



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 find 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.

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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 remnant “rhynchonellid 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 condriactians; 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 ctenacanthiforms 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 *Xenacanthus* 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 Breitenkreuz, 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 indeterminate 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 uruguayensis*, which were assigned to the family Acrolepidae; *Elonichthys macropircularis* to Elonichthyidae; *Rhadinichthys rioniger* to Rhadinichthyidae; *Itarichthys microphthalmus* to Pygopteridae; and *Daphnaechelus formosus* to Amblypteridae. Later, Beltan (1989) assigned the species *Irapintoseidon uruguayensis* and *Monesedeiphus depressus* to the order Cheirolepidiformes. In a recent review, Figueiredo and Gallo (2006) reassigned *Itarichthys microphthalmus* 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 familiae* 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

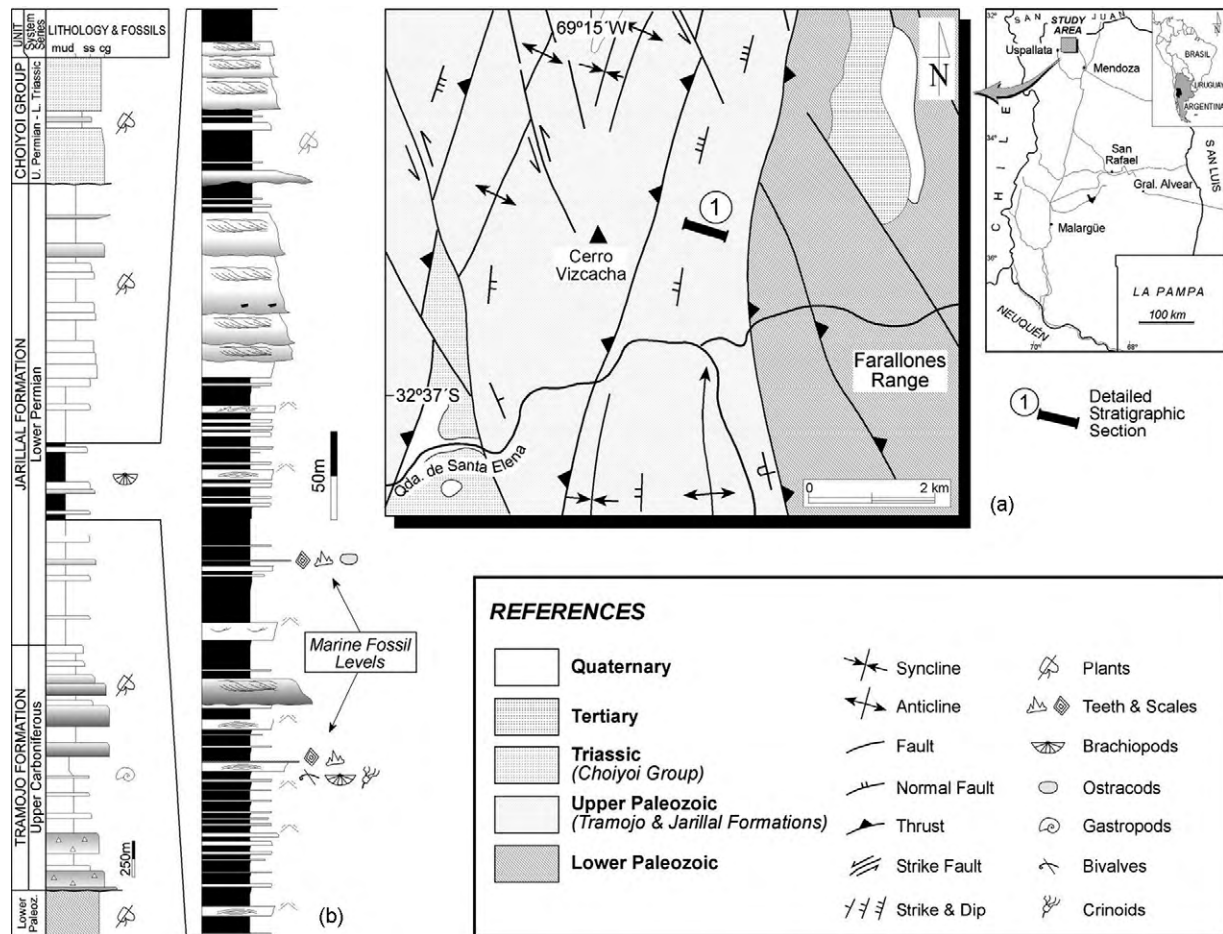


Fig. 1. Location map and section.

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 Westphalian-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. Hyodontiform 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 purposes and observed with Photo

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

The “basal actinopterygian” teeth and scales were described according to the morphotypes of Richter (1981, 1983), Richter et al. (1985, 1999; see also Würdig-Maciel, 1975), and Trinajstić (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 *Protacrodus* and differs from other Paleozoic chondrichthyan 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 *Protacrodus* 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 Breitenkreuz (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 assignment 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

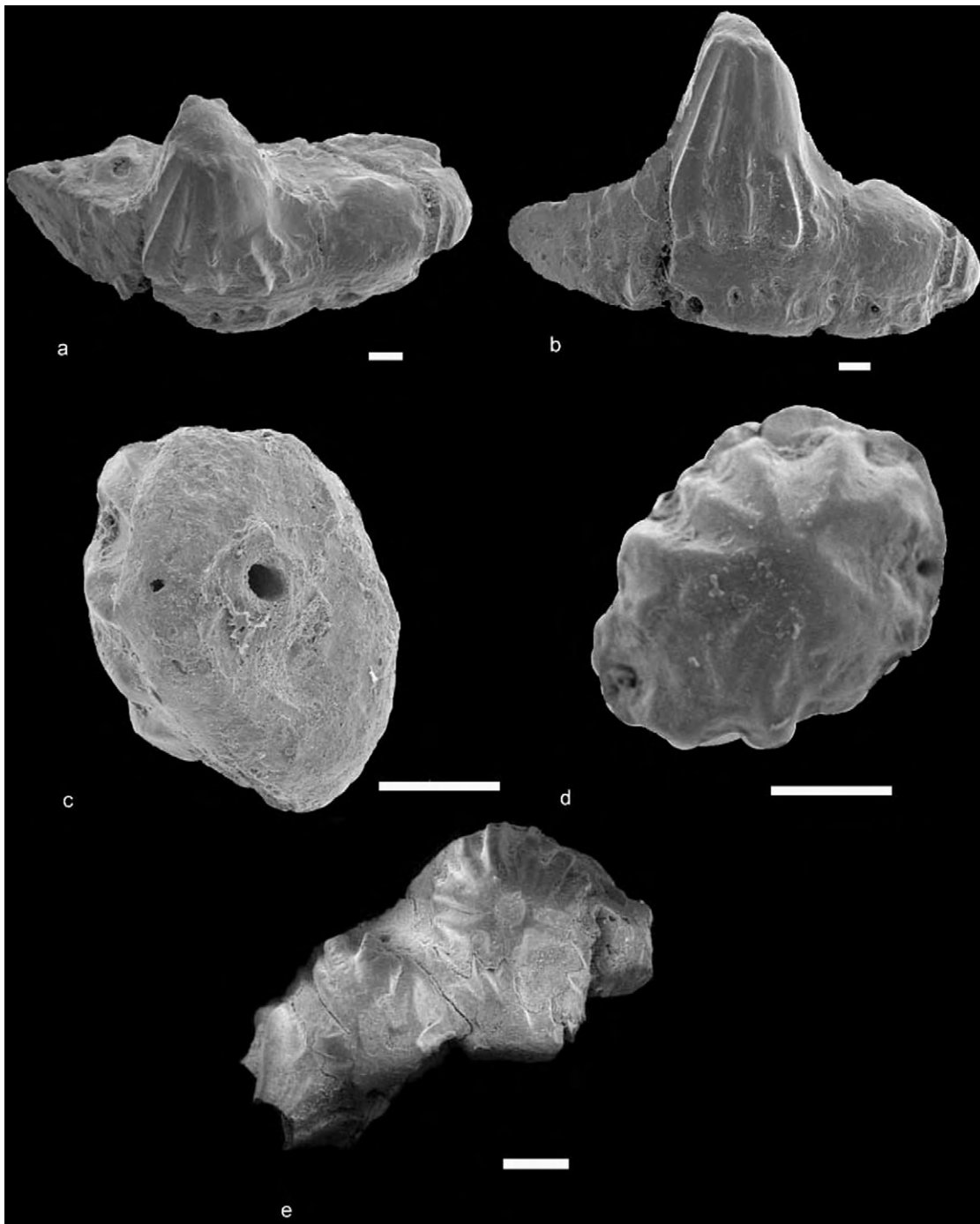


Fig. 2. El Jarillal formation. Hybodontiform tooth and scales. (a) MHNSR 603-14 cf. *Hybodus* sp. tooth almost occlusal view. (b) MHNSR 603-14 cf. *Hybodus* sp. tooth labial view. (c) MHNSR 603-16 *Petrodus* sp. basal view. (d) MHNSR 603-16 *Petrodus* sp. dorsal view. (e) MHNSR 603-15 Hybodontiform indet.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

(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 parasytematics 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, Trinajstić (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.

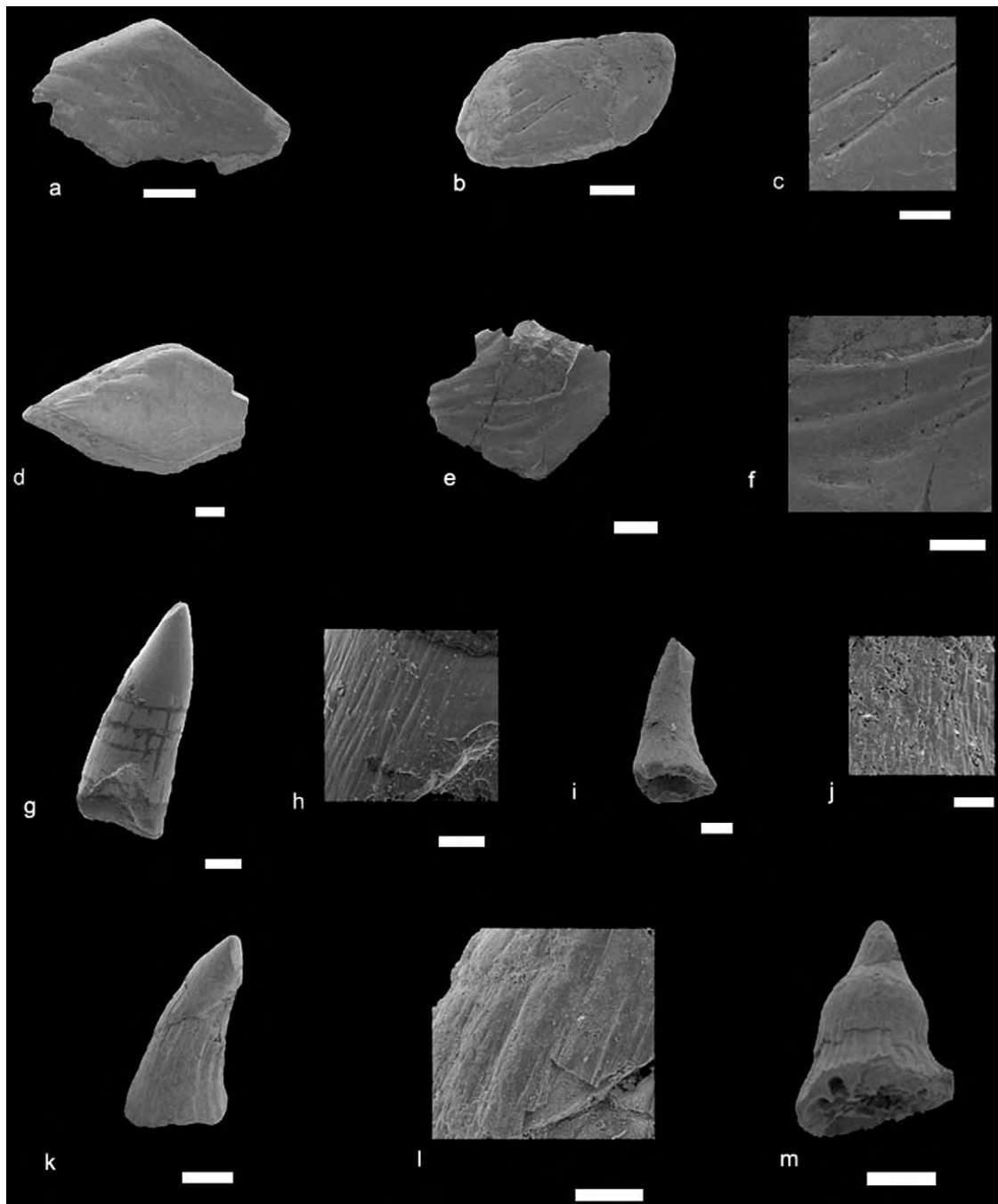


Fig. 3. El Jarillal Formation. “Basal actinopterygian” teeth and scales. (a) MHNSR 603-1 Scale type P1. (b) MHNSR 603-4 Scale type P2. (c) MHNSR 603-4. Scale type P2 detail of the surface. (d) MHNSR 603-7 Scale type X. (e) MHNSR 603-5 Scale type P2. (f) MHNSR 603-5 Scale type P2 detail of the surface. (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).

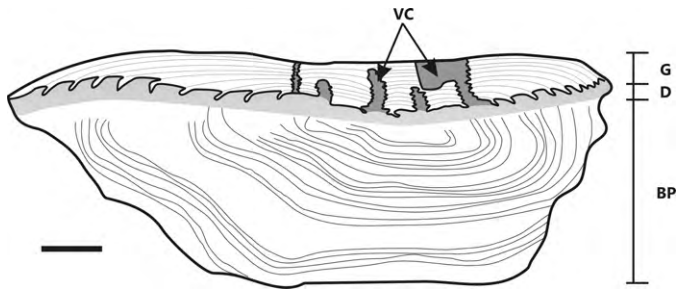


Fig. 4. MHNSR 603-66 Schematic draw of scale type P1 in cross section. VC, vascular canals; G, ganoin; D, dentine; BP, basal plate. Bar-scale = 100 μm .

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 Yaguari, Paso Aguiar, Mangrullo, and Frayle Muerto Formations (Piñeiro, 2006). The material also resembles morphotypes 6 and 7 of Trinajstić (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 *Elonichthys 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 O13 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 acrodine 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 \times). 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 Yaguari, 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-Maciél (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)
<i>Itapyrodus punctatus</i>	Irati Formation, Brazil	Early Permian	Ragonha (1978), Santos (1990), Chahud (2007), Chahud and Fairchild (2007), Chahud and Petri (2008), Chahud et al. (in press)
<i>Itapyrodus punctatus</i>	Pedra do Fogo Formation, Brazil	Early Permian	Richter (2004b)
Sphenacanthiformes			
Sphenacanthiformes indet.	Teresina Formation, Brazil	Late Permian	Richter (2004b)
<i>Sphenacanthus sanpauloensis</i>	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)
<i>Anisopleurodontis pricei</i>	Pedra do Fogo Formation, Brazil	Early Permian	Richter (2004b)
Agassizodontidae			
<i>Parahelicoprion mariosuarezi</i>	Copacabana Formation, Bolivia	Early Permian	Merino-Rodo and Janvier (1986), Janvier (1991)
<i>Tiaraju tenuis</i>	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			
<i>Orodus</i> sp.	Irati Formation, Brazil	Early Permian	Chahud (2007)
<i>Orodus milleri</i>	Teresina Formation, Brazil	Early Permian	Richter (2004a)
<i>Orodus milleri</i>	Estrada Nova Formation, Brazil	Late Permian	Würdig-Maciél (1975)
<i>Orodus ipeunaensis</i>	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. <i>Ctenacanthus</i> sp. <i>Ctenacanthus</i> sp. <i>Ctenacanthus maranhensis</i> <i>Ctenacanthus gondwanus</i>	Teresina Formation, Brazil Corumbataí Formation, Brazil Estrada Nova Formation, Brazil Pedra do Fogo Formation, Brazil Rio Bonito Formation, Brazil	Late Permian Middle-Late Permian Late Permian Early Permian Early Permian	Richter (2004a) Chahud and Fairchild (2007) Würdig-Maciel (1975) Santos (1946) Santos (1947), Richter et al. (1985)
Xenacanthiformes			
Xenacanthiformes indet. Xenacanthiformes indet. Xenacanthiformes indet. Xenacanthiformes indet. <i>Xenacanthus albuquerquei</i>	Pedra do Fogo Formation, Brazil Teresina Formation, Brazil Corumbataí Formation, Brazil Rio do Rasto Formation, Brazil Irati Formation, Brazil	Early Permian Late Permian Late Permian Late Permian Early Permian	Cox and Hutchinson (1991) Richter (2004a) Ragonha (1985) Dias (1996) Ragonha (1978), Chahud (2007), Chahud and Fairchild (2007), Chahud and Petri (2008) Chahud (2007)
<i>Xenacanthus albuquerquei</i>	Beds between Tubarão and Passa Dois groups, Brazil	Early Permian	Chahud (2007)
<i>Xenacanthus santosi</i> <i>Xenacanthus santosi</i> <i>Xenacanthus pricei</i> <i>Xenacanthus pricei</i> <i>Xenacanthus tocantinensis</i> <i>Wurdingeria oblitterata</i> <i>Triodus</i> sp.	Teresina Formation, Brazil Estrada Nova Formation, Brazil Teresina Formation, Brazil Estrada Nova Formation, Brazil Pedra do Fogo Formation, Brazil Teresina Formation, Brazil Passa Dois Group, Brazil	Late Permian Late Permian Late Permian Late Permian Early Permian Late Permian Late Permian	Klein et al. (1995), Richter (2004a) Würdig-Maciel (1975) Richter (2004a) Würdig-Maciel (1975) Richter (2004b) Richter (2005) Richter (2004b)
Hybodontiformes			
Hybodontiformes indet. Hybodontiformes indet. Hybodontiformes indet. Hybodontiformes indet. <i>Hybodus</i> sp.	Rio do Rasto Formation, Brazil Teresina Formation, Brazil Rio do Rasto Formation, Brazil Corumbataí Formation, Brazil Cerro 1584 Formation, Chile	Late Permian Late Permian Late Permian Late Permian Early-Middle Permian	Malabarba et al. (2003), Cisneros et al. (2004) Richter (2004a) Richter and Langer (1998) Chahud and Fairchild (2007) Richter and Breitung (1997)
Holocephali			
Bradyodonti indet.	Copacabana Formation, Bolivia	Early Permian	Merino-Rodo and Janvier (1986), Janvier (1991)
Acanthodii			
Acanthodii indet. Acanthodii indet.	Teresina Formation, Brazil Estrada Nova Formation, Brazil	Middle – Late Permian Late Permian	Mutter and Richter (2007) Würdig-Maciel (1975)
Actinopterygii			
Actinopterygii indet. Actinopterygii indet. Actinopterygii indet.	Mojón de Hierro Formation, Argentina Del Salto Formation., Argentina Vitiagua Formation. Bolivia	Early Permian Late Carboniferous-Early Permian Late Permian?-Early Triassic	González (1985) Manceñido (1973) Beltan et al. (1987), Janvier (1991), Arratia and Cione (1996)
Actinopterygii indet. Actinopterygii indet. Actinopterygii indet. Actinopterygii indet. Actinopterygii indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet.	Frayle Muerto Formation, Uruguay Paso Aguiar Formation, Uruguay Rio do Rasto Formation, Brazil Budó Formation, Itararé Group Pedra do Fogo Formation, Brazil Irati Formation, Brazil Rio do Rasto Formation, Brazil	Early Permian Late Permian Late Permian Late Carboniferous/Early Permian Early Permian Early Permian Late Permian	Mones (1986) Mones (1986) Dias (1996) Richter (2004b) Cox and Hutchinson (1991) Chahud (2007), Chahud and Fairchild (2007) Richter and Langer (1998), Malabarba et al. (2003), Cisneros et al. (2004) Würdig-Maciel (1975)
"Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. "Palaeonisciformes" indet. <i>Roslerichthys riomafrensis</i>	Estrada Nova Formation, Brazil Teresina Formation, Brazil Irati Formation, Brazil Mangrullo Formation, Uruguay Paso Aguiar Formation, Uruguay Frayle Muerto Formation, Uruguay Yaguari Formation, Uruguay Rio do Sul Formation, Brazil	Late Permian Late Permian Late Permian Early Permian Early Permian Early Permian Late Permian Early Permian	Klein et al. (1995) Richter et al. (1985) Piñeiro (2006) Piñeiro (2006) Mones (1986), Piñeiro (2006) Piñeiro (2006) Hammel (2005)
Actinopteri			
Family incertae sedis			
<i>Rubidus pascoalensis</i> <i>Arratiaichthys chilensis</i>	Rio do Rasto Formation, Brazil Peine Formation, Chile	Late Permian Late Permian	Richter (2002) Richter and Breitung (1997)
Acrolepididae			
<i>Acrolepis</i> sp. <i>Carbonilepis uruguayensis</i> <i>Gondwananichthys maximus</i> <i>Itararichthys microphthalmus</i>	Rio do Sul Formation, Brazil San Gregorio Formation, Uruguay San Gregorio Formation, Uruguay San Gregorio Formation, Uruguay	Early Permian Late Carboniferous?-Early Permian Late Carboniferous?-Early Permian Late Carboniferous?-Early Permian	Ruedemann (1929) Beltan (1978), Mones (1986) Beltan (1978), Mones (1986) Beltan (1978), Mones (1986)
Cosmoptychiidae			
<i>Mesonichthys antipodeus</i>	San Gregorio Formation, Uruguay	Late Carboniferous?-Early Permian	Beltan (1978), Mones (1986)
Elonichthyidae			
<i>Elonichthys</i> sp. <i>Elonichthys gondwanus</i> <i>Elonichthys macropercularis</i> <i>Santosichthys mafrensis</i> <i>Daphnaechelus fomosus</i> <i>Daphnaechelus</i> sp.	Río do Sul. Formation, Brazil Río do Sul. Formation, Brazil San Gregorio Formation, Uruguay Río do Sul. Formation, Brazil San Gregorio Formation, Uruguay Río do Sul Formation, Brazil	Early Permian Early Permian Late Carboniferous?-Early Permian Early Permian Late Carboniferous?-Early Permian Early Permian	Ruedemann (1929) Richter et al. (1985), Richter et al. (2000) Beltan (1978), Mones (1986) Malabarba (1988), Richter et al. (2000) Beltan (1978), Mones (1986) Richter (2004b)

Appendix A (Continued)

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

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