petrodus*-like) can be found in hybodontid sharks (Reif, 1978b) and the absence of compound scales could reflect growth-related factors (Maisey, 1982).

5.2. Osteichthyes

ACTINOPTERYGII Cope (1887)
Actinopterygii indet.

Only isolated actinopterygian scales and teeth were found. Most of them are fractured and worn down to some degree. Isolated scales and teeth of "basal actinopterygians" do not present enough morphological interspecific variation to allow systematic studies (Richter et al., 1999).

A parasystematics based on isolated actinopterygians remains was created by Würdig-Maciel (1975) and modified by Richter (1981, 1983) and Richter et al. (1985) introducing new morphotypes. Based on these morphotypes, a biostratigraphy was proposed. Besides, Trinajstic (1999) gave another scale parataxonomy for Devonian isolated scales of "basal actinopterygians" from Australia using the characterization according body areas of Esin (1995).

Scales and teeth similar to those described herein have been identified as pertaining to "Palaeonisciformes" or "paleoniscoid" fishes. However, taxa presently included in these groups have changed substantially and several workers consider them paraphyletic (Figueiredo and Gallo, 2006). Besides, there are other groups of "basal actinopterygians" in the late Paleozoic that present similar scales and teeth.

5.2.1. Scales

Scale type *sensu* Richter et al. (1985).

Fig. 3a.

Material: MHNSR-603-1 (figured), MHNSR 603-2, MHNSR 603-3, MHNSR 603-6, MHNSR 603-66 (figured, cross section): five scales.

Description: The scales are rhombic in shape, with a longer axis, entire margin. The free field is unornamented except for one scale (MHNSR 603-6) that presents some shallow *sulci*. Punctuations or pores are located towards the central portion of the scales. Daget et al. (2001) described similar pores and basoapical canals in recent polypterids as vascular canals. It is reasonable to assume that the pores in the Permian scales are similar structures. The outline is partially broken.

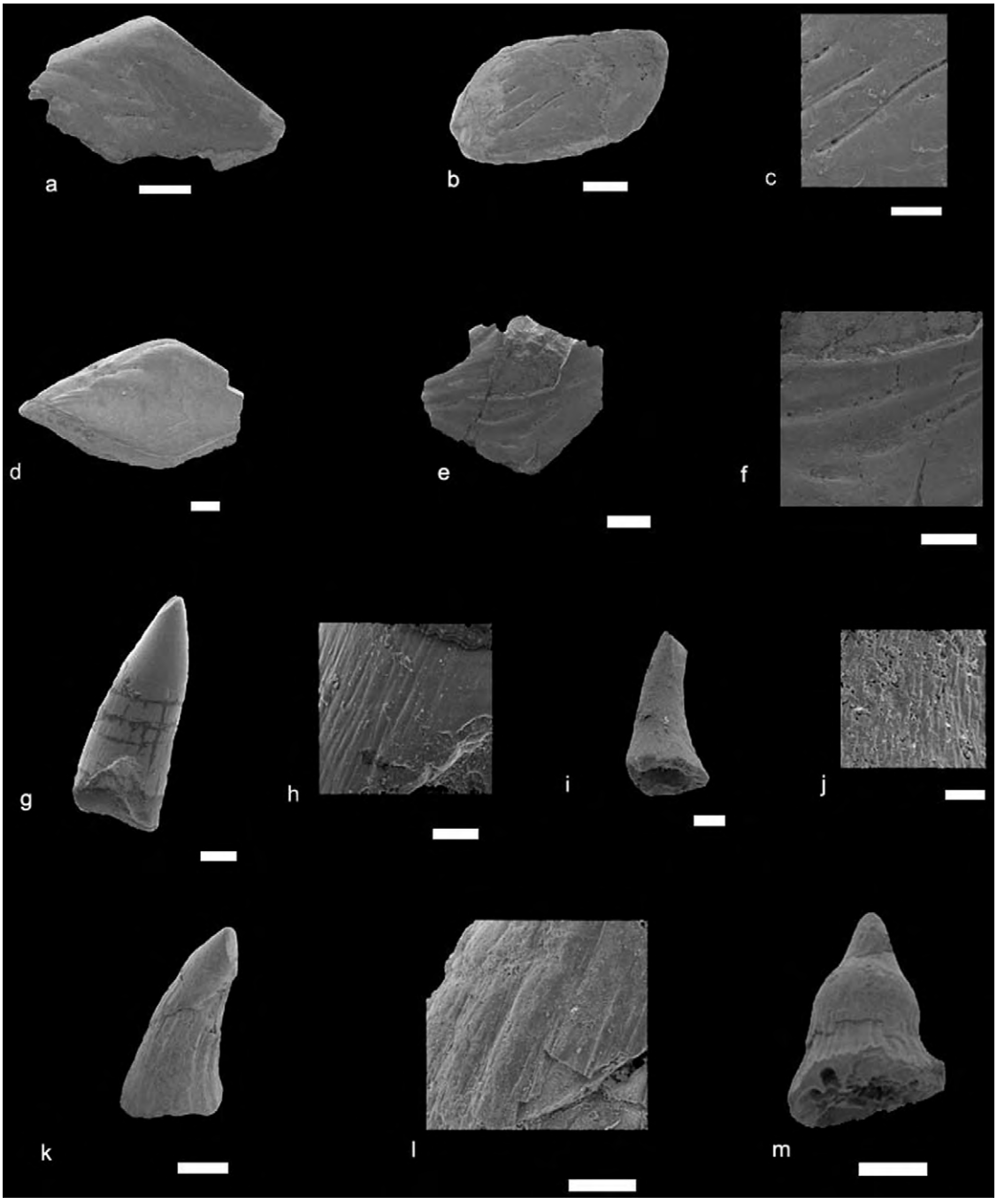

Fig. 3. El Jarillal Formation. "Basal actinopterygian" teeth and scales. (a) MHNSR 603-1 Scale type P1. (b) MHNSR 603-4 Scale type P2. (c) MNHSR 603-4. Scale type P2 detail of the surface. (d) MHNSR 603-7 Scale type X. (e) MHNSR 603-5 Scale type P2. (f) MHNSR 603-5 Scale type P2 detail of the surface. (g) MHNSR 603-10 Tooth type I 1. (h) MHNSR 603-10 Tooth type I 1 detail of the surface. (i) MHNSR 603-11 Tooth type I 8. (j) MHNSR 603-11 Tooth type I 8 detail of the surface. (k) MHNSR 603-12 Tooth type I 2. (l) MHNSR 603-12 Tooth type I 2 detail of the surface. (m) MHNSR 603-13 Tooth type Y. Bar-scale: 1 mm in subpart (k); 0.5 mm in subparts (a, e and m); 0.2 mm in subparts (c, d, f, g and i); 0.25 mm in subpart (l); 0.05 mm in subpart (h) and 0.02 mm in subparts (b and j).

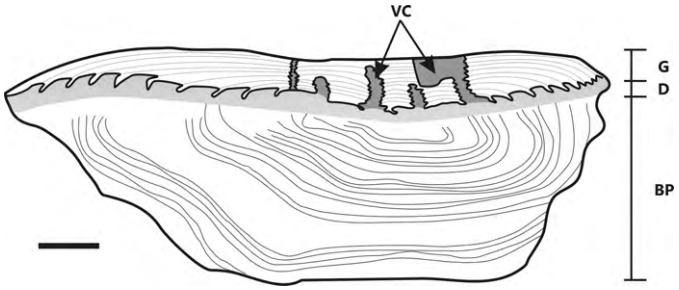

Fig. 4. MHNSR 603-66 Schematic draw of scale type P1 in cross section. VC, vascular canals; G, ganoin; D, dentine; BP, basal plate. Bar-scale = 100 μm.

In cross section (Fig. 4), a multilayered ganoin (G) forms the outer sheet of the scale. Some vascular canals (VC) open to the surface through the ganoin, these canals describes a zig-zag patron. The dentine (D) is a thin and massive layer that develops distally (in the ganoin boundary) hook-like structures. Below to this, there is a thick basal plate (BL). We cannot observe Sharpey's fibers neither osteocytes nor canals of Williamson.

Discussion: The general shape of scales MHNSR-603-1, MHNSR 603-3 and MHNSR 603-6 agree with that described to D area (latero-caudal) and MHNSR 603-2 to C area (midline) of Esin (1995). The poorly developed "peg and socket" structure agrees with subadult stage (Esin, 1995). The cross section reveals three conspicuous tissue layers, the histology observed agree widely with a palaeoniscoid-type scale (Richter, 1981; Sire et al., 2009).

The material most closely resembles the P1 morphotype of Richter et al. (1985), who mentioned that these scales are similar to some of the Permian species *Elonichthys punctatus*. Similar scales have been found in the Brazilian Estrada Nova, Corumbataí, Irati, and Palermo Formations (Würdig-Maciel, 1975; Richter, 1981; Richter et al., 1985) and the Uruguayan Yaguarí, Paso Aguiar, Mangrullo, and Frayle Muerto Formations (Piñeiro, 2006). The material also resembles morphotypes 6 and 7 of Trinajstic (1999), based in Devonian actinopterygians.

Scale type P2 *sensu* Richter et al. (1985).
Fig. 3b, c, e and f.

Material: MHNSR-603-4, MHNSR-603-5, two scales.

Description: The scales are rounded; sub-oval to rhombic in shape, with the external surface ornamented with antero-posterior and almost parallel wide ridges, and punctuations (pores) in the furrows or canals between ridges. The anterior and posterior margins are broken.

Discussion: The material mostly resembles subadult stages and corresponds to G or H areas of Esin (1995). These scales are similar to P2 morphotype of Richter et al. (1985). The scales also resemble some of the Permian species *Elonichtys punctatus* (Richter et al., 1985). Similar scales have been found in the Brazilian Irati Formation (Richter et al., 1985) and the Uruguayan Mangrullo Formation (Piñeiro, 2006). The 013 subtypes, section II of Carboniferous scales of Tway and Ziwek (1982) also resembles the El Jarillal scales.

Scale type X.
Fig. 3d.

Material: MHNSR-603-7: one scale.

Description: The anterior margin of the scale is partially broken. It is rhombic and the ganoin on the free posterior margin of the scale is delicately pectinated. There are some marginal punctuations or pores although the anterior margin lacks ornamentation, and the surface is smooth.

Discussion: The general shape agrees with subadult stages of D area scales of Esin (1995). The material does not resemble any of the morphotypes recognized by Richter (1981) and Richter et al. (1985). It most closely resembles the subtype 218, section III of Tway and Ziwek (1982).

5.2.2. Teeth

All the teeth reported in this section are conical in shape with a smooth acrodin cap and a pulp cavity opening in the base. When they have ridges, they are all around the tooth surface.

Tooth type I 1 *sensu* Richter et al. (1985).
Fig. 3 g and h.

Material: MHNSR-603-8, MHNSR-603-9, MHNSR-603-10 (figured): three teeth.

Description: The teeth are straight with a smooth shaft under OM, but presenting a gently ornamented surface with longitudinal and sometimes anastomosed ridges under SEM (aprox. 300×). Teeth are circular in cross section, with the apical cap of acrodine being hyaline.

Discussion: The teeth resemble the morphotype I 1 of Richter et al. (1985). Similar teeth have been found in sediments of the Brazilian Estrada Nova Formation (Richter et al., 1985) and the Uruguayan Mangrullo Formation (Piñeiro, 2006).

Tooth type I 8 *sensu* Richter et al. (1985).
Fig. 3i and j.

Material: MHNSR-603-11: one tooth.

Description: The ichthyodont is characterized by a curved and smooth shaft under OM, but the surface presents fusiform microtubercles under SEM. The tip is missing.

Discussion: The tooth resembles the type I 8 of Richter et al. (1985). Similar teeth have been found in the Brazilian Irati Formation (Richter et al., 1985).

Tooth type I 2 *sensu* Richter et al. (1985).
Fig. 3k and l.

Material: MHNSR-603-12: one tooth.

Description: The tooth is straight, with the surface ornamented with wide longitudinal ridges. Besides, there are smaller longitudinal folds both on the ridges and furrows (Fig. 3l). The cap is very pointed and narrow.

Discussion: The tooth appears to belong to type I 2 of Richter et al. (1985). Similar teeth have been found in the Brazilian Estrada Nova Formation (Richter et al., 1985) and the Uruguayan Mangrullo Formation (Piñeiro, 2006).

Tooth type Y.
Fig. 3m.

Material: MHNSR-603-13: one tooth.

Description: The tooth is short, its shaft is slightly curved, and is constricted near the base. It is ornamented with nearly evenly spaced longitudinal wide and blunt ribs.

Discussion: This morphotype does not belong to anyone described by Richter et al. (1985). It resembles the morphotype E figured by Richter et al. (1999) from the Brazilian Late Carboniferous Itaituba Formation although the latter lacks the small longitudinal folds.

6. Conclusions

Paleozoic vertebrates from Argentina are very poorly known. Moreover, this is the first report of vertebrate body remains from

the Permian of Argentina. Previously, only amphibian and reptile footprints were known for this period (e.g. Melchor and Sarjeant, 2004). The cf. *Hybodus* tooth from El Jarillal Formation reported here is the southernmost record of Hybodontiformes and the first tooth of the order described from the Paleozoic of South America.

The material is not useful as environmental proxy. For example, hybodontiform remains were found in the continental Rio do Rasto Formation (facies Armada of Estrada Nova Formation) and the marine Teresina Formation (facies Caveiras of Estrada Nova Formation) of Brazil (Richter and Langer, 1998; Malabarba et al., 2003; Cisneros et al., 2004; Richter, 2004a). However, the material was collected in beds considered marine by other source of evidence. Besides, we do not know of any record of the morphogenus *Petrodus* in freshwater beds (e.g. Case, 1970; Schultze, 1985; Goto, 1994; Itano et al., 2003; Elliot et al., 2004).

"Basal actinopterygian" scales and teeth morphotypes of El Jarillal Formation resemble some of those of Uruguayan and Brazilian Permian units. The scales types P1 and P2 are present in the Uruguayan Yaguarí, Paso Aguiar, Mangrullo, and Frayle Muerto Formations and Brazilian Estrada Nova, Corumbataí, Irati, and Palermo Formations, whereas the I 1 teeth are present in Estrada Nova, Mangrullo and Frayle Muerto Formations; I 2 teeth occur in Estrada Nova and Mangrullo Formations and I 8 teeth in Irati Formation. Two morphotypes are unknown in Brazilian or Uruguayan formations (scale type X and tooth type Y). However, morphotypes appear not to be useful for an accurate biostratigraphy.

Other taxa frequently reported from South American Permian units (Xenacanthiforms, Ctenacanthiformes, Dipnoi, Acanthodii or Coelacanthiformes) were not found so far in El Jarillal Formation of Argentina.

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Appendix A

South American Permian fish record.

Taxa	Stratigraphy	Age	References
Chondrichthyes			
Elasmobranchii			
Elasmobranchii indet.	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Elasmobranchii indet.	Copacabana Formation, Bolivia	Early Permian	Janvier (1991)
Petalodontiformes			
Petalodontiformes indet.	Corumbataí Formation, Brazil	Middle-Late Permian	Toledo et al. (1997), Toledo and Bertini (2005)
Petalodontidae indet.	Copacabana Formation, Bolivia	Early Permian	Merino-Rodo and Janvier (1986), Janvier (1991)
Petalodontidae indet.	Grupo Passa Dois, Brazil	Late Permian	Richter (2004b)
Itapyrodus punctatus	Irati Formation, Brazil	Early Permian	Ragonha (1978), Santos (1990), Chahud (2007), Chahud and Fairchild (2007), Chahud and Petri (2008), Chahud et al. (in press)
Itapyrodus punctatus	Pedra do Fogo Formation, Brazil	Early Permian	Richter (2004b)
Sphenacanthiformes			
Sphenacanthiformes indet.	Teresina Formation, Brazil	Late Permian	Richter (2004b)
Sphenacanthus sanpauloensis	Irati Formation, Brazil	Early Permian	Chahud et al. (in press)
Eugeneodontiformes			
Eugeneodontiformes indet.	Teresina Formation, Brazil	Late Permian	Richter (2004a)
Eugeneodontiformes indet.	Passa Dois Group, Brazil	Late Permian	Richter (2004b)
Anisopleurodontis pricei	Pedra do Fogo Formation, Brazil	Early Permian	Richter (2004b)
Agassizodontidae			
Parahelicoprion mariosuarezi	Copacabana Formation, Bolivia	Early Permian	Merino-Rodo and Janvier (1986), Janvier (1991)
Tiaraju tenuis	Teresina Formation, Brazil	Late Permian	Richter (2007)
Agassizodontidae indet.	Pedra do Fogo Formation, Brazil	Early Permian	Cox and Hutchinson (1991)
Orodontiformes			
Orodontiformes indet.	Beds between Tubarão and Passa Dois groups, Brazil	Early Permian	Chahud and Fairchild (2007)
Orodontiformes indet.	Irati Formation, Brazil	Early Permian	Chahud and Petri (2008)
Orodontidae			
Orodus sp.	Irati Formation, Brazil	Early Permian	Chahud (2007)
Orodus milleri	Teresina Formation, Brazil	Early Permian	Richter (2004a)
Orodus milleri	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Orodus ipeunaensis	Irati Formation	Early Permian	Chahud et al. (in press)
Symmoriformes			
Symmoriformes indet.	Budó Formation, Itararé Group	Late Carboniferous/ Early Permian	Richter (2004b)
Ctenacanthiformes			
Ctenacanthiformes indet.	Pedra do Fogo Formation, Brazil	Early Permian	Cox and Hutchinson (1991)
Ctenacanthiformes indet.	Irati Formation, Brazil	Early Permian	Chahud (2007), Chahud and Fairchild (2007), Chahud and Petri (2008)

Appendix A (*Continued*)

Taxa	Stratigraphy	Age	References
Ctenacanthiformes indet.	Teresina Formation, Brazil	Late Permian	Richter (2004a)
Ctenacanthus sp.	Corumbataí Formation, Brazil	Middle-Late Permian	Chahud and Fairchild (2007)
Ctenacanthus sp.	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Ctenacanthus maranhensis	Pedra do Fogo Formation, Brazil	Early Permian	Santos (1946)
Ctenacanthus gondwanus	Rio Bonito Formation, Brazil	Early Permian	Santos (1947), Richter et al. (1985)
Xenacanthiformes			
Xenacanthiformes indet.	Pedra do Fogo Formation, Brazil	Early Permian	Cox and Hutchinson (1991)
Xenacanthiformes indet.	Teresina Formation, Brazil	Late Permian	Richter (2004a)
Xenacanthiformes indet.	Corumbataí Formation, Brazil	Late Permian	Ragonha (1985)
Xenacanthiformes indet.	Rio do Rasto Formation, Brazil	Late Permian	Dias (1996)
Xenacanthus albuquerquei	Irati Formation, Brazil	Early Permian	Ragonha (1978), Chahud (2007), Chahud and Fairchild (2007), Chahud and Petri (2008)
Xenacanthus albuquerquei	Beds between Tubarão and Passa Dois groups, Brazil	Early Permian	Chahud (2007)
Xenacanthus santosi	Teresina Formation, Brazil	Late Permian	Klein et al. (1995), Richter (2004a)
Xenacanthus santosi	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Xenacanthus pricei	Teresina Formation, Brazil	Late Permian	Richter (2004a)
Xenacanthus pricei	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Xenacanthus tocantinensis	Pedra do Fogo Formation, Brazil	Early Permian	Richter (2004b)
Wurdingeria obliterata	Teresina Formation, Brazil	Late Permian	Richter (2005)
Triodus sp.	Passa Dois Group, Brazil	Late Permian	Richter (2004b)
Hybodontiformes			
Hybodontiformes indet.	Rio do Rasto Formation, Brazil	Late Permian	Malabarba et al. (2003), Cisneros et al. (2004)
Hybodontiformes indet.	Teresina Formation, Brazil	Late Permian	Richter (2004a)
Hybodontiformes indet.	Rio do Rasto Formation, Brazil	Late Permian	Richter and Langer (1998)
Hybodontiformes indet.	Corumbataí Formation, Brazil	Late Permian	Chahud and Fairchild (2007)
Hybodus sp.	Cerro 1584 Formation, Chile	Early-Middle Permian	Richter and Breitkreuz (1997)
Holocephali			
Bradyodonti indet.	Copacabana Formation, Bolivia	Early Permian	Merino-Rodo and Janvier (1986), Janvier (1991)
Acanthodi*i*			
Acanthodii indet.	Teresina Formation, Brazil	Middle – Late Permian	Mutter and Richter (2007)
Acanthodii indet.	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Actinopterygii			
Actinopterygii indet.	Mojón de Hierro Formation, Argentina	Early Permian	González (1985)
Actinopterygii indet.	Del Salto Formation., Argentina	Late Carboniferous-Early Permian	Manceñido (1973)
Actinopterygii indet.	Vitiacua Formation. Bolivia	Late Permian?-Early Triassic	Beltan et al. (1987), Janvier (1991), Arratia and Cione (1996)
Actinopterygii indet.	Frayle Muerto Formation, Uruguay	Early Permian	Mones (1986)
Actinopterygii indet.	Paso Aguiar Formation, Uruguay	Late Permian	Mones (1986)
Actinopterygii indet.	Rio do Rasto Formation, Brazil	Late Permian	Dias (1996)
Actinopterygii indet.	Budó Formation, Itararé Group	Late Carboniferous/Early Permian	Richter (2004b)
"Palaeonisciformes" indet.	Pedra do Fogo Formation, Brazil	Early Permian	Cox and Hutchinson (1991)
"Palaeonisciformes" indet.	Irati Formation, Brazil	Early Permian	Chahud (2007), Chahud and Fairchild (2007)
"Palaeonisciformes" indet.	Rio do Rasto Formation, Brazil	Late Permian	Richter and Langer (1998), Malabarba et al. (2003), Cisneros et al. (2004)
"Palaeonisciformes" indet.	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
"Palaeonisciformes" indet.	Teresina Formation, Brazil	Late Permian	Klein et al. (1995)
"Palaeonisciformes" indet.	Irati Formation, Brazil	Late Permian	Richter et al. (1985)
"Palaeonisciformes" indet.	Mangrullo Formation, Uruguay	Early Permian	Piñeiro (2006)
"Palaeonisciformes" indet.	Paso Aguiar Formation, Uruguay	Early Permian	Piñeiro (2006)
"Palaeonisciformes" indet.	Frayle Muerto Formation, Uruguay	Early Permian	Mones (1986), Piñeiro (2006)
"Palaeonisciformes" indet.	Yaguarí Formation, Uruguay	Late Permian	Piñeiro (2006)
Roslerichthys riomafrensis	Rio do Sul Formation, Brazil	Early Permian	Hammel (2005)
Actinopteri			
Family incertae sedis			
Rubidus pascoalensis	Rio do Rasto Formation, Brazil	Late Permian	Richter (2002)
Arratiaichthys chilensis	Peine Formation, Chile	Late Permian	Richter and Breitkreuz (1997)
Acrolepididae			
Acrolepis sp.	Rio do Sul Formation, Brazil	Early Permian	Ruedemann (1929)
Carbonilepis uruguayensis	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Gondwananichthys maximus	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Itararichthys microphtalmus	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Cosmoptychiidae			
Mesonichthys antipodeus	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Elonichthyidae			
Elonichthys sp.	Río do Sul. Formation, Brazil	Early Permian	Ruedemann (1929)
Elonichthys gondwanus	Río do Sul. Formation, Brazil	Early Permian	Richter et al. (1985), Richter et al. (2000)
Elonichthys macropercularis	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Santosichtys mafrensis	Río do Sul. Formation, Brazil	Early Permian	Malabarba (1988), Richter et al. (2000)
Daphnaechelus fomosus	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Daphnaechelus sp.	Rio do Sul Formation, Brazil	Early Permian	Richter (2004b)

Appendix A (*Continued*)

Taxa	Stratigraphy	Age	References
Rhadinichthyidae			
Rhadinichthys rioniger	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Amblypteridae			
Tholonosteon santacatarinae	Río Bonito Formation, Brazil	Late Permian	Richter et al. (1985, 2000)
Tholonosteon santacatarinae	Guatá Group, Brazil	Late Permian	Richter (2004b)
Tholonotus brasiliensis	Corumbataí Formation, Brazil	Late Permian	Dunkle and Schaeffer (1956), Richter et al. (1985, 2000)
Brazilichthyidae			
Brazilichthys macrognathus	Pedra do Fogo Formation, Brazil	Early Permian	Cox and Hutchinson (1991), Richter et al. (2000), Richter (2004b)
Haplolepidiformes			
Platysomidae			
Platysomidae indet.	Copacabana Formation, Bolivia.	Early Permian	Merino-Rodo and Janvier (1986), Janvier (1991)
Platysomidae indet.	Rio do Rasto Formation, Brazil	Late Permian	Dias (1996)
Family incertae sedis			
Angatubichthys mendesi	Corumbataí Formation, Brazil	Late Permian	Figueiredo and Carvalho (2004)
Neopterygii			
Palaeonisciformes			
Birgeriidae			
Birgeriidae cf. *Birgeria*	Vitiacua Fomation, Bolivia	Late Permian?-Early Triassic	Beltan et al. (1987)
Coccocephalicthyidae			
Coccocephalichthys tesselatus	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Mones (1986)
Irajapintoseidon uruguayensis	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1989)
Irajapintoseidon uruguayensis	Rio do Sul Formation, Brazil	Early Permian	Richter (2004b)
Monesedeiphus depressus	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1989)
Sarcopterygii			
Dipnoi indet.	Vitiacua Formation, Bolivia	Late Permian?-Early Triassic	Beltan et al. (1987)
Dipnoi indet.	Río do Rasto Formation, Brazil	Late Permian	Dias (1996), Richter and Langer (1998), Malabarba et al. (2003), Cisneros et al. (2004)
Dipnoi indet.	Pedra do Fogo Formation, Brazil	Early Permian	Cox and Hutchinson (1991)
Ceratodontidae			
Ceratodontidae indet.	Corumbataí Formation, Brazil	Middle-Late Permian	Toledo and Bertini (2005)
Gnathorhizidae			
Gnathorhizidae indet.	Corumbataí Formation, Brazil	Middle-Late Permian	Toledo and Bertini (2005)
Gnathorhizidae indet.	Río do Rasto Formation, Brazil	Late Permian	Toledo and Bertini (2005)
Crossopterygii indet.	Río do Sul Formation, Brazil	Early Permian	Ruedemann (1929)
Actinistia indet.	Pedra do Fogo, Brazil	Early Permian	Weiss and Oliveira (2007)
Actinistia indet.	Irati Formation, Brazil	Early Permian	Chahud (2007), Chahud and Fairchild (2007)
Actinistia indet.	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciel (1975)
Actinistia indet.	Frayle Muerto Formaiton, Uruguay	Early Permian	Piñeiro (2006)
Actinistia indet.	Yaguarí Formation, Uruguay	Late Permian	Piñeiro (2006)
Coelacanthus sp.	Rio do Sul Formation, Brazil	Early Permian	Richter (2004b)
Coelacanthus cf. *granulatus*	Vitiacua Formation, Bolivia	Late Permian?-Early Triassic	Sempere et al. (1992)

References

Agassiz, L.J.R., 1833-1843. Recherches sur les poissons fossiles 3. Imprimerie de Petitpierre, Neuchâtel.

Albanesi, G., Benedetto, J., Gagnier, P., 1995. *Sacabambaspis janvieri* (Vertebrata) y conodontes del Llandeiliano temprano en la Formación La Cantera, Precordillera de San Juan, Argentina. Boletín de la Academia de Ciencias de Córdoba 60, 519–543.

Amos, A.J., López-Gamundí, O., 1981. Las diamictitas del Paleozoico Superior en Argentina: su edad e interpretación. Actas del Octavo Congreso Geológico Argentino (San Luis) 3, 41–58.

Amos, A.J., Rolleri, E.O., 1965. El Carbónico marino en el valle de Calingasta-Uspallata (San Juan-Mendoza). Boletín de Informaciones Petroleras 368, 50–71.

Archangelsky, A., Archangelsky, S., 1987. Tafoflora de la Formación Tramojo, Paleozoico tardío, en la región de Uspallata, provincia de Mendoza, República Argentina. Ameghiniana 24, 251–256.

Archangelsky, A., Lech, R.R., 1986. Presencia de *Cancrinella* aff. *farleyensis* (Eth & Dunn) en las capas plegadas de la "Serie Tramojo", Pérmico inferior de la Precordillera de Mendoza. Actas de las Primeras Jornadas de Geología de Precordillera, Buenos Aires I 187–191.

Arratia, G., Cione, A., 1996. The record of fossil fishes of Southern South America. München Geowissenschaften Abhandlungen 30, 9–72.

Beltan, L., 1978. Découverte d'une ichthyofaune dans le Carbonifère supérieur d'Uruguay. Rapports avec les faunes ichthyologiques contemporaines des autres régions du Gondwana. Annales de la SociétéGéologique du Nord 351–357.

Beltan, L., 1981. *Coccocephalichthys tesselatus n.* sp. (Pisces, Actinopterygii) from the Upper Carboniferous of Uruguay. Anais do II Congresso Latino-Americano de Paleontología 1, Porto Alegre, pp. 95–105.

Beltan, L., 1989. New Permian actinopterygians families from Uruguay. Acta Musei Reginaehradecensis ScientiaeNaturales 22, 79–86.

Beltan, L., Freneix, S., Janvier, P., Lopez-Paulsen, O., 1987. La faune triasique de la formation de Vitiacua dans la région de Villamontes (Département de Chuquisaca, Bolivia). Neues Jahrbuch für Geologie und Paläeontologie Mitteil 2, 99–115.

Bonaparte, C.L., 1838. Synopsis vertebratorum systematis. Nuovi Annali delle Scienze Naturali 2, 105–133.

Bravard, A., 1858. Monografía de los terrenos terciarios del Paraná. pp. 1–107 (reprinted by the Imprenta del Congreso de la Nación, Buenos Aires, 1995).

Buggisch, W., von Gosen, W., Henjes-Kunst, F., Krumm, S., 1994. The age of Early Paleozoic deformation and metamorphism in the Argentine Precordillera—evidence from K-Ar Data. Zentralblatt fur Geologie Paläontogie 1, 275–286.

Caminos, R., Cordani, U., Linares, E., 1979. Geología y geocronología de las rocas metamórficas y eruptivas de la Precordillera y Cordillera Frontal de Mendoza. Actas del Segundo Congreso Geológico Chileno 1, Santiago de Chile, pp. 43–61.

Cappetta, H., 1987. Chondrichthyes II. Handbook of Paleoichthyology. Gustav Fischer Verlag, Stuttgart.

Cappetta, H., Duffin, C., Zidek, J., 1993. Chondrichthyes. In: Benton, M.J. (Ed.), The Fossil Record 2. Chapman & Hall, London, pp. 593–609.

Case, G.R., 1970. The occurrence of *Petrodus* and other fossil shark remains in the Pennsylvanian of Iowa. Annals of Iowa 40, 445–449.

Chahud, A. 2007. Paleontologia de vertebrados da transição entre os grupos Tubarão e Passa Dois (Neopaleozóico) no centro-leste do Estado de São Paulo. Unpublished PhD dissertation. Universidade de São Paulo, Instituto de Geociências, São Paulo, p. 184.
Chahud, A., Fairchild, T. R., 2007. Vertebrados Paleozóicos do Estado de São Paulo. In: Carvalho, I. de S., Cassab, R. de C. T., Schwanke, C., Carvalho, M. de A., Fernandes, A. C. S., Rodrigues, M. A. da C., Carvalho, M. S. S. de, Arai, M., and Oliveria, M. E. Q. (Eds.), Paleontologia: Cenarios de Vida, v.1. Interciência, Río de Janeiro, pp. 101-110.
Chahud, A., Fairchild, T.R., Petri, S. Chondrichthyans from the base of the Irati Formation (Early Permian, Parána Basin), São Paulo, Brazil. Gondwana Research, doi:10.1016/j.gr.2010.01.006.
Chahud, A., Petri, S., 2008. Chondrichthyes no Membro Taquaral, base da Formação Irati, no centro leste do Estado de São Paulo, Brasil. Revista de Geologia 21, 169–179.
Chorn, J., Reavis, E.A., 1978. Affinities of the Chondrichthyan Organ-Genera *Listracanthus* and *Petrodus*, vol. 89. The University of Kansas Paleontological Contributions, pp. 4–9.
Cieza de León, P., 1553. Crónica del Perú. El Señorío de los Incas. Fundación Biblioteca Ayacucho, Caracas, 2005, pp. 152–153.
Cione, A.L., Acosta Hospitaleche, C., Mennucci, J., Cocca, S., 2002. The first Triassic-Jurassic shark of South America. Neues Jahrbuch für Geologie und Paläeontologie Mitteil 1, 9–18.
Cisneros, J.C., Abdala, N.F., Malabarba, M.C., 2004. Pareiasaurids from the Rio do Rasto Formation (Late Permian) of Southern Brazil. X International Symposium on Early vertebrates/Lower vertebrates, (Gramado), pp. 12–13.
Cope, E.D., 1887. Zittel's manual of palaeontology. American Naturalist 21, 1014–1019.
Cox, B.C., Hutchinson, P., 1991. Fishes and amphibians from the Late Permian Pedra do Fogo Formation of Northern Brazil. Palaeontology 34, 561–573.
Cuvier, G., 1796. Notice sur le squelette d'une très-grande espèce de quadrupède inconnue jusqu'à présent, trouvé au Paraquay, et époséau cabinet d'histoire naturelle de Madrid. Magasin Encyclopèdique: ou Journal des Sciences, des Lettres et des Arts 1, 303–310.
D'Orbigny, A., 1842. Voyage dans l'Amérique méridionale (le Brésil, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), executé pendant les années 1826-1833, Tome 3, 3e part, Géologie. P. Bertrand, Paris, pp. 1–290.
Daget, J., Gayet, M., Meunier, F.J., Sire, J.Y., 2001. Major discoveries on the dermal skeleton of fossil and Recent plypteriforms: a review. Fishes and Fisheries 2, 113–124.
Darwin, C., 1846. Geological Observations. D. Appleton Co., London.
de Acosta, J., 1590. Historia natural y moral de las Indias. Fondo de Cultura Económica, Mexico, 1940, p. 35, 261.
De Römer, H.S., 1964. Sobre la geología de la zona de "El Choique", entre el cordón de los Farallones y el cordón de Bonilla, Quebrada Santa Elena, Uspallata (Provincia de Mendoza). Revista de la Asociación Geológica Argentina 19, 9–18.
Derycke-Khatir, C., 1992. Microrestes de Sélaciens et autres Vertébrés du Dévonien supérieur du Maroc. Bulletin of Museum national du Historia Naturelle 14, 15–61.
Derycke-Khatir, C., 2005. Microrestes de Vertébrés du Paléozoïque supérieur de la Manche au Rhin. Société Géologique du Nord, Publication 33, 1–363.
Derycke-Khatir, C., Vachard, D., Dégardin, J.P., de Buitrón, B., Hansen, M.C., 2004. Late Pennsylvanian and Early Permian chondrichthyan microremains from San Salvador Patlanoaya (Puebla, Mexico). X International Symposium on Early vertebrates/Lower vertebrates, (Gramado), pp. 14–15.
Derycke-Khatir, C., Vachard, D.J., Dégardin, M., Flores de Dios, A., Buitrón-Sánchez, B.E., Hansen, M., 2005. Late Pennsylvanian and Early Permian chondrichthyan microremains from San Salvador Patlanoaya (Puebla, Mexico). Geobios 38, 43–55.
Dessanti, R.N., Rossi, J.J., 1950. Nuevos hallazgos de fósiles carbónicos en la Quebrada de Uspallata. Revista de la Asociación Geológica Argentina 5, 149–158.
Dias, E.V., 1996. New fish (Actinopterygii, Platysomidae) from the Upper Permian of Paraná Basin, Brazil. Ameghiniana 33, 463.
Díaz Saravia, P., 2001. Upper Carboniferous fish micro-remains from western Argentina. Revista Española de Micropaleontología 33, 123–133.
Dunkle, D.H., Schaeffer, B., 1956. Preliminary description of a Paleoniscid Fish from the Late Paleozoic of Brazil. Boletim da Faculdade de Filosofia, Ciencias e Letras da Universidade de Sao Paulo 9, pp. 5–22.
Elliot, D.K., Irmis, R.B., Hansen, M.C., Olson, T.J., 2004. Chondrichthyans from the Pennsylvanian (Desmoinesian) Naco formation of Central Arizona. Journal of Vertebrate Paleontology 24, 268–280.
Esin, D., 1995. Ontogenetic development of the squamation in some Palaeoniscoid fishes. Bulletin of Museum national du Historia Naturelle 17, 227–234.
Falkner, T., 1764. Descripción de la Patagonia. Geografía, recursos, costumbres y lengua de sus moradores. Continente, Buenos Aires, 2008, pp. 1–156.
Figueiredo, F.J., Carvalho, B.C.M.C., 2004. A new actinopterygian fish from the Late Permian of the Paraná Basin, Southern Brazil. Arquivos do Museu Nacional, Rio de Janeiro 62, 531–547.
Figueiredo, F.J., Gallo, V., 2006. Actinopterígios paleopterígios: morfologia e taxonomía. In: Gallo, V., Brito, P.M., Silva, H.M.A., Figueiredo, F.J. (Eds.), Paleontologia de Vertebrados: Grandes Temas e Contribuições Científicas. Interciência, Rio de Janeiro, pp. 1–28.
Frakes, A., Crowell, J., 1969. Late Paleozoic glaciation. Part I, South America. Geological Society of America, Bulletin 80, 1007–1042.
Ginter, M., 2001. Chondrichthyan biofacies in the Late Famennian of Utah and Nevada. Journal of Vertebrate Paleontology 21, 714–729.
Ginter, M., 2002. Chondrichthyan fauna of the Frasnian–Famennian boundary beds in Poland. Acta Palaeontológica Polonica 47, 329–338.
Ginter, M., Hairapetian, V., Klug, C., 2002. Famennian chondrichthyans from the shelves of North Gondwana. Acta Geológica Polonica 52, 169–215.
Ginter, M., Piechota, A., 2004. The first Devonian holocephalian tooth from Poland. Acta Palaeontológica Polonica 49, 409–415.
González, C., 1985. El Paleozoico superior marino de la Patagonia extrandina. Ameghiniana 21, 125–142.
Goto, M., 1994. Palaeozoic and early Mesozoic fish faunas of the Japanese Island. The Island Arc 3, 247–254.
Gutiérrez, P., 1999. Informe palinológico de la hoja 3369-15, Potrerillos. Instituto de Geología y Recursos Minerales. Servicio Geológico Minero Argentino. Unpublished paper.
Hammel, M., 2005. A New Lower Actinopterygian from the Early Permian of the Paraná Basin, Brazil. Journal of Vertebrate Paleontology 25, 19–26.
Hamm, S., Cicimurri, D., Campbell, B., 2004. Chondrichthyans from the Pennsylvanian (Desmoinesian) Lake Neosho Shale Member of the Altamont Limestone in Southeastern Kansas. The 5th Annual Kansas Academy of Science Paleontology Symposium (Kansas), pp. 73–74.
Hay, O.P., 1902. Bibliography and catalogue of the fossil Vertebrata of North America. U. S. Geological Survey Bulletin 179, 1–168.
Itano, W.M., Houck, K.J., Lockley, M.G., 2003. *Ctenacanthus* and other Chondrichthyan spines and denticles from the Minturn Formation (Pennsylvanian) of Colorado. Journal of Paleontology 77, 524–535.
Ivanov, A., 2004. Permian chondrichthyans of the Middle and South Urals. X International Symposium on Early vertebrates/Lower vertebrates (Gramado), 21.
Janvier, P., 1991. The Permian and Triassic vertebrates of Bolivia. In: Suárez-Soruco, R. (Ed.), Fósiles y Facies de Bolivia (1) Vertebrados. Revista Técnica de YPFB, 12, pp. 389–391.
Johnson, G., 1981. Hybodontoidei (Chondrichthyes) from the Wichita-Albany Group (Early Permian) of Texas. Journal of Vertebrate Paleontology 1, 1–41.
Keidel, J., 1939. Las estructuras de corrimientos paleozoicos de la Sierra de Uspallata Provincia de Mendoza. Physis 14, 3–96.
Klein, C., Simões, M.G., Leipnitz, I.I., Richter, M., 1995. Interpretação dos dados tafonômicos na deposição de peixes e pelecípodes da Formação Teresina (Grupo Passa Dois), na região de Tiaraju, RS, Brasil. Boletim de Resumos 166.
López-Arbarello, A., Rauhut, O., Moser, K., 2008. Jurassic fishes fo Gondwana. Revista de la Asociación Geológica Argentina 63, 586–612.
Malabarba, M.C.L., 1988. A new genus and species of stem group actinopteran fish from the Lower Permian of Santa Catarina State, Brazil. Zoological Journal of the Linnean Society 94, 287–299.
Malabarba, M.C., Abdala, F., Weiss, F.E., Perez, P.A., 2003. New data on the Late Permian Vertebrate Fauna of Posto Queimado, Rio do Rasto Formation, Southern Brazil. Revista Brasileira Paleontología 6, 49–54.
Maisey, J.G., 1982. The anatomy and interrelationships of Mesozoic Hybodont sharks. American Museum Novitates 2724, 1–48.
Maisey, J.G., 1989. Hamiltonichthys mapesi, g. & sp. nov. (Chondrichthyes: Elasmobranchii), from the Upper Pennsylvanian of Kansas. American Museum Novitates 2931, 1–42.
Maisey, J.G., Naylor, G.J.P., Ward, D.J., 2004. Mesozoic elasmobranches, neoselachian phylogeny and the rise of modern elasmobranch diversity. In: Arratia, G., Tintori, A. (Eds.), Mesozoic fishes, Systematics, palaeoenvironments and biodiversity, 3. Friedrich Pfeil, Munich, pp. 17–56.
Manceñido, M., 1973. La fauna de la Formación del Salto (Paleozoico Superior de San Juan) Parte 1. Introducción y estratigrafía. Ameghiniana 10, 234–245.
May, W.J., Hall, J.D., 2002. Geology and vertebrate fauna of a new site in the Wellington Formation (Lower Permian) of Northern Oklahoma. Oklahoma Geology Notes 62, 63–66.
Mc Coy, F., 1848. On some new fossil fish of the Carboniferous Period. Annals and Magazine of Natural History 2, 115–133.
Merino-Rodo, D., Janvier, P., 1986. Chondrichthyan and actinopterygian remains from the Lower Permian Copacabana Formation of Bolivia. Geobios 19, 479–493.
Melchor, R., Sarjeant, W.S., 2004. Small Amphibian and Reptile Footprints from the Permian Carapacha Basin, Argentina. Ichnos 11, 57–78.
Mones, A., 1986. El contenido paleontológico de las Formaciones Carbónico-Pérmicas del Uruguay. Comunicaciones Paleontológicas del Museo de Historia Natural de Montevideo 14, 205–216.
Mutter, R.J., Neuman, A.G., 2006. An enigmatic chondrichthyan with Paleozoic affinities from the Lower Triassic of western Canada. Acta Palaeontologica Polonica 51, 271–282.
Mutter, R., Neuman, A.G., 2008. New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation of Western Canada. In: Cavin, L., Longbottom, A.E., Richter, M. (Eds.), Fishes and the Break-up of Pangaea. The Geological Society, London, pp. 9–41.
Mutter, R., Richter, M., 2007. Acanthodian remains from the Middle-Late Permian of Brazil. Geological Journal 42, 213–224.
Mutter, R., Tomassi, H.Z.D., Carmo, D.A., 2008. In pursuit of causes for the greatest mass extinction: the Permo-Triassic Boundary in the Southern Hemisphere–part II Investigating 260 million years old, meteorite-impacted sedimentary rocks in central-west Brazil. Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich 153, 81–91.

Owen, R., 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846. Part 1. Fishes. Longman, London.
Piñeiro, G., 2006. Nuevos aportes a la paleontología del Pérmico de Uruguay. In: Veroslavsky, N., Ubilla, M., Martinez, S. (Eds.), Cuencas sedimentarias de Uruguay-Paleozoico. DIRAC, Facultad de Ciencias, Montevideo, pp. 257–280.
Ragonha, E.W., 1985. Nova espêcie de Xenacanthodii (Chondrichthyes, Elasmobranchii) Formação Corumbataí, Taquarituba (SP). Resumos do IX Congresso Brasileiro de Paleontología (Sao Paulo) 132.
Ragonha, E.W., 1978. Chondrichthyes do Membro Taquaral (Formação Irati) no Estado de São Paulo. Dissertação de Mestrado, IGc-USP, 65 pp.
Rees, J., Underwood, C., 2002. The status of the shark genus Lissodus Brough, 1935 and the position of nominal Lissodus species within the Hybodontoidea (Selachii). Journal of Vertebrate Paleontology 22, 471–479.
Reif, W.E., 1978a. Types of morphogenesis of the dermal skeleton in fossil sharks. Paläontologische Zeitschrift 52, 110–128.
Reif, W.E., 1978b. Protective and hydrodynamic function of the dermal skeleton of elasmobranchs. Neues Jahrbuch für Geologie und Paläeontologie 1976-1978 133–141.
Riccardi, A., Sabattini, N., 1985. Supposed coleoids remains reinterpreted as fish scales. N. Neues Jahrbuch für Geologie und Paläeontologie Mitteil 11, 700–706.
Richter, M., 1981. Estudo morfologico e bio-estratigrafico de escamas da paleoictiofauna do Grupo Passa Dois (Permiano), Brasil. Porto Alegre. PhD thesis, Universidade Federal do Rio Grande do Sul, Curso de Pós-Graduacao em Geociencias.
Richter, M., 1983. Ultra-estrutura de dentes de Paleoniscídeos (Pisces) do Grupo Passa Dois, RS, Brasil. Iheringia 8, 131–145.
Richter, M., 2000. Peixes fósseis do Rio Grande do Sul. In: Holz, M., De Ros, L.F. (Eds.), Paleontologia do Rio Grande do Sul. CIGO/UFRGS, Rio Grande do Sul, pp. 163–175.
Richter, M., 2002. A ray-finned fish (Osteichthyes) from the Late Permian of the state of Santa Catarina (Paraná Basin) Southern Brazil. Revista Brasileira de Paleontología 3, 56–61.
Richter, M., 2004a. Late Permian (Guadalupian) shark remains (Chondrichthyes) from the Teresina Formation, Paraná Basin, Southern Brazil. X International Symposium on Early vertebrates/Lower vertebrates, (Gramado), pp. 28–29.
Richter, M., 2004b. Distribution of Permian Fishes of Brazil and their palaeoenvironments. 48th Annual Meeting17th-20th December 2004. Newsletter of The Palaeontological Association 57, p. 178.
Richter, M., 2005. A new xenacanthid shark (Chondrichthyes) from the Teresina Formation, Permian of the Paraná Basin, Southern Brazil. Revista Brasileira de Paleontología 8, 149–158.
Richter, M., 2007. First record of Eugeneodontiformes (Chondrichthyes: Elasmobranchii) from the Paraná Basin, Late Permian of Brazil. In: I. de S., Carvalho, Cassab, R. de C.T., Schwanke, C., Carvalho, M. de A., Fernandes, A.C.S., Rodrigues, M.A. da C., Carvalho, M.S. S. de, Arai, M., Oliveria, M.E.Q. (Eds.), Paleontologia: Cenarios de Vida, v.1. Interciência, Río de Janeiro, pp. 149–156.
Richter, M., Breitkreuz, C., 1997. Permian fish remains from the Peine Formation of northern Chile. Modern Geology 21, 171–184.
Richter, M., Langer, M.C., 1998. Fish remains from the Upper Permian Rio do Rasto Formation (Paraná Basin) of southern Brazil. Journal of African Earth Science 27, 158–159.
Richter, M., Neis, P., Smith, M., 1999. Acanthodian and Actinopterygian fish remains from the Itaituba Formation, Late Carboniferous of the Amazon Basin, Brazil, with a note on acanthodian ganoin. Neues Jahrbuch für Geologie und Paläeontologie Mitteil 12, 728–744.
Richter, M., Piccoli, A.E., Souza Lima, M.C., 1985. Variação morfológica de restos de paleoniscídeos (Pisces) no Permiano da Bacia do Paraná. MME/DNPM, Série Geologia 27, 111–122.
Richter, M., Sales Viana, M.S., Malabarba, M.C., 2000. Agnatos e Peixes. In: Ismar de Sousa Carvalho (Ed.), Paleontologia. Interciência, Rio de Janeiro, pp. 498–524.
Rocha Campos, A.A., Amaral, G., Aparicio, E.P., 1971. Algunas edades K-Ar de la "Serie Porfirítica" en la Precordillera y Cordillera Frontal de Mendoza, República Argentina. Revista de la Asociación Geológica Argentina 26, 311–316.
Ruedemann, R., 1929. Fossils from the Permian tillite of Sao Paulo, Brazil, and their bearing on the origin of tillite. Geological Society of American Bulletin 40, 417–426.
Santos, R.S., 1946. Duas novas formas de elasmobranquios do Paleozoico do meio do norte, Brasil. Anais da Academia Brasileira de Ciências 18, 282–285.
Santos, R.S., 1947. Um *Ctenacanthus* do Gondwana brasileiro. Anais da Academia Brasileira de Ciências 19, 247–253.
Santos, R.S., 1990. Paleoictiofáunula da Formaçâo Pedra do Fogo, bacia de Parnaíba, NE do Brasil. Holocephali-Petalodontidae. Anais da Academia Brasileira de Ciências 62, 347–355.
Schultze, H.P., 1985. Marine to Onshore Vertebrates in the Lower Permian of Kansas and their Paleoenviromental Implications, vol. 113. The University of Kansas Paleontological Contributions, pp. 1–18.
Sempere, T., Aguilera, E., Doubinger, J., Janvier, P., Lobo, J., Oller, J., Wenz, S., 1992. La Formation de Vitiacua (Permien Moyen à Supérieur-Trias? Inférieur, Bolivie du Sud): stratigraphie, palynologie et paléontologie. Neues Jahrbuch für Geologie und Paläeontologie Abhandlungen 185, 239–253.
Simpson, L.C., 1974. Acanthodes and Hybodus in the Permian of Texas and Oklahoma. Journal of Vertebrate Paleontology 48, 1291–1293.
Sire, J.Y., Donoghue, P.C.J., Vickaryous, E.M.K., 2009. Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. Journal of Anatomy 214, 409–440.
Spix, J.B., Martius, C.F.P., 1823-1831. Reise im Brasilien. München, 3 vol., pp. 1–412.
Taboada, A.C., 1998. Dos nuevas especies de Linoproductidae (Brachiopoda) y algunas consideraciones sobre el neopaleozoico sedimentario de las cercanías de Uspallata, Argentina. Acta Geológica Lilloana 18, 69–80.
Toledo, C.E.V., Bertini, R., 2005. Ocurrences of the fossil Dipnoiformes in Brazil and its stratigraphic and chronological distributions. Revista Brasilera de Paleontogía 8, 47–56.
Toledo, C.E.V., Brito, P.M.M., Bertini, R.J., 1997. Chronological meaning about the presence of petalodonts (Holocephali incertae sedis) in the Corumbataí Formation of São Paulo State (Brazil). In: Congreso Brasileiro Paleontología 15. Boletim de Resumos, São Pedro, p. 80.
Tornquist, A., 1904. Ein Radinichthys aus dem Karbon Südamerikas. Zeitschrift der Deutschen Geologischen Gesellschaft 56, 346–351.
Trinajstic, K., 1999. Scale morphology of the Late Devonian palaeoniscoid Moythomasia duriganga Gardiner and Bartram, 1977. Alcheringa 23, pp. 9–19.
Tway, L.E., Ziwek, J., 1982. Catalog of Late Pennsylvanian Ichthyoliths, Part I. Journal Vertebrate Paleontology 2, 328–361.
von Gosen, W., 1995. Polyphase structural evolution of the southwestern Argentine Precordillera. Journal of South American Earth Science 8, 377–404.
von Humboldt, A., 1814. Personal narrative of travels to the Equinoctial regions of the New Continent during the years 1799-1804. Vol. I. George Bell & Sons, London, 1907, pp. 1–505.
Weiss, F.D., Oliveira, S.G., 2007. Registro de Actinistia na Formação Pedra de Fogo, Permiano da Bacia do Parnaíba, no Estado do Tocantins, Brasil. Boletim Paleontologia em Destaque 53, 34.
Woodward, A.S. 1889. Catalogue of the Fossil Fishes in the British Museum (Natural History). Part 1. British Museum (Natural History), London, pp. 1–567.
Würdig-Maciel, N.L., 1975. Ichtiodontes e Ichtiodorulitos (Pisces) da Formaçâo Estrada Nova e sua aplicaçâo nao estratigrafia do Grupo Passa Dois. Pesquisas 5, 7–166.
Zangerl, R., 1981. In: Schultze, H.P. (Ed.), Handbook of Paleoichthyology. Chondrichthyes I Paleozoic Elasmobranchii. Gustav Fischer Verlag, Stuttgart.