The record of fossil fishes of southern South America

2 authors:

Gloria Arratia
University of Kansas

Alberto Luis Cione
Universidad Nacional de La Plata

Verlag Dr. Friedrich Pfeil

Münchner Geowissenschaftliche Abhandlungen

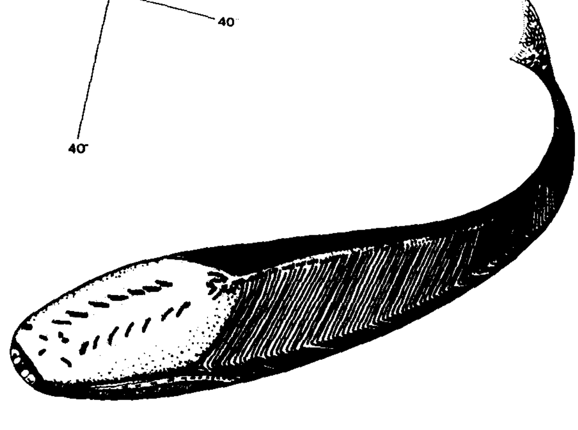
Reihe A

Geologie und Paläontologie

30

Contributions of Southern South America to Vertebrate Paleontology

Edited by Gloria ARRATIA



Münchner Geowiss. Abh.	(A)	**30**	9-72	36 figs., 2 apps.	München, April 1996

The Record of Fossil Fishes of Southern South America

by

Gloria ARRATIA* & Alberto CIONE**

"To the memory of OSVALDO REIG in recognition of his important contribution to South American Vertebrate Paleontology."

ABSTRACT

The record of fossil fishes of southern South America is analyzed. Lists of taxa, their geographic occurrences, ages, and sources of literature are presented in appendices.

The fish diversity changes considerably from place to place and among geological periods. Records of Paleozoic fishes (e.g., primitive agnathans, chondrichthyans, placoderms, acanthodians, actinopterygians, and sarcopterygians) are almost exclusively restricted to Bolivian localities. Triassic fishes (e.g., primitive neopterygians) are mainly recorded from Argentina, but are poorly known because of incomplete preservation. In contrast, Jurassic fishes from Chile are represented by numerous well-preserved forms (e.g., mainly teleosts, a few pycnodontiforms, semionotiforms, pachycormiforms), they constitute the best known southern South American fossil fishes. The teleostean varasichthyid group (including the Chilean genera *Bobbichthys, Domeykos, Protoclupea,* and *Varasichthys* and the Cuban genus *Luisichthys*) is one of the few monophyletic groups among the Jurassic basal teleosts. The Cretaceous and Cenozoic fish faunas comprise chondrichthyans, few primitive actinopterygians, few halecostomes, numerous teleosts, and a few sarcopterygians.

During the Late Cretaceous-Paleocene southern South America was inhabited by forms (e.g., ceratodontid sarcopterygians and polypteriform and lepisosteiform actinopterygians) which do not occur today in the South American continent. Most Late Cretaceous-Paleocene freshwater forms become extinct during the Paleocene and were replaced by genera still living in South America today. Among them, the teleostean groups are the best represented.

Key words: Southern South America, Fishes, Fossil record, Systematics, Geographical distribution.

RESUMEN

El registro fósil de peces del extremo austral de América del Sur - incluyendo principalmente Argentina, Bolivia y Chile - es analizado. Listas con taxones de peces, sus localidades, edades relativas y correspondiente fuentes literarias son presentadas en apéndices.

La diversidad de peces cambia considerablemente entre localidades y entre períodos geológicos. Por ejemplo, los peces paleozoicos (agnatos, condrictios, placodermos, acantodios, actinopterigios y sarcopterigios) son conocidos casi exclusivamente en localidades bolivianas. Los peces triásicos provienen principalmente de localidades argentinas, pero son pobremente conocidos. En comparación, las faunas ícticas jurásicas de Chile están representadas por numerosos peces en excelente estado de preservación y ellos constituyen el conjunto faunístico mejor conocido en América del Sur. Entre los teleósteos basales, el grupo varasíctido (incluyendo los géneros chilenos *Bobbichthys, Domeykos, Protoclupea* y *Varasichthys* y el género cubano *Luisichthys*) constituye uno de los escasos grupos monofiléticos que se conocen del Jurásico. Los peces cretácicos y cenozoicos están representados por condrictios, escasos actinopterigios primitivos, escasos halecostomos, numerosos teleósteos y algunos sarcopterigios.

* Gloria ARRATIA, Institut für Paläontologie, Museum für Naturkunde der Humboldt Universität, Invalidenstr. 43, D-10115 Berlin; Germany; and Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045, U.S.A.

** Alberto CIONE, Departamento Científico de Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo, Paseo del Bosque s / n°, 1900 La Plata, and CONICET, Argentina.

Münchner Geowiss. Abh. (A) **30**, S. 9-72, 36 figs., 2 apps.

Durante el Cretácico tardío-Paleoceneo, el extremo sur de América del Sur estuvo habitado por ciertos grupos (por ejemplo, sarcopterigios ceratodóntidos y actinopterigios tales como poliptéridos y lepisosteidos) los que no se encuentran en el continente sudamericano actualmente. La mayor parte de los formas cretácicas tardías de aguas continentales se extinguieron durante el Paleoceno y aparentemente fueron reemplazadas por muchos de los géneros modernos que actualmente viven en el continente. Entre esos grupos, los teleósteos son los mas abundantemente representados.

Palabras claves: Extremo sur de América del Sur, Peces, Registro fósil, Sistemática, Distribución geográfica.

Zusammenfassung

Das Auftreten fossiler Fische vom südlichen Südamerika wird analysiert. Taxa, ihre geographische Verbreitung, Alter und Literaturquellen sind in Appendices aufgeführt.

Die Diversität der Fischfaunen ändert sich beträchtlich von Ort zu Ort und innerhalb der Abfolge der geologischen Perioden. Der Nachweis paläozoischer Fische (primitive Agnathen, Chondrichthyes, Placodermata, Acanthodier, Actinopterygier und Sarcopterygier) ist nahezu ausschließlich auf Bolivien begrenzt. Triassische Fische (primitive Neopterygier) sind hauptsächlich von Argentinien beschrieben worden, allerdings sind sie ungenau bekannt, da die Erhaltung unvollständig ist. Im Gegensatz dazu sind die jurassischen Fische Chiles in zahlreichen gut erhaltenen Exemplaren (hauptsächlich Teleosteer, einige wenige Pycnodontiforme, Semionotiforme und Pachycormiforme) bekannt; sie stellen die besterforschten südamerikanischen Fische dar. Die varasichthyide Teleosteer-Gruppe (die chilenischen Gattungen *Bobbichthys, Domeykos, Protoclupea* und *Varasichthys* und die kubanische Gattung *Luisichthys* umfassend) stellt eine der wenigen monophyletischen Gruppen innerhalb der basalen Jura-Teleosteer dar. Kretazische und känozoische Faunen umfassen Chondrichthyes, einige primitive Actinopterygier, einige Halecostomen, zahlreiche Teleosteer und wenige Sarcopterygier.

Während der Übergangszeit von der oberen Kreide bis hinein ins Paleozän war das südliche Südamerika von Formen (ceratodontide Sarcopterygier und polypteriforme und lepisosteiforme Actinopterygier) bewohnt, die heute nicht mehr in Sudämerika auftreten. Die meisten Süßwasserfische der oberen Kreide und des Paleozäns sterben während des Paleozäns aus und werden durch Gattungen verdrängt, die noch heute in Südamerika auftreten. Unter diesen sind die Teleosteer am besten vertreten.

Schlüsselworte: Südliches Südamerika, Fische, Fossilnachweis, Systematik, geographische Verbreitung.

Introduction

Southern South America, including Argentina, Chile, and Bolivia, has a rich and diverse record of fossil fishes from the Mesozoic and Cenozoic. However, the knowledge of fossil fishes from these countries is unbalanced. The taxonomic information varies among localities of the same age; it varies among different geological periods, and it varies also between freshwater and marine environments. Uruguay records are mainly restricted to the Paleozoic.

Although paleontological and stratigraphic studies began in southern South America with D'ORBIGNY (1842) and DARWIN (1846), the study of fossil fishes began later, with the chondrichthyans (e.g., BRAVARD 1858; AMEGHINO 1898, 1900-1903). A pachycormiform, identified as *Protosphyraena* sp., was reported by WOODWARD (1897) and AMEGHINO (1899), and the teleosts with a characiform by WOODWARD (1900) and a catfish by COCKERELL (1925). Numerous papers recording a diverse fauna, mainly from Argentina, were published during the first half of this century. The second half has been characterized by numerous publications on fishes from the Paleozoic to the Tertiary found in several localities in Argentina, Bolivia, Chile, Peru, and Uruguay. Research in the Bolivian localities has been conducted mainly by French researchers. Studies on chondrichthyans and certain faunistic assemblages from the Jurassic to Cenozoic of Argentina and the Jurassic and Tertiary teleosts from Chile have been conducted continuously by native researchers mainly.

The record of fossil fishes of southern South America is characterized by (1) incomplete knowledge (just mention) of numerous forms, (2) descriptions based on fragments or very incomplete specimens (e.g., Cretaceous and Tertiary fishes from Bolivia), and (3) few descriptions of exceptionally well-preserved fishes such as those from Quebrada del Profeta in the Jurassic of northern Chile.

The diversity of fossil fishes of southern South America has never been reviewed. This is the first attempt to present a complete information on the fossil record followed by the phylogenetic relationships of some forms. Because of limitation of number of pages, comments on only certain groups are provided in the text; however, a list of taxa, their localities and source of references, are presented in two appendices for marine and freshwater environments. Here, the separation is sometimes arbitrary because of different interpretations for some localities. When it is necessary, these conflicting interpretations are discussed in the text.

Names and classification of high taxa follow NELSON (1994) as far as possible. Interpretation of semionotiforms follows OLSEN & McCUNE (1991) and of teleosts ARRATIA (1996).

Institutional abbreviations

Most of the Argentinian specimens mentioned in this paper are deposited at the Museo de La Plata, La Plata. Most Chilean specimens mentioned here are deposited at the Laboratorio de Biología, Santiago, Universidad de Chile; following the Chilean laws, most of the material will be re-catalogued at the Museo Nacional de Historia Natural, Santiago, Chile.

The following institutional abbreviations are used in text and figure captions:

Fig. 1: Map of southern South America illustrating the approximate position of some Paleozoic (**P**) and Triassic (**T**) localities. **1**, La Paz area (P). **2**, Cochabamba area (P). **3**, Sucre area (P). **4**, Chuquisaca (T). **5**, Tarija (P). **6**, Toconao area (P). **7**, Paramillos de Uspallata (T). **8**, Quebrada de Santa Clara (T). **9**, El Challao (T). **10**, Potrerillos (T). **11**, Quebrada de Los Leones (T). **12**, Cerro Bayo (T).

LBUCH, Laboratorio de Biología, Universidad de Chile, Campus Antumapu; **I.I.G.**, Instituto de Investigaciones Geológicas, Chile. Currently, the Servicio Nacional de Geología y Minas, Chile; **KUVP**, Division of Vertebrate Paleontology, Museum of Natural History, The University of Kansas, Lawrence, Kansas, U.S.A; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNHN SGO**, Museo Nacional de Historia Natural, Santiago, Chile; **PLV**, Universidad Nacional de Tucumán, Argentina; **PV. U.N.S.**, Paleontología de Vertebrados, Facultad de Ciencias Naturales, Universidad Nacional de Salta, Argentina; and **R**, Departamento de Geología, Universidad de Chile, Santiago.

Areas of Study

The fossil fishes reported here have been collected mainly in Argentina, Bolivia, and Chile. Records from southern Peru and Uruguay are also mentioned. Some localities cited (alphabetically) in this paper and their approximate geographic locations are indicated and illustrated (Figs. 1-4) below for better understanding and to avoid repetition throughout the text.

1. Marine localities

Cerritos Bayos and Cerro Blanco.- II Región, northern Chile; Jurassic: Callovian-Oxfordian
Cerro Lotena and Picún Leufú.- Neuquén Province, Argentina; Jurassic: Tithonian
Cochabamba area.- Bolivia; Ordovician
La Paz area.- Bolivia; Middle - Upper Devonian, Lower Permian
El Volcán.- Santiago, Región Metropolitana, Chile; Lower Cretaceous
Lebú.- VII Región, Chile; Eocene
Northeastern Santa Cruz Province.- Argentina; Eocene
Northeast Uruguay.- Uruguay: Carboniferous or Lower Permian
Paraná.- Entre Ríos Province, Argentina; Miocene
Plaza Huincul.- Neuquén Province, Argentina; Jurassic: Tithonian
Quebrada del Profeta.- Cordillera de Domeyko, II Región, northern Chile; Jurassic: Oxfordian
Quebrada Sandón.- Cordillera de Domeyko, II Región, northern Chile; Jurassic: Oxfordian
Quebrada Vaquillas Altas.- Cordillera de Domeyko, II Región, northern Chile; Jurassic: Sinemurian
Quiriquina island and near coast.- VIII Region, Chile; Upper Cretaceous: ?Maastrichtian
Sacaco area.- Peru; upper Miocene to lower Pliocene
San Jorge area.- Eastern Chubut Province, Argentina; Paleocene
San José and Colonia Departments.- Uruguay; upper Miocene to lower Pliocene
*Seripoma and La Higuera (*along *Grande river).*- Bolivia; Devonian
Southwestern Santa Cruz Province.- Argentina; Upper Cretaceous
Sucre area.- Bolivia; Early to ? Middle Devonian
Tarija area.- Bolivia; Upper Devonian
Tarija.- Bolivia; Upper Permian - Triassic
Tierra Amarilla.- III Region, Copiapó, northern Chile; Cretaceous

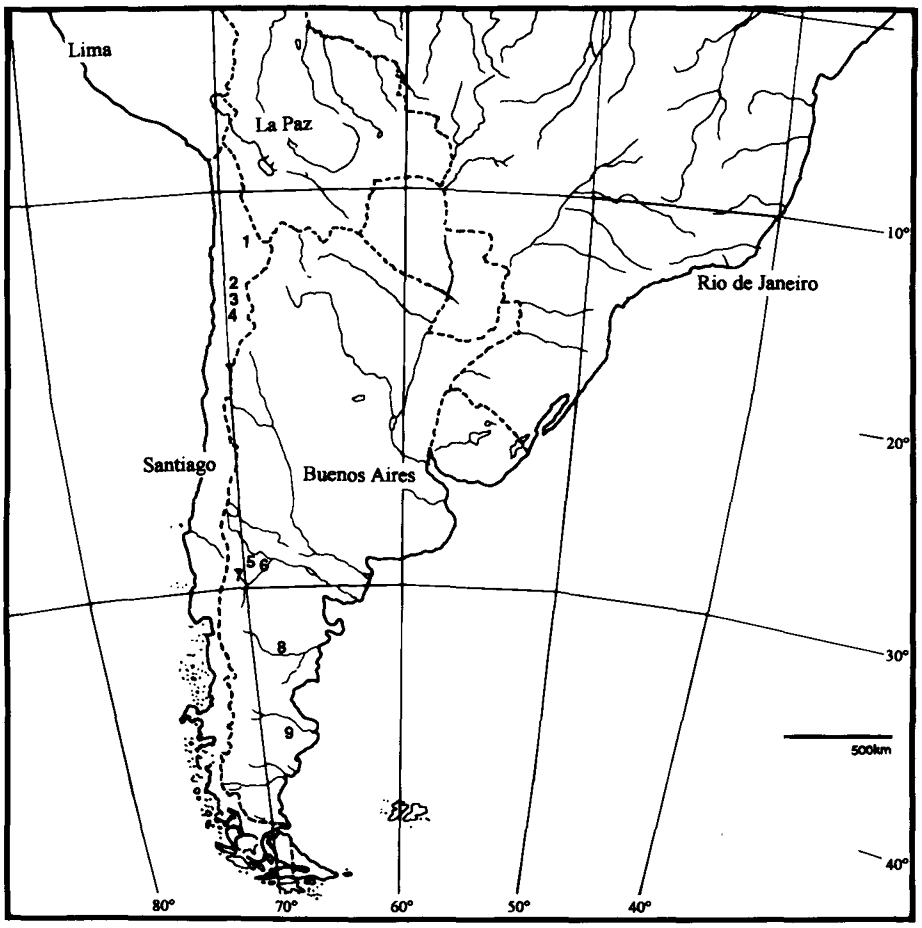


Fig. 2: Map of southern South America illustrating the approximate position of some Jurassic localities. **1**, Cerritos Bayos and Cerro Blanco. **2**, Quebrada del Profeta. **3**, Quebrada Sandón. **4**, Quebrada Vaquillas Altas. **5**, Cerro Lotena. **6**, Plaza Huincul. **7**, Picún Leufú. **8**, Cerro Cóndor.

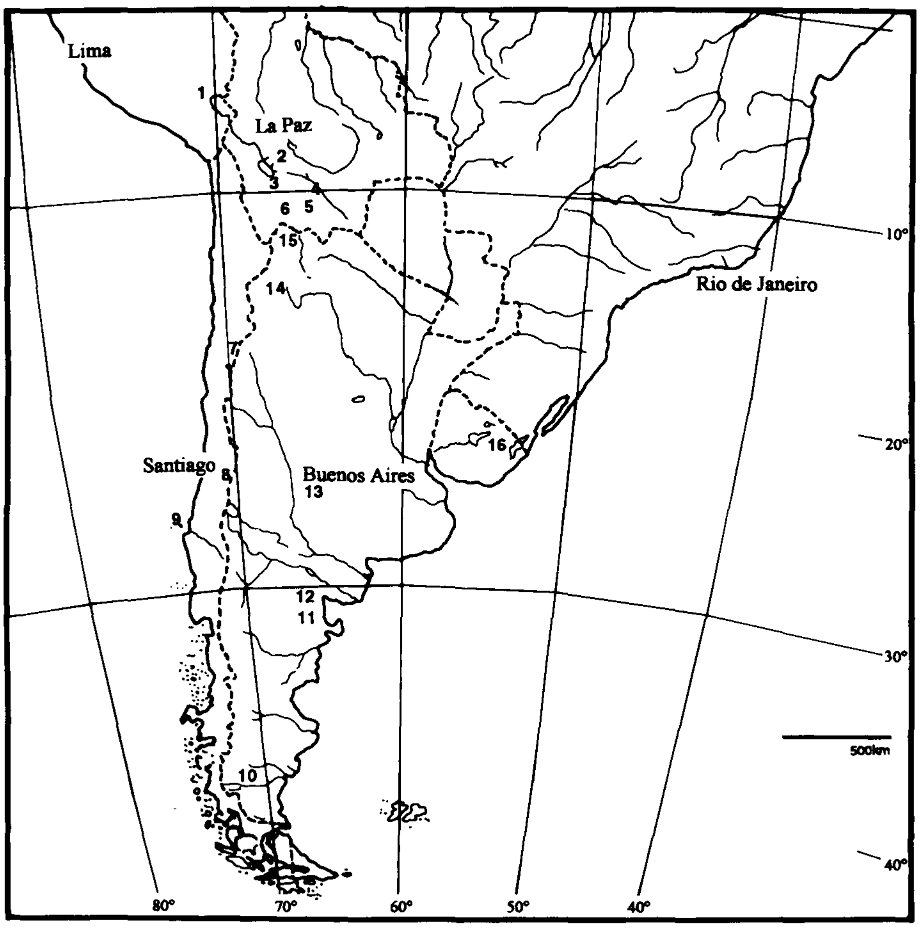


Fig. 3: Map of southern South America illustrating the approximate position of some Cretaceous localities. **1**, Laguna Umayo. **2**, Torotoro. **3**, Hotel Cordillera. **4**, Agua Clara. **5**, La Palca. **6**, Cayara. **7**, Tierra Amarilla. **8**, El Volcán. **9**, Quiriquina Island. **10**, Shehuen river. **11**, Estancia Los Alamitos. **12**, Arroyo Yaminué. **13**, Sierra del Gigante. **14**, Valle del Tonco. **15**, Cerro Colorado de Tres Cruces. **16**, Tacuarembó.

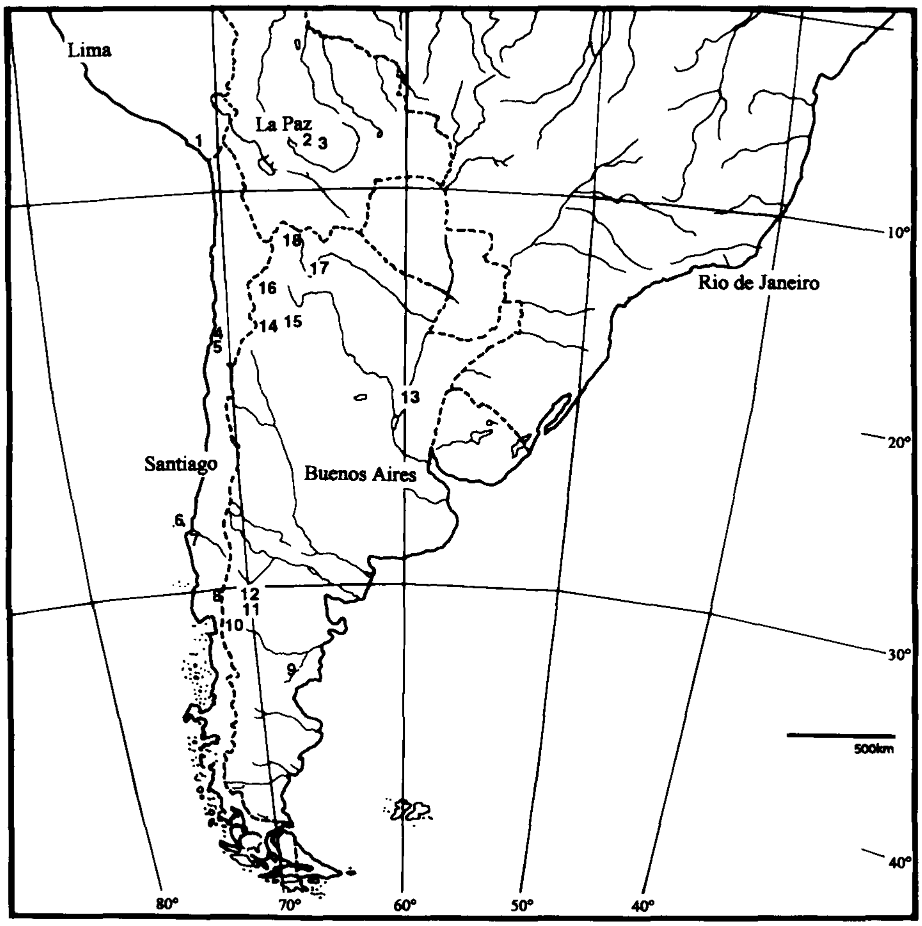


Fig. 4: Map of southern South America illustrating the approximate position of some Cenozoic localities. **1**, Sacaco. **2**, Rancho Blanco. **3**, Tiupampa. **4**, El Rincón. **5**, Bahía Inglesa. **6**, Quiriquina Island. **7**, Lebu. **8**, Lonquimay area. **9**, Cañadón Hondo. **10**, Puesto Galván. **11**, Laguna del Hunco. **12**, Ingeniero Jacobacci. **13**, Paraná. **14**, Valle de Santa María. **15**, Río Loro. **16**, Quebrada de la Yesera. **17**, Arroyo Abra del Trigo. **18**, Sierra del Mal Paso.

2. Freshwater localities

Most Cretaceous and Paleocene localities of Bolivia are listed here as freshwater localities even though that it is noted that the interpretation of the environment of these localities is controversial (see below for references).

Acre River.- Peru; Miocene
Agua Clara, Cayara, La Palca, Torotoro, ?Vila Vila, ?Hotel Cordillera.- Bolivia; Upper Cretaceous
Arroyo Abra del Trigo.- Jujuy Province, Argentina; Paleocene
Arroyo Yaminué.- Río Negro Province, Argentina; Upper Cretaceous
Cañadón Hondo.- Chubut Province, Argentina; Miocene
Cerro Bayo.- Mendoza Province, Argentina; Triassic
Cerro Colorado de Tres Cruces.- Argentina; Upper Cretaceous
Cerro Cóndor.- Neuquén Province, Argentina; ?Upper Jurassic
Cerro La Mina, La Junta, Puente Lolén, El Tallón, Cerro Rucañanco.- Cordillera de Lonquimay, VIII Región, Chile; Miocene
El Challao.- Mendoza Province, Argentina; Triassic
Estancia Los Alamitos.- Río Negro Province, Argentina; Upper Cretaceous
Estancia Blanco Rancho.- Bolivia; Paleocene
Estancia Roca Blanca.- Santa Cruz Province, Argentina; Lower Jurassic
Ingeniero Jacobacci.- Río Negro Province, Argentina; Lower Cretaceous
Jujuy area.- Argentina; Upper Cretaceous
Laguna del Hunco.- Chubut Province, Argentina; Eocene
Laguna Umayo.- Peru; Upper Cretaceous
Par Aike, Shehuen River.- Santa Cruz Province, Argentina; Upper Cretaceous
Paramillos de Uspallata.- Mendoza Province, Argentina; Triassic
Paraná.- Entre Ríos Province, Argentina; Miocene
Potrerillos.- Mendoza Province, Argentina; Triassic
Puesto Galvan.- Chubut Province, Argentina; Miocene
Quebrada Aguas Calientes.- Sierra de la Candelaria, Salta Province, Argentina; Upper Cretaceous
Quebrada de Los Leones.- Mendoza Province, Argentina; Triassic
Quebrada de Santa Clara.- Mendoza Province, Argentina; Triassic
Quebrada de la Yesera.- Salta Province, Argentina; Miocene
Río Loro.- Tucumán Province, Argentina; Eocene
Sierra de las Quijadas.- San Luis Province; Argentina; Lower Cretaceous
Sierra del Gigante.- San Luis Province, Argentina; Lower Cretaceous
Sierra del Mal Paso.- Jujuy Province, Argentina; Eocene
Tacuarembó.- Uruguay; Cretaceous
Tiupampa.- Bolivia; Paleocene
Toconao area.- II Región, northern Chile; Paleozoic
Valle de Santa María.- Catamarca Province, Argentina; Miocene
Valle del Tonco.- Salta Province, Argentina; Upper Cretaceous
Umayo lagoon.- Peru; Upper Cretaceous

Marine Fish Record

Study on marine fossil fishes in southern South America began at the end of the last century. The first finding was mentioned by BRAVARD (1858) and followed later by a few publications by AMEGHINO (1898, 1901, 1906 on chondrichthyans, based on ALESSANDRI 1896) and WOODWARD (1900). From that time until now, approximately 170 records of marine fishes have been published, about half of which corresponds to chondrichthyans (Appendix 1).

1. Agnathans, placoderms, and acanthodians

Interesting agnathans (e.g., *Andinaspis* and *Sacabambaspis*), placoderms (e.g., *Bolivosteus*), and acanthodians (e.g., *Climatius* and *Onchus*) have been reported from Bolivia (see GAGNIER 1992 and JANVIER 1992a, b for a synthesis) and Appendix 1 for a list of taxa and literature. Very well-preserved Ordovician vertebrate remains have been found in Bolivia. In consequence, Bolivian remains are extremely important for understanding the interrelationships and biogeography of early agnathans (see GAGNIER 1992; GAGNIER & BLIECK 1992).

The discovery of *Sacabambaspis janvieri* in the Cochabamba area represented the first record of an Ordovician vertebrate showing most of the dermal skeleton (Fig. 5) which permits comparisons with other early agnathans. The only Bolivian placoderm, *Bolivosteus chacomensis* GOUJET et al. (1985) belong to the rhenanids, a very derived group with the dermal armour reduced and the pectoral fins considerably enlarged.

The acanthodians are mainly represented by fin spines, tooth-bearing jaw bones, and isolated scales. The Bolivian acanthodians are included in the climatiids (with large broad-based fin spines) and ischnacanthids (with large tooth-bearing jaw bones).

2. Chondrichthyans from the Paleozoic to the Cenozoic

Stratigraphic and paleontological studies of marine beds in southern South America began with D'ORBIGNY (1842) and DARWIN (1846). AMEGHINO (1900-1903, 1906) gave the basic chronologic scale of the marine and continental Cenozoic of southern South America. AMEGHINO (op. cit.) correlated both standards largely based on vertebrate evidence. Other authors greatly refined the terrestrial and marine chronostratigraphic standards, e.g., SIMPSON (1940), PASCUAL et al. (1965), BERTELS (1975, 1980), RICCARDI & ROLLERI (1980), MARSHALL et al. (1983), DE MUIZON & DEVRIES (1985), and CIONE (1988). Recently, many radiometric (mostly K-Ar and fission tracks) and magnetostratigraphic studies were published (e.g., MARSHALL et al. 1986; BOWN & FLEAGLE 1993). However, some of the age assignments of continental units of the Patagonian late Paleogene and early Neogene (e.g., MARSHALL et al. 1986) do not agree with the chronological setting of the marine units (e.g., CAMACHO 1947; BERTELS 1975; CIONE 1988) and especially with the crucial level at the base of the marine Gaiman Formation in the Trelew-Gaiman area (LERICHE 1907; SIMPSON 1940; FERUGLIO 1949; CIONE 1988). Sharks and cetaceans have been especially relevant for giving an alternative interpretation (CIONE 1988; CIONE & COZZUOL, in prep.).

Elasmobranch studies began early in the region (BRAVARD 1858). Yet, their study is still incipient and based on fragmentary material.

Several stratigraphic units contain chondrichthyans in southern South America. They are Devonian, Permian, Late Cretaceous, Danian, late Eocene, late Oligocene, Miocene, Pliocene, and Holocene in age. The pre-Late Cretaceous record of chondrichthyans is poor (about 10 species; see Appendix 1), and restricted to a few Holocephali, Edestida, and Elasmobranchi known from Devonian and Permian localities of Bolivia (see Appendix 1; JANVIER 1976, 1978, 1987; JANVIER & SUÁREZ-RIGLOS 1986; MERINO-RODO & JANVIER 1986; GAGNIER et al. 1988).

Most Late Cretaceous-Cenozoic marine fishes are elasmobranchs, with minor representation of holocephalans and teleosts. This biased record is certainly due to taphonomic causes. Most elasmobranch-bearing rocks correspond to near-shore, high energy environments.

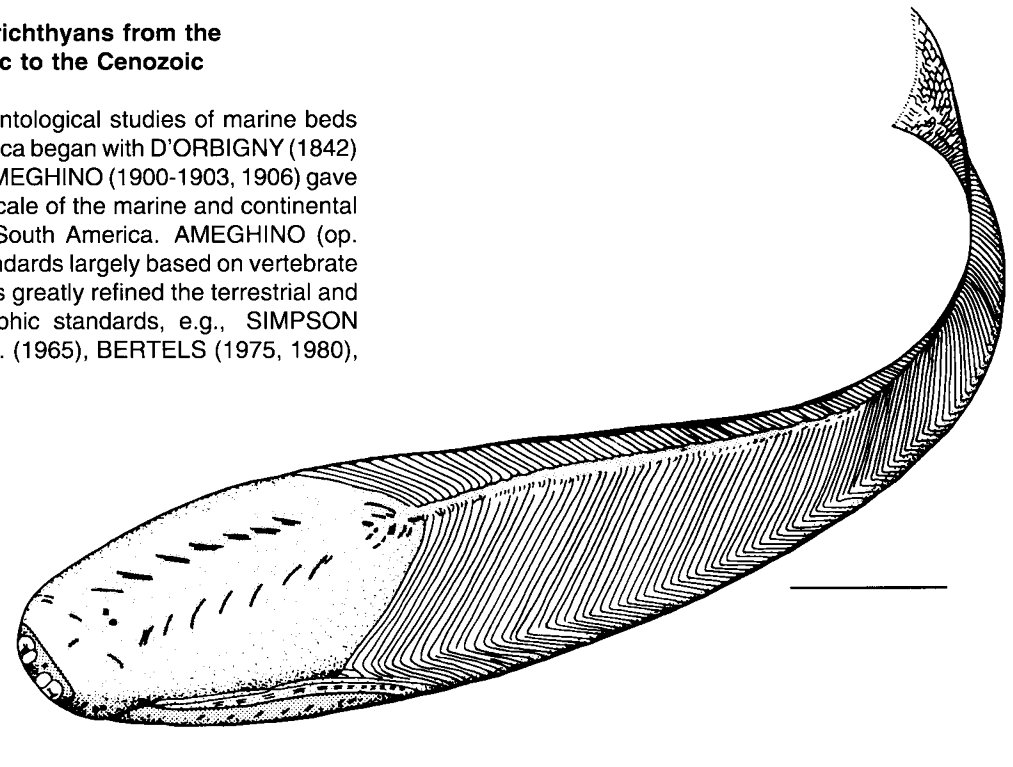


Fig. 5: *Sacabambaspis janvieri* GAGNIER, BLIECK & RODRIGO from the Ordovician of Bolivia (after GAGNIER 1992). Scale bar = 5 cm.

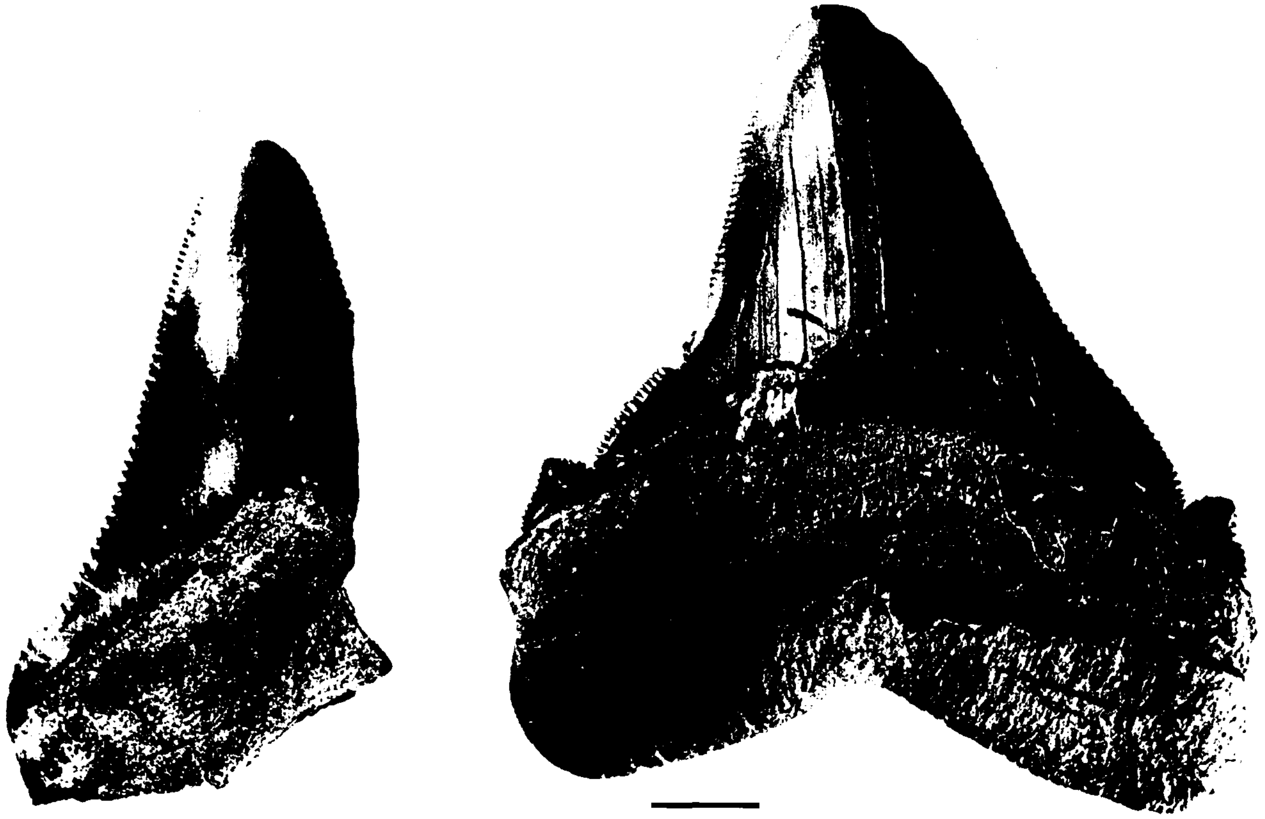


Fig. 6: Tertiary chondrichthyan *Carcharocles productus* (specimens from the Collection ROTH, MLP uncat.) from the early Miocene of Gaiman, Chubut, Argentina. Scale bar = 1 cm.

Cretaceous: Typical shark taxa from the "Piso Shehuenense" ("Shehuenan Stage") of southwestern Santa Cruz Province (Patagonia) have been reported by AMEGHINO (1898, 1901). Later, AMEGHINO (1906, 1935) included all these taxa in the Piso Salamanquense (Salamancan Stage). The Salamancan Stage is dated as late Danian-early Thanetian. The rocks assigned to the "Piso Shehuenense" are now included in part of the Mata Amarilla Formation which is Coniacian in age (RICCARDI & ROLLERI 1980). However, AMEGHINO did not describe or figure the material from the "Shehuenan." Odontaspidiids (cited as *"Scapanorhynchus" subulatus*), the "cretoxyrhinid" *Cretolamna appendiculata,* the anacoracid *Squalicorax* sp., two nominal species of palaeospinacids, and indetermined hexanchids were present (CIONE, pers. obser.; material at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires). All these sharks lived in the Cretaceous warm to warm-temperate seas almost worldwide. The endemic nominal species *Synechodus viedmai* and *Paraorthacodus patagonicus* (DUFFIN & WARD 1993) are referred to genera that were absent from the warmer areas (CIONE, in prep.). Actually, no recent collections are available and additional field work is needed in the Mata Amarilla Formation.

Maastrichtian assemblages in Bolivia include rhombodontoids, dasyatids, and sclerorhynchids. Most of the species recognized (with the exception of *Schizorhiza stromeri*) are endemic to Bolivia (DE MUIZON et al. 1983; CAPPETTA 1992). The Maastrichtian beds at Quiriquina (Chile) include many selachian remains but they need to be re-studied. Hexanchids, "cretoxyrhinids," sclerorhynchids, and odontaspidids or mitsukurinids are recorded (WETZEL 1930; OLIVER SCHNEIDER 1936a).

Selachians (especially batoids) useful for correlation have been reported from the Upper Cretaceous beds in the Bagua basin of Peru (CAPPETTA in MOURIER et al. 1988).

The great extinction at the end of the Cretaceous affected the diversity of sharks all around the world (CAPPETTA 1987). Cretaceous marine faunas were dominated by "cretoxyrhinids" (the "Cretoxyrhinidae" is probably paraphyletic), anacoracids, palaeospinacids, mitsukurinids, and hexanchids in Patagonia and by batoids in Bolivia. Several elasmobranch families became extinct in the Maastrichtian-Danian boundary (e.g., Anacoracidae, Rhombodontidae, Sclerorhynchidae). Other families persisted during the early Paleogene. The "cretoxyrhinid" *Cretolamna appendiculata* was reported from the Danian of northern Patagonia (CIONE 1988).

Paleocene-Eocene: After the great extinction at the Cretaceous-Danian boundary, the temperate marine assemblages of Chile and Argentinian Patagonia, as many others around the world (e.g., the Eocene of Seymour Island, Antarctica; CIONE et al. 1977; LONG 1992; CIONE & REGUERO 1994 and in press) were dominated by odontaspidiids (OLIVER SCHNEIDER 1936b; CIONE 1988). Unfortunately, South American Paleocene and Eocene marine assemblages are incompletely known.

Late Oligocene-early Miocene: At the turn of the century AMEGHINO (1898, 1900-1903, 1906) and other workers established the basic stratigraphic framework for the Eocene-Miocene marine nerithic sedimentary sequence

Fig. 7: Tertiary chondrichthyan *Galeocerdo aduncus* from the early Miocene of Gaiman, Chubut, Argentina. (Collection R. BRUNET uncat.; Puerto Madryn, Argentina). Scale bar = 1 cm.

that has received the global names "Patagoniano," "Patagoniense," "Formación Patagonia," and many others (extensive discussion can be found in FERUGLIO 1949; ZINSMEISTER 1981; CIONE 1988). The deposits are exceptionally rich in invertebrates and vertebrates (ZINSMEISTER 1981; CIONE 1988). The age and the limits of the subunits were angrily discussed by AMEGHINO and von IHERING (1903) defending certain ideas and HATCHER (1897) and ORTMANN (1902) with different ones. The controversy mostly focussed on the identification of supposed guide fossils (especially elasmobranchs and some invertebrates), the importance of some fossils as chronometers, and the age and correlation of several continental and marine units. AMEGHINO wrongly identified many Miocene sharks and invertebrates as Eocene taxa and considered that all of the Julian and Leonian rocks were older than it is presently accepted. BERTELS (1970; see also CIONE 1986a, 1988; CIONE & COZZUOL 1990) recognized two marine stages: the Julian Stage (late Eocene-early Oligocene; represented by the San Julián Formation) and the Leonian Stage (late Oligocene-early Miocene; represented by the Monte León and Gaiman Formations). Several authors that studied the continental sequences consider that the base of the Gaiman Formation is younger than the 18 M.y. (middle Burdigalian, late Oligocene-early Miocene; MARSHALL et al. 1986; MARSHALL & SALINAS 1990). However, cetacean and elasmobranch evidence suggests that the beds are Aquitanian in age (older than 21.5 M.y.; CIONE & COZZUOL, in prep.).

Fig. 8: Tertiary chondrichthyan *Hexanchus griseus* (specimen MLP 77-XII-13-2) from the early Miocene of Gaiman, Chubut, Argentina. Scale bar = 1 cm.

The first marine fishes of late Oligocene-early Miocene age were reported at the turn of the century (e.g., AMEGHINO 1898, 1900-1903, 1906; LERICHE 1907; PRIEM 1911; TOURNOÜER 1903).

The marine late Oligocene-early Miocene ichthyofaunas are well represented in Patagonia. At this time, the orders Carcharhiniformes and Lamniformes radiate and the size of sharks increases, especially in certain clades (e.g., *Carcharocles, Isurus;* ESPINOSA-ARRUBARENA et al. 1991). This radiation coincides with a polytaxic period according to FISHER & ARTHUR (1977); it has been related with the abundance of marine mammals (ESPINOSA-ARRUBARENA et al. 1991).

The marine Cenozoic fishes of southern South America are typical taxa of the shelf of warm temperate seas. Several shark taxa of the late Oligocene-early Miocene of Patagonia are cosmopolitan in warm temperate or even warm seas (e.g., *Isurus hastalis, I. retroflexus, Carcharocles productus* [Fig. 6], *Hemipristis serra, Galeocerdo aduncus* [Fig. 7], *Hexanchus griseus* [Fig. 8]). The living hexanchid *Hexanchus griseus* ranges from the early Miocene of Patagonia to today, thus it encompasses about 22 M.y. (CIONE 1988).

LERICHE (1907, 1926) considered that *Carcharocles productus* AGASSIZ and *C. chubutensis* AMEGHINO are junior synonyms of *C. megalodon* (Fig. 9). However, LERICHE (1926) correctly mentioned that the specimens of the early Miocene were smaller than those from the middle Miocene-Pliocene and had lateral denticles. CIONE (1988) suggested that the specimens with the former morphotype should be named. An available name is *C. productus.* Most authors consider that the living species *Carcharodon carcharias* should be included with *C. megalodon* and other fossil species in a single genus (*Carcharodon*; e.g., WELTON & ZINSMEISTER 1980; ESPINOSA-ARRUBARENA & APPLEGATE 1988).

The shark genus and species *Carcharoides totuserratus* (Fig. 10) was created by AMEGHINO (1901), forgotten, and recently resurrected by CAPPETTA (1987) and CIONE (1988). *C. totuserratus* seems to be the vicariant species of the northern *C. cattica* (see ANTUNES 1969). *Carcharoides* has a bipolar geographical distribution.

Two endemic species are the echinorhinid *Echinorhinus pozzii* AMEGHINO and the Galeomorphii *incertae sedis Megascyliorhinus trelewensis* CIONE. This latter was described as a carcharhiniform Scyliorhinidae. However, teeth of *Megascyliorhinus* show a vague similar external morphology to those of the Recent lamniform *Megachasma pelagios*. This tooth resemblance was considered convergent by CIONE (1986b).

Other fishes from upper Oligocene-lower Miocene rocks of Patagonia have been identified at generic or higher level; for instance, the squalid *Squalus*, the pristiophorid *Pristiophorus*, the heterodontid *Heterodontus*, the odontaspidid *Odontaspis*, myliobatid batoids, holocephalans, and labrid and molid teleosts.

AMEGHINO (1906, 1935) created several species of *Acrodus* (e.g., *A. basalduai*, *A. rothi*, *A. trelewensis*) and a new genus and species (*Pseudacrodus patagonensis*). The teeth are all referable to the Port Jackson shark *Heterodontus* (CIONE 1978, 1988). No characters were found in the Patagonian material deposited at Museo de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, that could permit to sustain AMEGHINO's species (CIONE 1988).

The supposed rostral tooth of a giant pristid (*Notopristis patagonicus* AMEGHINO) was found to be a dorsal finspine referable to *Heterodontus* (CIONE & PANDOLFI 1984).

AMEGHINO (1906) created the species *Squatina gigantea* without definition. Examination of the holotype permits to doubt the validity of this species. Recent species are not usually distinguished by their teeth. Additional studies on Recent material and comparison with fossil material are necessary. The material of Patagonia is designated here to *Squatina* sp.

The first pristiophorids in South America were described from the Monte León Formation in Patagonia (CIONE & EXPÓSITO 1980); both fossil or living are very rare. Pristiophorid teeth from Patagonia are the largest known. Rostral teeth of *Pristiophorus* from the Leonian reach up to 28.8 mm (CIONE & EXPÓSITO 1980) and those from the Aonikan up to more than 30 mm (CIONE 1988). The relatively large nominal species *Pristiophorus lanceolatus* of New Zealand has teeth reaching up to about 20 mm (KEYES 1979; CAPPETTA 1987) but most fossil and all other Recent pristiophorids are smaller. Several fossil species of *Pristiophorus* are recognized. All these species, except *Pristiophorus tumidens*, have been based on isolated rostral teeth. Unfortunately, rostral teeth

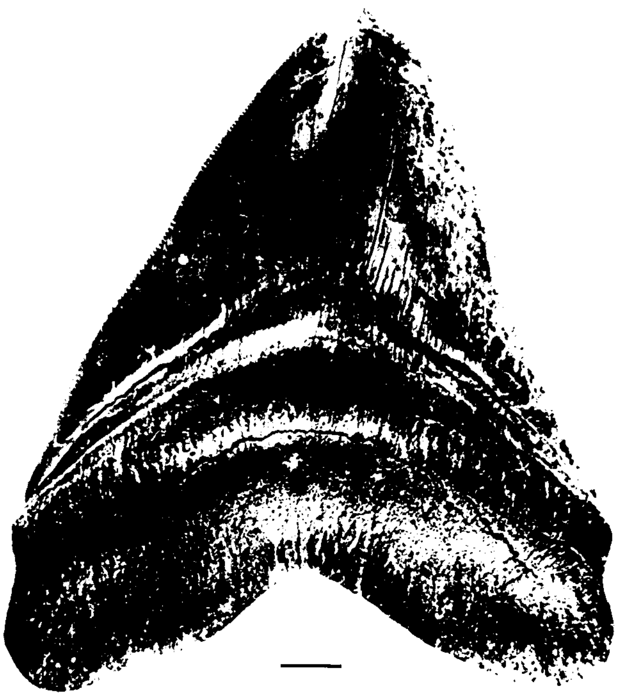


Fig. 9: Tertiary chondrichthyan *Carcharocles megalodon* (specimen MLP 86-V-1-159) from the middle-late Miocene of Paraná, Entre Ríos, Argentina. Scale bar = 1 cm.

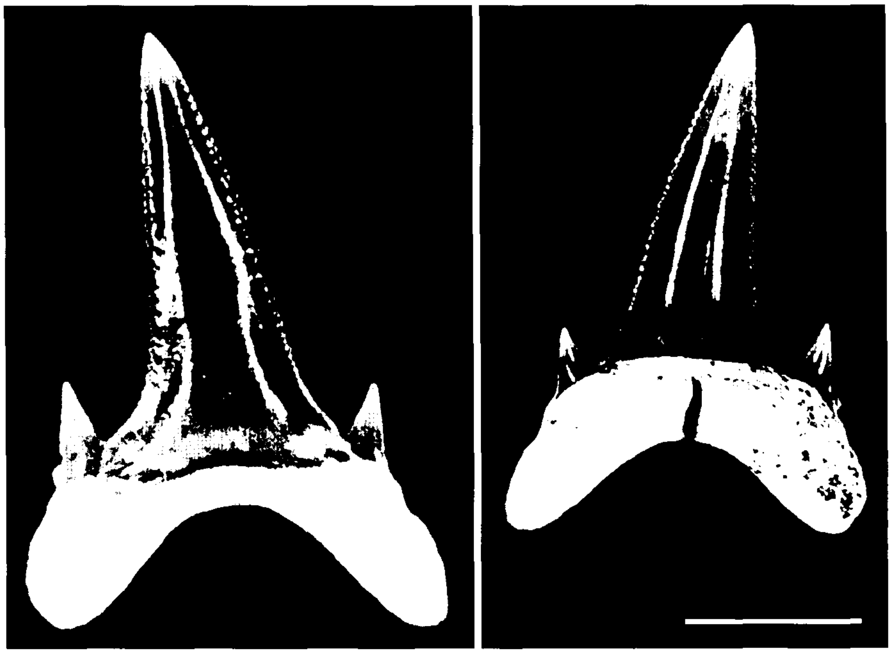
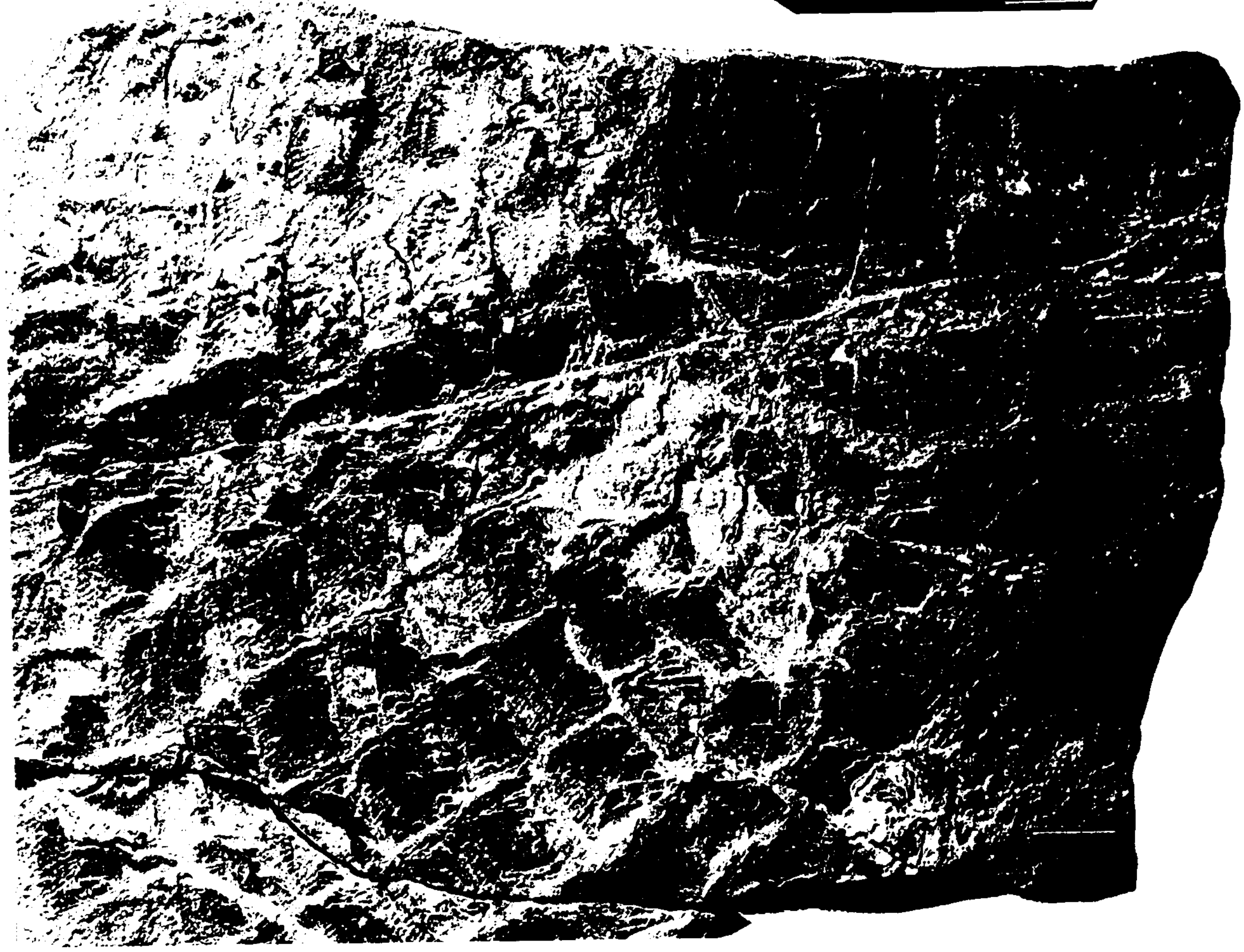


Fig. 10: Tertiary chondrichthyan *Carcharoides totuserratus* (specimen MLP 77-XII-13-2) from the early Miocene of Gaiman, Chubut, Argentina. Scale bar = 1 cm.

Fig. 11: Semionotiform fishes, probably *Lepidotes*. **A,** From Oxfordian of Quebrada del Profeta, northern Chile (specimen LBUCH uncat., dusted with NH_4Cl). **B,** From the Jurassic-Cretaceous boundary, Quebrada La Carreta, northern Chile (LBUCH uncat.). Scale bars = 1 cm.

A

B



of the different species of *Pristiophorus* (exception *P. tumidens*) are very similar and the alleged specific characters can be found as normal variation in a single specimen of *Pristiophorus cirratus* (see CIONE 1988). Recent species are separated by characters other than rostral teeth.

Middle-late Miocene: The high marine level of the middle Miocene sea permitted the ingression of marine waters in the Chacopampean plains at least to Paraguay and Bolivia (ULIANA & BIDDLE 1988; MARSHALL et al. 1993; CIONE & COZZUOL, in prep.). In the south, the marine influence was restricted to northeastern Patagonia. A typical warm temperate Miocene ichthyofauna occurs in the outcrops near Paraná, Argentina (Paraná Formation) and in southern Uruguay (Camacho Formation): the heterodontid *Heterodontus*, the squatinid *Squatina*, the abundant odontaspidid *Carcharias acutissima*, the lamnid *Isurus hastalis*, the "otodontid" *Carcharocles megalodon*, the hemigaleid *Hemipristis serra*, the also abundant carcharhinids *Carcharhinus* and *Galeocerdo aduncus*, the squalid *Squalus*, the batoids Dasyatidae and Myliobatoidei (D'ALESSANDRI 1896; FRENGUELLI 1920; CIONE 1978, 1988; PEREA et al. 1985; PEREA & UBILLA 1989, 1990).

In the Puerto Madryn Formation in Argentina, the dominant lamnid *Isurus hastalis*, the otodontid *Carcharocles megalodon*, the squatinid *Squatina* sp., and the myliobatid *Myliobatis* occur (CIONE 1978, 1988, and pers. obser. in material from Trelew and La Plata museums).

Hexanchids, lamnids (e.g., *Isurus hastalis*), odontaspidids (e.g., *Carcharias*), and "otodontids" (e.g., *Carcharocles megalodon*) occur in lower-middle Miocene rocks in central Chile (GIGNOUX 1913; OLIVER SCHNEIDER 1936b, 1937).

Lamnids (e.g., *Isurus oxyrhinchus*, *I. hastalis*), cetorhinids (e.g., *Cetorhinus maximus*), and batoids (e.g., *Aetobatus* sp.) have been reported from middle Miocene beds at El Rincón, in the coast of northern Chile (LONG 1993).

Several carcharhiniforms, batoids, and the odontaspid *Carcharias* occur in Miocene sediments of Ecuador (LONGBOTTOM 1979). This is the last record of the genus on the western coast of South America (see COMPAGNO 1984).

The assemblage at Paraná is different from the Patagonian ichthyofauna. Whereas at Paraná carcharhinids, hemigaleids, and odontaspidids dominate, Patagonian ichthyofaunas are ruled by lamnids. Invertebrates suggest warm water both for Paraná and northern Patagonia (DEL RÍO 1988).

Heterodontus and pristiophorid species were almost worldwide in the Tertiary (CAPPETTA 1987; CIONE 1988; CIONE & EXPÓSITO 1980). *Heterodontus* species live in the Pacific today (COMPAGNO 1984), whereas pristiophorids do not inhabit modern South American coasts (COMPAGNO 1984). Actually, only a small population of the endemic species *Pristiophorus schroederi* occurs in the (northwestern) Atlantic (SPRINGER & BULLIS 1960). Both groups greatly reduced their distribution after the Miocene. The finds of *Pristiophorus* in the Puerta del Diablo Formation and *Heterodontus* in the Paraná Formation constitute the last records of these genera in the South Atlantic and in the Atlantic, respectively.

Contrasting with the late Oligocene-early Miocene ichthyofaunas, middle Miocene shark assemblages are poorly diversified in Patagonia (CIONE 1978, 1988; CIONE & TONNI 1981; PEREA et al. 1985; PEREA & UBILLA 1989, 1990).

Latest Miocene, Pliocene, and Pleistocene: Until 1993, the only published latest Miocene and Pliocene sharks come from Sacaco (El Jahuay, Aguada de Lomas, Montemar, Sud-Sacaco, Sacaco levels) in Peru (DE MUIZON 1981). They are represented by the holocephalan *Callorhynchus* cf. *C. callorhynchus*, the hexanchid *Hexanchus gigas* (= *griseus*), the heterodontid *Heterodontus* sp., the pristiophorid *Pristiophorus* sp., the lamnids *Isurus hastalis*, *I.* cf. *I. oxyrhinchus*, and *Carcharodon carcharias*, the "otodontid" *Carcharocles megalodon*, the odontaspidid *Carcharias* aff. *taurus*, the carcharhinid *Carcharhinus* sp. indet., *C.* cf. *C. egertoni*, and *C.* cf. *C. priscus*, the sphyrnid *Sphyrna prisca*, and batoids Myliobatoidei. Notwithstanding the low latitude of Sacaco, the warm-temperate ichthyofaunas (CAPPETTA in DE MUIZON 1981) coexisted with penguins, probably indicating the influence of the Humboldt Current. The ichthyofauna was diversified and the elasmobranch composition was similar to that of the Paraná assemblage. According to DE MUIZON & DEVRIES (1985) the *Isurus hastalis* - *Carcharodon carcharias* Miocene-Pliocene lineage shows phyletic transformation. In the Peruvian Pliocene, only *Carcharodon carcharias* is known (DE MUIZON & DEVRIES 1985). However, *Isurus hastalis* did not become extinct in other areas in the Pliocene.

Recently, a relative diverse shark assemblage was described from Pliocene rocks at Bahía Inglesa, near Caldera in northern Chile (LONG 1993). The assemblage includes the hexanchid *Hexanchus griseus*, the "otodontid" *Carcharodon megalodon*, the lamnids *Isurus oxyrhinchus* and *Carcharodon carcharias*, the hemigaleid *Galeorhinus galeus*, the carcharhinid *Carcharhinus albimarginatus*, and rajid batoids. The Pliocene fishes of Bahía Inglesa are the best described assemblages of marine Neogene fishes in Chile (LONG 1993).

A few Pleistocene and Holocene shark teeth have been reported from Buenos Aires Province of Argentina (*Galeorhinus* sp., *Carcharodon carcharias*, *"Odontaspis"* [probable *Carcharias*], *Myliobatis* sp.; AMEGHINO 1898; CIONE 1983; TONNI & CIONE 1984). All are recorded within their present geographic range.

In Chile and central-southern Argentina, the fossil marine fish assemblages (except the Pleistocene-Holocene) are different from those that occur at the same latitude today, due to the dramatic climatic and hydrologic changes in the Late Cenozoic.

Most of the marine assemblages of Cretaceous to Miocene age in the area (except those of Paraná, Uruguay, and Peru) are ichthyofaunas with dominance of odontaspidid and lamnid sharks lacking the warmer carcharinid assemblages. A contrasting example is the tropical assemblage of the Miocene Pirabas Formation (Amazon area of Brazil) that is an assemblage with predominance of Carcharhinidae and other tropical fishes (SANTOS & TRAVASSOS 1960).

The extant representants of those genera occurring in Argentina and Uruguay live in the Argentinian Biogeographic Province today (LÓPEZ 1964). Those taxa characteristic of the cold temperate Magallanian Biogeographic Province are not represented in the fossil assemblages. The important environmental changes caused by global climatic and marine current modifications and tectonism are mostly late Miocene-Pleistocene events.

3. Primitive actinopterygians from the Paleozoic to Cretaceous

Some Paleozoic osteichthyan remains have been documented in western Argentina (TORNQUIST 1904 ;MANCEÑIDO 1973; GONZÁLEZ 1985; RICCARDI &

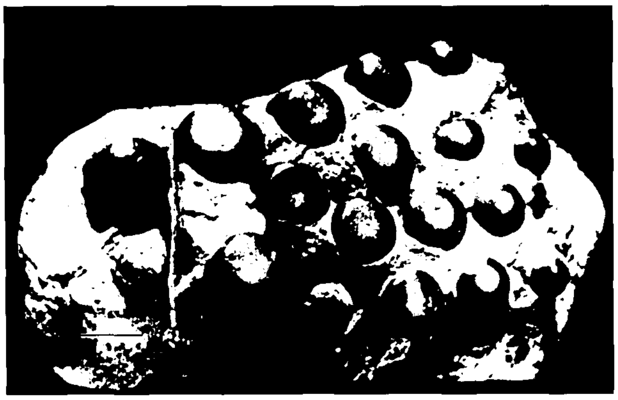


Fig. 12: Vomerine dentition of *Lepidotes* cf. *L. maximus* from the Tithonian of Argentina (specimen PV. U.N.S. 10010). Scale bar = 1 cm.

SABATTINI 1985) and in Bolivia (JANVIER 1992b). Occurrences are usually composed of isolated scales and bones.

Primitive actinopterygians, including cheirolepiforms, palaeonisciforms, and neopterygians are scarcely known in southern South America because of incomplete preservation. One exception is *Atacamichthys greeni* from the Oxfordian of Chile, which is the most complete described taxon among non-teleostean southern South American primitive actinopterygians (ARRATIA & SCHULTZE 1987).

Paleozoic: Scales of a "palaeoniscid" are recorded in the Famennian Iquiri Formation of Tarija Department in Bolivia (JANVIER & SUÁREZ-RIGLOS 1986). A cleithrum of a *Mimia*-like "palaeoniscoid" has been found in the Sicasica Formation (Frasnian) of La Paz area, Bolivia (GAGNIER et al. 1989). Some platysomid teeth are recorded in the Lower Permian Copacabana Formation in La Paz area (MERINO-RODO & JANVIER 1986).

A diversified fish fauna belonging to the orders Cheirolepidiformes and Palaeonisciformes has been reported from the Upper Carbonifeous-Lower Permian of San Gregorio Formation, Río Negro, northeast Uruguay. The fishes are known from incomplete but well-preserved specimens. BELTAN (1977, 1981, 1989) described eleven new species of primitive actinopterygians from Uruguay, two of which were included in two new families of the Cheirolepidiformes. The rest of the species were classified as belonging to families with a broad Gondwanan distribution during the Paleozoic (e.g., Acrolepidae, Elonichthyidae, Rhadinichthidae, Pygopteridae, and Amplypteridae).

An almost complete specimen from the Permian Paine Formation (near Toconao, northern Chile) has been described as a new gen. et sp. by RICHTER & BREITKREUZ (in press). This is the first formal description of a Paleozoic palaeoniscoid from southernmost South America.

Jurassic: Primitive Jurassic actinopterygians are known from Argentinian and Chilean localities (semionotiform neopterygians) and from Quebrada del Profeta, northern Chile (the halecostome *Atacamichthys*, undescribed pycnodonts, and pachycormiforms; see Appendix 1).

Rests of semionotiforms have been recently (1994) collected in the Sinemurian of Vaquillas Altas, northern Chile, by ARRATIA, SCHULTZE & party. These are the oldest semionotiforms known from the Jurassic in the area. The presence of *Lepidotes* from the Callovian of Cerritos Bayos was reported by BIESE (1957, 1961) and ARRATIA (1987a), and from the Oxfordian of Quebrada del Profeta by ARRATIA (1987a; Fig. 11A). All this material is incompletely preserved and is still undescribed.

Lepidotes cf. *L. maximus* from the Tithonian of Argentina was first mentioned by WEAVER (1931). Later, ARAMAYO (1981; Fig. 12) assigned an incomplete vomerine dentition and scales to *Lepidotes maximus* because, according to this author, the material is undistinguishable from the European *Lepidotes maximus* WAGNER (see CIONE & PEREIRA 1990). The question arises whether the similarity in dentition is enough to identify these remains as belonging to the European species or could be the result of morpho-functional convergence.

Atacamichthys greeni, like the teleosts of Quebrada del Profeta, is known from several specimens which also have preserved soft structures such as muscles, notochordal fibrous sheath, cartilages, and blood vessels (Figs. 13, 14). It represents the first described primitive halecostome from the Jurassic of northern Chile and from South America (ARRATIA & SCHULTZE 1987).

Other halecostomes reported from Cerritos Bayos and Quebrada del Profeta, northern Chile, are pachycormiforms (BIESE 1961; ARRATIA 1987a). It is unknown where the pachycormiform material from Cerritos Bayos, mentioned by BIESE (1961), is deposited; after ARRATIA' search in different collections it is better to be considered as lost. Incomplete tails of a few pachycormiforms are known from Quebrada del Profeta, and because of the structure of the caudal centra and the position of the caudal fin-rays they were assigned to the pachycormiforms in a preliminary way (ARRATIA 1987a). Recently, ARRATIA, SCHULTZE & party collected in Quebrada del Profeta part of body and head bones of pachycormiform-like fishes (ARRATIA et al., in process).

Cretaceous: Cretaceous pycnodonts and semionotiforms are scarcely known in the area. The pycnodontiforms are represented by the genera *Macromesodon* and *Paramicrodon*. The genus *Macromesodon* has been collected in southern Argentina (BOCCHINO 1977). [BIESE (1958) described *Microdon chilensis* from the Early Cretaceous of Copiapo; this taxon was included in the genus *Paramicrodon* by SCHULTZE (1981a) (see Appendix 1).]

Numerous semionotiforms (Fig. 11B), like a school of fishes which suddenly found their fate, are preserved in Quebrada La Carreta, northern Chile, at the Jurassic-Cretaceous boundary. This material is not preserved three-dimensionally as the fishes from the Late Jurassic of Quebrada del Profeta, northern Chile.

4. Teleosts from the Jurassic to the Tertiary

Marine teleosts are known from several Jurassic localities in southern South America. For instance: Vaquillas Altas (Chile; Sinemurian); Cerritos Bayos, Cerro Blanco (Chile; Oxfordian, Kimmeridgian); Quebradas del Profeta and Sandón (Chile; Oxfordian); Termas del Flaco (Chile; Late Jurassic), Plaza Huincul and Arroyo Picún Leufú (Argentina; Tithonian).

The oldest, and apparently more primitive, teleosts are those from the early Sinemurian of Quebrada Vaquillas Altas which were known from a few specimens reported as proleptolepiforms by ARRATIA (1987a). Recently,

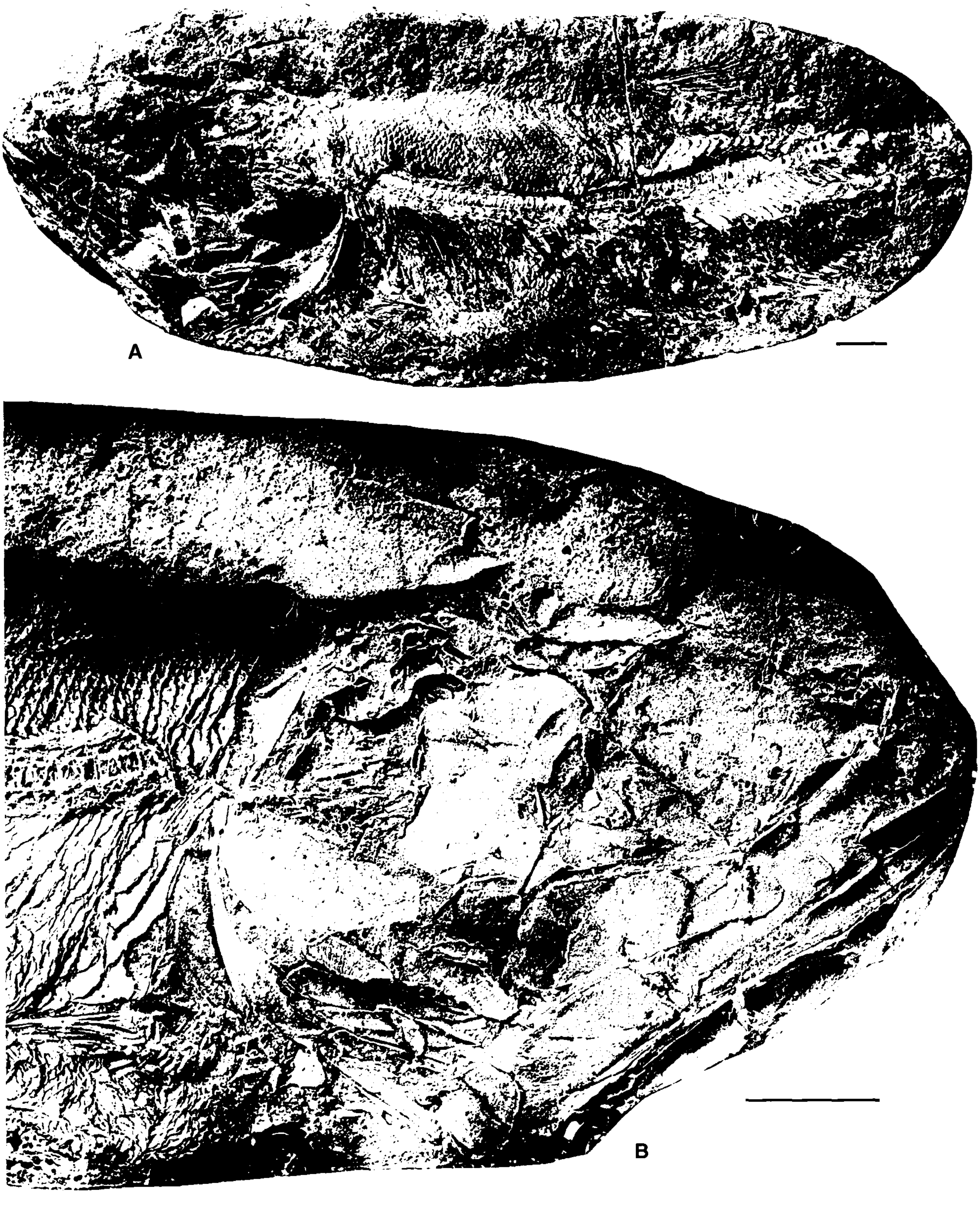


Fig. 13: *Atacamichthys greeni* ARRATIA & SCHULTZE from the Oxfordian of Quebrada del Profeta, northern Chile. **A**, Lateral view (specimen LBUCH 248). **B**, Latex cast of head of specimen illustrated in A (dusted with NH_4Cl). Scale bar = 1 cm.

ARRATIA, SCHULTZE & party collected numerous specimens including complete cranial roofs, opercular apparatuses, lower jaws, caudal fins, etc., and many partially disarticulated individuals. All specimens are very small with tiny, thin bones of few millimeters in size.

Certain teleosts from Cerritos Bayos were identified as *Trissops* (= *Thrissops*) by BIESE (1957, 1961). According to ARRATIA (1987a) these fishes are not *Thrissops* and should be considered indetermined teleosts. Among the material collected by BIESE and deposited at the National Museum of Natural History, Washington, there are at least two different kinds of teleosts (ARRATIA

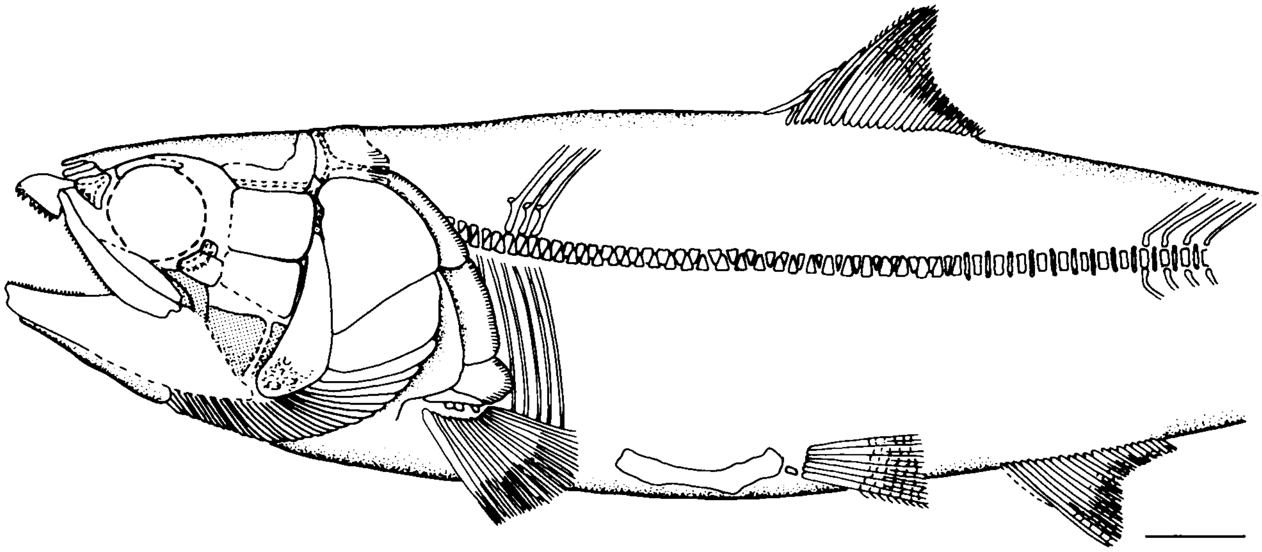


Fig. 14: Restoration in lateral view of *Atacamichthys greeni* (after ARRATIA & SCHULTZE 1987). Scale bar = 1 cm.

1987a) which are incompletely preserved. One taxon is only known from its caudal region and it was identified as Teleost sp. 2 by ARRATIA (1991: fig. 26); Teleost sp. 2 appears as the probable sister group of Teleost sp. 1 (from Quebrada del Profeta) in ARRATIA's (1991) phylogenetic hypothesis of relationships of basal teleosts. The other taxon is represented only by some vertebrae (ARRATIA 1987a: pl. II, figs. 1-4). BIESE (1961) mentioned the presence of clupeiforms, which was repeated by GASPARINI (1979). No clupeiform is among the fishes collected by BIESE that ARRATIA examined. Another teleost from this area is *Protoclupea* sp., which was collected in the west sector of Cerritos Bayos, in Cerro Blanco (ARRATIA & SCHULTZE 1985). *Protoclupea* sp. is the only fish known from that locality. Fishes from Cerro Blanco and Cerritos Bayos have preserved soft tissues like body muscles, a preservation similar to that of the fishes from Quebrada del Profeta described by SCHULTZE (1989).

Usually, only hard parts of organisms are preserved as fossils, but the fishes from Quebrada del Profeta present an outstanding condition of preservation, with three-dimensionally preserved muscles (Figs. 13A, 15A). Preserved are muscle fibers with mitochondria and nuclei, blood vessels, swim bladder, intestine and melanophores (ARRATIA 1987a; SCHULTZE 1989), and food content (Fig. 15B). Such preservation even permitted SCHULTZE (1989: figs. 4, 5) to restore the body muscles of *Protoclupea chilensis* (see Fig. 16). SCHULTZE (1989) argued that the soft tissues of the fishes were impregnated by calcium phosphate during life, whereas the decay of the remaining soft tissue induced the formation of the calcareous concretions around the fishes.

The best known assemblages of fishes from southern South America are the Jurassic teleosts from Quebrada del Profeta. Up to now, eight teleostean species have been described (ARRATIA 1981a, 1982a, 1986a, b; ARRATIA et al. 1975 a, b, c; ARRATIA & SCHULTZE 1985; Appendix 1); another one, ?*Pholidophorus domeykanus* (see ARRATIA et al. 1975b), is actually under revision by ARRATIA because the fish does not belong within the Pholidophoridae *sensu* NYBELIN (1966). Among the teleosts, one monophyletic assemblage, the varasichthyid group, can be identified (ARRATIA 1994). It includes at least the Chilean genera *Domeykos, Varasichthys,* and *Protoclupea* (Figs. 17A-C, 18A-C).

Chongichthys dentatus (Fig. 19) and *Antofagastaichthys mandibularis,* other teleosts of Quebrada del Profeta, are known from incomplete specimens lacking the tail. *Chongichthys* differs from members of the varasichthyid group in the presence of elongate lower jaws, of narrow preopercles lacking the posterior expansion bearing a finely crenulate posterior margin (ARRATIA 1981a, 1982a, 1986a, 1994), and of scales without the lines crossing the circuli in the middle field (ARRATIA 1986a: text-fig. 12A, B).

Recently, M. NOVACEK and party discovered Late Jurassic teleosts in Termas del Flaco (central Chile). The few specimens collected by the American team - and actually deposited at the Museo Nacional de Historia Natural, Santiago - open new possibilities of finding new Jurassic localities bearing fishes south to the Atacama desert. Because of poor preservation it is not possible to assign these fishes taxonomically (ARRATIA, pers. obser.).

While the Oxfordian teleosts from Chile have heavily ossified bones, the few teleosts known from the Tithonian of southern Argentina are more delicate, with thinner bones. Most of these fishes, poorly preserved, were previously asigned to the genus *Leptolepis* by DOLGOPOL (1939, 1940a). These identifications were revised by CIONE & PEREIRA (1990). *"Leptolepis" argentinus, "L." australis,* and *"L." patagonicus* were proposed by these authors in the category of *nomen vanum.* Another teleost was identified as *Leptolepis dubius* by DOLGOPOL (1939) because of certain similarities with the European species. NYBELIN (1974) included the European species in a new genus, *Tharsis,* which is the most common teleost in the Kimmeridgian-Tithonian of Germany (ARRATIA, pers. obers.). The Argentinian *Leptolepis dubius* does not pertain to *Tharsis dubius* (CIONE & PEREIRA 1990) and was left as ?*"Leptolepis dubius"* by CIONE & PEREIRA (1990) waiting for more material before to propose a taxonomic assignment. A supposed coelacanth (*Bunoderma baini* DOLGOPOL) was identified as a Teleostei *incertae sedis* by CIONE & PEREIRA (1990).

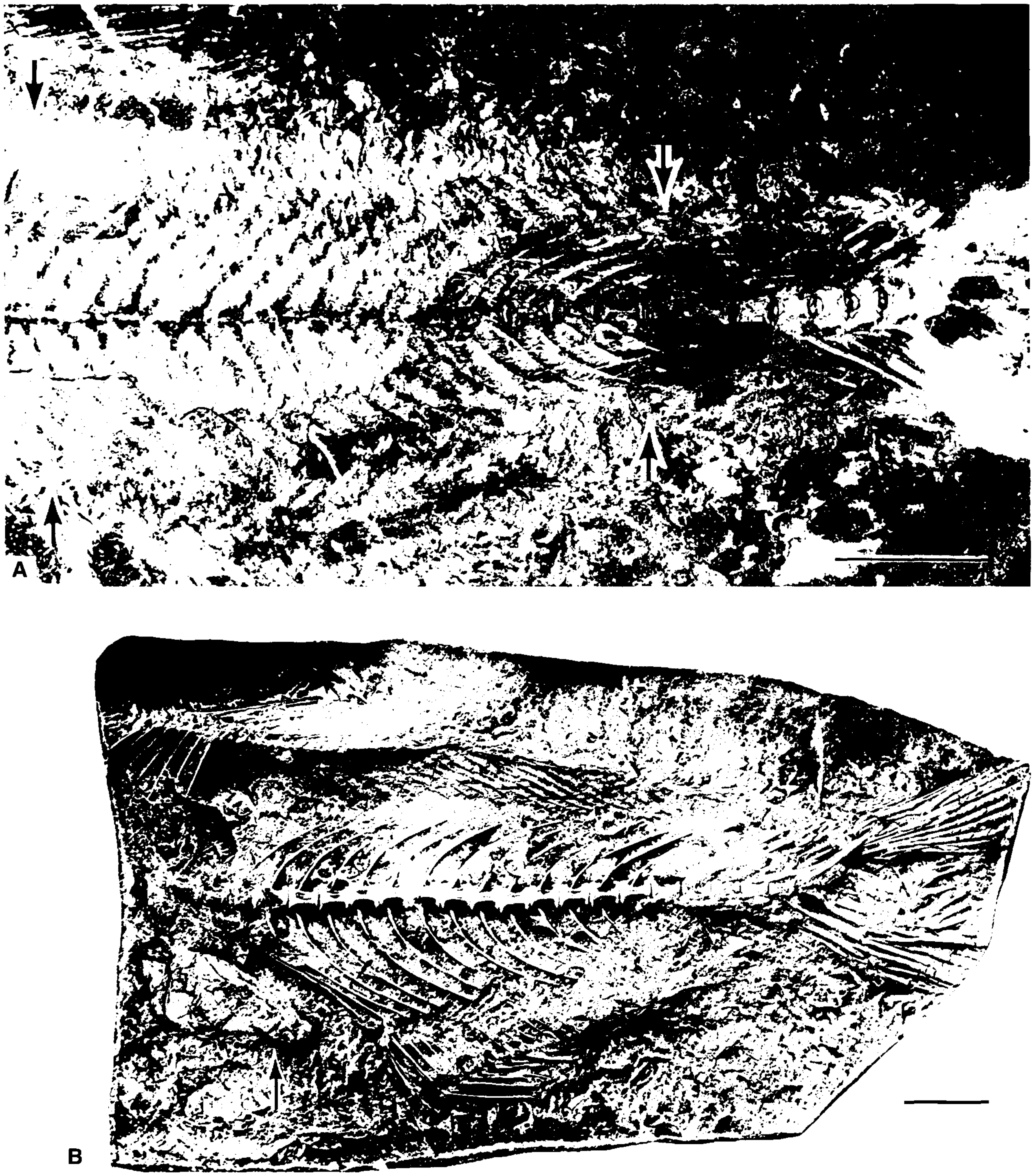


Fig. 15: Preservation of fishes from northern Chile. **A**, Note the preservation of muscles (indicated by arrows) in the caudal region of the body of *Protoclupea chilensis* ARRATIA, CHANG & CHONG from the Late Jurassic of Quebrada del Profeta (specimen KUVP 71205b). **B**, Note the fish head in the body cavity of an indeterminate teleost from Cerro Islote (LBUCH uncat., dusted with NH_4Cl). Scale bars = 1 cm.

The poor preserved material from the Argentinian localities does not facilitate comparison with the Late Jurassic fish fauna from Chile, which is very well preserved and in addition, looks very different. All the Jurassic teleosts from Argentina should be re-studied so that their taxonomy could be clarified. At present, the available information does not permit to hypothesize anything about their phylogenetic positions within Teleostei.

Cretaceous: Cretaceous teleosts of southern South America are poorly known. CABRERA (1927) described *Haplospondylus clupeoides* (Fig. 20) from the Early Cretaceous of southern Argentina. This fish was left as *"Haplospondylus" clupeoides* by CIONE & PEREIRA (1990). CIONE (1985) and CIONE & PEREIRA (1990) included *"Haplospondylus"* within the Clupeomorpha, not assignable to any of the divisions of GRANDE (1985). This assignment was based on the presence of ventral (and

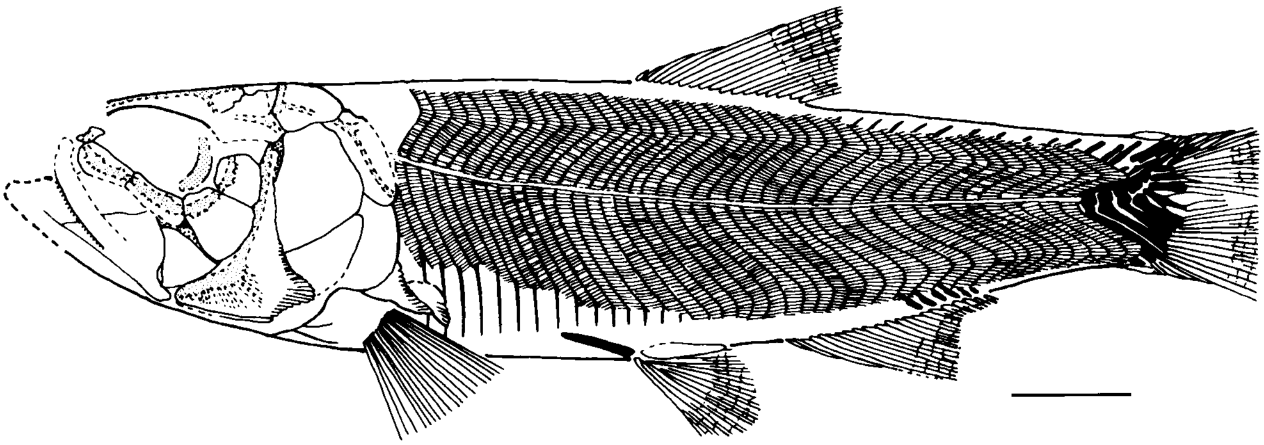


Fig. 16: *Protoclupea chilensis* showing muscle reconstruction (slightly modified by ARRATIA from SCHULTZE 1989).

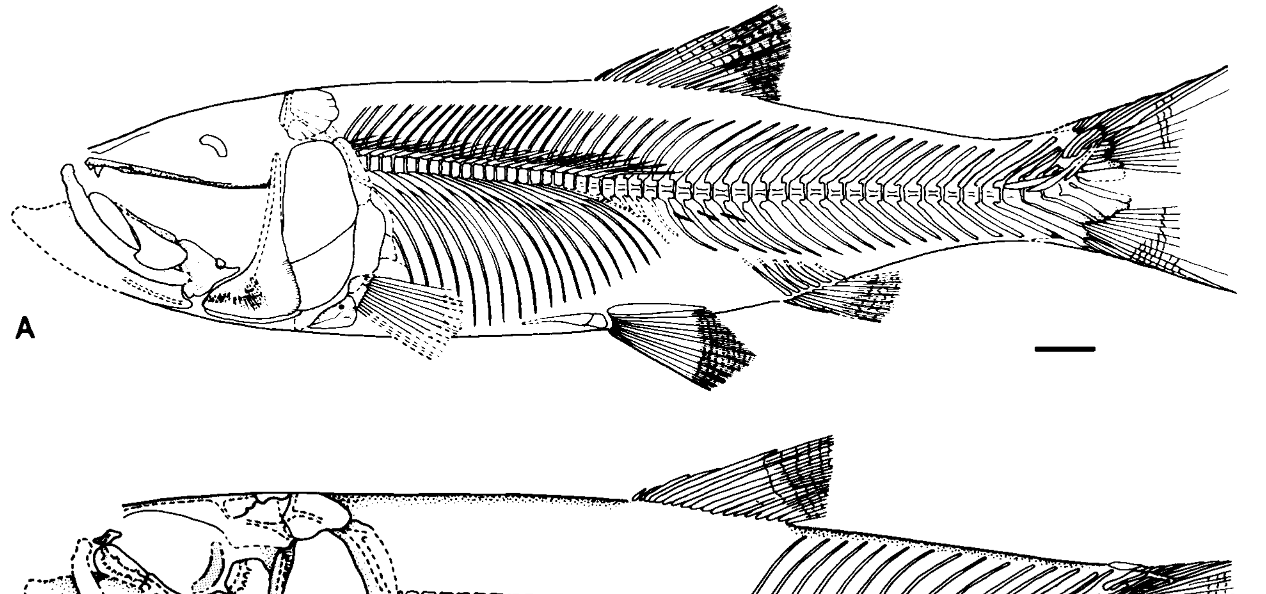


Fig. 17: Restorations in lateral view of certain Jurassic teleosts from the Oxfordian of Quebrada del Profeta, northern Chile. **A**, *Domeykos profetaensis* ARRATIA & SCHULTZE (after ARRATIA 1994). **B**, *Protoclupea chilensis* ARRATIA, CHANG & CHONG (after ARRATIA & SCHULTZE 1985). **C**, *Varasichthys ariasi* ARRATIA (after ARRATIA 1987a). Scale bars = 1 cm.

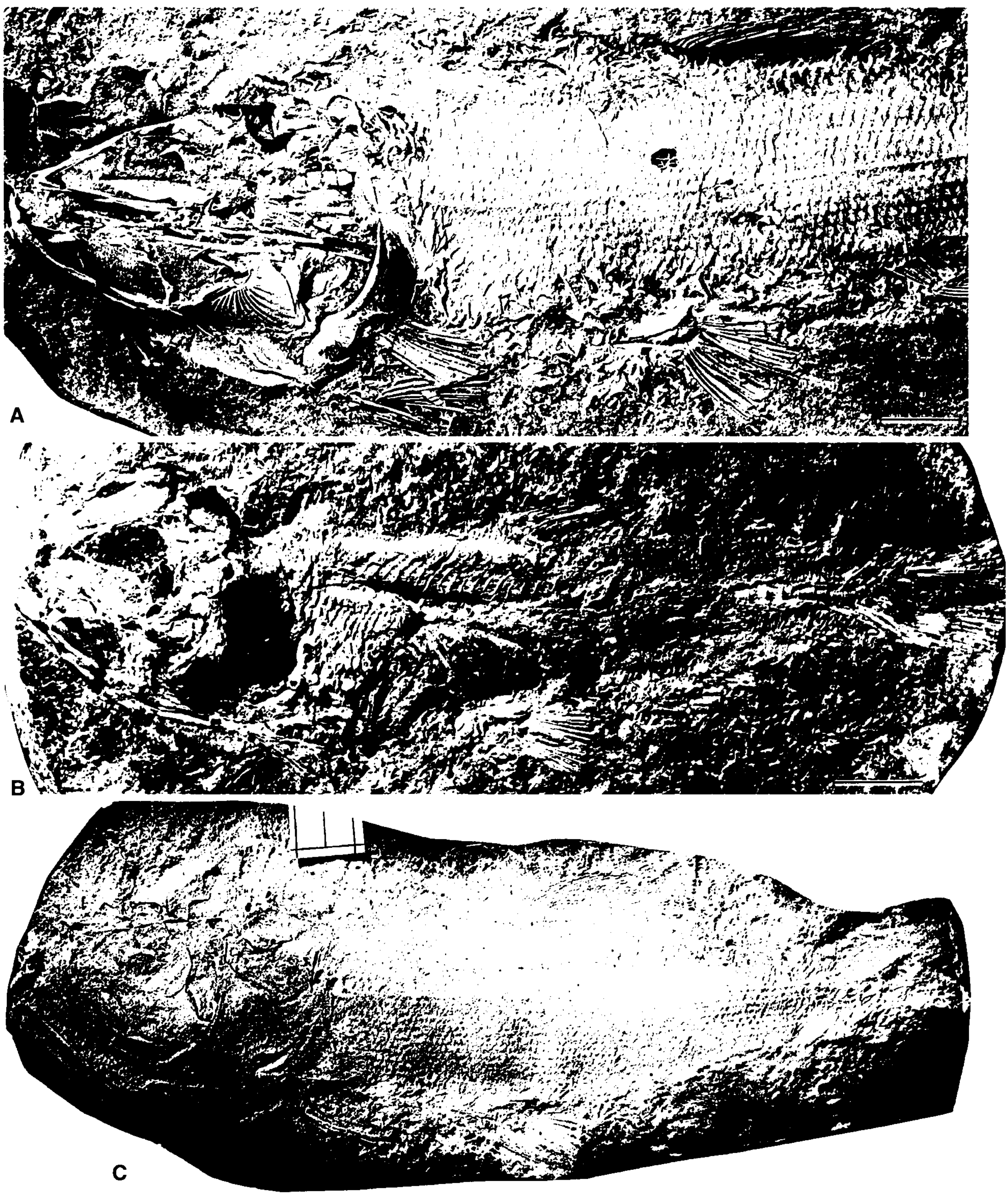


Fig. 18: Jurassic teleosts of Quebrada del Profeta, northern Chile. **A**, *Domeykos profetaensis* ARRATIA & SCHULTZE (latex cast of specimen LBUCH 12-260972, holotype dusted with NH_4Cl). **B**, *Protoclupea chilensis* ARRATIA, CHANG & CHONG (R-396, holotype). **C**, *Bobbichthys opercularis* (ARRATIA, CHANG & CHONG) (MNHN SGO. PV 306, holotype dusted with NH_4Cl). Scale bars = 1 cm.

probable dorsal) scutes. Numerous epineural and epipleural intermuscular bones, the general aspect of the cranium, and the structure of the scales were considered suggestive (CIONE 1985). From the listed characters only the presence of scutes is unquestionable a clupeomorph character. To determine the position of the fish within the Clupeomorpha it is important to know whether the fish has recessus lateralis, a supratemporal commissure passing through the parietals and supraoccipital, an epiotic fossa, and other features. The material is too poorly preserved, however, to identify these features.

The only specimen of *"Haplospondylus"* was collected close to San Martín Lake, in the Early Cretaceous Río Mayer Formation. Only very few Early Cretaceous clu-

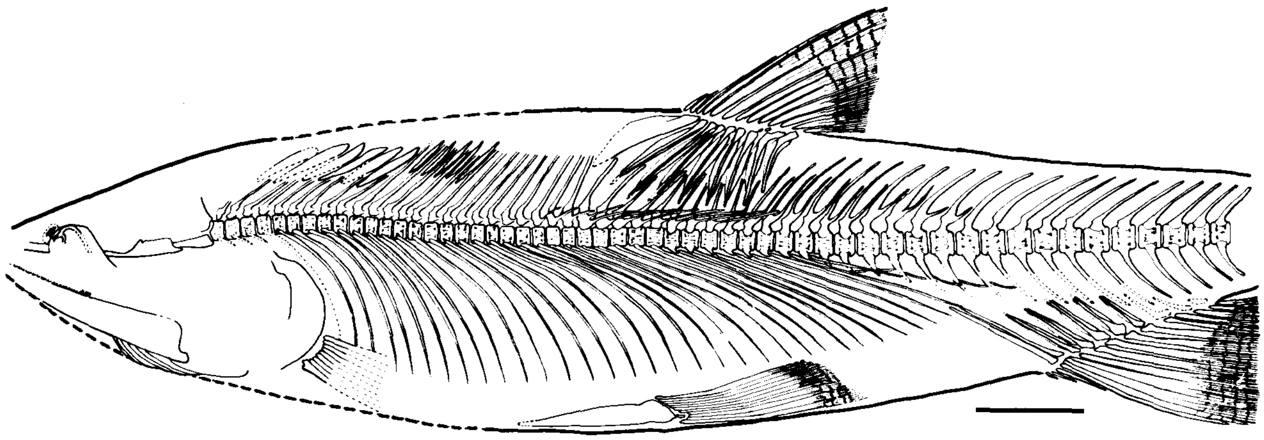


Fig. 19: *Chongichthys dentatus* ARRATIA from the Oxfordian of Quebrada del Profeta, northern Chile (after ARRATIA 1982a). Scale bar = 2 cm.

peomorphs are known all over the world; their knowledge is very important to clarify some characters of the basal clupeomorphs.

Other Cretaceous teleosts, such as those mentioned by D'ERASMO (1934; see Appendix 1) are also only poorly known. Cretaceous teleosts have also been collected in Tierra Amarilla, Copiapó, northern Chile. They do not have the exceptional preservation of the Oxfordian fishes from Chile, still they represent at present the best preserved Cretaceous specimens of southern South America (ARRATIA, in progress).

Middle Miocene to early Pliocene: Teleosts of Miocene and Pliocene age are known from El Rincón and Bahía Inglesa in Chile and Sacaco in Peru (Appendix 1). All of the records correspond to incomplete specimens and most of them are identified to the family level only. The teleosts Triglidae indet., Centropomidae aff. *Psamoperca*, Xiphiidae indet., Scombridae indet. Clupeidae Alosinae indet., Tetradontiformes indet., Cybiidae indet., and Siluriformes cf. Ariidae have been reported from Sacaco (HOFFSTETTER 1968; CAPPETTA in DE MUIZON 1981; DE MUIZON & DEVRIES 1985). The scombrid *Thunnus* and indetermined serranids occur in the Middle Miocene and Pliocene of Chile (LONG 1993).

Holocene: Teleost remains occur in the Holocene Las Escobas Formation in northwestern Buenos Aires Province. These correspond to the extant perciform species *Pogonias cromis* (CIONE & TORNO 1987).

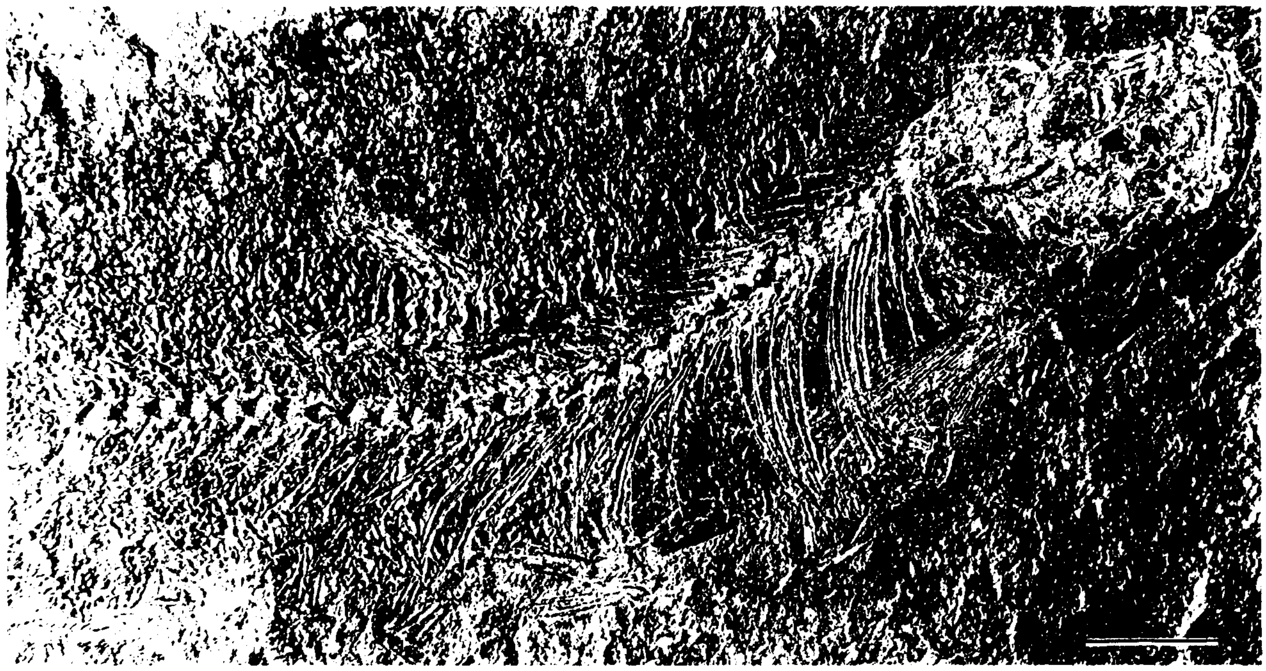


Fig. 20: *"Haplospondylus" clupeoides* CABRERA from the Lower Cretaceous of Lago San Martin region, Argentina (specimen MLP 25.XI.21.1, holotype). Scale bar = 1 cm.

Freshwater Fish Record

Studies on fossil freshwater fishes of southern South America began at the end of the last century with the dipnoan *Ceratodus iheringi* by AMEGHINO (1898, 1899, 1900-1903, 1904, 1906). WOODWARD (1900) reported the presence of the characiform *Colossoma macropomum.* At present, about 150 records are known from the region (Appendix 2).

The known record from southern South American of fossil freshwater fishes is rather poor if we compare it with that of mammals and with the approximately 2,950 species of Recent South American fishes (ARRATIA in press), and specifically with the approximately 500 species living actually in freshwater of Argentina and Chile (RINGUELET et al. 1967; ARRATIA 1981b; ARRATIA et al. 1983; CIONE 1986a). Many nominal fossil fish species have not been described and figured sufficiently or remain undescribed. Others have not been compared adequately with the numerous taxa inhabiting today South American freshwater environments.

The sparse and fragmentary nature of the record limits strongly testing of phylogenetic and paleobiogeographic hypotheses. Many important families or higher taxa of the Recent ichthyofauna have not yet a fossil record, i.e., Synbranchiformes, Galaxiidae, many families of Characiformes, Siluriformes, and Gymnotiformes.

1. Chondrichthyans from the Late Cretaceous

Numerous Late Cretaceous freshwater chondrichthyans are known from many localities in Argentina and Bolivia and one (Acre river) in Peru (see Appendix 2). The chondrichthyans include members of the Rajiformes (e.g., Sclerorhynchidae) and Myliobatiformes (e.g., Dasyatidae and Rhombodontidae). Sclerorhynchids are Late Cretaceous rajiformes characterized by a long, flattened rostrum, with a lateral set of rostral teeth which possess an enameloid cap and a peduncle with a closed basal face (CAPPETTA 1987). Many sclerorhynchids were amphibiotic (CIONE & PEREIRA 1985), like pristids are today. VAN VALEN (1988) wrongly assigned the family to the Paleocene based on HERMAN (1972) who created the new species *"Sclerorhynchus palaeocenicus"* for the Thanetian of Morocco.

The Late Cretaceous fish fauna from Chile is only known from one chondrichthyan, *Pucapristis branisi* from the Purilactis Formation (CIONE et al. 1985). This taxa was first described from Bolivia by SCHAEFFER (1963) and later by POWELL (1979) from Salta Province, Argentina. In contrast to Chile, a rich diversified fish fauna is known from the Upper Cretaceous of Argentina and from Bolivia. Unfortunately, the information about the age of some of the Bolivian localities that were formerly described as Late Cretaceous is unclear and some of them now are interpreted as early Paleocene (DE MUIZON et al. 1983, 1984; MARSHALL et al. 1985; GAYET 1992; GAYET et al. 1992). Numerous chondrichthyans are known from many localities belonging to the El Molino Formation in Bolivia, and some batoid remains from the Vilquechico Formation in Peru, and Los Alamitos and the Coli Toro Formations in Argentina (see Appendix 2).

The three Bolivian species of *Dasyatis* (*D. molinoensis, D. schaefferi,* and *D. branisai*) are endemic to the Andes basin (CAPPETTA 1992). Their knowledge is based on teeth found in Torotoro, Hotel Cordillera, and La Palca.

Up to now, 11 species of selachians are known from the Late Cretaceous of Bolivia. No sharks have been found, only batoids. All species are restricted to the Andes basin, except *Schizorhiza stromeri* which also occur in North America, western, northern, northeastern Africa and Middle East (CAPPETTA 1992). According to this author, the environmental conditions where these animals lived during the Late Cretaceous in Bolivia were probably marine.

2. Primitive actinopterygians from the Paleozoic to Tertiary

Paleozoic: Paleozoic freshwater fishes are extremely rare in southern South America and usually are represented by scales and bony fragments (e.g., BELL 1985). Some records are misidentifications (e.g., in FRENGUELLI 1952) or erroneous age assignments (e.g., in RUSCONI 1949a, b).

Triassic-Early Jurassic: Most nominal neopterygian species have been reported from Triassic rocks from Mendoza, Argentina. Most of these taxa correspond to usually well-preserved fishes found in continental Triassic rocks and described by C. RUSCONI in different publications. RUSCONI (1949a, b) reported "chondrosteans," "holosteans," and primitive teleosts. However, most of these fishes have to be re-studied because identifications are not reliable (BÁEZ et al. 1984). Only the perleids *Mendocinichthys* (= *Mendocinia*) *brevis* BORDAS 1944 (from Potrerillos Formation; re-studied by SCHAEFFER 1955) and *Pseudobeaconia bracaccini* BORDAS 1944 (from Las Cabras Formation; re-studied by HUTCHISON 1973) are well documented. Fish bearing rocks range from the Ladinian to Carnian (BÁEZ et al. 1984).

Actinopterygian remains such as lower jaws, teeth, and scales were described by BELTAN et al. (1987) from the Late Triassic Vitiacua Formation in Bolivia (now probably Early Triassic: P. JANVIER, in litteris). A dentalosplenial is suggestive of the genus *Birgeria.*

Bones and scales of semionotiform-like specimens, probable *Lepidotes,* are known from the ?Late Triassic-Early Jurassic of Bolivia (WENZ in GOÑI & HOFFSTETTER 1964) and of Uruguay (WALTHER 1932). The structure of the surface of the Bolivian scales studied under Scanning Electron Microscopy by GAYET & MEUNIER (1986) does not contradict the previous interpretation of this material as belonging to *Lepidotes.*

GAYET (1992: 455, material studied) listed only "isolated bones" of *Lepidotes* sp. from Quebrada de Charagua. However, the author noted that "isolated bones were found together with scales but because of their fragmentation nothing definite can be said of them." Notwithstanding so, GAYET, based on such weak evidence, determined the material as belonging to *Lepidotes* sp.

Late Jurassic: Jurassic freshwater actinopterygians are rare in South America. Primitive and advanced actinopterygians have been found together in the same Jurassic locality (see Appendix 2). BORDAS (1943) identified one

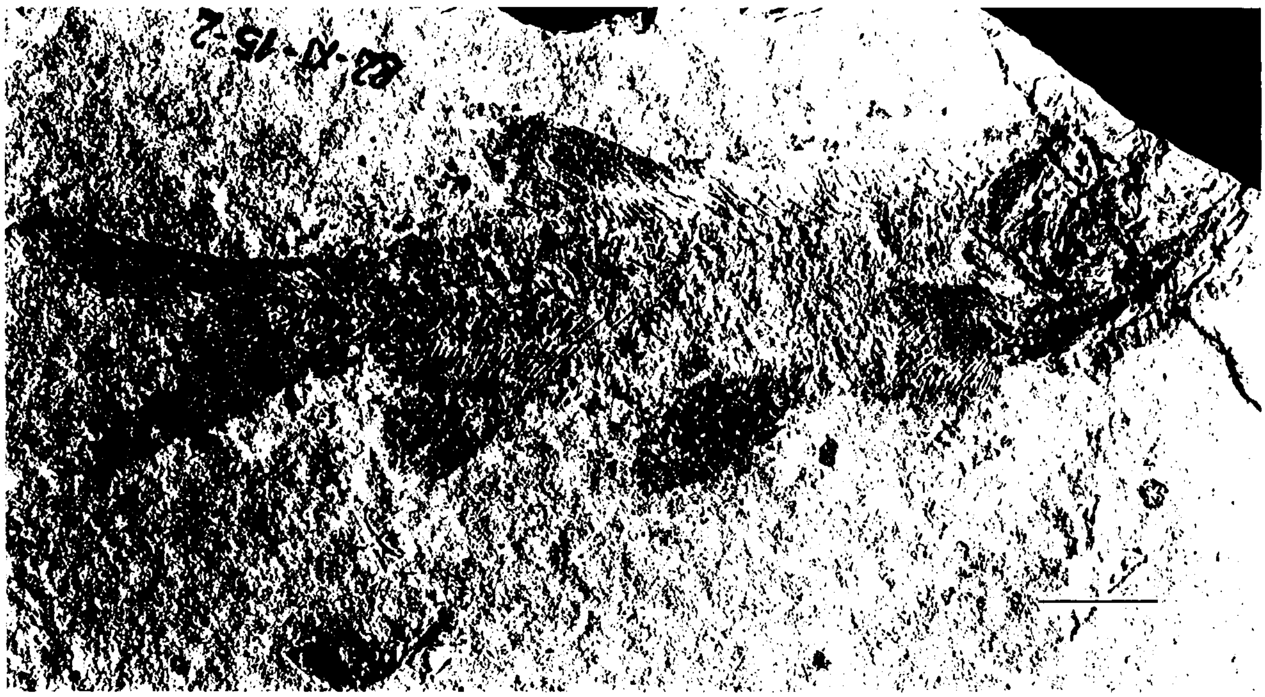


Fig. 21: *Coccolepis groeberi* (Bordas) from the Late Jurassic of Río Chubut medio, Argentina (specimen MLP 82-XI-15-2, holotype). Scale bar = 1 cm.

fish, *Oligopleurus groeberi,* from the Late Cretaceous of Río Chubut medio. BOCCHINO (1978) redescribed it and assigned it to the palaeonisciform genus *Coccolepis. Coccolepis groeberi* (Figs. 21, 22) is currently interpreted as having a probable Late Jurassic age (CIONE & PEREIRA 1987). It is one of the few South American palaeoniscoids known from almost complete specimens.

Cretaceous: An abbreviated presentation of the main taxa of Late Cretaceous age is presented below.

Pycnodontiformes.- Mandibular dentitions and vomerine tooth plates of pycnodontiforms have been found in Argentina and Bolivia. They have been included in the genus *Coelodus,* within the family Pycnodontidae. *Coelodus* has been recorded in Argentina and Bolivia (WENZ 1969; BENEDETTO & SÁNCHEZ 1972; CIONE 1977; GAYET 1992; SCHULTZE 1992a; see Appendix 2) and also in Santander, Colombia (PORTA 1970).

Semionotiformes.- Jurassic and Cretaceous semionotiforms are based on a few poorly preserved specimens which have been assigned to the Semionotiformes because of overall morphological similarities such as the aspect of scales, body shape, etc. The available information is so general that it does not permit to infer whether the South American genera *Neosemionotus* BOCCHINO 1973 and *Australepidotes* BOCCHINO 1974 are valid taxa because their diagnoses are based on a combination of primitive features. We are unable to distinguish one single apomorphic character in the respective generic diagnoses which clearly could separate them from other semionotiform genera. These fishes were considered to be Late Cretaceous in age (BOCCHINO 1973; YRIGOYEN 1975). Currently, the Lagarcito Formation in San Luis, where the fishes were collected, is assigned to the Early Cretaceous.

Lepidotes patagonicus AMEGHINO 1906 is assignable to the family Semionotidae (CIONE, pers. obser.). The material (scales and teeth in the Museo de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires) was not described nor figured; consequently, the species is a *nomen nudum. Paraikichthys ornatissimus* AMEGHINO 1900-1903 (also undescribed, and also a *nomen nudum*) is probably assignable to *Lepidotes.* This species was not mentioned by AMEGHINO in 1906, where he only recognized *L. patagonicus.*

Most information from the material collected in the Upper Cretaceous of Bolivia is based on isolated bones and scales which have been interpreted as semionotiforms. GAYET (1982a), based on isolated scales, interpreted them as belonging to *Lepidotes mawsoni* WOODWARD; recent studies contradict such assignment and the scales are now interpreted as belonging to Semionotidae n. gen. (GAYET 1992).

GAYET (1982a) stated that the scales assigned to *Lepidotes* were much thicker than those of *Lepisosteus* and were cushion-like (thicker in the center). GAYET et al. (1984) mentioned that the ganoine layer is reduced in *Lepidotes* from the Cretaceous of Bolivia and Brazil. One of us (A. CIONE) examined two large specimens of *Atractosteus spatula* in the Natural History Museum, London, and in the American Museum of Natural History, New York, U.S.A. Scales show the ganoine layer greatly reduced and an important allometric growth in thickness. The scales of the dorsal middle line are very similar to those from the El Molino and Yacoraite Formations. Large specimens of *Lepidotes* also show ganoine reduction (e.g., specimen of *Lepidotes maximus* in the Senckenberg Museum, Frankfurt, Germany).

Lepidotes is unknown in levels of proved Tertiary age. AMEGHINO (1906) did not refer *Lepidotes* from Patagonia to the Eocene as was stated by GAYET (1982a). The bearing rocks are Coniasian in age (CIONE 1988).

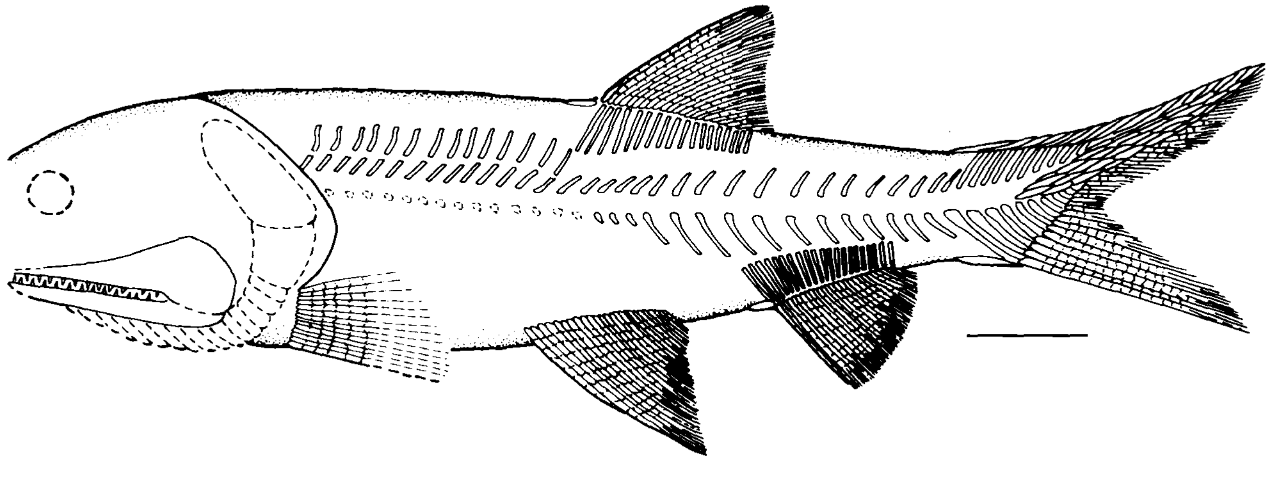


Fig. 22: *Coccolepis groeberi* (BORDAS), restoration in lateral view (slightly modified from CIONE & PEREIRA 1987). Scale bar = 3 cm.

Lepisosteiformes.- Recent lepisosteiforms are known from two genera, *Atractosteus* and *Lepisosteus*, living in North America and Cuba today (WILEY 1976). In contrast, the fossil record has a broader distribution including Africa, Europe, India, and North America.

The first South American record of lepisosteids (scales and some teeth) is from Tiupampa and Vila Viscarra in Bolivia (GAYET in DE MUIZON et al. 1983). However, the scales were later assigned to Polypteriformes (GAYET 1992: 447; teeth were not mentioned). New material, mostly isolated scales, incomplete vertebrae, teeth, fragments of indetermined cranial bones, bases of lepidotrichia from several localities in Bolivia (see Appendix 2) have been identified as *Lepisosteus* sp. and those from the Los Alamitos Formation were interpreted as cf. *Atractosteus* (Appendix 2).

3. Mesozoic and Tertiary Teleosts

Jurassic: Two Teleostei *incertae sedis* (e.g., *Lusiella inexcutata* and *"Tharrias" feruglioi;* Figs. 23, 24) are recorded from the same locality as *Coccolepis groeberi.* These species are known from well-preserved material. *Luisiella inexcutata* BOCCHINO 1967 must be re-studied to define its taxonomic assignment and phylogenetic relationships. *"Tharrias" feruglioi* (BORDAS 1943) is known from numerous specimens; it was redescribed by CIONE & PEREIRA (1987) and left as a Teleostei *incertae sedis* because of its combination of characters, most of them primitive among the basal Teleostei *sensu stricto.* Two species described by DOLGOPOL (1949a), *Tharrias shamani* and *Leptolepis leanzai,* were considered undistinguishable from *"T." feruglioi* by CIONE & PEREIRA (1987) and therefore were determined as synonyms of *"T." feruglioi.*

Late Cretaceous: Numerous Late Cretaceous localities are known in southern South America (see Apendix 2). Among these the Coli Toro, Los Alamitos, Yacoraite, El Molino, and Vilquechico Formations are the best known.

CIONE & LAFITTE (1980) described what it is considered one of the most ancient siluriforms, associated with the lungfish *Ceratodus iheringi,* turtles, and dinosaurs in the Coli Toro Formation at Arroyo Yaminué, central Río Negro Province. In Los Alamitos and other correlated units, fragmented spines of the most ancient siluriforms occur (CIONE 1987). There are two types of spines that have been tentatively referred to ariids and diplomystids. This assignment is based on close phenetic similarity of pectoral and dorsal spines and has to be confirmed with more complete specimens. The diplomystid *Olivaichthys viedmensis* inhabits nearby rivers and lakes and the ariid *Netuma barba* inhabits the seashore and rivers of north-

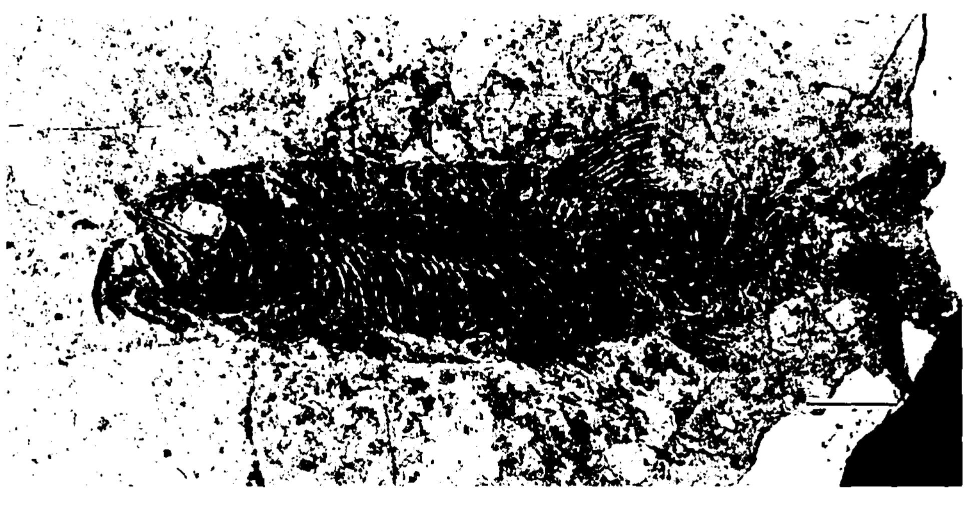


Fig. 23: *Luisiella inexcutata* BOCCHINO from the Upper Jurassic of Río Chubut medio, Argentina (specimen MLP 35-III-1-45, holotype). Scale bar = 1 cm.

Fig. 24: *"Tharrias" feruglioi* (BORDAS) from the Upper Jurassic of Río Chubut medio, Argentina (specimen MLP 48-I-1-2, previously described as *Leptolepis leanzai*). Scale bar = 1 cm.

ern Patagonia today. In the same locality, some percoid upper pharyngeal tooth plates were found (CIONE 1987). Upper and lower pharyngeal tooth plates are currently being studied by A. CIONE and J. CASCIOTTA.

There are several Upper Cretaceous units (Yacoraite, El Molino, and Vilquechico Formations) with abundant fossil fishes (and other vertebrates) ranging from southern Peru to northwestern Argentina. These fossil assemblages are relevant to understand the evolution of the neotropical ichthyofaunas. These continental to marginal marine deposits are approximately correlative with each other and were deposited in the Aimara Basin of RICCARDI (1987). This is the Andean Basin of REYES (1972) and BONAPARTE & POWELL (1980), a part of the Andean Basin of most authors and the Subandean basin of MALUMIÁN et al. (1983).

The age of these units have been extensively discussed but most authors agree that the age of the formations is mostly Late Cretaceous. VAN VALEN (1988) discussed the evidence of chronologic significance considering the units *in toto* as Cretaceous or Tertiary. VAN VALEN was interested in the possible survival of dinosaurs in the Cenozoic. The recorded mammals suggested an Early Tertiary age (PASCUAL & ORTIZ JAUREGUIZAR 1992). However, Vilquechico mammals are not in situ and Tiupampa mammals occur in a level that presently is considered pertaining to the Paleocene Santa Lucía Formation (e.g., GAYET et al. 1992; SEMPERE & MARSHALL in press). The only reported Cretaceous fish in the beds with mammals at Tiupampa was *Enchodus* cf. *oliverai* (GAYET in DE MUIZON et al. 1983). However, this record is a mistake as GAYET (1992) recognized. She did not clarify why the interpretation is wrong for the teeth found in Tiupampa. Isolated teeth found in other localities are assignable to *Enchodus* (see below).

The richest vertebrate fauna is that of Tiupampa. In contrast to previous publications, GAYET et al. (1992) distinguished three fossil levels of the El Molino Formation. Two fossil levels at Tiupampa belong to the basal middle and upper El Molino Formation; a third fossil level is located about 130 m above the base of the Cretaceous section (MARSHALL et al. 1985). Because all faunal assemblages were assigned previously to the Late Cretaceous, the new interpretation of the ages of the El Molino Formation changes the age of many teleosts reported from the Bolivian localities that were previously considered as the most ancient representatives of many teleostean groups. According to GAYET et al. (1992) and GAYET (1992), some representatives of clupeomorphs, cypriniforms, siluriforms, aulopiforms (= her "salmoniforms"), and probable cyprinodontiforms (see below; Appendix 2) would be Late Cretaceous in age.

We include the El Molino Formation in this section despite the fact that it was deposited in waters of different salinity. According to CAPPETTA (1992) the chondrichthyans from Torotoro, El Molino Formation, are probably marine. The clupeomorph *Gasteroclupea branisai* has been collected from localities where supposed freshwater and marine fishes occur together (GAYET 1992: 459) or brackish-water localities bearing ostracods (CAMOIN et al. 1991), or marine or freshwater localities (GAYET et al. 1993a). Enchodontids were reported from Agua Clara and Hotel Cordillera, El Molino Formation; they are known from marine environments in other parts of the world. Four pharyngeal bones assigned to a supposed cypriniform, *Molinichthys inopinatus*, are known from the same localities; as GAYET (1992) acknowledged, cypriniforms are only known from freshwater environments; her *Ramallichthys* (GAYET 1986) recognized by GAYET (1992: 467) as the ancestor of Cypriniformes and the only marine cypriniform seems to be a gonorynchiform (GRANDE 1992 and in press).

Because the present information is unclear (e.g., CAPPETTA 1992; GAYET 1992; CAMOIN et al. 1992; GAYET et al. 1993a) we consider that there is not conclusive evidence that the environment(s) in which the teleosts lived during the Late Cretaceous in Bolivia could be assigned to fresh, brackish, or marine waters. Therefore, in the following presentation the paleoenvironmental conditions are not discussed.

An abbreviated presentation of the main teleostean taxa of Late Cretaceous age is presented below.

Teleostei indeterminate.- *Neolycoptera gracilis* DOLGOPOL 1939 is a nominal species from the Yacoraite Formation from a drilling core in Jujuy, Argentina. The type material is apparently lost but it seems to be badly preserved; it must be considered a *nomen dubium*. DOLGOPOL did not give reasons to refer it to the Osteoglossiformes (CIONE 1986a).

Clupeiformes.- Late Cretaceous clupeomorphs are only known from *Gasteroclupea branisai*. Girdle bones of the species from the Yacoraite Formation were identified first as bivalves (SCOCCO 1948; ORRUMA 1974). SIGNEAUX in BRANISA et al. (1964) reported this fish from the El Molino Formation and assigned the new species, *Gasteroclupea branisai*, to a new subfamily, the Gasteroclupeinae. Later, *G. branisai* has been reported from numerous localities in the Yacoraite Formation and the El Molino Formation (see Appendix 2). According to GAYET (1992) and GAYET et al. (1992), it is also present in the Paleocene of Bolivia.

Even though *Gasteroclupea branisai* is known from complete specimens, isolated skull bones and girdles, a complete morphological description is not available yet. GRANDE (1985: 261) included *Gasteroclupea* in the Pristigasteroidea because the genus and the superfamily present one synapomorphy (loss of interlobar notch in third hypural of caudal skeleton) and "because it is remarkable similar in appearance to the peculiar *Pristigaster*." The inclusion of this species in the Pristigasteridae, subfamily Pristigasterinae, is based on four characters, e.g., bony process on the first pleural rib articulating with shoulder girdle, loss of pelvic fins, more than 23 predorsal bones, and more than 57 anal pterygiophores. GAYET (1992: fig. 6b) retained *Gasteroclupea* in the subfamily Gasteroclupeinae because *Gasteroclupea* has subrectangular and symmetrical dorsal scutes bearing a median crest. These scutes look like those present in *Diplomystus* and *Ellimmichthys* and not as those found in *Pristigaster*.

"Cypriniformes."- No Recent or fossil cypriniform is known from South America. GAYET (1982b) created a new genus and species, *Molinichthys inopinatus,* based on a doubtful interpretation of an incomplete bone that she considered a fifth pharyngeal bone of a cypriniform (Fig. 25). Only the incomplete holotype has ever been illustrated (GAYET 1982b, 1992) and the remaining evidence (other three incomplete and isolated "fifth pharyngeal bones") never have been described or illustrated. So we are left with our own interpretation of GAYET's figures. We cannot find support for such an interpretation, nor FINK et al. (1984) or GAUDANT (1993). The latter is the only one who apparently has been able to examine the holotype. The response by GAYET et al. (1993b) to FINK et al.'s and GAUDANT's criticisms about the interpretation of an incomplete bone as a fifth pharyngeal bone of a cyprinid or to a family *incertae sedis* is again unsatisfactory ["Il a déjà été répondu ailleurs (GAYET 1986b) à ce sujet. D'autres découvertes de matérial dans le même

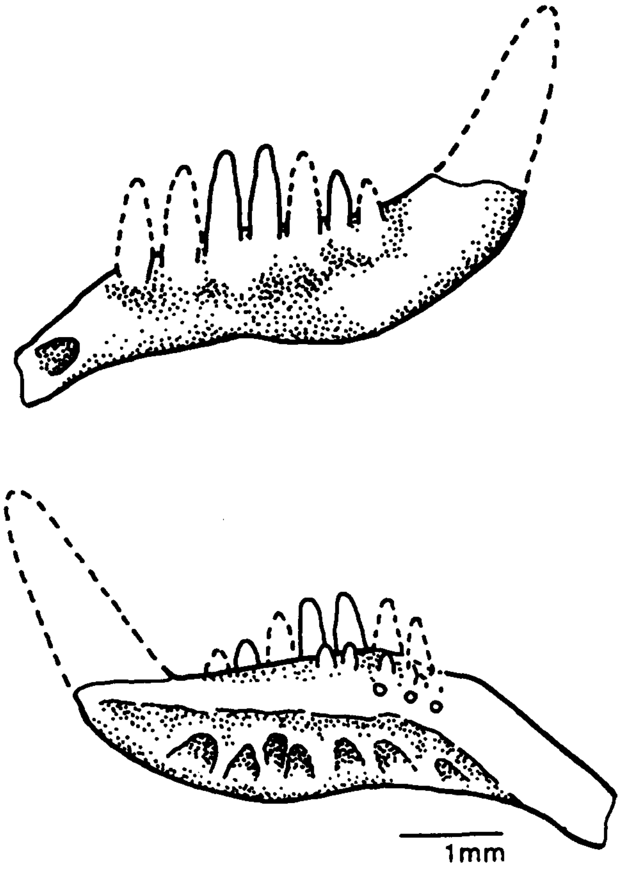


Fig. 25: Two views of a so-called fifth pharyngobranchial bone of *Molinichthys inopinatus* GAYET from the Upper Cretaceous of Bolivia (after GAYET 1992).

gisement seron déscrites en temp utile."] Unfortunately, GAYET has not realized that more than 13 years after *Molinichthys inopidatus* was described as a cypriniform, the scientific community (except GAUDANT) has not been able to examine the so-called fifth pharyngeal bone(s). The other finds never have been described, therefore reception of these tenuous arguments and responses is not good.

We disagree with GAYET that by enlarging the diagnosis of the family Cyprinidae or by considering these fragments as "Cypriniformes family *incertae sedis*" something is gained. The main point is that there is no morphological evidence to consider the bony fragments as belonging to the "Order Cypriniformes sensu Fink & Fink, 1981" as GAYET (1992: 466) did. After the available evidence, the authors agree with GAUDANT (1993) that *Molinichthys inopinatus* should be considered a *nomen vanum.*

Characiformes.- Isolated teeth from the Late Cretaceous localities of the El Molino Formation (and the Paleocene of Santa Lucía Formation) have been assigned to the families Erythrinidae (e.g., cf. *Hoplias*), Serrasalmidae (e.g., Myleinae indet.), and Characidae (e.g., Tetragonopterinae gen. and sp. indet.) (GAYET 1992). It is unclear how most of these determinations were done because material used for comparison was not listed. As it is known, South America actually has more than one thousand characiform species (GÉRY 1977) for most of which detailed studies on the teeth are missing and the few

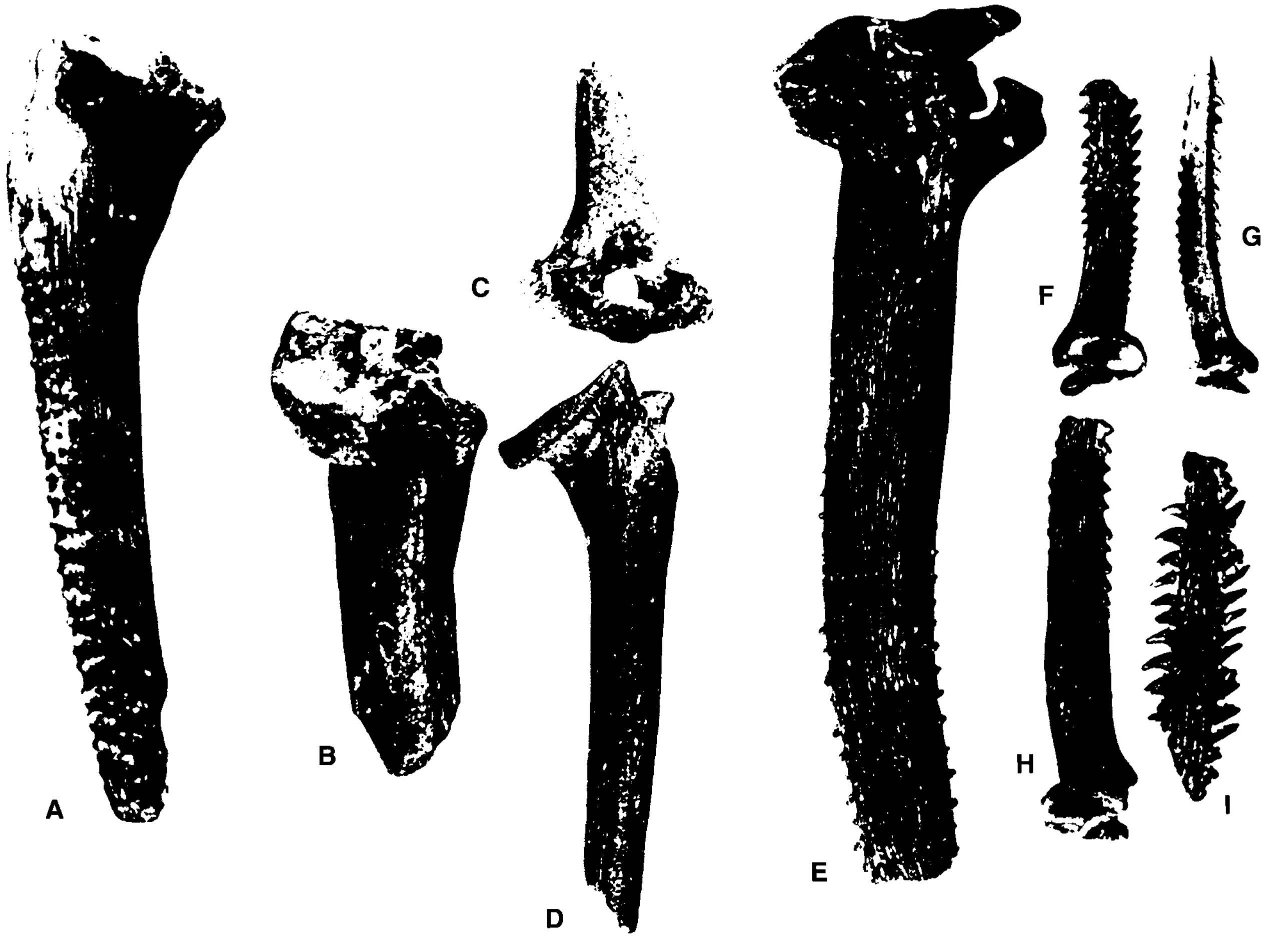


Fig. 26: Siluriform pectoral and dorsal spines from the late Miocene of Paraná, Entre Ríos, Argentina. **A**, Ariidae indet. (specimen MACN 15993.2). **B-D**, Loricariidae indet. (specimens MACN 15984, MLP 41-XII-13-1578, and MLP 41-XII-13-1428, respectively). **E-I**, Pectoral spines of Doradidae indet. (specimens MLP 41-XII-13-1462).

available publications show intraindividual and intraspecific variation.

Additional problems remain: For instance, GAYET (1982c) cited the presence of cf. *Triporteus* and cf. *Rhoadsia* in Hotel Cordillera, El Molino Formation. GAYET (1992) identified specimens from that locality as cf. *Hoplias*, Myleinae, and Tetragonopterinae gen. and sp. indet., and previous identifications were not mentioned; therefore it is unclear what is synonymous of what and why.

The Cretaceous Bolivian teeth may belong to characiforms. However, until detailed comparisons .with extant members of the group are not available and because the diagnoses based on teeth are insatisfactory, we do not feel confident with the taxonomic assignments which should be considered preliminary.

No characiform record is known from other Late Cretaceous localities of southern South America such as those belonging to the Yacoraite, Coli Toro, and Los Alamitos Formations.

Siluriformes.- Remains of Late Cretaceous siluriforms are known from several localities in Argentina, Bolivia, and Peru (see Appendix 2). First they were reported from different localities within the Yacoraite and Coli Toro Formations (e.g., by SCOCCO 1948; CIONE & LAFITTE 1980; CIONE 1985; CIONE & PEREIRA 1985), and later from the Los Alamitos Formation (CIONE 1987). Most of these remains represent siluriform spines and have been interpreted as indetermined siluriforms, cf. Ariidae (Fig. 26A), and cf. Diplomystidae. The best preserved material comes from the El Molino Formation, e.g., Ariidae cf. *Rhineastes* and *Andinichthys* sp. which include three-dimensionally preserved cranial bones, pectoral girdles, and pectoral and dorsal spines.

Catfish spines from the Los Alamitos Formation were interpreted as belonging to cf. Diplomystidae because of the overall similarity in the configuration of striae and grooves with those present in the living *Olivaichthys viedmensis.* If this assignment is correct it would correspond to the oldest record of the extant family Diplomystidae which is considered the most primitive among the 33 extant catfish families (e.g., CHARDON 1968; FINK & FINK 1981; ARRATIA 1987b, 1992).

Numerous catfish remains including neurocranial bones, Weberian apparatuses, and teeth reported from various localities in Bolivia have been assigned to Ariidae, genus *Rhineastes* (GAYET 1992: 474), or to cf. *Rhineastes* (GAYET 1992: 473). Independently of these contradictory assignments from page to page in GAYET (1992), *Rhineastes*, a genus described from the Eocene of North America (LUNDBERG 1975), does not belong to the Ariidae after LUNDBERG (1992). The North American *Rhineastes* has very thick and large bones. The Bolivian material which has been identified as *Rhineastes* is represented by large and thick bones belonging to specimens of one to two meters length (GAYET 1992). Except of the size, it is unclear which are the characters that support such an identification. A comparison between the Eocene North American *Rhineastes* and the so-called *Rhineastes* from Bolivia has not been presented.

Another Bolivian fossil catfish, *Andinichthys* sp., is known at least by an incomplete braincase (see ARRATIA & GAYET 1995: fig. 3B); however, it was listed as known by only isolated neurocranial bones, pectoral girdles, and pectoral and dorsal spines by GAYET (1992). The reason why this material was left as *Andinichthys* sp. is unknown. These two species were included in the family Andinichthyidae, in a superfamily *incertae sedis* by GAYET (1992: 477), in a superfamily named Andinichthyiodea a few pages in front in the same volume (GAYET et al. 1992: 409), and in the suborder Andinichthyoidei (GAYET et al. 1993a: 293).

GAYET (1988) erected the family Andinichthyidae on incomplete neurocrania belonging to *Andinichthys bolivianensis* which at that time was interpreted as Late Cretaceous in age, but currently as a Paleocene form. The family diagnosis is based mainly on features of the cephalic sensory canal system; one feature, the presence of a complete supratemporal commissure, was interpreted by GAYET as a unique character among catfishes. Further examination of the material demonstrated that a complete supratemporal commissure is not present in *Andinichthys bolivianensis* and a rudimentary canal, probably an atrophied supratemporal commissure, is found in one specimen of *Andinichthys* sp. (ARRATIA & GAYET 1995: figs. 2A, 3B). No unique derived character supports the family Andinichthyidae and its combination of characters, as defined by GAYET (1988), is not unique either.

"Aulopiformes."- Three taxa assigned to the suborders Enchodontoidei (*Enchodus* sp.) and Ichthyotringoidei (?*Apateodus* sp. and Ichthyotringoidei n. gen. and sp.) have been reported from the El Molino Formation (GAYET 1992).

Enchodus sp. is known only from isolated teeth. "Isolated teeth of slightly sigmoidal shape can be referred to the genus *Enchodus*" (GAYET 1992: 464). The same material was previously assigned to *Enchodus* cf. *oliverai* (GAYET in DE MUIZON et al. 1983), and because of the small size of the teeth was recently interpreted as *Enchodus* sp. by GAYET (1992).

?*Apateodus* is only known from teeth "close to *Apateodus* as defined by GOODY (1969)." Furthermore GAYET (1992: 466) partially based her identification on the fact that the teeth were found "in association with selachian, *Enchodus*, pycnodontid, and eotetragonopterid teeth, a fact which agrees with a marine environment known from this genus (WOODWARD 1901)." However, in the same localities (e.g., Agua Clara and Hotel Cordillera), bones were found that GAYET (1992) interpreted as belonging to a cypriniform and characiforms. Cypriniform and characiforms are primary freshwater fishes, but they are interpreted as marine or freshwater in GAYET et al. (1993: 293).

A third "aulopiform" known only by a badly preserved, incomplete long rostrum was left as Ichthyotringoidei gen. et sp. indet. by GAYET (1992). This assignment is unsupported because no rostral features were described or figured.

Cyprinodontiformes.- A few complete specimens and isolated pharyngeal teeth from Bolivian localities were preliminarily assigned to cf. Cyprinodontiformes by GAYET (1992). Cyprinodontiforms are characterized by a symmetrical caudal skeleton where the parhypural opposes the epural and the hypurals are fused. Apparently such is not the condition of the cf. Cyprinodontiformes from Bolivia because they have a "very primitive pattern with six hypurals of nearly equal size." It is unclear why the isolated teeth were assigned to cf. Cyprinodontiformes "because the pharyngeal teeth are often similar in different fishes" (fide GAYET 1992: 481).

"Nothing can be said about the paleoenvironment of cf. Cyprinodontiformes of Bolivia." (GAYET 1992: 483). That is a surprising statement because the specimens were collected in the "Cenomanian marine Miraflores Formation," in Agua Clara and Hotel Cordillera that were interpreted as marine environment for *Enchodus* and ?*Apateodus* by GAYET (1992), and in Estancia Blanco Rancho and Pajcha Pata (where the catfish *Andinichthys* was found) which seem to be freshwater. GAYET et al. (1993a: 293) interpreted them as being marine or freshwaters.

"Tetraodontiforms."- "Eotrigonodontidae" is present in the El Molino Formation (GAYET in DE MUIZON et al. 1983). It is represented by *Stephanodus*-like teeth. In the Yacoraite Formation, CIONE found a tooth very similar to those of this genus. However, PATTERSON in ESTES & SANCHIZ (1982) commented that similar teeth occur in the pharyngeal dentition of Pycnodontiformes. The teeth figured from the Lower Cretaceous rocks of Spain (ESTES & SANCHIZ 1982) are small (to 1.5 mm total length), and there are no buccal teeth of eotrigonodontids in the same locality. CAPPETTA (1972) figured teeth of *Stephanodus* from the Upper Cretaceous of Africa that are much larger and similar to those from the El Molino and Yacoraite Formations. Additionally, APPLEGATE (1970) related the North American material to pycnodonts. THURMOND & JONES (1983) referred similar pharyngeal teeth, identified as *Hadrodus priscus* LEIDY to the new family of Semionotiformes, the Hadrodontidae. Pycnodontiforms occur in all Late Cretaceous formations in the area, but no oral eotrigonodontid tooth was reported. In consequence, we consider that the presence of this family in the Late Cretaceous of Bolivia and Argentina, based on pharyngeal teeth that are similar to those occurring in other taxa, is tenuous.

A new species, *Stephanodus minimus,* was erected on numerous pharyngeal teeth collected in several Bolivian localities (GAYET 1992). The only diagnostic character of the new species is a round posterior process on the teeth. However, specimens despicted by GAYET (1992: figs. 29b, c, d) do not show a round process different from that shown by material depicted by CAPPETTA (1972) and ESTES & SANCHIZ (1982). In consequence, we consider that *Stephanodus minimus* is a *nomen vanum.*

"Dicarlesia (Carlesia) incognita" HUENE.- Coming from a site near the railroad station El Quemado close to San Pedro de Jujuy, Jujuy Province, Argentina, "VON HUENE (1931: 183, 184) described a small mandible which he named *Carlesia incognita* (= *Dicarlesia incognita*) von Huene, 1932: 192 *nec Carlesia* Kraglievich 1926b, a genus of fossil Rodentia. According to Simpson (1932a: 9), von Huene believed that this specimen had the general

aspect of a Mesozoic mammal, although Simpson believed that it was comparable to a reptile, possible to a Lacertilia. We feel, however, that this specimen is probably a bony fish." (DE MUIZON et al. 1983: 261). It is unclear whether DE MUIZON et al. (1983) examined the specimen or not.

Paleocene: Teleosts are known from a few Paleocene localities of Argentina (e.g., in the Mealla and Maiz Gordo Formations) and of Bolivia (e.g., in Santa Lucía Formation). Few taxa, e.g., Teleostei indet., the siluriform *Corydoras revelatus* (its locality is Arroyo Abra del Trigo according to GIUDICI & OLIVER GASCÓN 1982; COCKERELL 1925, named this locality as "Sunchal"), and the atheriniform "*Cyprinodon* (?) *primulus*" are known from Argentina (see Appendix 2). In contrast, a large diversity of teleosts has been reported from the Paleocene of Bolivia.

Osteoglossiformes.- According to GAYET et al. (1992), osteoglossiforms are represented in the Paleocene of Bolivia by the family Osteoglossidae, e.g., *Phareodusichthys tavernei* and Osteoglossinae n. gen. and n. sp. The age given to these forms is confusing. For instance, GAYET (1992: 460) reported squamules, teeth, incomplete jaws, and incomplete skulls from several localities belonging to the lower and middle members of the El Molino Formation (Late Cretaceous according to GAYET et al. 1992) and from Tiupampa, Santa Lucía Formation, Paleocene, according to the same authors. However, the horizon and locality given in the description of the new genus and species *Phareodusichthys tavernei,* is only "Tiupampa (Bolivia), Santa Lucía Formation" (GAYET 1992: 463). Furthermore, remains assigned to Osteoglossinae n. gen. and sp. are also from Tiupampa, Santa Lucía Formation and all illustrations of these forms correspond to fragments from Tiupampa. The question is: which remains would correspond to the Late Cretaceous section of the El Molino Formation?

ARGOLLO et al. (1987) reported the presence of a premaxilla at Huarachani (middle member of the El Molino Formation after GAYET et al. 1992). This material was interpreted as *Brychaetus.* "Similar premaxillae occur at Tiupampa in addition of parts of mandibles and squamules (fragments of scales)" (GAYET 1992: 461). Some specimens represented by the anterior part of the mandible were assigned to the Hiodontidae by GAYET (in DE MUIZON et al. 1983, 1984) while other were identified as cf. *Phaerodus* by GAYET in DE MUIZON et al. (1983). Later, GAYET (1992) assigned these specimens and the new premaxillae of Tiupampa to a new genus and species which presents a combination of features of *Brychaetus* and *Phareodus.* If our interpretation is correct, cf. *Phaerodus* and the Hiodontidae of GAYET in DE MUIZON et al. (1983, 1984) are synonyms of *Phareodusichthys tavernei.* Still another problem remains: Is *Brychaetus* of ARGOLLO et al. (1987) a synonym of *Phareodusichthys tavernei*? According to GAYET (1992: 461), the *Brychaetus* premaxilla of ARGOLLO et al. from Huarachani is similar to those occurring in Tiupampa. However, Huarachani was not cited as a locality of *P. tavernei* (see GAYET 1992: 463).

Clupeiformes.- The only reported clupeomorph is *Gasteroclupea branisai* (see above) from Tiupampa, Santa Lucía Formation (GAYET 1992).

Characiformes.- Isolated teeth, mandibular fragments (e.g., *Hoplias* n. sp.) and incomplete neurocrania (Characiformes indet.) have been included in various characiform groups by GAYET (1992, see table 2). Some of them were assigned to the Late Cretaceous and Paleocene, others to the Paleocene alone (see Appendix 2).

Numerous fragments of mandibles and isolated teeth were assigned to a new species of *Hoplias* (even probably to a new genus) by GAYET (1992: 467). GAYET (1992: 467) referred dentaries and isolated conical teeth from the Paleocene Santa Lucía Formation of Bolivia to "*Hoplias* nov. sp. or perhaps to a new genus close to it." GAYET (1992: 469) mentioned that "According to Géry (1977) three genera belong to the living family Erythrinidae: *Hoplias* which have two or three small canines plus a series of conical teeth, *Erythrinus* and *Hoplerythrinus*, which are more specialized but have no canines. The Bolivian genus has only one small canine followed by a series of conical regular teeth in contrast to what can be observed in *Hoplias* in which the conical teeth are irregular in size." However, GÉRY (1977: 99) actually stated that the maxillary bone (not the dentary) has "2 or 3 small canines plus a series of conical teeth." Additionally, teeth of *Hoplias* are pedicelated and those from Bolivia are not.

Isolated teeth from Tiupampa were assigned to cf. Rhoadsinae gen. and sp. nov. These teeth do not correspond to a previous identification of *Rhoadsia*, based on only one tooth, by GAYET (1982c).

Siluriformes.- Siluriform remains are known from Tiupampa, Santa Lucía Formation (e.g., *Andinichthys*, *Incaichthys*, and *Hoffstetterichthys*) and from several localities in Santa Lucía Formation (cf. *Rhineastes*). Despite the comments that "Siluriformes are increadibly numerous and varied in Bolivian localities" (GAYET 1992: 474), they are poorly known. Despite the scarce morphological information they were assigned to new families and genera without comparative studies with the numerous living siluriform faunas of South America (see above for *Andinichthys*).

Two new genera and species, *Incaichthys suarezi* and *Hoffstetterichthys pucai,* were erected by GAYET (1990) and included in separated families *incertae sedis* by GAYET (1992). The descriptions of both genera are based on incomplete neurocrania; Weberian apparatuses have although been collected and assigned to species (GAYET 1992), they are undescribed yet. The combinations of characters diagnosing these genera are doubtful. In addition, GAYET (1992: 479) reported the presence of new genera belonging to "Family indet." and of "Gen. indet.," all of them from Tiupampa. The new genera are represented by incomplete skulls and the Gen. indet. by Weberian apparatuses, pectoral girdles, and pectoral and dorsal spines.

All these forms are supposed to be members of a a superfamily *incertae sedis* (GAYET 1992) or a superfamily named Andinichthyoidea (GAYET et al. 1992) or a suborder Andinichthyoidei (GAYET et al. 1993a) for which diagnostic characters are unknown. According to GAYET (1992: 479) "All of those skulls belong to the same superfamily because they have a similar pattern of the arrangement, shape and size of the skull roof." Unfortunately, the Bolivian material has not been adequately compared.

Perciformes.- Head bones, lower and upper jaws, quadrates, hyomandibulars, vertebrae, dorsal spines, and proximal axonosts from the Santa Lucía Formation were iden-

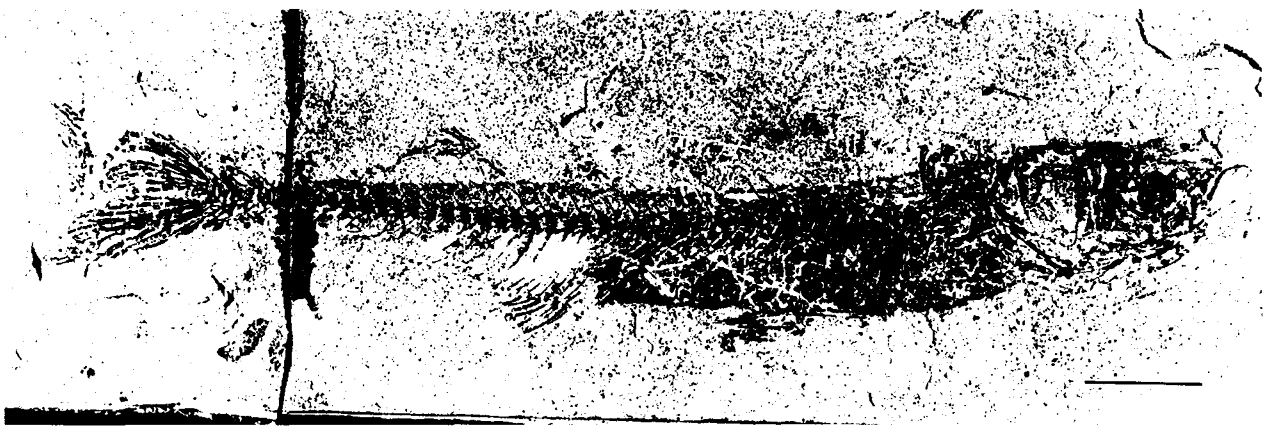


Fig. 27: *Basilichthys* aff. *regius* from the Miocene of Puesto Galván, Chubut, Argentina (specimen MLP 88-III-20-14). Scale bar = 2 cm.

tified as belonging to the family Centropomidae by GAYET (1992; previously they were assigned to Percichthyidae by GAYET in DE MUIZON et al. 1983) because the Bolivian vertebrae are similar to those in centropomids and because the upper and lower jaws differ from those in *Percichthys* and *Percilia* (fide ARRATIA 1982b).

Eocene: Eocene teleosts are known from several localities in Argentina, in the Lumbrera Formation (= Margas Coloradas Superiores), the Huitrera Formation (= Laguna del Hunco), and the Cañadón Hondo Formation.

Siluriformes indet. and cyprinodontiforms (e.g., Poeciliidae indet.) are recorded from the Lumbrera Formation (see Appendix 2).

In northwestern Patagonia, interesting catfishes and anurans have been recorded in sediments of the "Serie Andesítica" of FERUGLIO (1927). The Laguna del Hunco Formation (ARAGÓN & ROMERO 1984) or the La Huitrera Formation (VOLKHEIMER & LAGE 1981) is a lacustrine unit overlaying ignibrites with a radiometric date of 57 ± 3 Ma (ARCHANGELSKY 1974; Lower Eocene according to BERGGREN et al. 1985). DOLGOPOL (1941) created the species *Arius* (?) *argentinus* and *Bachmania chubutensis*. However, both are synonyms (*Bachmania* is retained) and are not assignable to Ariidae. The fishes have a remarkable feature, the presence of very large conical buccal teeth. They compare to the tenth of the dorsal spine length. These catfishes present some primitive features such as six hypurals (PEREIRA 1988). A. L. CIONE and M. AZPELICUETA are currently re-studying the material.

Near the Atlantic coast at San Jorge Gulf, lacustrine sediments known as Cañadón Hondo Formation (ANDREIS 1977) bear percichthyids (and also anurans and mammals, though at different levels). Mammals permit to date the unit as Casamayoran (early Eocene, or latest Paleocene; MARSHALL et al. 1983). ARGUIJO & ROMERO (1981), based on floral studies by BERRY (1932) dated it as late Eocene-Oligocene. BÁEZ (1986) discussed it and concluded that the levels with flora can be younger than those with anurans and fishes.

Percichthys hondoensis SCHAEFFER 1947, from Cañadón Hondo, Argentina, is the most ancient record of Percichthyidae. The supposed Paleocene record from Chile is currently considered Miocene (see below). *Guayquichthys ferugliof* DOLGOPOL 1949b from the same locality in Cañadón Hondo Formation is a junior synonym of *Percichthys hondoensis* (see ARRATIA 1982b; CIONE 1986a).

Miocene: Miocene localities are known from Argentina (e.g., Anta, Ñirihuau, Collón Curá, San José, Entre Ríos or Ituzaingó Formations), Bolivia (e.g., Yecua Formation), and Chile (e.g., Cura-Mallín Formation); they bear a diverse ichthyofauna.

GAYET & MEUNIER (1991a) reported remains of gymnotoids (e.g., *Ellisella*) from beds of late Miocene age from Alto Moile river in Bolivia.

The fishes of the Quebrada de La Yesera (Anta Formation) are known since the end of the 1940's when the geologists ZUNINO & MAURI of the Yacimientos Petrolíferos Fiscales, Argentina, sent several specimens to B. SCHAEFFER at the American Museum of Natural History, New York. SCHAEFFER identified them preliminaryly as the Cretaceous enchodontid *Enchodus* and the Cretaceous and Tertiary clupeid *Knigthia*. BARDACK (1961) identified the material as two new species of cichlids, *Aequidens saltensis* and *Acaronia longirostrum*, and the new clupeid genus and species *Austroclupea zuninoi*. Notwithstanding that the original identification by SCHAEFFER was never published, it provoked great confusion in the Argentinian geological community. The bearing unit was repeatedly assigned to the Cretaceous due to the supposed occurrence of *Enchodus* (e.g., GARCÍA 1957; IBAÑEZ 1960; PASCUAL & ODREMAN RIVAS 1973).

Atherinids and perciforms occur in the Ñirihuau Formation outcrops in the Ñorquinco-Cushamen-Ñirihuau Basin in western Patagonia.

Propygidium primaevus BOCCHINO 1964 from a locality facing Cerro David, Río Negro in the Ñirihuau Formation was considered the first fossil record of the catfish family Trichomycteridae. After study of the holotype, the only referred specimen, CIONE & TORNO (1988) concluded that it does not correspond to a catfish but to an acanthopterygian, possibly a percichthyid.

From Puesto Galván, near the Arroyo Leleque (Chubut), BOCCHINO (1971) reported a silverside (*Basilichthys* aff. *regius*; Fig. 27), a sailfish (*Istiophorus* sp.), and an anchovie (Engraulidae indet.). However, a preliminar examination of the material shows that not only the first but also the second specimen are referable to Atherinidae. The badly preserved specimen of the "anchovie"

Fig. 28: *Paleocichla longirostrum* (BARDACK) from the Tertiary of Catamarca, Argentina (specimen MLP 92-V-3-4, dusted with NH_4Cl). Scale bar = 1 cm.

only permits to determine it as Teleostei indet. The original identification caused speculation about a marine ingresion. However, the Atherinidae includes freshwater, marine, and amphibiothic taxa.

Diatomitic lacustrine sediments of Friasian age (Middle Miocene; see MARSHALL et al. 1983) near Ingeniero Jacobacci, western Río Negro Province, assigned to the Collón Curá Formation, include *Percichthys*, anurans, and mammals.

Several lithostratigraphic units in Salta, Tucumán, and La Rioja Provinces are correlated with the marine Paraná Formation and the Entre Ríos Formation (Friasian-Huayquerian). The Río Salí, San José, and Entre Ríos Formations include freshwater fishes. FAVERI (1978) reported poecilid cyprinodontiforms from the San José Formation at the Santa María Valley in Catamarca. The specimens have an acceptable preservation. Many male specimens have a modified anal fin (gonopodium) used for reproduction. The gonopodium is formed by three very large, thick, untwisted and unbranched anal-fin rays (probably the third, fourth, and fifth) in the fossil material. The anal-fin pterygiophores are also enlarged and thickened. Gonopodia are found in the cyprinodontiform Poecilidae Poecilinae, Anablepidae Anablepinae, and Goodeidae (PARENTI 1981). Goodeids have a slightly modified anal fin. Anablepines (*Anableps* and *Jenynsia*) have anal-fin rays twisted around each other. *Anableps* also has dorsally located eyes. Poecilines have rays 3, 4, and 5 greatly developed, strong pterygiophores, and gonadopophysis built by the haemacanths of the second and third caudal vertebrae. The enlarged haemal arches were not observed in the fossil material. Based on the shared characters, these fishes are identified privisionally as poecilines. Similar fishes also occur in the Río Salí Formation of Tucumán. This material will be re-studied by one of us.

An important fish assemblage (with numerous catfishes and characiforms) occurs at the Paraná river cliffs near the city of Paraná, Entre Ríos Province, Argentina. Fishes from this locality have been known since last century (BRAVARD 1858). However, they have been very insufficiently studied (AMEGHINO 1898; WOODWARD 1900; PRIEM 1911; see CIONE 1978, 1986a). The catfish *Silurus agassizi* BRAVARD 1858 was not described nor figured and must be considered *nomen nudum* (CIONE 1986a). FRENGUELLI (1920) figured a skull that he assigned to that species which makes the determination obviously invalid. Recently, PEREIRA (1988) determined catfishes (e.g., sorubiminids, pimelodids, loricariids, callichthyids, ariids, doradiids, auchenipterids; Fig. 26B-I) in the site. The quotation of *Potamotrygon* by AMEGHINO (1898), without figuration nor description, is probably a mistake (CIONE 1986a).

Characiforms as the serrasalmid *Colossoma macropomus* occur also in the Miocene, at the Paraná river cliffs (CIONE 1986a). This species has been collected also in La Venta Group (Middle Miocene of Colombia; LUNDBERG et al. 1986, 1988). The records from the Entre Ríos Formation and La Venta Group corroborate the biogeographic relationship postulated by other faunal elements (e.g., *Rhamphostomopsis*, dugongs, cetaceans).

FRAILEY (1986) reported a local fauna along the Acre river on the border between Peru and Brazil. Only one formation, the Iñapari Formation of presumed Pliocene-Pleistocene age, is shown from outcrops along Acre river. Later work indicates that at least two formations are present. The upper is dated as Holocene. The underlying formation is unnamed and was referred to Tertiary red beds by CAMPBELL & FRAILEY (1984) based on a pre-

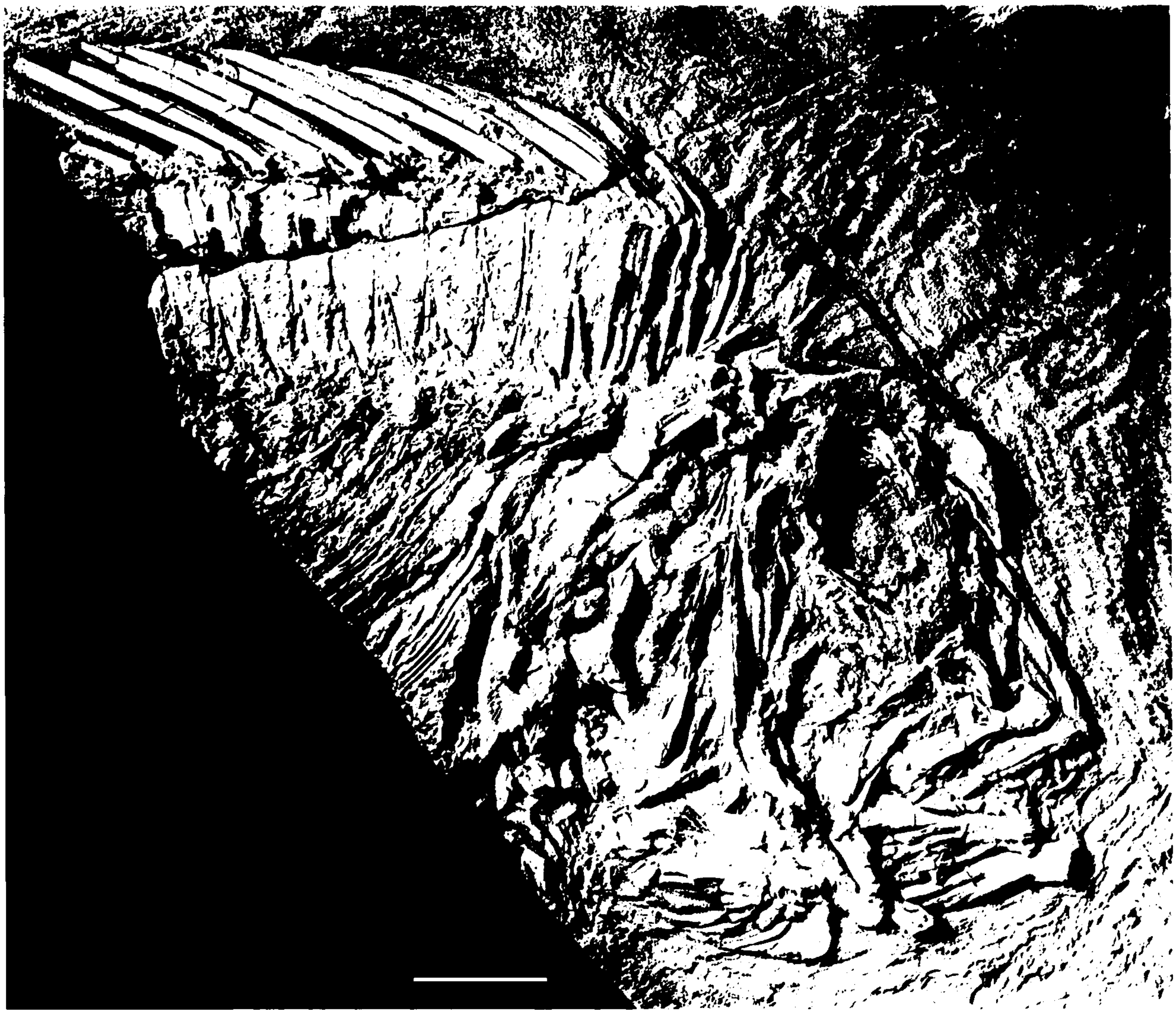


Fig. 29: Geophagine 1 sensu CASCIOTTA & ARRATIA (1993) from the Miocene of Salta, Argentina (PLV 6, dusted with NH_4Cl). Scale bar = 1 cm.

sumed correlation to some part of the undifferentiated Tertiary red beds of SINGEWALD (1927) and OPPENHEIM (1937). This assemblage includes typical Brazilian fishes, e.g., potamotrygonids, osteoglossids, pimelodiids, callichthyids, doradiids, and the serrasalmid *Colossoma* (FRAILEY 1986). The material has not been described nor figured yet. Most of the fishes have been identified at La Plata Museum, by A. CIONE.

CHANG et al. (1978) and ARRATIA (1982b) described new species of percichthyids from Lonquimay mountains, Cura-Mallín Formation, Chile, originally dated as Paleocene but currently considered Miocene (SUÁREZ & EMPARÁN 1988; SUÁREZ et al. 1990; RUBILAR & ABAD 1990). Recently, RUBILAR & ABAD (1990), RUBILAR & WALL (1990), and RUBILAR (1994) reported a diversified new fauna comprising new perciforms, characiforms, atheriniforms, and catfishes. Among these forms, the percichthyids are the dominant element represented by several taxa (Appendix 2).

Among the Miocene fauna from southern South America, the cichlids and the percichthyids are the only ones that have been studied in detail, as shown below.

Cichlids.- The first comprehensive description of southern South American cichlids are those from specimens from La Yesera, Anta Formation, studied by BARDACK (1961).

KULLANDER (1986) considered the species *Aequidens saltensis* to be most likely a geophagine, possibly adscribed to *Aequidens* by virtue of the dorsal fin-ray count (XIII, 13) and vertebral count (11 or 12 + 16). He also maintained that *Acaronia longirostrum* has a vertebral count too high for a member of this genus and that it could be an extinct lineage. KULLANDER (1986: 317) affirmed that South American fossil cichlids "should be reexamined when the osteology of Recent forms, both of the Old and New World, is better known."

CASCIOTTA & ARRATIA (1993) described new material from La Yesera and other localities from Anta Formation (in Salta and Catamarca, Argentina) and compared it with numerous living representatives belonging to about 20 genera of American cichlids. The fossil fauna includes crenicichlines (e,g., *Paleocichla longirostrum:* Fig. 28; and cf. *Chenichla*) and other forms that have been preliminaryly assigned to the geophagines (cf., *Gymnogeophagus* and Geophagines 1 and 2; Fig. 29). *Acaronia longirostrum* erected by BARDACK (1961), was considered a

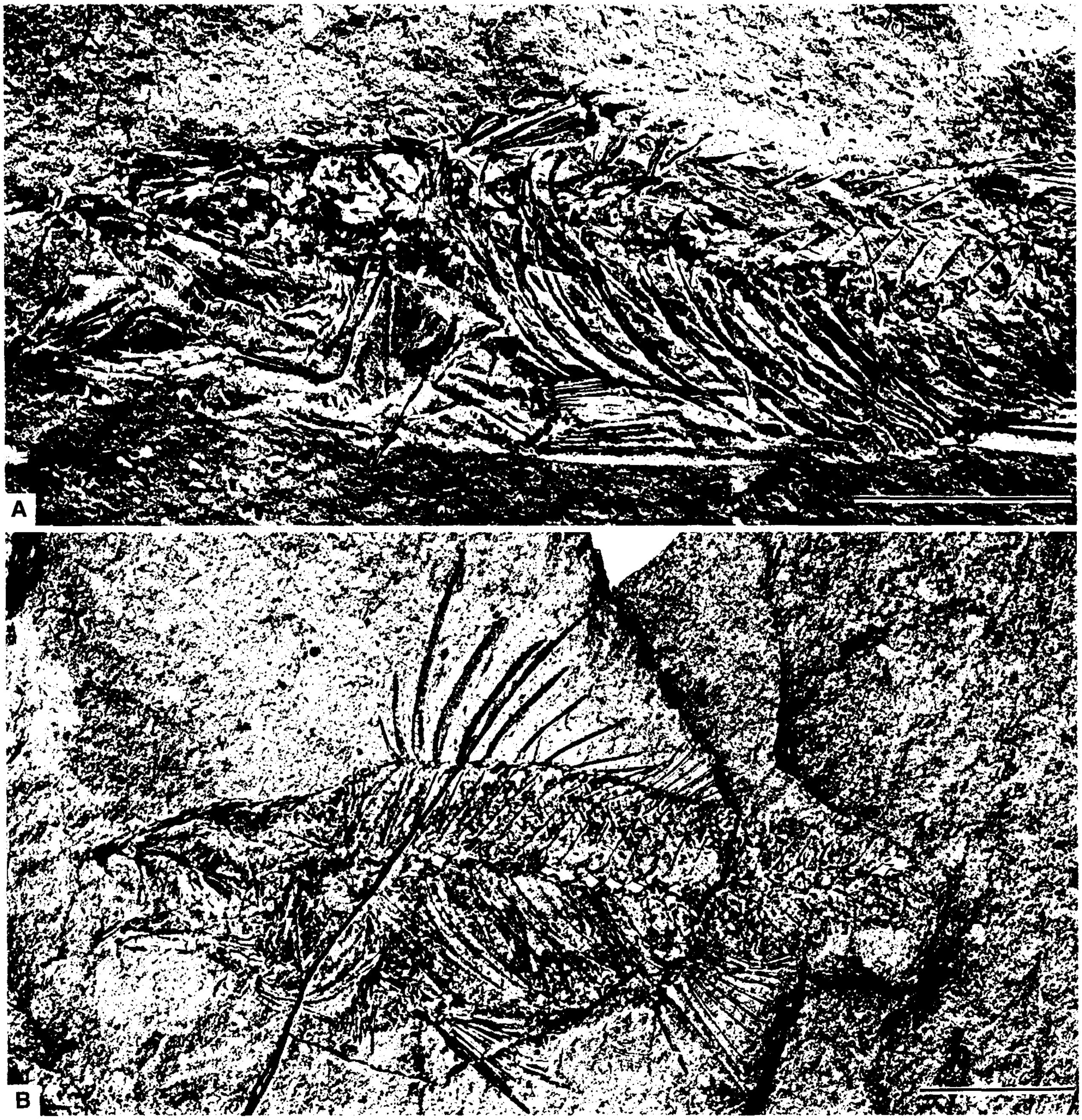


Fig. 30: *Percichthys lonquimayiensis* CHANG, ARRATIA & ALFARO from the Miocene of Lonquimay region, southern Chile. **A**, Specimen I.I.G. MA 21 (holotype). **B**, Specimen I.I.G. No. 2990. Scale bars = 1 cm.

new genus, *Paleocichla* (CASCIOTTA & ARRATIA 1993). *Paleocichla* is characterized by a combination of characters such as a high supraoccipital crest, the premaxillary ascending arm longer than the dentigerous arm and reaching about half of the orbit, seven lateral line foramina in the lower jaw, the coulter area longer than deep, an elongate body with 31 or 32 vertebrae, etc. A detailed description, as far as the preservation permits, is known from *Paleocichla longirostrum,* and is one of the most complete descriptions of a fossil cichlid. In contrast, the other cichlid species from the Anta Formation are known from incomplete specimens and therefore were not assigned to species awaiting more material.

Other South American fossil cichlids have been recorded from the Eocene of Brazil (e.g., *Macracara prisca* WOODWARD).

Percichthyids.- At least five species of percichthyids are known from the Miocene of Chile. These are *Percichthys lonquimayiensis* (Fig. 30A-B), *P. sandovali*, *P. sylviae*, *Percichthys* sp., and *Santosius*? sp. The number of fossil species exceeds the number of Recent percichthyids inhabiting the freshwater of central and southern Chile (e.g., *Percichthys trucha* and *P. melanops*). In addition, another perciform, *Percilia*? sp. has been reported from the Miocene of Chile. Most fossil species have been erected on certain meristic and morphometric features, number of serrations on infraorbital and preopercular bones, number of predorsal bones, number of spines supported by the first dorsal pterygiophore, etc. We are aware that the determination of fossil species encounters numerous problems, one of them being the number of specimens studied (a few in this case). As all of these fossil species of *Percich-*

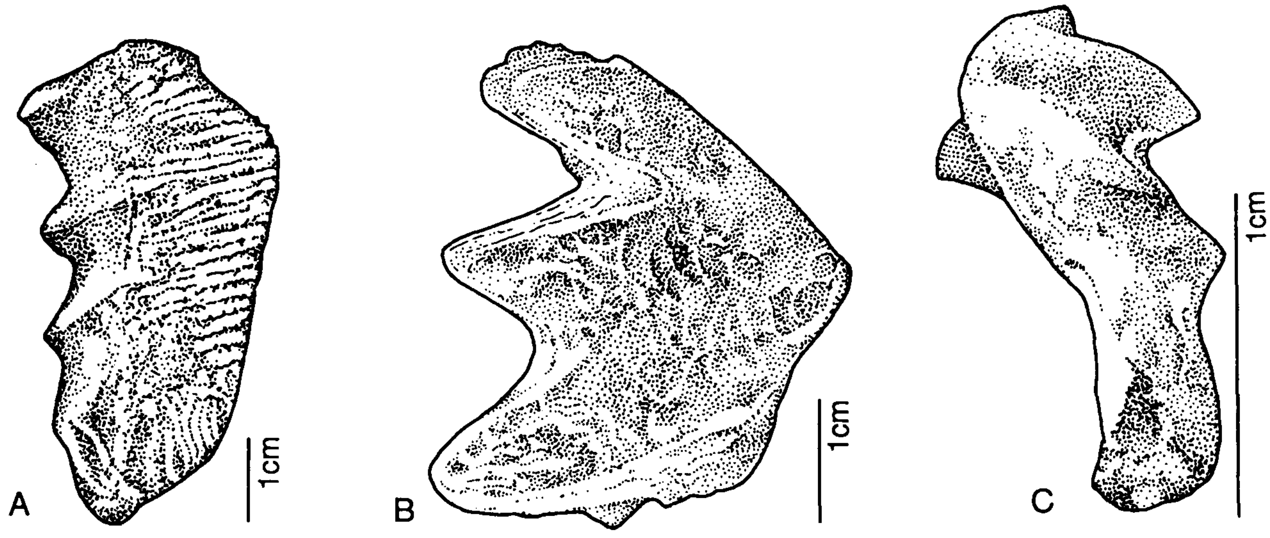


Fig. 31: Sarcopterygians from the Upper Cretaceous and Paleocene of Peru and Bolivia (drawn from SCHULTZE 1992b). **A**, Ceratodont n. gen. et sp. Left prearticular tooth plate (Paleocene; Tiupampa, Bolivia). **B**, *Ceratodus* sp. Left preaticular tooth plate (Maastrichtian; Laguna Umayo, Peru). **C**, *Lepidosiren* cf. L. *paradoxa.* Right prearticular tooth plate (Paleocene; Tiupampa, Bolivia).

thys have been erected on a few specimens, the intraspecific variation, common phenomenon in Recent species (ARRATIA 1982b and in process), cannot be detected.

RUBILAR (1994) identified one specimen from El Tallón as *Santosius*? sp. based on the shape of the epurals fide ARRATIA (1982b: text-fig. 77) and the angle formed by the dorsal and ventral limbs of the preopercle (cf., ARRATIA 1982b: text-figs. 43, 85). One diagnostic feature of *Santosius* (*sensu* ARRATIA 1982b) is the presence of large infraorbital bones; this feature is poorly preserved in the specimen from El Tallón. Comparing different features, RUBILAR (1994) concluded that (1) the genera *Percichthys, Santosius,* and *Percilia* can be distinguished from each other because of the shape of the epural bones; and (2) that *Percichthys* can be distinguished from *Santosius* on the angle formed by the dorsal and ventral limbs of the preopercle.

Pliocene: Catfishes and percichthyids have been recorded in fluvial beds in the lower part of the marine cliffs between Pehuen-có and Punta Alta (Monte Hermoso Formation), in southern Buenos Aires Province. These levels are the stratotype of the Montermosan Stage, which is dated as early Pliocene by MARSHALL et al. (1979; magnetostratigraphic and radiometric data in western Argentina), but it can also be assigned to late Pliocene (CIONE 1986a).

Pleistocene: From the Lujanian Stage (upper Pleistocene) sediments near Bahía Blanca (Cantera Vita, in the flooding area of the Río Sauce Grande) remains of Brazilian fauna as the callichthyids *Corydoras* the pimelodid *Pimelodella,* and Loricariidae indet. occur in rare association with the percichthyid *Percichthys.* No species of the austral *Percichthys* nor the Brazilian Loricariidae inhabit this area nowadays.

Holocene: In marine sediments of Las Escobas Formation, La Plata, Argentina, some freshwater fishes occur. Teeth of *Leporinus* (Leporinidae; TONNI & CIONE 1984), probable washed in by rivers, occur besides shark and cetacean remains.

4. Late Cretaceous and Tertiary sarcopterygians

Late Cretaceous: Freshwater sarcopterygians are known from incomplete specimens, mainly represented by teeth. They have been assigned to the dipnoans *Ceratodus iheringi* which has been collected in Río Negro Province in Argentina (C. AMEGHINO 1916; WICHMANN 1924, 1927; PASCUAL & BONDESIO, 1976; CIONE & LAFITTE 1980; CIONE 1987), *Ceratodus* sp. from the Late Cretaceous of Peru (Fig. 31B; SCHULTZE 1992b), and *Lepidosiren* cf. *L. paradoxa* from the Late Cretaceous of Peru and Bolivia (e.g., SCHULTZE 1992b).

Carlos AMEGHINO collected many marine and freshwater fishes from Par Aike, Río Shehuen (Mata Amarilla Formation), Argentina. However, no new collections have been made so that it is difficult to be certain that the material could not have been collected in northern and more recent sites. In 1898, his brother Florentino named a new species, *Ceratodus iheringi,* after a single tooth plate coming from the Shehuenense of this site. This "stage" is not recognized as valid today (see CIONE 1988). Florentino never described the material, though it was figured (AMEGHINO 1904, 1906: 102, pl. IX). Additional material was reported from the same locality and from the southern part of Mendoza by WICHMANN (1924, 1927) and PASCUAL & BONDESIO (1976), and from Los Alamitos by CIONE (1987).

The ceratodont tooth plates from Santa Cruz and Río Negro Provinces, Argentina (AMEGHINO 1906; WICHMANN 1927; CIONE 1987) resemble ceratodont tooth plates of Late Jurassic age of North America and from the Early Cretaceous of North Africa (SCHULTZE 1992b). MARTIN (1981a) proposed a close relationship between *Ceratodus iheringi* and *C. madagascariensis* based on the presence of only four ridges and the acquisition of a crushing surface early in ontogeny. According to SCHUL-

TZE (1992b: 443), "there is no distinct character to support a relationship of the Patagonian tooth plates with any particular Jurassic or Cretaceous *Ceratodus* tooth plates."

One single *Lepidosiren* pterygoid tooth plate has been found in the Cretaceous of Pajcha Pata in Bolivia and interpreted as *Lepidosiren* cf. *L. paradoxa* (SCHULTZE 1992b). The Cretaceous tooth plate and the Paleocene tooth plates are very similar according to SCHULTZE. The oldest fossil *Lepidosiren* record is from Peru (Maastrichtian?) (SIGÉ 1968).

Paleocene: Ceratodont tooth plates are known from the Paleocene of Santa Lucía Formation of Tiupampa and Torotoro in Bolivia (Fig. 31A). They were identified as *Ceratodus* sp. and Ceratodont n. gen. and n. sp. by SCHULTZE (1992b). *Lepidosiren* records are also known from the Eocene of Argentina (Fig. 31C; see Appendix 2).

Analysis of the Fossil Record of Southern South America

The examination of about 350 records presented in Appendices 1 and 2 shows that it is very difficult to draw generalizations. Still some general comments can be put forward.

Analysis of fossil localities

The analysis of localities and of their faunal composition shows that a few localities and formations, e.g., Paleozoic localities in the Anzaldo, Sicasica, Belén, Santa Rosa, Copacana Formations, and others in Bolivia, the Jurassic locality of Quebrada del Profeta in Chile, Late Cretaceous-Paleocene El Molino and Santa Lucía Formations in Bolivia, and the Miocene Quebrada La Yesera in Argentina represent faunal assemblages comprising a diverse fish fauna. Most of the other localities do not illustrate the diversity of the faunal composition, but show only isolated examples. However, these isolated representatives are important because they eventually could stimulate search for more material in certain areas. For instance:

The Sinemurian locality of Quebrada Vaquillas Altas was known from a few remains of fishes collected by A. NARANJO and mentioned in NARANJO & COVACEVICH (1979). Two proleptolepid remains were illustrated by ARRATIA (1987a: pl. VI, figs. 3-4). Recent field work in the locality has yielded numerous specimens which represent the best preserved proleptolepid-like assemblage in the world.

Analysis of faunal composition

The analysis of the fish taxa shows that about 30 % of the total fossil record corresponds to chondrichthyans. Chondrichthyans represent approximately 50 % of marine fishes and 8 % of freshwater fishes. The last value may be an artificial one because it is uncertain whether the Bolivian Late Cretaceous beds bearing chondrichthyans are marine or not (CAPPETTA 1992).

The osteichthyans correspond to 70 % of the total fossil fish record, approximately 40 % of marine fishes and 92 % of freshwater fishes.

Among osteichthyans the teleosts are the best represented group with 60 %. Among freshwater fishes they correspond to 88 %. These values correlate with the current information on living fishes because the teleosts are the largest group among vertebrates (LAUDER & LIEM 1983; NELSON 1994).

Among freshwater teleosts the most common representatives are the ostariophysans, mainly catfishes. Again that correlates well with the current information on Recent faunal composition because catfishes represent the dominant group comprising 13 endemic families in South America (ARRATIA in press). Among catfishes the following taxa have fossil representatives: Ariidae, Auchenipteridae, Callichthyidae, Doradidae, Loricariidae, Nematogenyidae, Pimelodidae, and possibly Diplomystidae with cf. Diplomystidae (see Appendix 2). Most fossil members of these families are known from Tertiary records, however Ariidae and cf. Diplomystidae have a long history on the continent, starting with the Late Cretaceous. It is possible that other modern catfish families are also represented among the indetermined siluriforms listed in Appendix 2; unfortunately the preserved fragments do not bear diagnostic features that could allow to assign them to family level.

Among the fossil osteichthyans the sarcopterygians are known from a few representatives (one marine representative from the Late Permian of Bolivia [Appendix 1] and at least three freshwater forms, e.g., Ceratodont n. gen. and n. sp., *Ceratodus,* and *Lepidosiren* [Appendix 2]). Only one lungfish, *Lepidosiren paradoxa,* is known in South America, actually. The comparison illustrates that living South American *Lepidosiren* is a survival of a group that was better represented during the Late Cretaceous-Tertiary in South America. *Lepidosiren* lives in the Brazilian Sub-Region of South America and reaches northern Argentina at its southernmost distribution (RINGUELET et al. 1967; ARRATIA in press a). It had a broader distribution in the past, inhabiting also regions of Peru and Bolivia where it does not occur today (SIGÉ 1968; SCHULTZE 1992b).

Only about 5 % of the whole southern South American record has been identified to generic level and 38 % to specific level. Numerous forms have been left as indetermined within a family or order.

The modern freshwater fish fauna of South America is characterized by its high endemism (DARLINGTON 1957; RINGUELET 1975; ARRATIA et al. 1983; ARRATIA in press). In contrast, the fossil record of osteichthyans shows that 10 genera occurred in other continents also - e.g., *Atractosteus, Belonostomus, Birgeria, Ceratodus, Enchodus, Lepidotes, Lepisosteus, Pachycormus, Protosphyraena,* and *Stephanodus.* The southern South American representatives assigned to these genera have been identified on bony fragments (e.g., cf. *Birgeria, Lepidotes*), teeth and/or scales (e.g., *Atractosteus, Ceratodus, Enchodus, Lepisosteus, Protosphyraena*, *Stephanodus*), or simply they represent citations (e.g., *Pachycormus*). The possibility exists that some of these identifications could be mistakes; therefore it is suggested that all these identifications be revised when more material is available. Furthermore, on the light of poor knowledge of these forms, it seems wise not to consider them in paleobiogeographic hypotheses supporting probable connections between South America and other continents.

Fossil fish assemblages

Paleozoic, Mesozoic, and Cenozoic faunal assemblages show dramatic differences in fish diversity in southern South America.

Paleozoic fish assemblages are only known from Bolivia. Only isolated bones and scales have been found in Argentina. They are good examples of the radiation of certain groups whereas others were not represented, or at least they have not been recovered yet. For instance:

Phylogenetic analyses show that the Ordovician vertebrates of the southern hemisphere form a monophyletic group that is the plesiomorphic sister group of northern hemisphere ones and of heterostracans (GAGNIER 1992). The discovery of *Sacabambaspis janvieri* represents the first record of an Ordovician vertebrate showing most of the dermal skeleton which permitted comparisons with all other agnathans. The other Ordovician vertebrate from Bolivia (*Andinaspis suarezorum* GAGNIER 1992) is certainly distinct from *Sacabambaspis*, but is represented by the holotype only.

At least five chondrichthyan species, one placoderm and one actinopterygian are known from the ?Silurian-Devonian Tarabuco, Sicasica, Belén, and Huamampampa Formations. This Paleozoic assemblage differs from that of the Lower Devonian of the Santa Rosa Formation with only Acanthodii, e.g., nine species belonging to orders Climatiida and Ischnacanthida, and Acanthodii incertae sedis.

The most peculiar chondrichthyan from the Devonian of Bolivia is certainly *Zamponiopteron* (JANVIER & SUAREZ-RIGLOS 1986), a form with ankylozed, calcified paired fins and unique to Bolivia, to date.

Only one placoderm, the rhenanid *Bolivosteus* is present in the Devonian of Bolivia; placoderm and osteolepid assemblages has been recently discovered in the Late Devonian of Venezuela (GAGNIER in press).

The thelodont *Turinia gondwana* is strikingly similar to scales from the Middle and Late Devonian of Antarctica and Australia (JANVIER 1992a). The same applies to the chondrichthyan *Antarctilamna*.

This local radiation and endemism that apparently already were playing roles in the Paleozoic are observed in all geological periods in southern South America up to the present time (RINGUELET 1975; ARRATIA 1983 and in press; ARRATIA et al. 1983; ARRATIA & MENU MARQUE 1984).

Diversified Mesozoic fish assemblages are known from a few localities. Most localities are represented by scarce fish forms (one or two), therefore these are not considered in this section.

Triassic assemblages belonging to a single locality are unknown in southern South America. The available information represents isolated records.

Important Jurassic fish assemblages of a single locality are those of Quebrada del Profeta and Cerritos Bayos in Chile, a few localities of Vaca Muerta Formation in Argentina, and the freshwater locality of Cerro Cóndor in Argentina. One locality, potentially very rich in primitive teleosts, pycnodontiforms, and other indetermined neopterygians is the Sinemurian Quebrada Vaquillas Altas in northern Chile.

Quebrada del Profeta is known from pycnodontiforms, semionotiforms, pachycormiforms, *Atacamichthys*, ?pholidophorids, and at least eight teleost species (Appendix 1). Recent field work in the locality will increase the list because of new findings. The other Jurassic locality of Cerritos Bayos, also in northern Chile, has apparently a similar composition of fossil fishes as that of Quebrada del Profeta at high hierarchic levels, e.g., pycnodontiforms, semionotiforms, pachycormiforms, and teleosts. Nevertheless, there are differences at the generic and specific levels.

The Argentinian Tithonian localities of Vaca Muerta Formation bear semionotiforms and indeterminate teleosts. The fishes from this formation comprise a faunal assemblage different from those of the older Chilean localities Quebrada del Profeta and Cerritos Bayos. All of them are also different from the Tithonian freshwater locality Cerro Cóndor. The palaeonisciform *Coccolepis* and the teleosts *Luisiella* and *"Tharrias"* are recorded from Cerro Cóndor.

Late Cretaceous localities are known from the Yacoraite, Los Alamitos, and the El Molino Formations in Argentina and Bolivia. Again, the faunal assemblages, as far as known, differ between these formations. For instance:

The Yacoraite Formation bears a chondrichthyan (*Pucapristis*), pycnodontiforms, and three teleosts (?osteoglossiform, clupeiform, and catfish). In contrast, the fauna of the Los Alamitos Formation has a chondrichthyan, a lepisosteid (cf. *Atractosteus*), a dipnoan, and teleosts.

The fish fauna of Bolivia has been collected in numerous localities (see Appendix 2; CAPPETTA 1992; GAYET 1992; GAYET et al. 1992) of the El Molino Formation. It comprises chondrichthyans (nine species), two polypteriforms, two pycnodontiforms, one semionotiform, lepisosteid (*Lepisosteus*), about a dozen teleosts, and one dipnoan. Polypteriforms are only known from Bolivian localities in southern South America.

The faunal assemblages from Paleocene beds of the El Molino and Santa Lucía Formations in Bolivia show a diversified fauna comprising pycnodontiforms (e.g., *Coelodus*), supposed semionotiforms, polypteriforms, lepisosteids, teleosts (e.g., osteoglossiforms, clupeiforms, characiforms, siluriforms, perciforms, cf. cyprinodontiforms), and dipnoans (e.g., Ceratodont n. gen. and sp., *Ceratodus, Lepidosiren*). With the exception of non-teleostean fishes, teleosts seem to be represented by the same groups that today occur in South American freshwaters.

Numerous osteoglossiform remains have been reported from the Bolivian localities and assigned at least to *Phareodusichthys* and Osteoglossinae n. gen. (GAYET 1992). In contrast, only two osteoglossomorph genera, *Arapaima* and *Osteoglossum*, occur in the continent at present time.

Other Tertiary localities are mainly or exclusively known from teleosts (see Appendix 2).

Among the 27 genera of Tertiary freshwater teleosts reported from the area, 16 correspond to extant genera, e.g., *Corydoras, Hypostomus, Colossoma, Percichthys, Pimelodella,* and *Pimelodus*. Paleocene fishes are commonly known from extinct genera, e.g., *Andinichthys, Hoffstetterichthys, Incaichthys,* and *Phareodusichthys.*

Comparison between fossil and modern fish faunas

An overview of the southern South American fossil record shows that:

1. Most fish taxa living up to the Late Cretaceous-Paleocene become extinct by the Paleocene (e.g., pycnodontiforms, *Ceratodus* and Ceratodont n. gen. et sp.) and were apparently replaced by modern genera.
2. During the Late Cretaceous-Paleocene forms (e.g., polypteriforms, lepisosteids) which actually do not occur in the continent inhabited southern South America. These forms occur today in Africa (polypteriforms), North America and Cuba (lepisosteids), and Australia (*Ceratodus*).
3. Among the teleostean groups actually inhabiting the South American continent - osteoglossiforms, clupeiforms, ostariophysans, osmeriforms, synbranchiforms, perciforms, atheriniforms, and cyprinodontiforms - the osteoglossiforms, the clupeiforms, the characiforms, the catfishes, and the cyprinodontiforms seem to be represented in the Late Cretaceous fossil record.
4. The following groups of living freshwater teleosts do not have fossil representatives yet: the synbranchiforms and the osmeriforms (e.g., galaxiids).
5. Most families of characiforms are not represented (e.g., Anostomidae, Ctenoluciidae, Curimatidae, Gasteropelecidae, Hemiodontidae, and Lebiasinidae). Numerous catfish families have no fossil representatives yet (e.g., Ageneiosidae, Aspredinidae, Astroblepidae, Cetopsidae, Helogenidae, Hypophthalmidae, Scoloplacidae, and Trichomycteridae). No fossil representative is known of the six gymnotiform families actually living in South America.

The oldest record of some teleostean groups are known from South America; for instance, the catfishes from the Yacoraite and Los Alamitos Formations in Argentina and the El Molino Formation in Bolivia (Appendix 2), and the characiforms and probably the cyprinodontiforms from the El Molino Formation.

South America is the only continent where numerous remains of Cretaceous catfishes have been found, even though there are well-known Cretaceous freshwater beds in North America (e.g., Hell Creek Formation, see ESTES et al. 1969), in Africa (In Beceten, Niger, Lower Senonian, see BROIN et al. 1974) and India (Pisdura, see JAIN & SHANI 1983). There is no evidence of catfishes in Early Cretaceous freshwater sediments such as in the La Cruz Formation (BOCCHINO 1973, 1974), in the La Cantera Formation (CIONE & PEREIRA 1990) in San Luis, Argentina, and in the Tacuarembó Formation in Uruguay (MONES 1972).

GAYET (1982c) reported the presence of the most ancient Characidae from southern South America. She assigned them to the Recent genera *Triportheus* (Bryconinae) and *Rhoadsia* (Rhoadsinae, a geographically restricted taxon reported only from western Ecuador and Costa Rica; GÉRY 1977). As above discussed, there are different genera with the morphology shown in GAYET's (1982c, 1992) figures. The characiforms from El Molino Formation are the most ancient record of Characiformes if we except the debated record of marine characiforms in the Cenomanian of Portugal (GAYET 1985).

Other teleostean groups are already known from the Early Cretaceous in other parts of the world. For instance, the osteoglossomorphs from numerous Chinese lacustrine deposits (CHANG & JIN 1996), the clupeomorphs from the Early Cretaceous of Brazil, and the gonorynchiforms from the Early Cretaceous of Spain and Brazil (POYATO-ARIZA 1994 and MAISEY 1991 and 1993, respectively).

Some fossil fishes that were living in the past in South America, do not occur on the continent today. This fact has made it difficult to accept some of the identifications because the material on which they are based is fragmentary. Among these groups are:

Polypteriforms.- They reached apparently southern South America in the Late Cretaceous-Paleocene. Their knowledge is mainly or only based on scales that have been interpreted as belonging to polypteriforms because of similarities in the micro- and macromorphology of scales of extant polypteriforms (GAYET & MEUNIER 1991a, b, 1992a, b; MEUNIER & GAYET 1995).

Lepisosteids.- They occur in southern South America in the Late Cretaceous - Paleocene. The southernmost locality from where fragments have been recorded is Estancia Los Alamitos in southern Argentina. Remains assigned to *Lepisosteus* sp. have been found in Bolivian localities (Appendix 2). The determinations of lepisosteids from Argentina and Bolivia have been doubted because of the quality of the material. In contrast, complete specimens were recovered from the Early Cretaceous of Brazil (WENZ & BRITO 1992, 1996) which confirm the presence of this group in the South American continent in past times.

Dipnoans.- They were apparently well represented in the area during the Late Cretaceous and Paleocene and remain on the continent with only one representative, *Lepidosiren paradoxa.* Today lungfishes are restricted to the southern continents: the Lepidosirenidae, *Protopterus* and *Lepidosiren,* to Africa and South America respectively, and the Neoceratodontidae, *Neoceratodus,* to Australia. *L. paradoxa* seems to have a long history in the continent, because there are not differences between the Late Cretaceous-Tertiary and Recent representatives. On the other hand, *Neoceratodus* is considered a relict of an older radiation of the Ceratodontidae (SCHULTZE 1992b). This family had a worldwide distribution in the Mesozoic still occurring during the Cretaceous in Africa, Madagascar, Australia, North America, and South America (see SCHULTZE 1992b for other references).

Systematic Considerations

As a whole, the systematics of most southern South American fossil fish groups is poorly understood and the deficiency lies on the fact that most fishes are incompletely known because of poor preservation. However, there are a few exceptions such as the Ordovician *Sacabambaspis*, the Jurassic halecostome *Atacamichthys* and some of the Jurassic basal teleosts from northern Chile, the cichlids from the Miocene of Salta and Catamarca in Argentina, and the percichthyids from the Miocene of Lonquimay area in Chile.

Unfortunately, based on incomplete evidence and doubtful taxonomic assignments numerous forms have been used to postulate significant changes in systematics (e.g., for Cypriniformes) and to postulate general paleobiogeographic and paleoenviromental hypotheses (GAYET 1982b, 1992; GAYET et al. 1992, see below). We think that the first requirement for such work is a solid taxonomic framework.

Phylogenetic relationships of some South American fishes

Sacabambaspis: The first record of an Ordovician vertebrate showing most of the dermal skeleton is that of *Sacabambaspis* from Bolivia. The genus *Sacabambaspis* is known from one species, *S. janvieri.* Recent hypotheses of phylogenetic relationships suggest that *Sacabambaspis* shares only one synapomorphy (large ventral and dorsal shields covering the head) with the heterostracans (JANVIER 1981, 1984; BLIECK et al. 1991; ELLIOT et al. 1991).

Recent phylogenetic studies suggest that the Bolivian genus *Sacabambaspis* and the Australian genus *Arandaspis* form a monophyletic group (the Arandaspida) sharing two synapomorphies at least (presence of individual platelets on the branchial openings and pineal and parapineal apparatuses placed side-by-side) (Fig. 32). The clade [*Sacabambaspis* + *Arandaspis*] is proposed as the sister group of heterostracans (GAGNIER 1992; GAGNIER & BLIECK 1992).

Andinaspis suarezorum GAGNIER from the Ordovician of the Capinota Formation, Bolivia, was included within the Arandaspididae (GAGNIER 1992), but its phylogenetic relationships are still unknown.

Atacamichthys: The halecostome genus *Atacamichthys* from Quebrada El Profeta, northern Chile, is known from one species, *A. greeni.* Following the characters of PATTERSON & ROSEN (1977) it was considered an halecostome actinopterygian by ARRATIA & SCHULTZE (1987). The halecostome features are a mobile maxilla and the presence of a supramaxilla and median neural spines. ARRATIA & SCHULTZE (1987) added two characters, a notch in the posterior margin of the maxilla and supradorsal cartilages. However, a notch in the posterior margin of the maxilla is shared by *Atacamichthys* and various fossil primitive halecostomes and halecomorphs, e.g., Recent *Amia*, pholidophorids, leptolepids, and *Varasichthys.*

There are only a few characters common between *Atacamichthys* and the halecomorphs, e.g., shape of hyomandibular bone and the absence of intermuscular bones (the latter is a primitive character). There are many features in common between *Atacamichthys* and the so-called primitive teleosts (*sensu* PATTERSON 1977 and PATTERSON & ROSEN 1977) such as the formation of vertebral centra, L-shaped dermopterotic, lack of coronoid bones, absence of teeth on prearticular bone, and presence of two hypohyal bones. On the other hand, *Atacamichthys* has two large suborbitals like pachycormids. A large dorsal postcleithrum and a small ventral one occur in *Atacamichthys*, in macrosemiids, pachycormids, and *Hulettia.*

The combination of morphological features of *Atacamichthys* is unique among halecostomes; it has very clear autapomorphies such as a very elongate autopalatine, triangular endopterygoid and several sensory tubules in the antorbital. Still, the fish was not assigned to a family by ARRATIA & SCHULTZE (1987). Due to its combination of features, *Atacamichthys* was hypothetized to be closer to *Eurycormus*, and below *Pholidophorus* (Fig. 33), on the lineage towards the teleosts *sensu stricto* (*Leptolepis coryphaenoides* and above; see Fig. 34 below). Since the placement of Pachycormiformes and Aspidorhynchiformes within the Teleostei *sensu* PATTERSON (1973) has been questioned (ARRATIA & LAMBERS 1996) it is clear that the putative basal teleosts of PATTERSON (1973, 1977) and PATTERSON & ROSEN (1977) have to be revised. Therefore, *Atacamichthys* may have a more basal position than that proposed by ARRATIA & SCHULTZE (1987).

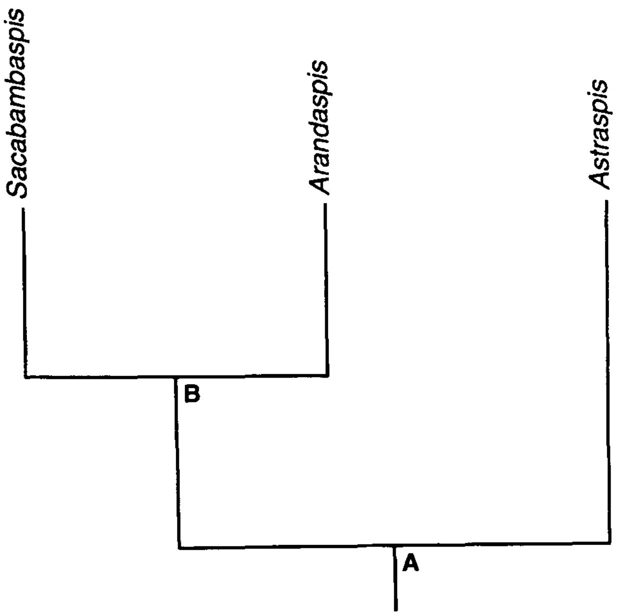


Fig. 32: An hypothesis of phylogenetic relationships of *Sacabambaspis* (after GAGNIER 1992). The characters supporting nodes are listed below. **Node A:** Large median plates covering head; development of oral plates. **Node B:** Individual platelets on branchial openings; pineal and parapineal apparatuses placed side-by-side. Characters for *Astraspis* lineage: Reduction of number of branchial openings and their dorsal position; development of acellular bone.

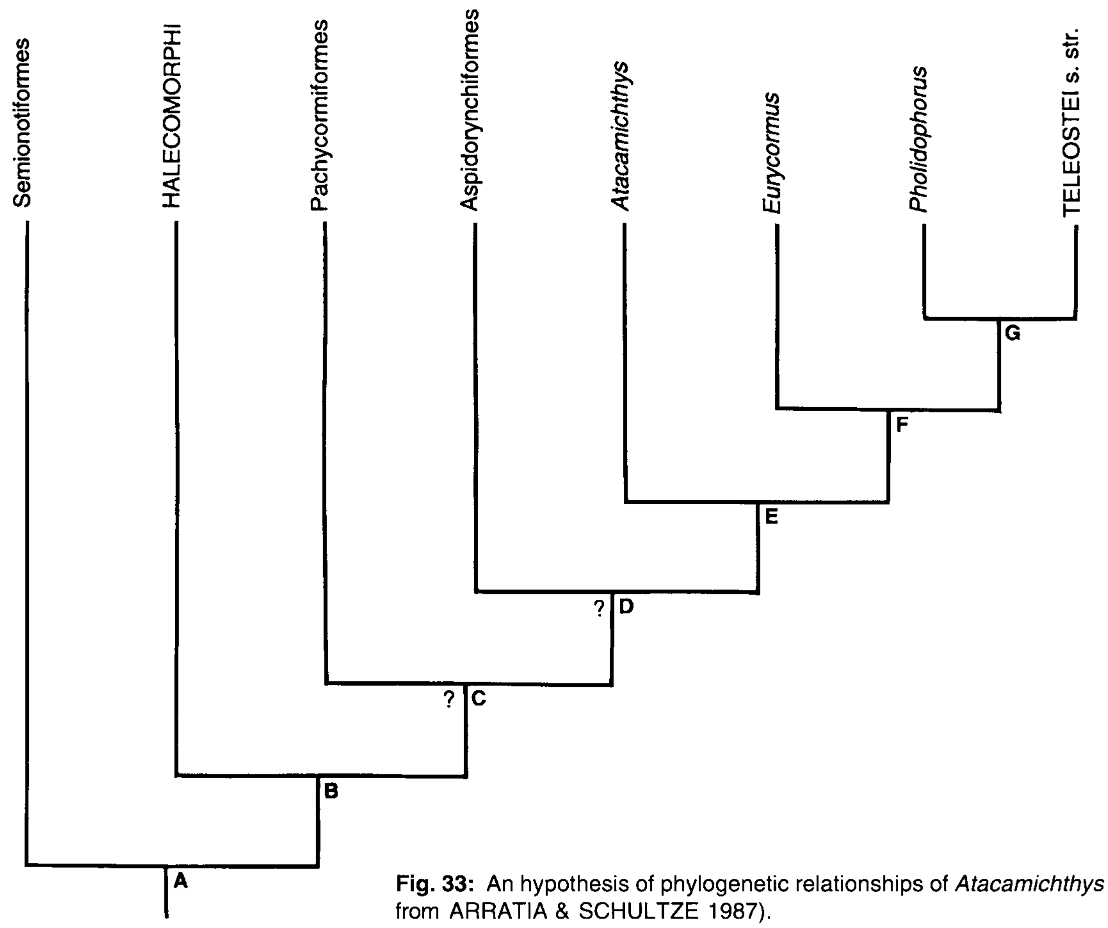


Fig. 33: An hypothesis of phylogenetic relationships of *Atacamichthys greeni* (modified from ARRATIA & SCHULTZE 1987).

Basal teleosts: Phylogenetic studies among southern South American Jurassic and Cretaceous teleosts are known only from certain Chilean Jurassic teleosts (see ARRATIA 1991, 1994, 1996). Among the Tertiary fishes, phylogenetic studies including both fossil and Recent taxa are only known from cichlids (CASCIOTTA & ARRATIA 1993).

Among basal Jurassic teleosts only two monophyletic groups are recognized, the Ichthyodectiformes (see PATTERSON & ROSEN 1977; ARRATIA 1994, 1996) and the varasichthyid group including the four Chilean genera and one Cuban genus. The monophyly of the varasichthyid group is supported by several synapomorphies, e.g., parasphenoid without teeth, retroarticular bone excluded from the joint surface of quadrate, more than three postcleithra, pectoral axillary process formed by bony elements, and pelvic axillary process formed by an elongate bone. According to the available evidence, *Domeykos* is the plesiomorphic sister group of other members of the varasichthyid group. ARRATIA's (1994, 1996) phylogenetic analyses showed that the Cuban teleost *Luisichthys* is also a member of this varasichthyid group, the sister group of *Protoclupea* (Fig. 34). *Bobbichthys*, first described as *Leptolepis opercularis* by ARRATIA et al. (1975a), is not so well preserved as other taxa of the Oxfordian of Chile. Information on the neurocranium of *Bobbichthys* is incomplete, as well that on the retroarticular bone, and that of the caudal skeleton are not informative because of poor preservation; therefore, comparison with other taxa from the Oxfordian of Chile is difficult. Still, *Bobbichthys* is better considered another member of the varasichthyid group because it shares the following synapomorphies: the presence of more than three postcleithra (ARRATIA 1986a: text-fig. 4B, C), pectoral axillary process formed by bony elements, and pelvic axillary process formed by an elongate bone.

One teleostean taxon which deserves comments is Teleost sp. 1 (*sensu* ARRATIA 1991) only known from its caudal skeleton and fin. Teleost sp. 1 presents the most primitive caudal skeleton and caudal fin among Teleostei *s. str.* with the presence of epaxial and hypaxial basal fulcra, fringing fulcra in both the dorsal and ventral lobes of the caudal fin, a reduced epaxial procurrent ray, four epurals, seven uroneurals, at least eight hypurals, and 20 principal caudal rays. Such combination of primitive features, together with the presence of heavily ossified caudal autocentra which are fused to their neural and haemal arches and autocentra constricting the notochord separate Teleost sp. 1 from all so-called primitive teleosts of PATTERSON (1973, 1977) and PATTERSON & ROSEN (1977) such as pachycormiforms, aspidorynchiforms, pholidophoriforms, etc. Teleost sp. 1 appears as the plesiomorphic sister group of *Leptolepis coryphaenoides* + more advanced teleosts in ARRATIA's (1994: text-fig. 9) phylogenetic hypothesis of relationships.

Another teleost from the Late Jurassic of Chile is *Chongichthys dentatus*. Because of its combination of features *Chongichthys dentatus* was included in its own family by ARRATIA (1982a) and interpreted as a Teleostei *incertae sedis*. SCHAEFFER & PATTERSON (1984) listed *Chongichthys* as a teleost placed somewhere between *Tharsis* and the Osteoglossomorpha in the phylogenetic hypotheses of PATTERSON & ROSEN (1977) and PATTERSON (1977). Recent phylogenetic hypothe-

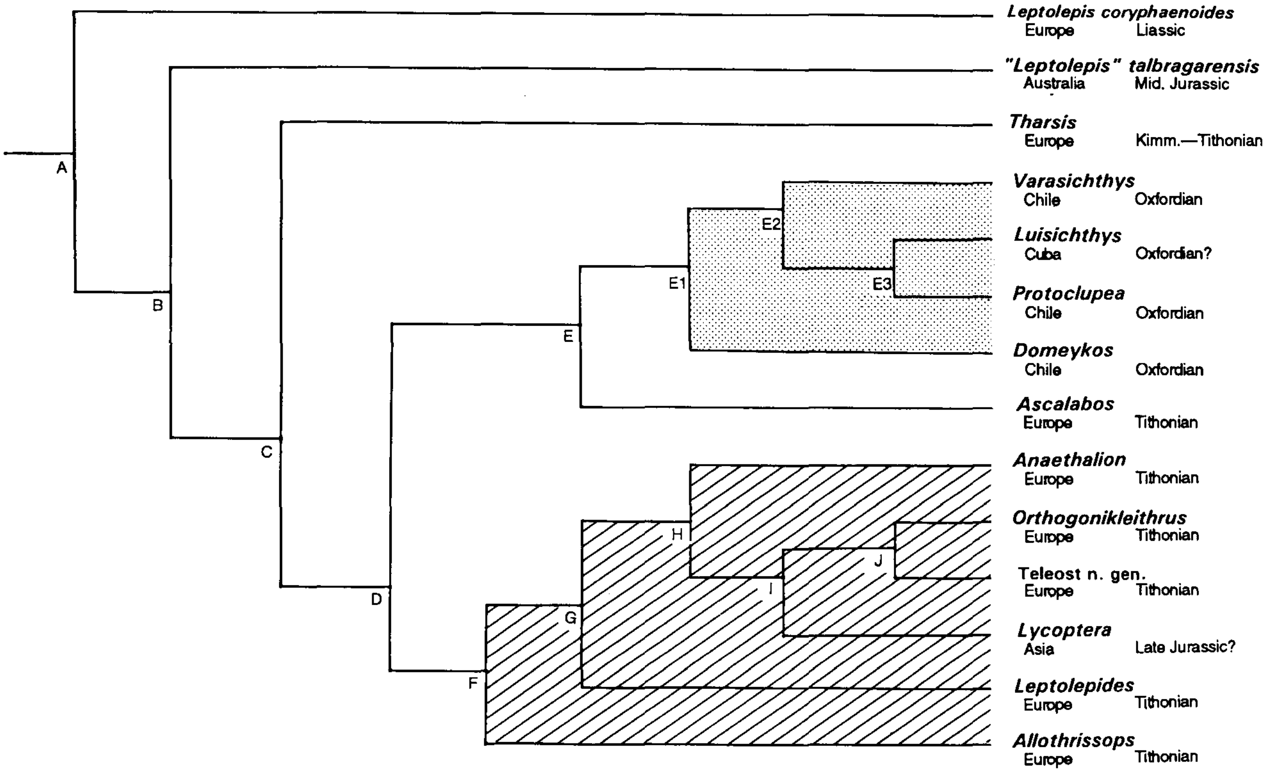


Fig. 34: An hypothesis of phylogenetic relationships of the varasichthyid group (for explanation of characters see ARRATIA 1994). Uniquely derived characters are indicated with an asterisk (*). The combined outgroup includes *Pholidophorus* spp., *Pholidolepis* sp., and *Proleptolepis* spp. **Node A:** Middle caudal centra with fused neural and haemal arches (*); preural vertebrae (excluding preural centrum 1) of adult individuals with fused haemal arches; parhypural in adult individuals laterally fused to its centrum; two sets of uroneurals, a long anterior one and a short posterior set; two "urodermals" (*); fringing fulcra present in dorsal lobe of caudal fin; 19 principal caudal fin-rays, nine in the lower lobe of caudal fin. **Node B:** Middle pitline groove not crossing the parietal and extending onto the pterotic; suborbital bones absent; suprapreopercle absent (*). **Node C:** Sutures between cartilage bones in braincase retained throughout life (*); ossified aortic canal absent (*); without canal for occipital arteries in basioccipital bone (*); spiracular canal absent (*); foramen for glossopharyngeal nerve in exoccipital (*); caudal vertebrae with sculptured autocentra; midcaudal centra strongly constricting the notochord (*); a few epipleural bones in anterior caudal region. **Node D:** Fringing fulcra absent in both lobes of caudal fin; long dorsal segmented procurrent rays present; primitively with cycloid scales with crenulate posterior margin. **Node E:** Middle pitline crossing the parietal and extending onto pterotic (a reversal); cycloid scales posterior to pectoral girdle with circuli crossed by transverse lines in middle field (*). **Node E1:** Parasphenoid without dentition (*); retroarticular bone excluded from joint facet for quadrate (*); more than three postcleithra present (*); pectoral axillary process formed by bony elements (*); pelvic axillary process formed by an elongate bone (*). **Node E2:** Preural vertebrae (excluding preural centrum 1) of adult individuals with unfused haemal arches; parhypural in adult individuals with unfused haemal arch; neural arch over first ural centrum reduced or absent; with 20 principal caudal fin-rays (a reversal), with ten principal rays in lower lobe. **Node E3:** Five or four ural neural arches modified as uroneurals; two uroneurals extending forward beyond the second ural centrum. **Node F:** Main lateral line emerging at about middle region of supracleithrum; hypural 10 absent; hypural 9 absent (*). **Node G:** Five or four ural neural arches modified as uroneurals; two long anterior uroneurals (loss or fusion of one; less than three uppermost uroneural present (*); longest anterior uroneural(s) not extending forward to preural centrum 2 or 3 (*); first uroneural reaching preural centrum 2; two uroneurals extending forward beyond second ural centrum; one "urodermal" present (*); proximity of fulcra or dorsal procurrent rays to neural spines, epurals, and posterior uroneurals. **Node H:** Bases of dorsalmost principal rays of caudal fin aligned with hypurals so that no fin-ray base overlies more than one hypural. **Node I:** Posterior opening of mandibular sensory canal placed lateral to angular bone (*); seven hypurals present (*); cycloid scales without crenulate posterior margin. **Node J:** Postarticular process of lower jaw poorly developed; parhypural in adult individuals with haemal arch laterally unfused to its centrum; neural spines of ural centra 1 and 2 or 'first' ural centrum absent; neural arch over first ural centrum reduced or absent; abrupt dorsal flexion of tail begins at preural centrum 1 or 'first' ural centrum.

ses (ARRATIA 1991, 1994, 1996) differ from those by PATTERSON & ROSEN in the position of *Tharsis* and osteoglossomorphs (see Fig. 34). The phylogenetic position of *Chongichthys* is still unknown.

Perciforms: Recent freshwater perciforms are known by few representatives in southern South America. Among these the austral families Percichthyidae and Perciliidae comprise six species of *Percichthys* living in Chile and Argentina and two species of *Percilia*, endemic to Chile (ARRATIA 1981b, 1982b).

ARRATIA (1982b) defined the Percichthyidae *sensu stricto* and restricted it to the freshwaters of southern South America. The diagnoses of the Percichthyidae and *Percichthys* are based on a combination of features (ARRATIA 1982b: 42). JOHNSON (1984: 469) based on the condition of the ctenoid scale and "on other several well nested synapomorphies" (which were not provided), in-

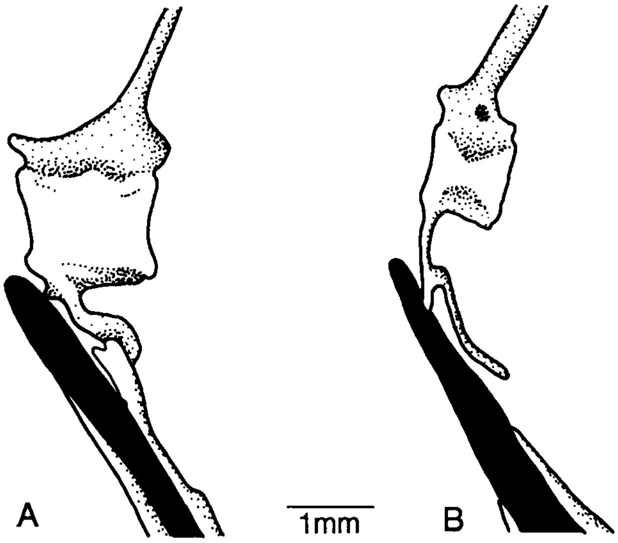


Fig. 35: Position of the second anal pterygiophore and first caudal centrum in *Percichthys lonquimayiensis* according to ARRATIA (1982b).

cluded the South American genera *Percichthys* and *Percilia* and several Australian forms, e.g., *Bostockia, Macquaria, Nannatherina, Percalates,* and *Plectroplites*, within the Percichthyidae. Further studies by ARRATIA agree with her hypothesis (1982b) that the genus *Percilia* is separated from South American and Australian percichthyids (ARRATIA, in prep.).

Percichthys is one of the best known fossil genera, based on both fossil and Recent evidence. As far as known the oldest record is from the Eocene of Argentina (*Percichthys hondoensis*). Other three formally described species and several *Percichthys* sp. are known from Miocene beds of Chile and Argentina (see Appendix 2).

ARRATIA (1982b) noted the contact between the second anal pterygiophore and the first caudal vertebral centrum in *Percichthys lonquimayiensis* (Fig. 35). Later, the same condition was reported for *P. sylviae* (RUBILAR & ABAD 1990) and *Percichthys* sp. (RUBILAR 1994). This feature is not present in the extant *Percichthys* nor in the Miocene *P. sandovali.* By comparison with other percoids, this character state is derived and therefore a synapomorphy of a clade including *P. lonquimayiensis, P. sylviae,* and *Percichthys* sp. Whether *Percichthys* sp. *sensu* RUBILAR (1994) is a new species or falls into the range of variation of *P. lonquimayiensis* or of *P. sylviae* has to be demonstrated.

The relationships among *Percichthys* species have not been published yet. However, the present evidence reveals that the fossil species *Percichthys lonquimayiensis, P. sylviae,* and *Percichthys* sp. from Chile share one synapomorphy, the contact between the second anal pterygiophore and first caudal vertebral centrum (Fig. 35). If this interpretation is correct, then the species of the genus *Percichthys* can be grouped in clades below the generic level.

The diversification of the percichthyids suggested for the Miocene deposits of the Lonquimay area (Appendix 2) would represent an interesting speciation of these forms in the area. As for the cichlids, we do not know the historical events that explain the speciation rate in *Percichthys* during the early Tertiary.

Cichlids: At present, the family Cichlidae is one of the most speciose in South American freshwater. Although the total number of species in unknown, KULLANDER (1986) estimated over 250 species on the continent. Currently, cichlids do not inhabit freshwaters of Chile and of the Argentinian Patagonia; they are restricted to the Brazilian Sub-Region of RINGUELET (1975) and ARRATIA et al. (1983).

Based on both fossil and Recent American cichlids, CASCIOTTA & ARRATIA (1993) proposed a hypothesis of phylogenetic relationships (Fig. 36). *Paleocichla*, the best known fossil cichlid from South America, and Geophagine 1, incomplete fossil form, were considered together with 23 taxa of Recent cichlids. Figure 36 represents a new hypothesis contrary to the phylogenetic relationships proposed by authors such as REGAN (1906), DE MIRANDA RIBEIRO (1915), and STIASSNY (1991).

According to CASCIOTTA & ARRATIA's (1993) hypothesis, the basal position among American cichlids is occupied by the Chaetobranchine Group [*Astronotus* + [*Chaetobranchus* + *Chaetobranchopsis*]]. Geophagine 1 is more derived than the Chaetobranchine Group, but it is the plesiomorphic sister group of all other cichlids (Fig. 36). The Crenicichline Group of STIASSNY (1991) comprises *Cichla, Crenicichla,* and *Teleocichla.* In CASCIOTTA & ARRATIA's hypothesis, *Paleocichla* is the sister group of *Cichla* and both are the sister group of *Crenicichla* spp. and *Crenicichla semifasciata.* According to the available data, the Crenichline Group is probable the only one among American cichlids whose monophyly is certain. For characters supporting nodes see Figure 36.

Both fossil taxa, *Paleocichla* and Geophagine 1, from the Miocene deposits, are more advanced than the Recent representatives of the Chaetobranchine Group. As CASCIOTTA & ARRATIA (1993) noted, the Miocene cichlids were already as advanced as Recent forms.

"The diversification of the cichlids shown by the Miocene deposits of Salta and Catamarca [Appendix 2] reveals that high speciation of cichlids is not a Recent event. Unfortunately, we do not know the historical events that explain the speciation rate in cichlids during the early Tertiary." (CASCIOTTA & ARRATIA 1993: 235).

Dipnoans: As above stated, most knowledge of fossil southern South American lungfishes is based on tooth plates. This is the common condition for the fossil record; skull roof bones are rare.

At present, the Mesozoic dipnoan interrelationships have been based on two approaches, one based on cranial patterns (SCHULTZE 1981b) and other based on tooth plates (MARTIN 1981b, 1982a, b, 1983, 1984). Because tooth plates are common in the fossil record, MARTIN could include most of the known Mesozoic species; in contrast SCHULTZE (1981b) could include only a few Mesozoic taxa.

MARTIN (1983, 1984) used the number of ridges (less than seven and less than six) as features of the crushing tooth plates, position of the pterygoid process, among other features. However, all these are homoplastic characters appearing in parallel many times on his cladogram. "Even the main synapomorphy for all Mesozoic tooth plates (short first ridge on the upper tooth plates) does not apply for all; the primitive (plesiomorphic) features (long first ridge) appears many time on his cladogram (North American Ceratodontidae; Madagascar, South American, and Indian Pychoceratodontidae)." (SCHUL-

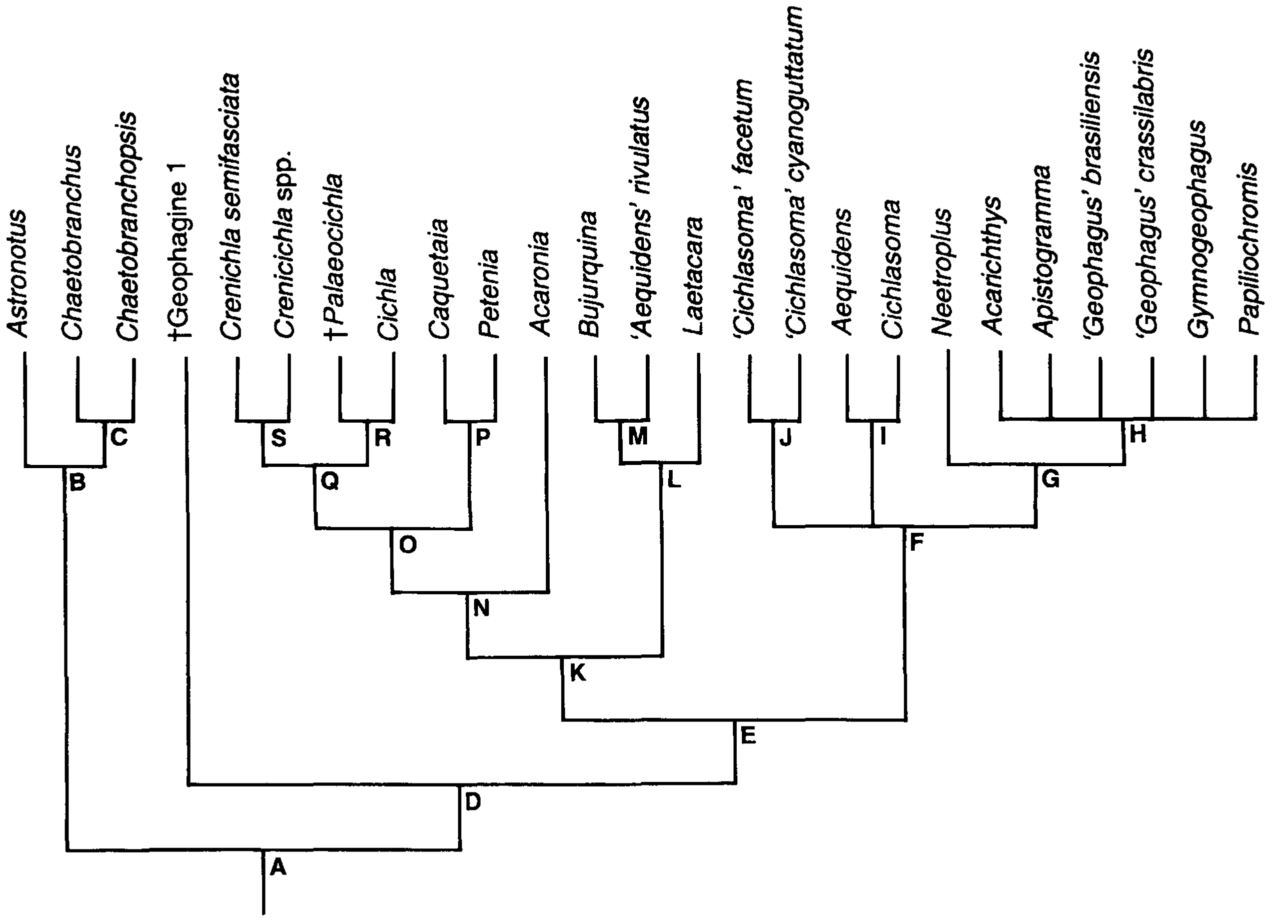


Fig. 36: An hypothesis of phylogenetic relationships of certain fossil and Recent cichlids (for explanation of characters see CASCIOTTA & ARRATIA 1993). Uniquely derived characters are indicated with an asterisk (*). **Node A:** Strongly interdigitating suture between vomerine wing and parasphenoid bar (*); lacrimal as a single element. **Node B:** Characteristic microbranchispines bearing numerous spines; complex tendon system of pharyngocleithralis internus muscle. **Node C:** Uncinate process of first epibranchial bone much longer than anterior arm of epibranchial (*). **Node D:** Six preopercular sensory canal pores. **Node E:** Four foramina in bony tube enclosing mandibular canal running in dentary. **Node F:** Tooth patches on ceratobranchial 4 separated from outer rakers. **Node G:** One supraneural. **Node H:** Five foramina in bony tube enclosing mandibular canal running in dentary; one cavity in frayed zone at caudal edge of four upper pharyngeal tooth plate. **Node I:** Uni- or tri-serial predorsal scale pattern. **Node J:** Bicuspid teeth (hooked) in upper and lower jaws. **Node K:** One concavity in frayed zone at caudal edge of fourth upper pharyngeal tooth plate. **Node L:** Uni- or tri- serial predorsal scale pattern. **Node M:** Anterior ceratohyal with groove for hyoid artery partially or completely walled. **Node N:** Remnant of Meckel cartilage between retroarticular and anguloarticular obliquely placed; unicuspid and recurved posteriorly teeth covering more than 50 % of surface of lower pharyngeal jaw; neural arch and spine of second caudal vertebra directed dorso-caudad. **Node O:** Low supraoccipital crest; tooth patches on ceratobranchial 4 separated from outer rakers; (at least) two relatively large foramina placed on lateral surface of neural arch of second caudal vertebra; medial extrascapula straight, not curved along its length nor at its distal tip. **Node P:** Absence of medial tube and of cephalic lateral line foramen 0; process on dentigerous arm ridge present; retroarticular bone extended caudad as in *Caquetaia* and *Petenia* (*). **Node Q:** Enlarged sphenotic foramen (*); presence of anteriorly notched vomer (*); remnant of Meckel cartilage between retroarticular and angular horizontally placed; five foramina in bony tube enclosing mandibular canal running in dentary; minuscule gill rakers on lateral sides of lower pharyngeal jaw; more than five inner tooth rows in upper and lower jaws; uniscuspid and recurved posteriorly teeth covering more than 50 % of surface of lower pharyngeal jaw; urohyal with a rostrally directed process (*); 34 to 41 vertebrae (*); lowermost postcleithrum with a rostrally directed spinous process (*); pharyngocleithralis muscle not originating from lateral surface of cleithrum (*); elaboration of obliquus inferioris muscle associated with first and second postcleithra (*). **Node R:** compound lacrimal including second infraorbital; lower pharyngeal jaw not fully sutured along saggital axis (*); two or more concavities in frayed zone at caudal edge of fourth pharyngeal tooth plate; tooth patches on ceratobranchial 4 not separated from outer rakers; characteristic microbranchispines bearing numerous spines absent. **Node S:** Uncinate process of first epibranchial and anterior arm of epibranchial equal in length or uncinate process a bit longer than anterior arm; (at least) two relatively large foramina placed on lateral surface of neural arch of second caudal vertebra.

TZE 1992b: 442).

MARTIN (1982b) synonymized South American ceratodonts with Madagascan and North African species. The result is a close relationship between African forms and Gondwana lungfishes, and consequently a close paleogeographic connection between Gondwana continents (also proposed by SOUZA CUNHA & FERREIRA 1980). In contrast, PASCUAL & BONDESIO (1976) linked Patagonia and Australia via Antarctica on the basis of similarities between *Ceratodus iheringi* and *Neocera-*

todus. A connection between Patagonia and Madagascar, based on similarities between *C. iheringi* and *C. madagascariensis* was hypothetized by MARTIN (1981a). These hypotheses are based on close similarities between taxa, not on unique derived characters.

After studing the South American lungfishes, SCHULTZE (1992b) hypothetized that:

1. The most closely related *Ceratodus* species between South America and Africa (e.g., *Ceratodus brasiliensis* and *C. africanus*) and between South America and Madagascar (*C. iheringi* and *C. madagascariensis*) may indicate historical relationships between South America and Africa.
2. Some Cretaceous ceratodonts show marine tolerance and, therefore, a land connection in the Cretaceous was not required to allow dispersal of ceratodonts.
3. *Lepidosiren* from South America and *Protopterus* from Africa are close relatives.
4. Both *Lepidosiren* and *Protopterus* may not be useful for indication of historical relationships between South America and Africa if the ancestor shared with either *Ceratodus humei* or *C. propteroides* was present in the Late Cretaceous.

Acknowledgments

The authors like to thank P. JANVIER (Muséum national d'Histoire naturelle, Paris) and H.-P. SCHULTZE (Museum für Naturkunde, Berlin) for comments and suggestions to the manuscript and for help with literature and providing unpublished information; P. LAMBERS (University of Groningen), for comments on the manuscript. A. CIONE thanks A. RICCARDI and E. TONNI for comments and discussions.

This work has been partially supported by several institutions. G. ARRATIA thanks to the Alexander von Humboldt Foundation, Bonn, for two Research Awards and for the Humboldt-Forschungspreis (1995); the National Geographic Society, Washington (grant No. 5118-93; The Division of Vertebrate Paleontology, Museum of Natural History, The University of Kansas, Lawrence, Kansas, and the Institut für Paläontologie, Museum für Naturkunde, Berlin. A. CIONE thanks the CONICET for permanent support to his research.

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APPENDIX 1

List of marine fishes, their localities and stratigraphy, and source of references. Within a High taxon the lower taxa are ordered alphabetically and from old to younger ages.

Taxa	Locality	Stratigraphy	References
CLASS PTERASPIDOMORPHI			
Andinaspis suarezorum	Unknown locality in the area of Cochabamba; Bolivia	Ordovician	GAGNIER 1992, 1993
Sacabambaspis janvieri	Cochabamba area; Bolivia	Anzaldo Formation; Ordovician	GAGNIER 1992, 1993; GAGNIER et al. 1989
Turiniagondwana	Seripona; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1989
CLASS PLACODERMI			
?Antiarch	Precordillera of San Juan; Argentina	Devonian	FRENGUELLI 1952; JANVIER & SUÁREZ-RIGLOS 1986
Bolivosteus chacomensis	La Paz area (between La Paz and Oruro); Bolivia	Belén Formation; Middle Devonian	GOUJET et al. 1985; JANVIER 1992a; GOUJET et al. 1993
CLASS Chondrichthyes			
Chondrichthyes gen. et sp. indet.	Bolivia	Sicasica, Belén and Huamampampa Formations; Middle to Upper Devonian	JANVIER 1992a
SUBCLASS HOLOCEPHALI			
Bradyodonti gen. et sp. indet.	La Paz area; Bolivia	Copacabana Formation; Lower Permian	MERINO-RODO & JANVIER 1986
Petalodontida gen. et sp. indet.	La Paz area; Bolivia	Copacabana Formation; Lower Permian	MERINO-RODO & JANVIER 1986
Pucapampella rodrigae	Sucre and La Paz areas (Sucre, ?Chuquisaca and La Paz Departments); Bolivia	Sicasica, Belén and Huamampampa Formations; Middle to Upper Devonian	JANVIER & SUÁREZ-RIGLOS 1986; JANVIER & DINGERKUS 1991; JANVIER 1992a
Zamponiopteron triangularis	La Paz and Sucre areas; Bolivia	Sicasica, Belén, and Huamampampa Formations; Middle Devonian	JANVIER & SUÁREZ-RIGLOS 1986; JANVIER 1992a
Zamponiopteron cf. *Z. triangularis*	La Paz and Sucre areas; Bolivia	Sicasica, Belen, and Huamampampa Formation; Devonian	GAGNIER et al. 1989
Zamponiopteron falciformis	La Paz and Sucre areas; Bolivia	Sicasica, Belén and Huamampampa Formations; Middle to Upper Devonian	JANVIER & SUÁREZ-RIGLOS 1986; JANVIER 1992a
Zamponiopteron spinifera	Bolivia	Sicasica, Belén and Huamampampa Formations; Middle to Upper Devonian	JANVIER & SUÁREZ-RIGLOS 1986; JANVIER 1992a
Order Eugeneodontiformes:			
Parahelicoprion mariosuarezi	Jacha Khatawi; Bolivia	Copacabana Formation; Lower Permian	MERINO-RODO & JANVIER 1986; JANVIER & SUÁREZ-SORUCO 1989; JANVIER 1992a
SUBCLASS ELASMOBRANCHII			
Antarctilamna scriponensis	Seripona-La Higuera; Department of Chuquisaca; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988; JANVIER 1992a
Antarctilamna sp.	La Paz area; Bolivia	Belén Formation; Middle Devonian	JANVIER, in litteris
Bolivacanthus sagitalis	Seripona-La Higuera; Department of Chuquisaca; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988; JANVIER 1992a
"Cladodus" sp.	La Paz area; Bolivia	Copacabana Formation; Lower Permian	MERINO-RODO & JANVIER 1986
Ctenacanthus	Chaqkeri, Chuquisaca; Bolivia	Iquiri Formation;	CHAMOT 1965 in JANVIER & SUÁREZ-RIGLOS 1986
Cretolamna appendiculata	Southwestern Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1898, 1901, 1906, 1935

Cretolamna appendiculata	Northern Patagonia; Argentina	Roca Formation; Paleocene	CIONE 1988
Ischyrhiza or *Dalpiazia*	Fundo El Triunfo; Peru	Celendin Formation; Upper Cretaceous	MOURIER et al. 1988
Lamnidae	T-Bagua; Peru	Bagua Formation; Upper Cretaceous	MOURIER et al. 1988
Orectolobiformes cf. *Chilocyllium*	Fundo El Triunfo; Peru	Celendin Formation; Upper Cretaceous	MOURIER et al. 1988
Paraorthacodus patagonicus	Southwestern Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1935; DUFFIN & WARD 1993
Pucabatis cf. *P. hoffstetteri*	Pongo de Rentema; Peru	Bagua Formation; Upper Cretaceous	MOURIER et al. 1988
"Scapanorhynchus" subulatus	Southwestern Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1898, 1901 1906, 1935
Scapanorhynchus subulatus	Quiriquina island and near coast; Chile	Upper Cretaceous	OLIVER SCHNEIDER 1936a; GASPARINI 1979; BIRÓ 1982
Sclerorhynchidae gen. indet. 1	Fundo El Triunfo; Peru	Celendin Formation; Upper Cretaceous	MOURIER et al. 1988
Sclerorhynchidae gen. indet. 2	T-Bagua; Peru	Bagua Formation; Upper Cretaceous	MOURIER et al. 1988
Squalicorax sp.	Southwestern Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO, 1898, 1901, 1906, 1935
Synechodus viedmani	Southwestern Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1898, 1901, 1906, 1935; DUFFIN & WARD 1993
Triakidae nov. gen.	Fundo El Trinfo; Peru	Celendin Formation; Upper Cretaceous	MOURIER et al. 1988
Trilidae nov. gen.	Pongo de Rentema; Peru	Bagua Formation; Upper Cretaceous	MOURIER et al. 1988
Carcharias sp.	Northern Patagonia; Argentina	Roca Formation; Paleocene	CIONE 1988
Carcharias striata	San Jorge area, eastern Chubut Province; Argentina	Salamanca Formation Paleocene	CIONE 1988
Carcharias substriata	San Jorge area, eastern Chubut Province; Argentina	Salamanca Formation; Paleocene	CIONE 1988
Carcharias whitei	San Jorge area, eastern Chubut Province; Argentina	Salamanca Formation; Paleocene	CIONE 1988
Carcharias macrota	Northeastern Santa Cruz Province; Argentina	San Julián Formation; upper Eocene	CIONE 1988
Carcharias acutissima	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Miocene	CIONE 1978
Carcharias acutissima	San José and Colonia Departments in southwestern Uruguay	Camacho Formation; upper Miocene-lower Pliocene	PEREA & UBILLA 1989
Carcharocles sp.	Northeastern Santa Cruz Province; Argentina	San Julián Formation; upper Eocene	CIONE 1988
Carcharocles productus	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaimán Formations; Oligocene-lower Miocene	CIONE 1988
Carcharocles megalodon	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Miocene	CIONE 1978
Carcharocles megalodon	Sacaco area; Peru	Pisco Formation; Late Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Carcharocles megalodon	Northeastern Patagonia; Argentina	Puerta del Diablo Formation; Late Miocene-lower Pliocene	CIONE 1988
Carcharocles megalodon	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
Carcharoides totuserratus	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaiman Formations; Oligocene-lower Miocene	CIONE & EXPÓSITO 1980; CIONE 1978, 1988
Carcharhinus sp.	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Middle Miocene	CIONE 1978
Carcharhinus sp.	San José and Colonia Departments in southwestern Uruguay; Sacaco area; Peru	Camacho Formation; upper Miocene-lower Pliocene Pisco Formation; upper Miocene-lower Pliocene	PEREA & UBILLA 1989 CAPPETTA in DE MUIZON 1981

Carcharhinus albimarginatus	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
Carcharhinus cf. *C. egertoni*	Sacaco area; Peru	Pisco Formation; upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Carcharhinus cf. *C. priscus*	Sacaco area; Peru	Pisco Formation; Late Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Carcharias aff. *taurus*	Sacaco area; Peru	Pisco Formation; Late Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Carcharodon carcharias	Sacaco area; Peru	Pisco Formation; Pliocene	CAPPETTA in DE MUIZON 1981
Carcharodon carcharias	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
Cetorhinus maximus	El Rincón; northern Chile	Middle Miocene	LONG 1993
Odontaspis elegans	Boca-Lebu Stage; Chile	Eocene	OLIVER SCHNEIDER 1936a
Odontaspis sp.	From north of Patagonia to Santa Cruz Province; Argentina	Gaiman Formation; Oligocene-lower Miocene	CIONE 1988
Echinorhinus pozzii	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaiman Formations; Oligocene-lower Miocene	AMEGHINO 1906; CIONE 1988
Heterodontus sp.	From north of Patagonia to Santa Cruz Province; Argentina	Gaiman Formation; Oligocene-lower Miocene	CIONE 1978, 1988; CIONE & PANDOLFI 1984
Heterodontus sp.	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Miocene	CIONE 1978
Heterodontus sp.	Sacaco area; Peru	Pisco Formation; Late Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Hexanchus griseus	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaiman Formations; Oligocene-lower Miocene	CIONE 1988
Hexanchus griseus	Northeastern Patagonia; Argentina	Puerta del Diablo Formation; Late Miocene-lower Pliocene	CIONE 1988
Hexanchus griseus	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
Hexanchus gigas (= *griseus*)	Sacaco area; Peru	Pisco Formation; Late Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Hemipristis serra	North of Patagonia; Argentina	Gaiman Formation; Oligocene-lower Miocene	CIONE 1988
Hemipristis serra	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Middle Miocene	CIONE 1978
Isurus hastalis	From north of Patagonia to Santa Cruz Province; Argentina	Gaiman Formation; Oligocene-lower Miocene	CIONE & EXPÓSITO 1980; CIONE 1988
Isurus hastalis Province; Argentina	Cliff near Paraná, Entre Ríos Middle Miocene	Paraná Formation; CIONE 1978	FRENGUELLI 1920;
Isurus hastalis	El Rincón; northern Chile	Middle Miocene	LONG 1993
Isurus hastalis	Northeastern Patagonia; Argentina	Puerta del Diablo Formation; upper Miocene-lower Pliocene	CIONE 1988
Isurus hastalis	Sacaco area; Peru Late Miocene- lower Pliocene	Pisco Formation;	CAPPETTA in DE MUIZON 1981
Isurus retroflexus	From north of Patagonia to Santa Cruz Province; Argentina	Gaiman Formation; Oligocene-lower Miocene	CIONE 1988
Isurus oxyrhinchus	El Rincón and Bahía Inglesa; northern Chile	Middle Miocene and Pliocene	LONG 1993
Isurus cf. *I. oxyrhinchus*	Sacaco area; Peru	Pisco Formation; upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Megascyliorhinus trelewensis	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaimán Formations; Oligocene-lower Miocene	CIONE 1986b, 1988
Pristiophorus sp.	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaimán Formations; Oligocene-lower Miocene	CIONE & EXPÓSITO 1980; CIONE 1978, 1988
Pristiophorus sp.	Sacaco area; Peru	Pisco Formation; upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Squatina sp.	From north of Patagonia to Santa Cruz Province; Argentina	Monte León-Gaimán Formations; Oligocene-lower Miocene	AMEGHINO 1906; CIONE 1978, 1988
Squatina sp.	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Miocene	CIONE 1978
cf. *Squalus*	San José and Colonia Departments in southwestern Uruguay	Camacho Formation; upper Miocene-lower Pliocene	PEREA & UBILLA 1989

Callorhynchus cf. *C. callorhynchus*	Sacaco area; Peru	Pisco Formation; upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Galeocerdo aduncus	Clift near Paraná, Entre Ríos Province; Argentina	Paraná Formation; middle Miocene	CIONE 1978
Sphyrna prisca	Sacaco area; Peru	Pisco Formation; upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Galeorhinus galeus	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
Myliobatis sp.	From north of Patagonia to Santa Cruz Province; Argentina	Gaiman Formation; Oligocene-lower Miocene	CIONE & EXPÓSITO 1980; CIONE 1978
Myliobatis sp.	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; Middle Miocene	CIONE 1978
cf. *Myliobatis*	San José and Colonia Depart-mentsin southwestern Uruguay;	Camacho Formation; upper Miocene-lower Pliocene	PEREA & UBILLA 1989
Dasyatidae	Cliff near Paraná, Entre Ríos Province; Argentina	Paraná Formation; middle Miocene	CIONE, per. obser.
Rajidae indet.	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
?Chondrichthyes			
Sinacanthus boliviensis	Department of Chuquisaca, Bolivia	Seripoma and Santa Rosa Formations; Lower Devonian	GAGNIER et al. 1988; JANVIER 1992a
CLASS ACANTHODII			
Indet. acanthodian	La Paz area (between La Paz and Oruro) and Sucre area Bolivia	Tarabuco, Sicasica, Belén and Huamampampa Formations; Middle-Lower Devonian	JANVIER, in litteris
Acanthodii *incertae sedis:*			
Climatius enodicosta	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988
Nodonchus rectus	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988
Onchus punctatus	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988
Onchus sicaeformis	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988
Onchus sp.	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988
Order Climatiida:			
Climatius enodicosta	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988; JANVIER 1992a
Gyracanthus seriponensis	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988; JANVIER 1992a
Gyracanthyus sp.	Seripona and La Hiquera along the Río Grande; Bolivia	Santa Rosa Formation; Lower Devonian	JANVIER 1992
Climatiidae gen. et sp. indet.	Sucre area; Kirusillas near Sudanez; Bolivia	Tarabuco Formation; Lower Devonian	JANVIER 1992a
Order Ischnacanthida			
Gomphonchus pluriformis	Seripona-La Higuera; Bolivia	Santa Rosa Formation; Lower Devonian	GAGNIER et al. 1988; JANVIER 1992a
Ischnacanthida gen. et sp. indet.	Sucre area; Kirusillas near Sudanez; Bolivia	Tarabuco Formation; Lower Devonian	JANVIER 1992a
CLASS ACTINOPTERYGII			
Actinopterygii gen. et sp. indet.	La Paz and Tarija areas; Bolivia	Sicasica, Belén, and Iquiiñi Formations; Upper Devonian	JANVIER & SUÁREZ-RIGLOS 1986; GAGNIER et al. 1989; JANVIER 1992
Actinopterygii gen. et sp. indet.	Villamontes, Tarija; Bolivia	Vitacua Formation; Upper Permian-?Lower Triassic	BELTAN et al. 1987
Cheirolepidiformes			
Irajapintoseidon uruguayensis	Río Negro, northeast Uruguay	?San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1989
Monesedeiphus depressus	Río Negro, northeast Uruguay	?San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1989

Palaeonisciformes			
Moythomasia-like form	Tarija; Iquiri Formation; Bolivia	Devonian	JANVIER & SUÁREZ-RIGLOS 1986
Palaeonisciform n. gen. et sp.	Paine Formation near Toconao, northern Chile	Carboniferous	RICHTER & BREITKREUZ (in press)
Carbonilepis uruguayensis	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Coccocephalichthys tessellatus	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1981; MONES 1986
Daphnaechelus formosus	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Elonichthys macropercularis	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Gondwanichthys maximus	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Itatarichthys microphthalmus	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Mesonichthys antipodeus	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Radinichthys rioniger	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Tholonosteus santacatarinae	Río Negro, northeast Uruguay	San Gregorio Formation; Upper Carboniferous-Lower Permian	BELTAN 1977; MONES 1986
Platysomidae gen. et sp. indet.	La Paz area; Bolivia	Copacabana Formation; Permian	MERINO-RODO & JANVIER 1986
?Saurichthyiformes			
Saurichthys-like	Lomas Negras; NE Calama city; northern Chile	Lower Cretaceous	ARRATIA 1994
HALECOMORPHI			
incertae sedis			
Caturid-like halecomorph	Cantera El Ministerio; Neuquén Province, Argentina	Tithonian	CIONE et al. 1987; CIONE in LEANZA & ZEISS 1990
Pycnodontiformes			
Pycnodontiformes indet.	Quebrada Vaquillas Altas; northern Chile	Jurassic, Sinemurian	ARRATIA, pers. obser.
Pycnodontiformes indet.	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1987a
Paramicrodon chilensis	Mina Abundancia, III Región, Chile	Aptian	BIESE 1958; SCHULTZE 1981a
Paramicrodon chilensis	Volcán region, SE Santiago; Chile	Lower Cretaceous	SCHULTZE 1981a
Macromesodon agrioensis	Bajada del Agrio; Neuquén Province; Argentina	Agrio Formation; Lower Cretaceous	BOCCHINO 1977; CIONE & PEREIRA 1990
Semionotiformes			
Lepidotes indet.	Cerritos Bayos; northern Chile	Jurassic, Oxfordian	BIESE 1957, 1961; ARRATIA 1987a
Lepidotes maximus	Cerro Lotena and Picún Leufú, Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	WAGNER in WEAVER 1931; ARAMAYO 1981; CIONE & PEREIRA 1990
cf. *Lepidotes*	Cantera El Ministerio, Neuquén Province; Argentina	Jurassic, Tithonian	CIONE et al. 1987; CIONE in LEANZA & ZEISS 1990
Semionotiformes indet.	Quebrada de San Pedrito, Copiapó; northern Chile	Triassic	SCHULTZE in CHONG & GASPARINI 1976
Semionotidae indet.	Sierra de las Quijadas; San Luis Province; Argentina	Lagarcito Formation; Lower Cretaceous	BOCCHINO 1974

HALECOSTOMI			
Atacamichthys greeni	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA & SCHULTZE 1987
cf. *Belonostomus*	Cantera El Ministerio; Neuquén; Argentina	Jurassic, Tithonian	CIONE et al. 1987; CIONE in LEANZA & ZEISS 1990
Notodectes argentinus	Mina La Valenciana; W of Malargüe, Mendoza Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1949; CIONE & PEREIRA 1990
Pachycormiform-like	Quebrada Vaquillas Altas, northern Chile	Sinemurian	ARRATIA, pers. obser.
Pachycormiformes indet.	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1987a
Pachycormus indet.	Cerritos Bayos; northern Chile	Jurassic, Oxfordian	BIESE 1961; ARRATIA 1987a
Pachycormidae indet.	Cantera El Ministerio; Neuquén Province; Argentina	Jurassic, Tithonian	CIONE et al. 1987; CIONE in LEANZA & ZEISS 1990
"Pholidophorus" argentinus (*Nomen vanum*)	Arroyo Picún Leufú; Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1939; CIONE & PEREIRA 1990
?*Pholidophorus domeykanus*	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA et al. 1975b; ARRATIA 1987a
?*"Platysomus pehuenchensis"*	Department of Malargüe; Mendoza Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	RUSCONI 1946c; CIONE & PEREIRA 1990
TELEOSTEI			
Teleostei *incertae sedis*:			
Antofagastaichthys mandibularis	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1986a, 1987a
Bobbichthys opercularis	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA et al. 1975b; ARRATIA 1986a, 1987a
Bunoderma baini	Plaza Huincul; Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1940b; CIONE & PEREIRA 1990
Chongichthys dentatus	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1982a, 1986, 1987a
Domeykos profetaensis	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA & SCHULTZE 1985; ARRATIA 1987a
"Leptolepis" argentinus (*Nomen vanum*)	Plaza Huincul; Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1940b; CIONE & PEREIRA 1990
"Leptolepis" australis (*Nomen vanum*)	Arroyo Picún Leufú; Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1939; CIONE & PEREIRA 1990
?*"Leptolepis dubius"*	Arroyo Picún Leufú; Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1939; CIONE & PEREIRA 1990
"Leptolepis" patagonicus (*Nomen vanum*)	Plaza Huincul; Neuquén Province; Argentina	Vaca Muerta Formation; Jurassic, Tithonian	DOLGOPOL 1940a; CIONE & PEREIRA 1990
"Leptolepis" sp.	North of Cerro Cuchillo, Estancia Cristina, Santa Cruz Province; Argentina	Río Mayer Formation; Early Cretaceous	D'ERASMO 1934; CIONE & PEREIRA 1990
Proleptolepids indet.	Quebrada Vaquillas Altas, Cordillera de Domeyko; northern Chile	Jurassic, Early Sinemurian	ARRATIA 1987
Protoclupea atacamensis	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA & SCHULTZE 1985
Protoclupea chilensis	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA et al. 1975c; ARRATIA & SCHULTZE 1985
Protoclupea sp.	Cerritos Bayos, Cerro Blanco; northern Chile	Jurassic, Middle-Late Oxfordian	BAEZA 1976; ARRATIA 1987a
Varasichthys ariasi	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1981a, 1984, 1987a
Teleost sp. 1	Quebrada del Profeta, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1991
Teleost sp. 2	Cerritos Bayos; northern Chile	Jurassic, Oxfordian	ARRATIA 1991
Indet. teleosts			
(= *Thrissops* of Biese)	Cerritos Bayos; northern Chile	Jurassic, Kimmeridgian	BIESE 1961; ARRATIA 1987a
Indet. teleosts	Cerritos Bayos; northern Chile	Jurassic, Kimmeridgian	ARRATIA 1987a

Indet. teleosts	Sandón, Cordillera de Domeyko; northern Chile	Jurassic, Oxfordian	ARRATIA 1987a
Tharsis-like	Cantera El Ministerio, Neuquén Province; Argentina	Jurassic, Tithonian	CIONE et al. 1987; CIONE in LEANZA & ZEISS 1990
Indet. teleost	South coast of Arroyo Bajo Comisión, Santa Cruz Province; Argentina	Río Mayer Formation; Lower Cretaceous	CIONE in AGUIRRE & URRETA 1981
Indet. teleosts	Tierra Amarilla, Copiapó; Chile	Cretaceous	ARRATIA, pers. obser.
Indet. teleost (= *"Cimolichthys"*? sp.)	North of Cerro Cuchillo, Estancia Cristina, Santa Cruz Province; Argentina	Río Mayer Formation; Upper Cretaceous	D'ERASMO 1934; CIONE & PEREIRA 1990
Clupeiformes			
Alosinae indet.	Sacaco area; Pisco Formation; Peru	Upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
"Haplospondylus" clupeoides	Around San Martin Lake, Santa Cruz Province; Argentina	Río Mayer Formation; Lower Cretaceous	CABRERA 1927;CIONE 1985; CIONE & PEREIRA 1990
Siluriformes			
cf. Ariidae	Sacaco area; Pisco Formation; Peru	Upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Tetraodontiformes			
Tetraodontiformes indet.	Sacaco area; Pisco Formation; Peru	Upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Cybiidae indet.	Sacaco area; Pisco Formation; Peru	Upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Scorpaeniformes			
Triglidae indet.	Sacaco area; Pisco Formation; Peru	Late Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Perciformes			
aff. *Psamoperca*	Sacaco area; Pisco Formation; Peru	Upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Xiphiidae indet.	Sacaco area; Pisco Formation; Peru	Upper Miocene-lower Pliocene	CAPPETTA in DE MUIZON 1981
Serranidae indet.	Bahía Inglesa; northern Chile	Pliocene	LONG 1993
Thunnus sp.	El Rincón and Bahía Inglesa; northern Chile	Middle Miocene and Pliocene	LONG 1993
Pogonias cromis	Northeastern Buenos Aires Province and southern Uruguay	Las Escobas Formation; Holocene	CIONE & TORNO 1987
CLASS SARCOPTERYGII			
Coelacanthus cf. *C. granulatus*	Tarija department, basal part of Bolivia	Late Permian Viticua Formation;	JANVIER 1992b; SEMPERE et al. 1992

APPENDIX 2

List of freshwater fishes, their localities, and stratigraphy. Within a high taxon the lower taxa are ordered alphabetically and from old to younger ages. Fishes from El Molino Formation are placed tentatively herein because there is not conclusive evidence about their paleoecological conditions.

Taxa	Locality	Stratigraphy	References
CLASS CHONDRICHTHYES			
SUBCLASS ELASMOBRANCHII			
Hybodontoidea			
Lissodus selachos	Puesto de Marileo, Ingeniero Jacobacci; Río Negro Province; Argentina	Coli Toro Formation; Upper Cretaceous	ESTES 1964; CASAMIQUELA 1978, 1984
Batomorphii			
Batomorphii indet.	Estancia Los Alamitos; Río Negro Province; Argentina	Los AlamitosFormation; Upper Cretaceous	CIONE 1987
Sclerorhynchidae			
Ischyrhiza sp.	Cerro Colorado de Tres Cruces;Jujuy Province; Argentina	Upper Cretaceous	CIONE, pers. obs.
Ischyrhiza hartenbergeri	Agua Clara, La Palca, Torotoro, Vila Vila, Hotel Cordillera; Bolivia	Molino Formation; Upper Cretaceous	CAPETTA 1975, 1992; GAYET et al. 1992
Pucapristis branisi	Quebrada de Aguas Calientes, Sierra de la Candelaria; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	SCHAEFFER 1963; POWELL 1979
Pucapristis branisi	Laguna Umayo; Peru	Vilquechico Formation; Upper Cretaceous	CIONE et al. 1985
Pucapristis branisi	La Palca, Pajcha Pata, Sayari, Torotoro, Vila Vila, Río Flora, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	CAPPETTA 1992; GAYET et. al. 1992
Schizorhiza aff. *stromeri*	Agua Clara, La Palca, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	BRANISSA et al. 1964; CAPPETTA 1992; GAYET et al. 1992
Rhombodontidae			
Pucabatis hoffstetteri	La Palca, Torotoro, Vila Vila; Bolivia	El Molino Formation; Upper Cretaceous	CAPPETTA 1975, 1992; GAYET et al. 1992
Pucabatis n.sp.	Agua Clara; Bolivia	El Molino Formation; Upper Cretaceous	CAPPETTA 1992
Dasayatidae			
Dasyatis branisai	Torotoro, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	CAPPETTA 1975, 1992; GAYET et al. 1992
Dasyatis molinoensis	La Palca, Torotoro; Bolivia	El Molino Formation; Upper Cretaceous	CAPPETTA 1975, 1992; GAYET et al. 1992
Dasyatis schaefferi	La Palca, Torotoro, Hotel Cordillera, Tiupampa; Bolivia	Molino Formation; Upper Cretaceous-Paleocene	CAPPETTA 1975, 1992; GAYET et al. 1992
Dasyatis n. spp.	Agua Clara, Rancho Hoyada; Bolivia	El Molino Formation; Upper Cretaceous	CAPPETTA 1992
Potamotrygonidae indet.	Acre river; Peru	Miocene	RICHTER 1984; FRAILEY 1986
Potamotrygonidae indet.	Cliffs near Paraná, Paraná basin	Ituzaingó Formation; upper Miocene	DEYNAT & BRITO 1994
CLASS OSTEICHTHYES			
Osteichthyes indet.	Estancia Roca Blanca, Departament of Magallanes; Santa Cruz Province; Argentina	Roca Blanca Formation; Jurassic, Liassic	HERBST 1965; BONAPARTE 1981; CIONE & PEREIRA 1987
Osteichthyes indet.	Salitral Ojo de Agua; Río Negro Province; Argentina	Allen Formation; Upper Cretaceous	POWELL 1987
Osteichthyes indet.	Ingeniero Jacobacci, Río Negro Province; Argentina	Angostura Colorada Formation; Upper Cretaceous	CASAMIQUELA 1984
CLASS ACTINOPTERYGII			
Actinopterygii incertae sedis			
Anatoia semiovata	Quebrada de Los Leones; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b

Anatoia debilis	Quebrada de Los Leones; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b
Caninchaia draghii	Quebrada de Los Leones; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b
Cenechoia paramillense	Paramillos de Uspallata; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1946a
Cenechoia sulcata	Paramillos de Uspallata; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1947
Challaia striata	El Challao; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b
?*Challaia magna*	Cerro Bayo; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1949a
?*Challaia minor*	Cerro Bayo; Mendoza Province; Argentina	Cacheuta Formation;Triassic	RUSCONI 1948a
?*Cleithrolepis cuyanus*	Quebrada de Santa Clara; Mendoza Province; Argentina	Las Cabras Formation; Triassic	BORDAS 1944
Echentaia obesa	Quebrada de Los Leones; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b
Eurynotus uspallatensis	Paramillos de Uspallata; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1946b
Guaymallenia paramillensis	Paramillos de Uspallata; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1946b
Gyrolepidoides cuyanus	Potrerillos; Mendoza Province; Argentina	Las Cabras Formation; Triassic	CABRERA 1944
?*Gyrolepidoides multistriatus*	Paramillos de Uspallata; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1946b
Mendocichthys brevis (= *Mendocinia*)	El Challao; Mendoza Province; Argentina	Potrerillos Formation; Triassic	BORDAS, 1944; SCHAEFFER 1955
Neochallaia leonensis	El Challao; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1952a
Neochallaia minor	Cerro Bayo; Mendoza Province; Argentina	Cacheuta Formation;Triassic	RUSCONI 1949b, 1952
?*Platysomus cajonensis*	Arroyo Cajón Grande, Malargüe; Mendoza Province; Argentina	Triassic	RUSCONI 1948c
?*Platysomus pehuenchensis*	Cerro Bayo; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1948a
?*Pholidophorus dentatus*	Quebrada de Los Leones; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b
?*Pholidophorus vallejensis*	Paramillos de Uspallata; Mendoza Province; Argentina	Cacheuta Formation; Triassic	RUSCONI 1947
Psamabaya tellecheai	Quebrada de Los Leones; Mendoza Province; Argentina	Potrerillos Formation; Triassic	RUSCONI 1946b
?*Radinichthys tellechai*	Cerro Bayo; Mendoza Province; Argentina	Cacheuta Formation;Triassic	RUSCONI 1948a
Actinopterygii indet.	Barda Blanca, valley of Río Grande; S Mendoza Province; Argentina	Jurassic, lower Bajocian	JAWORSKI 1926; CIONE & PEREIRA 1987
Cladistia			
Dagetella sudamericana	Vila Vila, Tiupampa Bolivia	El Molino Formation; Santa Lucía Formation; Upper Cretaceous and Paleocene	GAYET & MEUNIER 1992; MEUNIER & GAYET in press
Palaeonisciformes			
? *Birgeria*	Department of Chuquisaca; Bolivia	Vitiacua Formation; Upper Triassic	BELTAN et al. 1987
Palaeoniscoid indet.	Chinches Formation; northern Chile	Paleozoic, Lower Carboniferous	BELL 1985
Coccolepis groeberi	Sierra del Gigante; San Luis Province; Argentina	La Cantera Formation; Early Cretaceous	CIONE in BONAPARTE 1981
Coccolepis groeberi	Cerro Cóndor, río Chubut medio; Chubut Province; Argentina	?Upper Jurassic	BORDAS 1942; BOCCHINO 1978; CIONE & PEREIRA 1987

Perleidiformes			
Pseudoceaconia bracaccini	Quebrada de Santa Clara; Mendoza Province; Argentina	Las Cabras Formation; Triassic	BORDAS 1944
Pseudobeaconia elegans	Quebrada de Santa Clara; Mendoza Province; Argentina	Las Cabras Formation; Triassic	BORDAS 1944
HALECOSTOMI incertae sedis			
Pycnodontiformes			
Coelodus toncoensis	Valle del Tonco; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	BENEDETTO & SANCHEZ 1971
Coelodus toncoensis	Maimará; Jujuy Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985
Coelodus toncoensis	Las Bateas, Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985
Coelodus toncoensis	Quebrada del Arroyo de los Salteños; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE 1977
Coelodus toncoensis	Torotoro; Bolivia	El Molino Formation; Upper Cretaceous-lower Paleocene	SCHULTZE 1992a
Coelodus toncoensis	Río de los Patos, Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	BENEDETTO & SÁNCHEZ 1971, 1972; GASPARINI & BUFFETAUT 1980
Pycnodontidae gen. et sp. indet.	La Palca (Chaunaca Formation); Agua Clara, Pajcha Pata, Rancho Hoyada, Vila Vila, Hotel Cordillera, Vilcapujio (El Molino Formation); Bolivia	Upper Cretaceous	DE MUIZON et al. 1983; GAYET 1992
Pycnodontiformes indet.	Cerro Colorado de Tres Cruces; Jujuy Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE, pers. obser.
HALECOMORPHI			
Semionotiformes			
Austrolepidotes cuyanus	Sierra de las Quijadas; San Luis Province; Argentina	Lagarcito Formation; Lower Cretaceous	BOCCHINO 1974; CIONE & PEREIRA 1990
Lepidotes sp.	Quebrada de Charagua; Bolivia	Castellón Formation; Upper Triassic-Lower Jurassic	WENZ in GOÑI & HOFFSTETTER 1964; GAYET 1992
Lepidostyle enigmatica	Agua Clara, Chocaya, Vila Vila, Hotel Cordillera (?); Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992; MEUNIER & GAYET 1992
Lepidotes patagonicus (*Nomen nudum*)	Par Aike, Shehuen River, Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1900-1903, 1904; ARAMAYO 1981
Lepidotes pussillus	Sierra de las Quijadas; San Luis Province; Argentina	Lagarcito Formation; Lower Cretaceous	BOCCHINO 1974; CIONE & PEREIRA 1990
Neosemionotus sp.	Sierra de las Quijadas; San Luis Province; Argentina	Lagarcito Formation; Jurassic, Tithonian	BOCCHINO 1974
Neosemionotus puntanus	Sierra de las Quijadas; San Luis Province; Argentina	Lagarcito Formation; Lower Cretaceous	BOCCHINO 1974; CIONE & PEREIRA 1990
Paraikichthys ornatissimus (*Nomen nudum*)	Par Aike, Shehuen river; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1900
Semionotiform-like	Uruguay	Tacuarembó Formation; Upper Triassic-Lower Jurassic	WALTHER 1932; MONES 1972
Semionotidae indet.	Sierra de las Quijadas; San Luis Province; Argentina	Lagarcito Formation; Lower Cretaceous	BOCCHINO 1974; CIONE & PEREIRA 1990
Ginglymodi			
cf. *Atractosteus*	Estancia Los Alamitos; Río Negro Province; Argentina	Los Alamitos Formation; Upper Cretaceous	CIONE 1987
Lepisosteidae indet.	Cerro Colorado de Tres Cruces; Jujuy Province; Argentina	Yacoraite Formation Upper Cretaceous	CIONE, pers. obser.
Lepisosteidae indet.	El Abra; Argentina	Upper Cretaceous	CIONE, pers. obser.
Lepisosteus sp.	Agua Clara, Chocaya, Rancho Hoyada, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992
Pachycormiformes			
Protosphyraena sp.	Par Aike, Shehuen River; Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1899

Aspidorhynchiformes			
Belonostomus sp.	Puesto de Marileo, Ingeniero Jacobacci; Río Negro Province; Argentina	Coli Toro Formation; Upper Cretaceous	CASAMIQUELA 1984
?Teleostei			
"Pholidophoridae" indet.	Sierra del Gigante; San Luis Province; Argentina	La Cantera Formation; Lower Cretaceous	BOCCHINO in FLORES 1969
TELEOSTEI			
Indet. teleosts	Mina Aguilar, Jujuy Province; Argentina	Mealla Formation; Paleocene	CIONE in PASCUAL et al. 1981
Indet. teleosts	West slope of Sierra del Mal Paso, near Vizcarra river; Jujuy Province; Argentina	Lumbrera Formation; Eocene	PASCUAL et al., 1981
Indet. teleosts	Valleys of Ñirihuau, Villegas and Pichileufú rivers; coal mine of Cushamen, Río Negro; Chubut Province; Argentina	Ñirihuau Formation; Miocene	FERUGLIO 1949
Indet. teleosts	East side of the Cerro del Carbón anticlinal, southwest Bariloche, Río Negro Province; Argentina	Ñirihuau Formation; Miocene	DESSANTI 1972
Indet. teleosts	Tarija; Bolivia	Pleistocene	HOFFSTETTER 1963
Indet. teleosts	Tagua-Tagua; Chile	Cenozoic, "Upper Pleistocene"	CASAMIQUELA 1970
Teleostei incertae sedis			
Luisiella inexcutata	Cerro Cóndor; Río Chubut medio; Chubut Province; Argentina	?Upper Jurassic	BOCCHINO 1967; CIONE & PEREIRA 1987
"Tharrias" feruglioi	Cerro Cóndor; Río Chubut medio; Chubut Province; Argentina	?Upper Jurassic	BORDAS 1943; DOLGOPOL 1949a; CIONE & PEREIRA 1987
Osteoglossiformes			
Brychaetus	Huarachani; El Molino Formation; Bolivia	?Upper Cretaceous	ARGOLLO et al. 1987
Neolycoptera gracilis (*Nomen dubium*)	Jujuy; Argentina Upper Cretaceous	Yacoraite Formation;	DOLGOPOL 1939; CIONE 1986a
Phareodusichthys tavernei	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Osteoglossinae n. gen.	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Osteoglossidae indet.	Acre river, Peru	Miocene	RICHTER 1984; FRAILEY 1986
Clupeiformes			
Austroclupea zuninoi	Quebrada de la Yesera; Salta Province; Argentina	Anta Formation; Miocene	BARDACK 1961
Gasteroclupea branisai	Valle del Tonco, Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	BENEDETTO & SANCHEZ 1971; REYES 1972; CIONE & PEREIRA 1985; CIONE et al. 1985
Gasteroclupea branisai	Cerro Colorado de Tres Cruces, Jujuy Province; Argentina	Yacoraite Formation; Upper Cretaceous	SCOCCO 1948, identified as bivalves; BENEDETTO & SÁNCHEZ 1971
Gasteroclupea branisai	Barro Negro, near Tres Cruces, Mal Paso; Jujuy Province; Argentina	Yacoraite Formation; Upper Cretaceous	ORRUMA 1974, identified as bivalves; LEANZA 1989; BENEDETTO & SANCHEZ 1971
Gasteroclupea branisai	Mal Paso, Jujuy Province; Yacoraite Formation; Argentina	Upper Cretaceous	FERNÁNDEZ et al. 1973
Gasteroclupea branisai	La Puerta, Juramento Riverside; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	LEANZA 1989
Gasteroclupea branisai	Sierra de Santa Bárbara; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985
Gasteroclupea branisai	Cuesta del Obispo; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985
Gasteroclupea branisai	Rosario de la Frontera; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985

Gasteroclupea branisai	Agua Clara, Cayara, Chocaya, Hotel Cordillera, La Palca, Pata, Sevaruyo, Cayara, Estancia Blanco Rancho, Río Flora, Río Moile, Tiupampa; Bolivia	El Molino Formation; Upper Cretaceous; Paleocene	BRANISA et al. 1964; GAYET 1992; GAYET et al. 1992
(?) Cypriniformes			
Molinichthys inopinatus (*Nomen vanum*)	Agua Clara, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992
Characiformes			
Characidae indet.	Cerro La Mina, La Junta, Puente Lolén, El Tallón, Cerro Rucañanco; Chile	Cura-Mallín Formation; Miocene	RUBILAR 1994
Serrasalmidae			
Myleinae gen. et sp. indet.	Vila Vila, Hotel Cordillera, Vilcapujio (El Molino Formation); Tiupampa (Santa Lucía Formation); Bolivia	Upper Cretaceous; Paleocene	GAYET 1992
cf. Serrasalminae	Tiupampa (Santa Lucía Formation); Villa Pacheco (Impora Formation); Bolivia	Paleocene	GAYET 1992
Serrasalminae indet.	Cerro Rucañanco; Lonquimay; Chile	Cura-Mallín Formation; Miocene	RUBILAR 1994
Serrasalmus	Utoguinea river, Hallaga, Uyacali; Peru	Miocene	WILLARD 1961 and 1966 cited in HOFFSTETTER 1970
Colossoma macropomum	Paraná; Entre Ríos Province; Argentina	Entre Ríos Formation; Miocene	WOODWARD 1900; PRIEM 1911; CIONE 1978, 1986a
Colossoma sp.	Acre river, Peru	Miocene	RICHTER 1984; FRAILEY 1986
Erythrinidae			
cf. *Hoplias*	Laguna Umayo; Peru	Vilquechico Formation; Upper Cretaceous	GAYET 1992
cf. *Hoplias*	Agua Clara, Hotel Cordillera (El Molino Formation) Tiupampa, (Santa Lucía Formation); Bolivia	Upper Cretaceous, Paleocene	GAYET 1992
Hoplias n. sp.	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Characidae			
Tetragonopterinae gen. et sp. indet.	Agua Clara, Hotel Cordillera (El Molino Formation); Tiupampa (Santa Lucía Formation); Bolivia	Upper Cretaceous, Paleocene	GAYET 1992
cf. Rhoadsiinae gen. et sp. nov	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Siluriformes			
Siluriformes indet.	Arroyo Yaminué; Río Negro Province; Argentina	Coli Toro Formation; Upper Cretaceous	CIONE & LAFITTE 1980
Siluriformes indet.	Valle del Tonco; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous RINI & BUFFETAUT 1980	CIONE & PEREIRA 1985; CIONE et al. 1985; GASPA-
Siluriformes indet.	Las Bateas, Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985
Siluriformes indet.	Cerro Colorado de Tres Cruces; Jujuy Province; Argentina	Yacoraite Formation; Upper Cretaceous	SCOCCO 1948
Siluriformes indet.	Rosario de la Frontera; Salta Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE et al. 1985
Siluriformes indet.	Laguna Umayo; Peru	Vilquechico Formation; Upper Cretaceous	GAYET 1988
Siluriformes indet.	Río Moile; Bolivia	Yecua Formation; Miocene	GAYET 1992
Siluriformes indet.	Localities between Sierra del Mal Paso and Sierra de Aguilar; Jujuy Province; Argentina	Lumbrera Formation; Eocene	FERNÁNDEZ et al. 1973; CIONE 1978, 1986a
Siluriformes indet.	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992

Andinichthys bolivianensis	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Andinichthys sp.	Pajcha Pata, Estancia Blanco Rancho (El Molino Formation); Pajcha Pata, Tiupampa, (Santa Lucía Formation); Bolivia	Upper Cretaceous, Paleocene	GAYET 1992
cf. Ariidae	Estancia Los Alamitos; Río Negro Province; Argentina	Los Alamitos Formation; Upper Cretaceous	CIONE 1987
cf. Ariidae	Maimará; Jujuy Province; Argentina	Yacoraite Formation; Upper Cretaceous	CIONE & PEREIRA 1985 CIONE et al. 1985
cf. *Arius*	Paraná; Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	PEREIRA 1988
Auchenipteridae indet.	Paraná, Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	PEREIRA 1988
Bachmania chubutensis (= *Arius argentinus*)	Laguna del Hunco; Chubut Province; Argentina	La Huitrera Formation; Eocene	DOLGOPOL 1941; FERUGLIO 1949; CIONE 1978, 1986a; PEREIRA 1988
Callichthyidae indet.	Paraná, Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	CIONE , pers. obser.
Callichthyidae indet.	Acre river; Peru	Miocene	RICHTER 1984; FRAILEY 1986
Corydoras revelatus	Arroyo Abra del Trigo; Jujuy Province; Argentina	Maiz Gordo Formation; Paleocene	COCKERELL 1925; BARDACK 1961; CIONE 1978, 1986a; GIUDICI & GASCÓN OLIVER 1982
Corydoras cf. *C. paleatus*	Arroyo de Azul, Buenos Aires Province; Argentina	Luján Formation; Pleistocene	ZETTI et al. 1972; CIONE 1982, 1986a
Corydoras cf. *C. paleatus*	Paso de Otero; Buenos Aires Province; Argentina	Luján Formation; Pleistocene	CIONE 1982, 1986a
cf. Diplomystidae	Estancia Los Alamitos; Río Negro Province; Argentina	Los Alamitos Formation; Upper Cretaceous	CIONE 1987
Doradidae indet.	Paraná; Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	CIONE 1978, 1986a; PEREIRA 1988
Doradidae indet.	Acre river, Peru	Miocene	RICHTER 1984; FRAILEY 1986
Hoffstetterichthys pucai	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Hypostomus sp.	Paraná; Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	AMEGHINO 1898; CIONE 1978, 1986a; PEREIRA 1988
Incaichthys suarezi	Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Nematogenys sp.	Upper Río Queuco and Lonquimay; Chile	Cura Mallín Formation; Miocene	RUBILAR & WALL 1990; RUBILAR 1992, 1994
Pimelodidae indet.	Acre river, Peru	Miocene	RICHTER 1984; FRAILEY 1986
Pimelodella cf. *P. laticeps*	Arroyo de Azul; Buenos Aires Province; Argentina	Pleistocene	ZETTI et al. 1972; CIONE 1982, 1986a
Pimelodella cf. *P. laticeps*	Paso de Otero; Buenos Aires Province; Argentina	Luján Formation; Pleistocene	CIONE 1982, 1986a
Pimelodus sp. 1	Paraná; Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	CIONE 1978, 1986a; PEREIRA 1988
Pimelodus sp. 2	Paraná; Entre Ríos Province; Argentina	Entre Ríos Formation; Miocene	CIONE 1978, 1986a; PEREIRA 1988
Pimelodus sp.	Pehuen có, Buenos Aires Province; Argentina	Monte Hermoso Formation; Pliocene	AMEGHINO 1898; CIONE 1986a
Rhamdia cf. *R. sapo*	Paso de Otero; Buenos Aires Province; Argentina	Luján Formation; Pleistocene	CIONE 1982, 1986a
cf. *Rhineastes* sp.	Agua Clara, Chocaya, Pajcha Pata, Rancho Hoyada, Sayari, Vila Vila, Hotel Cordillera, La Palca, Estancia Blanco Rancho, Vilcapujio, Tiupampa (Río Pucarani) (El Molino Formation); Chaupi Khocha, Maragua, Pajcha Pata, Tiupampa (Santa Lucía Formation); Villa Pacheco (Impora Formation); Bolivia	Upper Cretaceous; Paleocene	GAYET 1992

Sorubiminae indet.	Paraná, Entre Ríos Province; Argentina	Ituzaingó Formation; Miocene	PEREIRA 1988
Gymnotiformes			
Ellisella kischbaumi	Río Alto Moile; Bolivia	Yecua Formation; Upper Miocene	GAYET & MEUNIER 1991a
Aulopiformes			
?*Apateodus* sp.	Agua Clara, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992
Enchodus sp.	Agua Clara, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992
?Ichthyotringoidei n.gen. and sp. indet.	Torotoro; Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992
Atheriniformes			
Atherinidae indet.	Puesto Galván, Chubut Province; Argentina	Ñirihuau Formation; Miocene	BOCCHINO 1971; CIONE pers. obser.
Atherinidae indet.	Cerro La Mina, El Tallón; Lonquimay; Chile	Cura-Mallín Formation; Miocene	RUBILAR 1994
Basilichthys aff. *regius*	Puesto Galván; Chubut Province;Argentina	Miocene	BOCCHINO 1971
cf. Cyprinodontiformes	Agua Clara, Pajcha Pata Wila Khasa, Hotel Cordillera, Estancia Blanco Rancho; Bolivia	El Molino Formation; Upper Cretaceous; Paleocene	GAYET 1992; GAYET et al. 1992
Poeciliidae indet.	Estancia Pampa Grande, between La Cueva and Toro; Argentina	Lumbrera Formation; Eocene	CIONE in PASCUAL et al. 1981
Poeciliidae indet.	Río Loro, Mataderos River (Siambón), De los Panchones river, Tucumán Province; Argentina	Lumbrera Formation; Eocene	PORTO et al. 1982
Poeciliidae indet.	Santa María Valley; Catamarca Province; Argentina	San José Formation; Miocene	FAVERI 1978; CIONE 1986a
Poeciliidae indet.	Several localities in Tucumán Province; Argentina	Río Salí Formation; Miocene	FAVERI 1978; CIONE 1986a
Perciformes			
Perciformes indet.	Estancia Los Alamitos, Río Negro Province; Argentina	Los Alamitos Formation; Upper Cretaceous	CIONE 1987
Perciformes indet.	Puesto Galván; Chubut Province Argentina	Ñirihuau Formation; Miocene	CIONE , pers. obser.
(?) Centropomidae indet.	Estancia Blanco Rancho, Tiupampa; Bolivia	Santa Lucía Formation; Paleocene	GAYET 1992
Cichlidae			
Aequidens saltensis	Quebrada de la Yesera, Salta Province; Argentina	Anta Formation; Miocene	BARDACK 1961; CIONE 1978, 1986a
cf. *Crenicichla*	Quebrada de la Yesera, Salta Province; Argentina	Anta Formation; Miocene	CASCIOTTA & ARRATIA 1993
Geophagine 1	Quebrada de la Yesera, Salta Province; Argentina	Anta Formation; Miocene	CASCIOTTA & ARRATIA 1993
Geophagine 2	Quebrada de la Yesera, Salta Province; Argentina	Anta Formation; Miocene	CASCIOTTA & ARRATIA 1993
cf. *Gymnogeophagus*	Quebrada de la Yesera, Salta Province; Argentina	Anta Formation; Miocene	CASCIOTTA & ARRATIA 1993
Paleocichla longirostrum	Quebrada de la Yesera, Salta Province (Anta Formation); and Serie de Loro Huasi, Quebrada de Cachiyuyal, Santa María de Catamarca; Argentina	Miocene	BARDACK 1961; CASCIOTTA & ARRATIA 1993
Percichthys hondoensis	Cañadón Hondo, Chubut Province; Argentina	Cañadón Hondo Formation; Eocene	SCHAEFFER 1947; CIONE 1978; 1986a; ARRATIA 1982b
Percichthys lonquimayiensis	Cordillera de Lonquimay; Chile	Cura Mallín Formation; Miocene	CHANG et al. 1978; ARRATIA 1982b; RUBILAR 1994

Percichthys sandovali	Cordillera de Lonquimay; Chile	Cura Mallín Formation; Miocene	ARRATIA 1982b; RUBILAR 1994
Percichthys sylviae	Cordillera de Lonquimay; Chile	Cura Mallín Formation; Miocene	RUBILAR & ABAD 1990; RUBILAR 1994
Percichthys sp.	Las Bayas-Cerro David; Río Negro Province; Argentina	Ñirihuau Formation; Miocene	BOCCHINO 1964; CIONE 1978, 1986a, 1988
Percichthys sp.	Ingeniero Jacobacci; Río Negro Province; Argentina	Collón Curá Formation; Miocene	CIONE 1986a
Percichthys sp.	El Tallón, Lonquimay; Chile	Cura Mallín Formation; Miocene	RUBILAR 1994
Percilia ?. sp.	Cerro La Mina, El Tallón, Lonquimay; Chile	Cura-Mallín Formation; Miocene	RUBILAR 1994
?*Santosius* sp.	El Tallón, Lonquimay; Chile.	Cura-Mallín Formation; Miocene	RUBILAR 1994
Tetraodontiformes			
Stephanodus minimus	Agua Clara, Rancho Hoyada, Hotel Cordillera; Bolivia	El Molino Formation; Upper Cretaceous	GAYET 1992; GAYET et al. 1992
CLASS SARCOPTERYGII			
Dipnoi			
Ceratodus iheringi	Par Aike, Shehuen River, Santa Cruz Province; Argentina	Mata Amarilla Formation; Upper Cretaceous	AMEGHINO 1898, 1899, 1900-3, 1904, 1906; PASCUAL & BONDESIO 1976
Ceratodus iheringi	Arroyo Yaminué, Río Negro Province; Argentina	Coli Toro Formation; Upper Cretaceous	AMEGHINO 1898; PASCUAL & BONDESIO 1976; CIONE & LAFFITTE 1980
"Ptychoceratodus" iheringi	Estancia Los Alamitos, Río Negro Province; Argentina	Los Alamitos Formation; Upper Cretaceous	BONAPARTE 1987; CIONE 1987
Ceratodus sp.	Puesto de Marileo, Ingeniero Jacobacci, Río Negro Province; Argentina	Coli Toro Formation; Upper Cretaceous	WICHMANN 1924, 1927; CASAMIQUELA 1978,1984; PASCUAL & BONDESIO 1976; CIONE & LAFITTE 1980
Ceratodont n. gen. et sp.	Tiupampa, Bolivia	Santa Lucía Formation; Paleocene	SCHULTZE 1992b
Ceratodus sp.	Tiupampa, Bolivia	Santa Lucía Formation; Paleocene	SCHULTZE 1992b
Lepidosiren cf. *L. paradoxa*	Laguna Umayo, Perú	Vilquechico Formation; Upper Cretaceous	SIGÉ 1968; MARSHALL et al., 1985
Lepidosiren cf. *L. paradoxa*	Pajcha Pata; Bolivia	El Molino Formation; Upper Cretaceous	SCHULTZE 1992b
Lepidosiren cf. *L. paradoxa*	Tiupampa, Bolivia	Santa Lucía Formation, Paleocene	SCHULTZE 1992b
Lepidosiren paradoxa	Localities between Sierra del Mal Paso and Sierra de Aguilar, Jujuy Province; Argentina	Lumbrera Formation; Eocene	FERNÁNDEZ et al. 1973; CIONE 1978, 1986a