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Tropical freshwater teleosts from Miocene beds of eastern Patagonia, southern Argentina

Téléostéens d'eau douce brésiliens dans des couches d'âge miocène dans le nord-est de la Patagonie, Argentina

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Abstract

Loricariid and pimelodid-like siluriforms—along with undetermined percomorph—are described for the first time from Patagonia. Vertebrate fossils, including fish, mammals and birds, were found in beds attributed to the top of the Puerto Madryn Formation. These levels supposedly corresponded to the "Rionegrense marino" of former authors. Mammals occurring in the site suggest a Huayquerian age for the fossiliferous beds. The base of the Huayquerian was dated at about 9 Ma and the top is younger than 6.5 Ma. Radioisotopic dating in the marine shell beds of the Puerto Madryn Formation ranges from 11 to 9 Ma. Consequently, the section described here appears to be younger than the typical Puerto Madryn Formation from which it is separated by an unconformity. The section is correlated with the type Río Negro Formation from northern Patagonia, which also includes Huayquerian fossils. Freshwater fishes were previously unknown in beds younger than the middle Miocene in southern South America. This is also the southernmost record of loricariid fishes. The association of aquatic continental and terrestrial vertebrates indicates for the first time in Península Valdés beds of freshwater origin. The evidence apported by fossils is also in agreement with global climate trends. The local extinction of loricariids in Patagonia possibly occurred much later than the time of deposition.

Résumé

Siluriformes Loricariidae et Pimelodid-like sont décrit pour la première fois dans la Patagonie, Argentina. Ces poissons ont été trouvé avec Percomorpha indéterminés, mammifères et oiseaux continentales. Les Loricariidae trouvés sont les plus australes connues. Les fossiles on été enregistrés dans niveaux attribué à la Formation Puerto Madryn. Ces niveaux on été correlationés avec le "Rionegrense marino" des autheurs anciennes. Les mammifères trouvés dans le site suggérent une âge Huayquérien. La limite inférieur du Huayquérien a été daté ca 9 Ma et le plafond est plus jeune que 6,5 Ma. Études radiometriques indiquent que les niveaux marines de la Formation Puerto Madryn embrassent de 11 au 9 Ma. En consequence, la section décri ressemble être plus jeune que la Formation Puerto Madryn typique de laquelle est séparée pour une discordance. La section pourrait être correlacioné avec la Formation Río Negro typique du nord de la Patagonie laquelle aussi inclue mammifères huayquériens. Jusqu'à ce jour, poissons d'eau douce on été unconnue dans niveaux plus jeunes que le Miocène moyen dans la partie australe de l'Amérique du Sud. Bien plus, très peux vertébrés sont connues dans niveaux plus jeunes que le Miocène moyen dans la Patagonie. Jusqu'à ce travail, seulement quelques mammifères on eté raportées dans le Miocène et dans le Pleistocène supérieur dans la région. La peculiar association de vertébrés aquatiques d'eau douce et terrestres signale un climat au moins temperé pour le Miocène supérieur

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dans la Península Valdés. L'evidence apporté pour les fossiles est aussi d'accord avec la tendance climatique global. En fin, il est vraisemblable que la extinction locale de Loricariidae a été lieu plus tard que l'époque ou le niveau avec le fossiles a été déposé.

Keywords: Miocene; Argentina; Siluriformes; Loricariidae; Percomorpha; Continental; Paleogeography; Biochronology

Mots clés : Miocène ; Argentine ; Siluriformes ; Loricariidae ; Percomorpha ; Continental ; Paléógéographie ; Biochronologie

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1. Introduction

An assemblage of freshwater and terrestrial vertebrates was found in late Miocene beds assigned to the upper part of the Puerto Madryn Formation, in a coastal site located between Punta Delgada and Pico Lobo in the Península Valdés, eastern Chubut, southern Argentina (Fig. 1). The site was discovered by personnel of the Centro Nacional Patagónico (Puerto Madryn, Chubut) in 1997 and visited several times thereafter (see Dozo et al., 2002). No other association of this kind is known in Neogene beds of Patagonia. In the present paper, the fishes are described, the stratigraphic provenance is discussed, and some biogeographic and paleoclimatic features are noted. All the material is deposited in the Museo de Paleontología "Egidio Feruglio" of the city of Trelew, Chubut, Argentina.

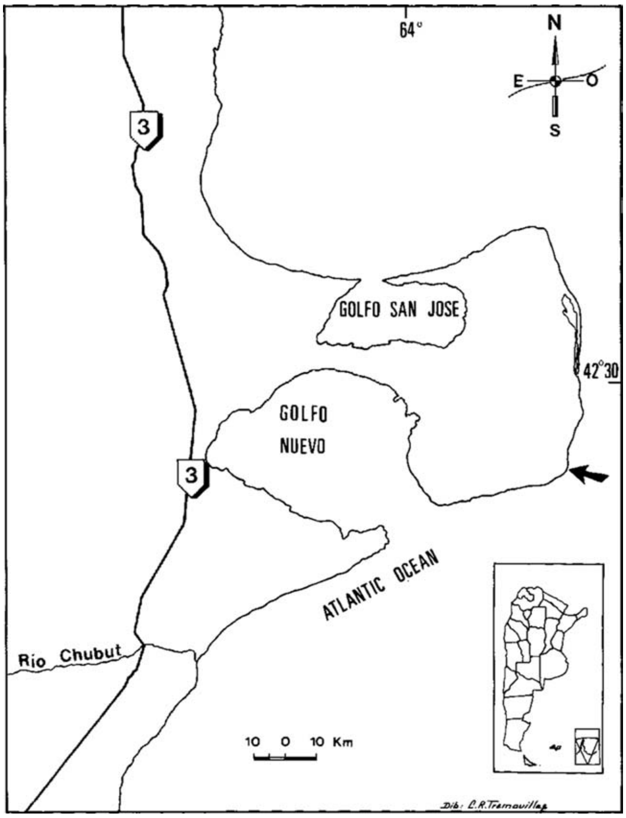

Fig. 1. Locality map (modified from Scasso and del Río, 1987). The arrow indicates Punta Delgada at Península Valdés.

2. Stratigraphic setting

Southern South America (Patagonia) was deeply invaded by the sea during the earliest Neogene but the Pampean area was emergent at this time. Since the middle-late Miocene, basculation of southern South America provoked that Patagonia had become almost free of marine sedimentation, excepting in its northeastern area. During this time, the sea deeply penetrated into the Pampean area as a large gulf, reaching at least to Bolivia (Yrigoyen, 1975; Uliana and Biddle, 1988; Aceñolaza, 2000; Cione et al., 2000; Marengo, 2000). First workers that described the sediments deposited in this encroachment were d'Orbigny (1842); Darwin (1846). Later, Doering (1882); Ameghino and Woodward (1897); Ameghino (1906); Rovereto (1921); Frenguelli (1926); Feruglio (1949) established the stratigraphic scheme that included the "Patagoniense," "Entrerriense," and "Rionegrense" stages for the local representation of the Neogene (for a synthesis, see Feruglio, 1949; Cione, 1988; Scasso and del Río, 1987). The "Patagoniense" and "Entrerriense" are marine in origin. The "Rionegrense" in its type locality, the río Negro area, is almost exclusively continental. However, in the Península Valdés area, beds assigned to the "Rionegrense" were mostly marine, with some strata of a putatively continental origin in the top. Capping the sequence, conglomerates called "Rodados tehuelches" widely crop out in eastern Patagonia (see Feruglio, 1949). All units older than the "Rodados tehuelches" were informal chronostratigraphic units, which were recognized on the basis of lithology, stratigraphic relationships and fauna (see discussion in Cione and Tonni, 1995a,b,1999).

The "Patagoniense" and "Entrerriense" are clearly separated by an unconformity but the "Entrerriense" was considered to pass transitionally to the "Rionegrense" in the Península Valdés region (Feruglio, 1949). In this context, the "Patagoniense" strata in the area have been included in the Gaiman Formation (Haller, 1979,1981) and, due to the alleged transitional relationships between the "Rionegrense" and "Entrerriense," the strata of both units were included in only one lithostratigraphic unit, the Puerto Madryn Formation (Haller, 1979; see also Scasso and del Río, 1987). More to the north, in the type area, the continental beds of the "Rionegrense" is more clearly distinguished from the "Entrerriense" which is named Formación Barranca Final there (Zambrano, 1980). Moreover, Andreis (1965; see also Angulo and Casamiquela, 1982) proposed the Río Negro Formation, and Kaaschieter (1965) the Belén Formation, for including the "Rionegrense" beds. Recently, Malumián (1999), in a gen-

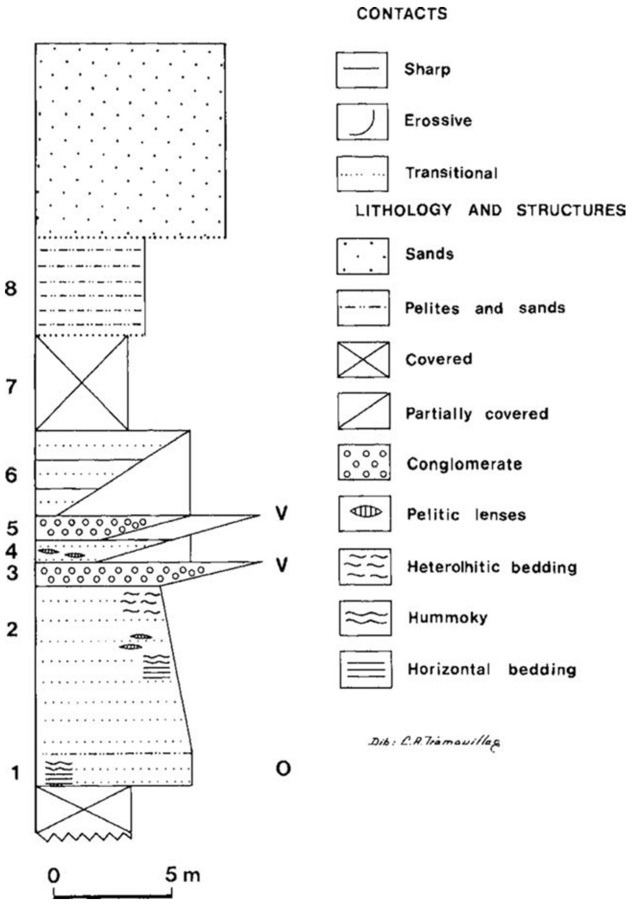

Fig. 2. Section at 3 km to the west of Punta Delgada (modified from Dozo et al., 2002). Fossils: V = vertebrates; O = oysters.

eral work, assigned the "Rionegrense" beds in Península Valdés to the Río Negro Formation. However, this author did not establish the boundaries.

The Puerto Madryn Formation consists of chestnut to yellow in color heterolithic and cross-bedded sandstones, muddy sandstones and sandy mudstones interbedded with white tuffs (Del Río et al., 2001). The unit includes abundant, well preserved invertebrate remains disposed frequently in shell beds. In the top of the sequence (the "Rionegrense"), gray colors predominate (Scasso and del Río, 1987). The Puerto Madryn Formation is about 150 m thick and is recognized as such in the Península Valdés area (Del Río et al., 2001). Correlative sediments crop out to the north. The unit has been distinguished in the lower río Chubut valley, to the south of Península Valdés (Mendía and Bayarsky, 1981). However, other authors suggested that they are not correlative (Scasso and del Río, 1987).

In the Puerto Madryn Formation, an upward-shallowing from open mid-shelf to more restricted shoreface–foreshore environments has been recently proposed for the whole sequence (Del Río et al., 2001). Transgressive, Maximum Highstand, and Regressive phases were recognized in the lowermost 75 m of the formation based on an integrated approach of assemblages and lithofacies arrangement (Del Río et al., 2001). The Maximum Highstand Phase refers to deposits accumulated when the sea level was at its maximum, before the regression took place (ibid.). Consequently, these authors use this term in a different way in which is used in sequence stratigraphy. The Regression Phase represents the gradual regression of the sea (Scasso and del Río, 1987) and corresponds to the "Rionegrense" of Feruglio (1949) and probably to the Río Negro Formation of Malumián (1999). As a result of sediment aggradation, the entire system prograded and depocentres shifted to the east and northeast during deposition. The uppermost part of the sequence include paleosoils (Del Río et al., 2001).

2.1. Profile at Rincón Chico

The fossiliferous locality with the continental fishes here described is located in the marine cliffs between Punta Delgada and Punta Lobo (about 3 km to the west from Punta Delgada; 42°47′ S, 63°40′ W), Estancia Rincón Chico, southeastern Peninsula Valdés, provincia del Chubut, Argentina (Fig. 1).

The sequence constitutes a coastal front of erosion that rises approximately 40 m above sea level (Fig. 2). The action of the eolian, gravitational and hydric gliding processes has caused that part of the sedimentary sequence be covered with recent deposits, especially in their basal section. The basal section of the profile is covered by 13 m of colluvial and alluvial material.

In the profile, eight main levels, numbered from the base, were distinguished (Fig. 2). The base is covered by the beach sediments.

Level 1 is 1.5 m thick and is mainly formed by medium grained sandstone of gray to gray clear chestnut color with occasional intercalations of white (in dry) and yellowish brown (in humid) mudstones. The level is fairly consolidated and includes horizontal stratification which, in sectors, is undulate. Towards to the top there is a thin bed of few disarticulated oysters. The oysters are whole and frequently arranged with the concavity of the valves down. This is the only presence of marine invertebrates in the section. We also did not find bioturbation.

Level 1 passes to level 2 by means of a transitional contact. It is 7.5 m thick, with medium grained sandstones of moderate consolidation and gray to gray clear chestnut color. The grain is finer towards the upper part of the level, with pelitic lenses of 1–3 cm maximum thickness. The dominant internal structure is horizontal bedding. Cross-bedding in trough becomes more conspicuous toward the top. Occasionally, there are flat cross-bedding of small scale, asymmetric and symmetrical ripple marks, and heterolithic facies with prevalence of flaser stratification for sectors. Black layers of opaque minerals with levels with yellowish chestnut ferruginous stains, inserted as fine sheets intercalated with gray sands with undulate stratification and levels with ripple marks are common.

A lenticular bed (level 3) of 1 m maximum thickness overlies level 2 with an erosive net contact. It is an oligomictic conglomerate with interbedded mudstones and fine and medium grained sands in sheets less than 1 cm thick. The coarser clastic fraction, whose grain size varies from thick to fine gravel, is composed of rounded pelitic intraclasts (in sectors discoidal), of white (in dry) and clear olive gray (in humid) color. Internally, the body presents cross-bedding in trough. The top of level 3 includes remains of continental vertebrates as bioclasts. The stronger consolidation of this level in comparison to the underlying and overlying levels is easily identifiable in the sequence because form a bank.

Level 4 is a sandy horizon of greenish gray color 1 m thick. It is partially covered and finely laminated. Occasionally, it presents pelitic lenses similar to those of levels 1 and 2. We found vertebrate remains on the sands but when we screened them a while, no fossil occurred. We do not discard that vertebrates come only from the levels 3 and 5.

Another lenticular body (level 5) of approximately 1 m thick, partially covered, overlies level 4 by means of an erosive contact. It is composed of an oligomictic conglomerate, similar to that of level 3, but with finer granulometry. In this level we also found vertebrates.

Level 6 is composed of 4 m of fine gray sandstones and greenish gray mudstones, horizontally interbedded, in some cases with criss-cross stratification of low angle. This level is partially covered except in those tracts where the biggest consolidation, generally of the sandy strata, causes small topographical projections.

The overlying colluvial and alluvial material (level 7) is 4 m thick and masks completely the profile.

The uppermost level (level 8) is a consolidated horizon 5 m thick of grayish green to yellowish mudstone with parallel lamination. To the top, a thin interstratification of fine and very fine gray sandstone occurs. The profile culminates with 8 m of eolic, partially vegetated sands that constitute the coastal dunes.

3. Systematic paleontology

Order SILURIFORMES sensu Grande, 1987.
Siluriformes indet.
Fig. 3.

Material: The material consists of fragmented pectoral spines: MPEF-PV 2500, 6 ex.; MPEF-PV 2501, 1 ex.; MPEF-PV 2502, 2 ex.; MPEF-PV 2503, 7 ex.

Description: Spines medium-sized (maximum shaft width measured, 5.5 mm), dorsoventrally compressed, without anterior serrations but with a strong anterior longitudinal rib (Fig. 3.1). Anterior part of dorsal and ventral faces without striae. Rest of dorsal and ventral faces with large longitudinal striae. Posterior face with a shallow sulcus, a large proximal foramen, and medium-sized serrations (Fig. 3(2)). Serrations placed immmediately distad to foramen, proximally perpendicular to axis of shaft. Dorsal process of spine base rectangular, with radial fine striae (Fig. 3(3,4)).

Discussion: The spines are overall most similar to “*Pimelodus*-group” (Lundberg et al., 1991) plus Heptapteridae with strong spines, especially *Pimelodella*, *Rhamdia*, *Brachyrhamdia*, and *Rhamdella*. Also resemble most genera of Ageneiosidae.

The spines are distinct from the weakly ossified and flexible spines of Cetopsidae, Trichomycteridae, many Heptapteridae, and some *Calophysus*-group Pimelodidae; from that of non-Trycomycteridae Loricarioidei because of absence of odontodes; from Doradidae, Aspredinidae, most Auchenip-

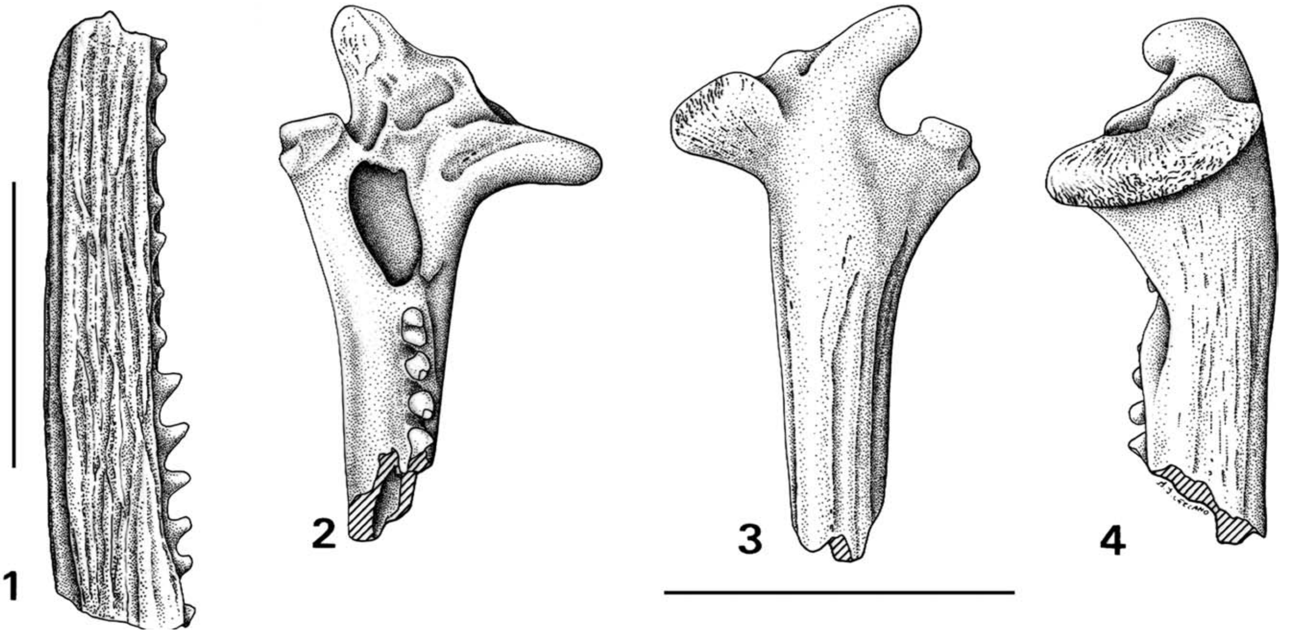

Fig. 3. 1. Pectoral-fin spine of Siluriformes indet., MPEF-PV 2503-1, showing the anterior longitudinal rib. 2. Pimelodid-like pectoral-fin spines, MPEF-PV 2500-1, posterior view with serrae. 3, 4. Anterior and dorsal view of the same specimen showing the articular surface of the head spine. Scale bars = 1 cm.

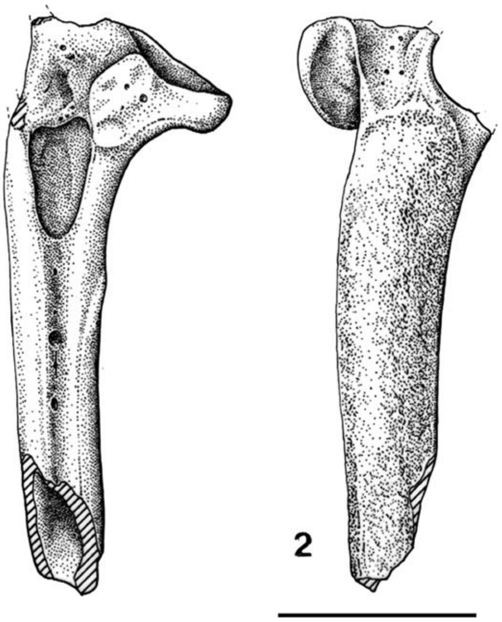

Fig. 4. Pectoral spine of Loricarioidei, MPEF-PV 2505-1. 1. Posterior view showing the large foramen, and the sulcus. 2. Dorsal view showing numerous odontode bases. Scale bar = 1 cm.

teridae and some Pimelodidae for the absence of very strong serrations along anterior edge; and from Diplomystidae for the type of serrations and the presence of a posterior sulcus.

Suborder LORICARIOIDEI

Figs. 4 and 5

Material: Most of the material is fragmentary. Pectoral and dorsal spines: MPEF-PV 2504-2 and 3, 2 ex.; MPEF-PV 2505, 4 ex. Plates: MPEF-PV 2507, 1 ex.; MPEF-PV 2508, 4 ex.; MPEF-PV 2509, 3 ex.; MPEF-PV 2510, 4 ex.; MPEF-PV 2511, 2 ex.

Description: Pectoral spines: Spines medium-sized (maximum shaft width measured, 7.0 mm), subcircular in section, without anterior serrations (Fig. 4(2)). Many bases of odontodes well defined, and densely packed on anterior surface of spine shaft. Posterior face with a very shallow sulcus and a large proximal foramen (Fig. 4(1)). Most spine fragments with a quadrangular, finely striated dorsal articular process; spine base with small holes and a central foramen. Another fragment with a small rectangular articular surface present, bearing granulations on surface, and a posterodorsally placed foramen.

Plates: The largest fragment (maximum length: 22.5 mm; Fig. 5(1)) semicircular in outline. Part of external plate surface unornamented and remaining area strongly ornamented and covered with bases of odontodes.

Family LORICARIIDAE

Figs. 5 and 6

Material: Cleithrum: MPEF-PV 2506, 1 ex. Skull roof undetermined bone: MPEF-PV 2512, 1 ex. Plate: MPEF-PV

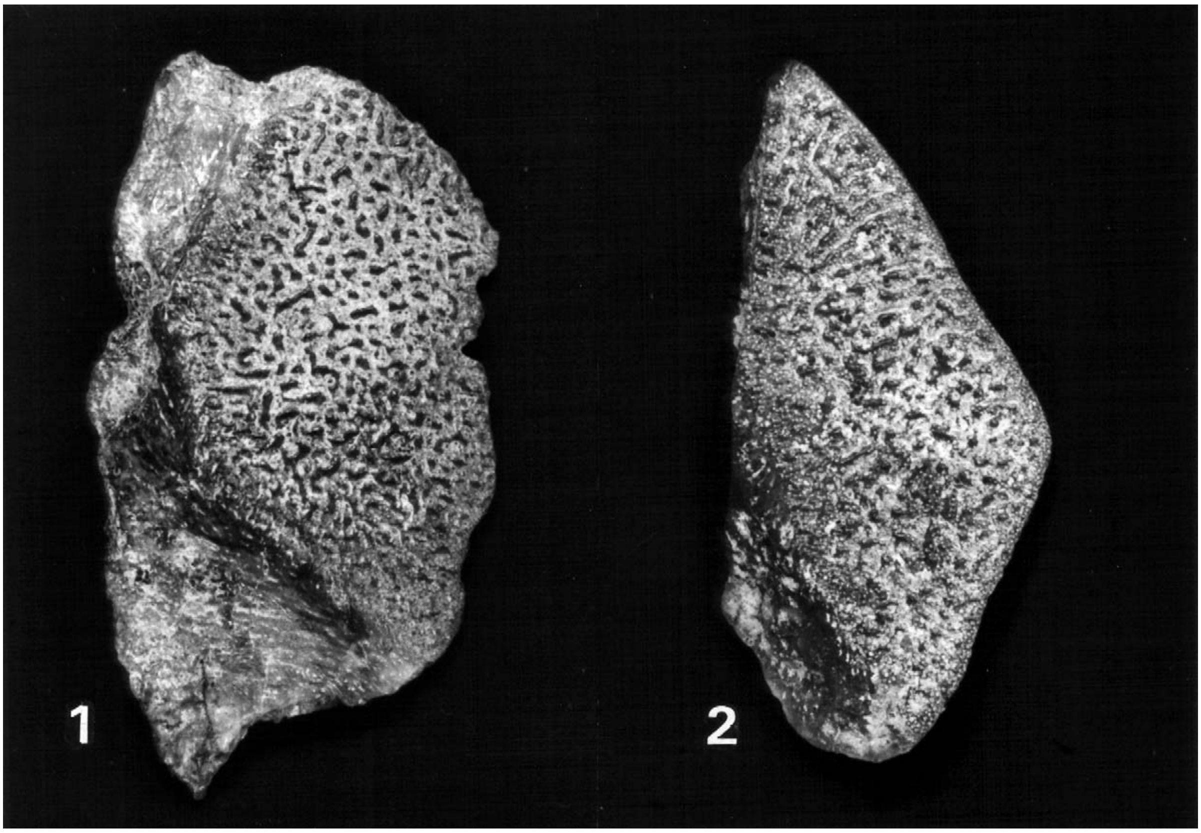

Fig. 5. 1. Plate of Loricarioidei, MPEF-PV 2511-1. 2. Plate of Loricariidae, MPEF-PV 2507-1, ×4.

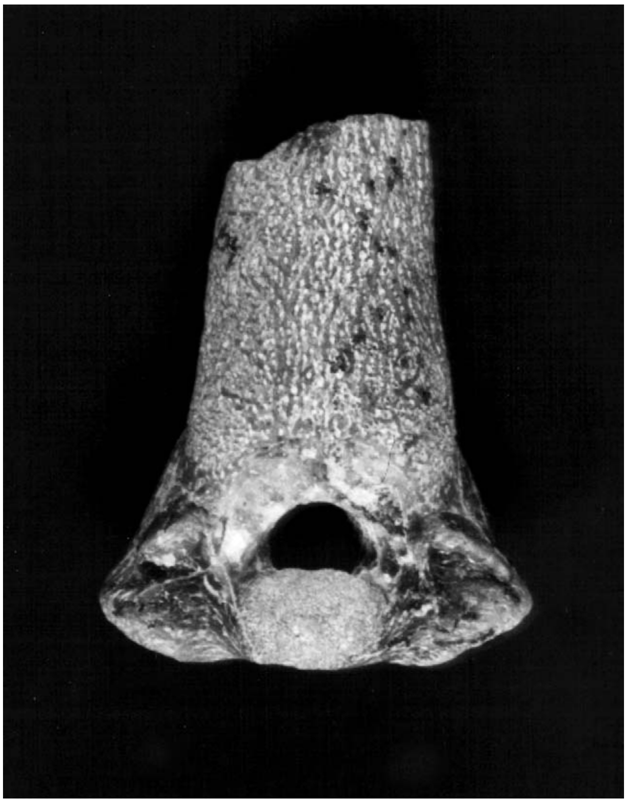

Fig. 6. Dorsal spine base of Loricariidae, MPEF-PV 2505-2, ×4.

2511-1. Dorsal spines: MPEF-PV 2505-2, 1 ex., MPEF-PV 2504-1, 1 ex.

Description: Plate (Fig. 5(2)): Plate with wide anastomosed costae (maximum width: 25.0 mm). Odontode bases numerous and distributed both on costae and sulci between costae.

Dorsal spines (Fig. 6): Spines medium-sized (maximum base width measured, 11.5 mm), subcircular in section, posteriorly flat without sulcus in one fragment and a very shallow sulcus in another. Anterior and lateral surfaces with longitudinal striae and bases of odontodes.

Cleithrum: Lateral piece of cleithrum, bearing a portion of an articular sulcus for pectoral spine. Lateral surface with odontode bases between costae.

Skull roof: Many ridges on surface covered by odontode bases.

Discussion: Some plates were eroded and odontode bases and costae are less well defined. The morphology of dorsal spines and the presence of odontode bases both on ridges and striae of cleithrum, skull roof, and plates strongly resemble features characteristic of Loricariidae.

ACANTHOPTERYGII

PERCOMORPHA

Figs. 5,7 and 8

Material: All material is fragmentary. Fin rays: MPEF-PV 2513, 1 ex.; MPEF-PV 2514, 7 ex. Dentary: MPEF-PV 2515-1–3, 3 ex.; MPEF-PV 2518, 1 ex.; MPEF-PV 2516, 5 ex. Fragment of anguloarticular: MPEF-PV 2515-4, 1 ex. Premaxilla: MPEF-PV 2519, 2 ex. Opercle: MPEF-PV 2517, 2 ex.

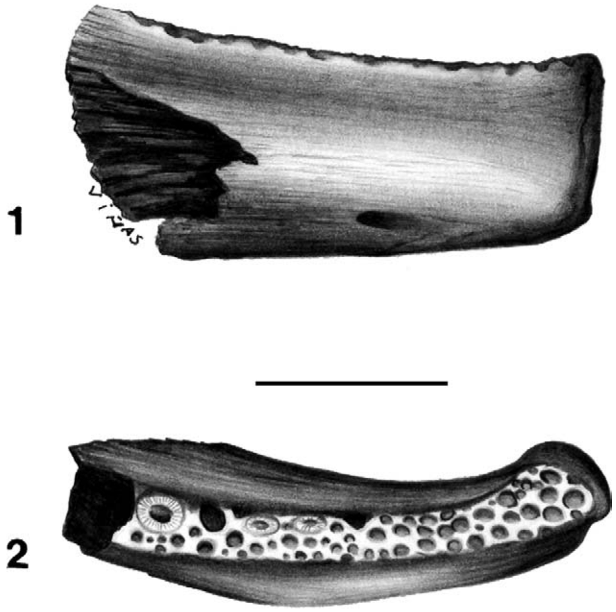

Fig. 7. Percomorpha, dentary, MPEF-PV 2518. 1. External view showing the roofed sensory mandibular canal. 2. Oclusal view showing large tooth sockets in the inner row. Scale bars = 1 cm.

Description: Fin spine: One fin spine with the articular portion preserved.

Opercles: Fragments bearing the articular area for hyomandibula. One of them with some striae on its external surface.

Dentaries (maximun symphyseal depth: 7.0 mm; Fig. 7): Only anterior fragments, including symphysis well preserved. External face with first and second foramina of laterosensory canal clearly distinguished; canal roofed between both foramina (Fig. 7(1)). Fragments dorsally bearing many rounded tooth sockets of different size. Along dorsal margin, three rows of tooth sockets present, inner one largest. Wall of those sockets growing dorsally forming a flamingo nest-like structure. Walls of those sockets thicker than wall of external ones, ornamented with numerous striae, radial in oclusal view. Largest socket placed at level of second laterosensory canal foramen (Fig. 7(2)).

Anguloarticular (maximun depth: 10.7 mm): Fragment of anguloarticular bearing articular fossa. External surface completely covered with striae. Posterior process well developed, lacking retroarticular.

Premaxilla: Small fragments of premaxillae, dentigerous branch shallow (Fig. 8(1)) with two rows of teeth distally (Fig. 8(2)), and an inner row of large tooth sockets. Several tooth rows of small sockets near symphysis (Fig. 8(3)). Largest sockets of same morphology than those described for dentary.

Discussion: The characteristic stiff fin spines are an obvious character of Acanthopterygii (Lauder and Liem, 1983). The material differs from Mugilomorpha and Atherinomor-

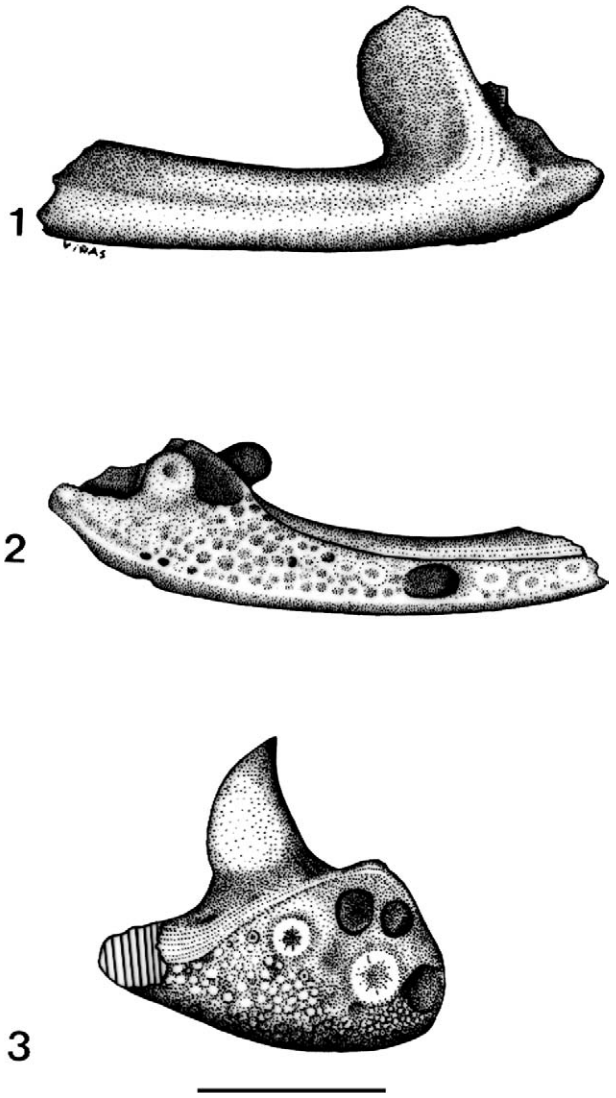

Fig. 8. Percomorpha, premaxillae. 1, 2. MPEF-PV 2519-1, lateral and oclusal views. 3. MPEF-PV 2519-2, oclusal view showing several rows on the symphysis. Scale bars = 1 cm.

pha and most closely resemble percomorphs. In the premaxillas and dentaries from Punta Delgada, teeth are not preserved but large sockets occur. Large sockets on dentary and premaxilla are usually associated with large (caniniform) teeth. Large canines are only ocassionally encountered in percoids (Sasaki, 1989). One of the taxa where canines are found is the Family Sciaenidae. However, the morphology of dentary canal in the fossil does not resemble that of sciaenids and the disposition of the intermediate teeth is different to that of sciaenids with large teeth such as *Macrodon* and *Cynoscion*.

4. Paleoenvironment

In the Punta Delgada area, Rovereto (1921 in Frenguelli, 1926) described and figured a profile that included the complete sequence of "Entrerriense," "Rionegrense continental," and "Rionegrense marino." Castro (1981) described the sedimentology of a profile and Scasso and del Río (1987: 303) described in detail another profile. These sections do not agree with that which includes the vertebrates described herein. However, we observed complete sections of "Entrerriense" closeby to the West, which appear to correspond with profiles of Castro (1981); Scasso and del Río (1987).

In the Punta Delgada section, the contact of the "Rionegrense continental" with the marine "Entrerriense" beds is not clear, but appears to be an erosive unconformity in a paleochannel.

The lower and middle portions of the sequence were certainly deposited in an aquatic environment. Dozo et al. (2002), based on geologic evidence, suggested that sedimentation occurred in a marine environment near to the coast, linked to intertidal environments and alternation of underaerial and underwater exhibition. The identified structures allow us to infer a dynamic of sedimentary transport characterized partly by alternation of wave action and channelized coastal currents, and calmer periods with sedimentation of silts and clays. The sedimentary characteristic identified in the profile appeared to present similarities with the facies 4b (interbedded sandstones and pelites) and 5 (crossbedded sandstones) defined by Scasso and del Río (1987) for other stratigraphical sections in the Península Valdés area. These facies correspond respectively to: (4b) sedimentation in tidal plains with sandy bars disposed perpendicularly to the coast and parallel to tidal channels with those that are linked genetically and (5) sedimentation in channels and streams in intertidal and undertidal area product of a normal sedimentation not related with catastrophic episodes.

A different interpretation, however, could be derived from stratigraphic and fossil evidence. The section with vertebrates appears to have been deposited in a paleochannel excavated into the typical marine, richly fossiliferous, beds of the "Entrerriense" (the "spectacular marine Miocene shell beds" of Del Río et al., 2001). In these marine beds, bivalves of the families Carditidae, Veneridae, Glycymeridae, Pectinidae, and Ostreidae, gastropods of the families Muricidae and Architectonicidae, echinoderms of the family Monophorasteridae and brachiopods of the family Terebratulidae are abundant (Scasso and del Río, 1987). Most occur in post-mortem accumulations. Contrasting with this richness, there are no marine fossils in all the sequence of Punta Delgada, except for a very thin oyster (Ostreidae) accumulation one shell thick in the base (level 1). Oysters are "secondary soft-bottom dwellers" (Del Río et al., 2001: 5). Specimens detected in the profile correspond to the "recliner boulder-shaped" ecophenotype of *Ostrea patagonica*, with shells that lie on the left convex valve (Del Río et al., 2001: 6). A complete marine section with remarkable invertebrate content and strongly cemented banks crops out at 200 m to the West. Scasso and del Río (1987: 303) had described the section at Punta Delgada including coquines with shells in life position, coquines with sandy matrix and bioturbation. Consequently, the section described by these authors is not ours.

According to Scasso and del Río (1987), shells occur in the facies 4b although they are not very abundant; bioturbation is composed of burrows 2 cm wide and vertical tubes 10 cm long. Facies 5 include abundant small shell fragments but bioturbation is occasional. We did not find shells nor bioturbation in the section excepting by the thin oyster bank. Quite the contrary, in levels 3–5, several fishes, birds and mammals mostly indicate a continental environment. Loricariid and pimelodid indicates freshwater environments. The percomorph are indeterminate but could represent a freshwater or diadromous group. In the same levels, birds and mammals strongly linked to freshwater habitats (threskiornitids, dendrocygnids, hydrochoerid capibaras) and terrestrial mammals (pampatheriids, glyptodontids, mylodontids, chinchillids, caviids, and macrauchenids) occur. Similar associations of freshwater and terrestrial vertebrates are found, at many other sites, such as the Huayquerian basal conglomerate of the Ituzaingó Formation in the Provincia de Entre Ríos (Cione et al., 2000) and the Pleistocene beds in the río Sauce Grande valley in southern Provincia de Buenos Aires (Cione and López Arbarello, 1995), both in Argentina. The basal fossiliferous conglomerate of the Ituzaingó Formation overlies the earliest Tortonian upper beds of the Paraná Formation, which is correlative with the marine sections of the Puerto Madryn Formation (dated between 11 and 9 Ma). The Ituzaingó and Paraná formations are separated by an important unconformity.

We here suggest that fossiliferous levels 3–5 were deposited in a freshwater channel, not far from the sea. This hypothesis is supported not only by vertebrate evidence but for the absence of any marine invertebrate or vertebrate remains. The undetermined percomorph would represent an unknown freshwater species or an occasional penetration of an active swimmer in the lower part of a stream (as many marine fishes do today). The lower level had some kind of marine influence indicated by the thin oyster bank. In the site, at least a short event of normal marine salinity enough to permit the establishment of the oysters occurred.

Del Río et al. (2001: 18) commented that “no definitive of brackish or freshwater (fluvial) have been found in the Península Valdés area, although important channel incision is evident to the southwest.” Consequently, the present section seems to include the first freshwater sediments discovered in the area.

The vertebrate bearing beds of Punta Delgada correspond to the time when Península Valdés was emergent and had hydrographic connections with western areas. Terrestrial environments were nearby, indicating that the regression of the sea was accomplished in eastern part of the Península Valdés.

5. Biochronology

The relatively poor preservation of mammal material only allowed identification to generic or higher level. However, taxa recorded permit some discussion of the chronology.

The pampatherid *Scirrotherium* occurs in the Honda Group (late middle Miocene, Colombia) and the “Conglomerado osífero” of the Ituzaingó Formation (Huayquerian, late Miocene, Entre Ríos, Argentina; Cione et al., 2000).

The glyptodontid belonging to the tribe Neuryurini is known from the Huayquerian (“Conglomerado osífero” and in different sites in the provinces of Buenos Aires, Catamarca y Tucumán) to the Lujanian (latest Pleistocene-earliest Holocene).

The mylodontids *Ranculcus* and *Megabradys* occur in the “Conglomerado osífero” (Cione et al., 2000); *Ranculcus* also occurs in the Kiyú Formation (Uruguay) and Solimões Formation (Brazil), which are referred to the Huayquerian (Marshall et al., 1983; Perea and Scillato-Yané, 1990; Latrubesse and Rancy, 1994; Perea et al., 1994).

The rodents Hydrochoeridae range from the Chasicoan to the Recent, but genus *Kiyutherium* only is known in the Huayquerian (“Conglomerado osífero”, Cerro Azul Formation of La Pampa and Río Negro Formation; Cione et al., 2000). Concerning the other rodents, the chinchillid *Lagostomopsis* is known since the Chasicoan to the Chapadmalalan, the Caviidae certainly from the Colloncuran to the Recent and the Dolichotinae certainly from the Laventan to the Recent (Dozo et al., 2002).

In summary, all taxa are late middle Miocene or younger. Two are known from the Laventan, one reaching the Huayquerian and the other, the Recent. Sediments and fauna in the Honda Group permit identification of the Laventan Stage/Age, intermediate between the Colloncuran and Mayoan (Madden et al., 1995). However, the stratotype is located in northern South America and their sediments are not in a sequence with older or younger mammal bearing beds and their location in the scale is mainly based on radiometric dating.

A genus occurs since the Chasicoan and reaches the Chapadmalalan and another ranges from the Huayquerian to the Lujanian. Finally, two taxa are only known from the Huayquerian. Consequently, taxa recorded suggest a Huayquerian age in the standard South American scale.

6. Age of the fossiliferous beds

The Huayquerian has been recognized as a South American chronostratigraphic and geochronologic unit younger than the Chasicoan and older than the Montehermosan. Since the paper by Pascual et al. (1965), Huayquerian has also been considered a “Land-mammal age” (Marshall et al., 1983; Flynn and Swisher, 1995). However, the present Codigo Argentino de Estratigrafía (1992) treats term as an informal designation (see, Cione and Tonni, 1995a,1996,2001).

The boundary between the Chasicoan and Huayquerian was proposed at about 9 Ma (Flynn and Swisher, 1995). According to these authors, radioisotopic dates, location of the boundary in the earliest part of Chron C3Ar, and using the chron terminology and time scale of Cande and Kent (1995); Berggren et al. (1997), the best estimate for the boundary Huayquerian/Montehermosan is about 6.8 Ma and certainly is older than 6.5 Ma. Actually, this estimate does not correspond to the boundary but to the most recent Huayquerian beds of the Andalhualá Formation in the provincia de Catamarca, northwestern Argentina (Cione et al., 2000). Besides, beds over the Andalhualá Formation might not be Montehermosan but Chapadmalalan in age (Cione and Tonni, 1996). Flynn and Swisher (1995) indicate that the interval Huayquerian/Montehermosan is paleomagnetically relatively well sampled in Bolivia and northwestern Argentina. However, both in Bolivia and Argentina, the alleged Montermosan strata are Chapadmalalan in age (Cione and Tonni, 1996). These Chapadmalalan beds are as old as 4.0 Ma and are the oldest dates for faunas of this age (Anaya and MacFadden, 1995; Cione and Tonni, 1996; Cione and Tonni, 2001). The interval Huayquerian/Montehermosan should encompass from 9.0 to 4.0 Ma. The upper part of the Andalhualá Formation, of Huayquerian age, should range to 6.8–6.5 Ma. Consequently, the Huayquerian/Montehermosan boundary should be younger than this age.

The youngest stage of the late Miocene, the Tortonian, ranges from 11.2 to 7.12 Ma (Handerbol et al., 1998). Consequently, the Huayquerian encompasses the middle and late part of the Tortonian and perhaps the base of the Messinian (youngest stage of the Miocene).

The age of the Puerto Madryn Formation was largely debated (for a synthesis see Del Río, 1988). In the last years, it was referred to the middle Miocene (Del Río, 1988,1990) and recently again to the late Miocene (Del Río et al., 2001; Scasso et al., 2001). The type section of the correlative Barranca Final Formation in Río Negro (northern Patagonia) was assigned to the middle to late Miocene (Guler et al., 2002).

Concentrates coming from an ash bed located in the upper levels of the “Rionegrense” at Bahía Cracker, eastern Chubut, were dated by means of $^{40}K/^{39}Ar$ (three dates: average 9.41 Ma; Zinsmeister et al., 1981). Scasso et al. (2001) correlated this ash level with the upper strata at Puerto Pirámide and the Lobería of Puerto Pirámide. Recently, numerous dates were obtained by means of $^{87}Sr/^{86}Sr$ analyses on shells of pectinids and oysters (Scasso et al., 2001). Dates encompasses from 18.4 to 8.7 Ma; these authors discard the oldest dates and retain those that range from 10.8 to 8.7 Ma as more reliable (average: 10.1 Ma). These dates are approximately in agreement with a date $^{40}K/^{39}Ar$ of 10 Ma on escorias from the type Chasicoan in the Provincia de Buenos Aires (Schultz et al., 1998).

Radioisotopic dating in the marine shell beds of the Puerto Madryn Formation ranges from 11 to 9 Ma. The Huayquerian is younger than 9 Ma. So, according to radioisotopic and biostratigraphic evidence, the section described is younger than the typical Puerto Madryn Formation from which is actually separated by an unconformity. The section would be correlated with the type Río Negro Formation from northern Patagonia, which also include Huayquerian fossils.

7. Biogeography

The Neotropical Region was divided into two major subunits: the Austral and Brazilian ichthyogeographic Subregions (Ringuelet, 1975; Arratia, 1997; Almirón et al., 1997; Casciotta et al., 1999; Fig. 9). Most of the diversity is concentrated in the Brazilian Subregion, the area to which loricariid catfishes are now limited (Ringuelet, 1975; Arratia et al., 1983; Arratia, 1997; Fig. 9). Loricariidae is one of the two most diversified families in the Americas (more than 80 genera and 640 species; Arratia, 1997; Ambruster and Provenzano, 2000) and is largely responsible along with characids and cichlids for the remarkable diversity of the subregion.

The Austral ichthyofauna is more closely related to West Gondwanan faunas (e.g. Australia and New Zealand; Ringuelet, 1975) and the Brazilian ichthyofauna to African faunas (Gosline, 1975; Patterson, 1975). Both subregions were greatly affected by the Andean tectonism that may have influenced the origin of many endemic taxa (e.g. *Orestias* spp.).

Loricariid catfishes are mostly confined to tropical and subtropical climates were they are extremely diverse (Vari and Malabarba, 1998; Fig. 9). Their diversity dramatically diminishes southward. In the southernmost area of the present distribution, southwestern Pampean region, loricariids are only represented by two species: *Hypostomus commersoni* and *Loricarichthys anus*. In a recent book dealing with freshwater fish distribution, loricariid distribution is depicted as ranging to the latitude of the Río de la Plata (Berra, 2001). However, the southernmost loricariids occur in the laguna Cochicó of the lagunas Encadenadas del sudoeste, more than 400 km to the southwest (36°30′–37°30′ S, 061°–063°30′ W; Miquelarena and López, 1995). Until recently, the southernmost distribution of loricariids was considered to be the Salado Basin including the lagunas Encadenadas del noreste (Ringuelet, 1975; Fig. 9). The lagunas Encadenadas del sudoeste were connected to the Salado Basin by the arroyo Vallimanca but were highly saline. However, the recent higher annual precipitation (more than 200 mm in excess; Tonni et al., 1999) has diluted salinity in the lagunas Encadenadas del sudoeste, thus permitting dispersion of many fishes.

Consequently, the new Miocene locality of Punta Delgada is more than 500 km southward of the extant southernmost range of the family Loricariidae. Although identification of the other catfish material in the site is uncertain, it does not correspond to one of the living Austral taxa (i.e. Nematogenyidae, Trychomycteridae, or Diplomystidae).

Since the early 19th century, it is well known that the Earth’s climate has cooled over the last 100 million years. Since the Cretaceous, the “hot-house” world of the late Mesozoic (a time interval without significant polar ice-sheets) has turned to the “ice-house” world in which we now live (Markwick, 1998). The presence of loricariids in the Península Valdés area suggests that the climate was much warmer than today, perhaps at least as warm as that of the middle part of Buenos Aires province. Present loricariids are distributed

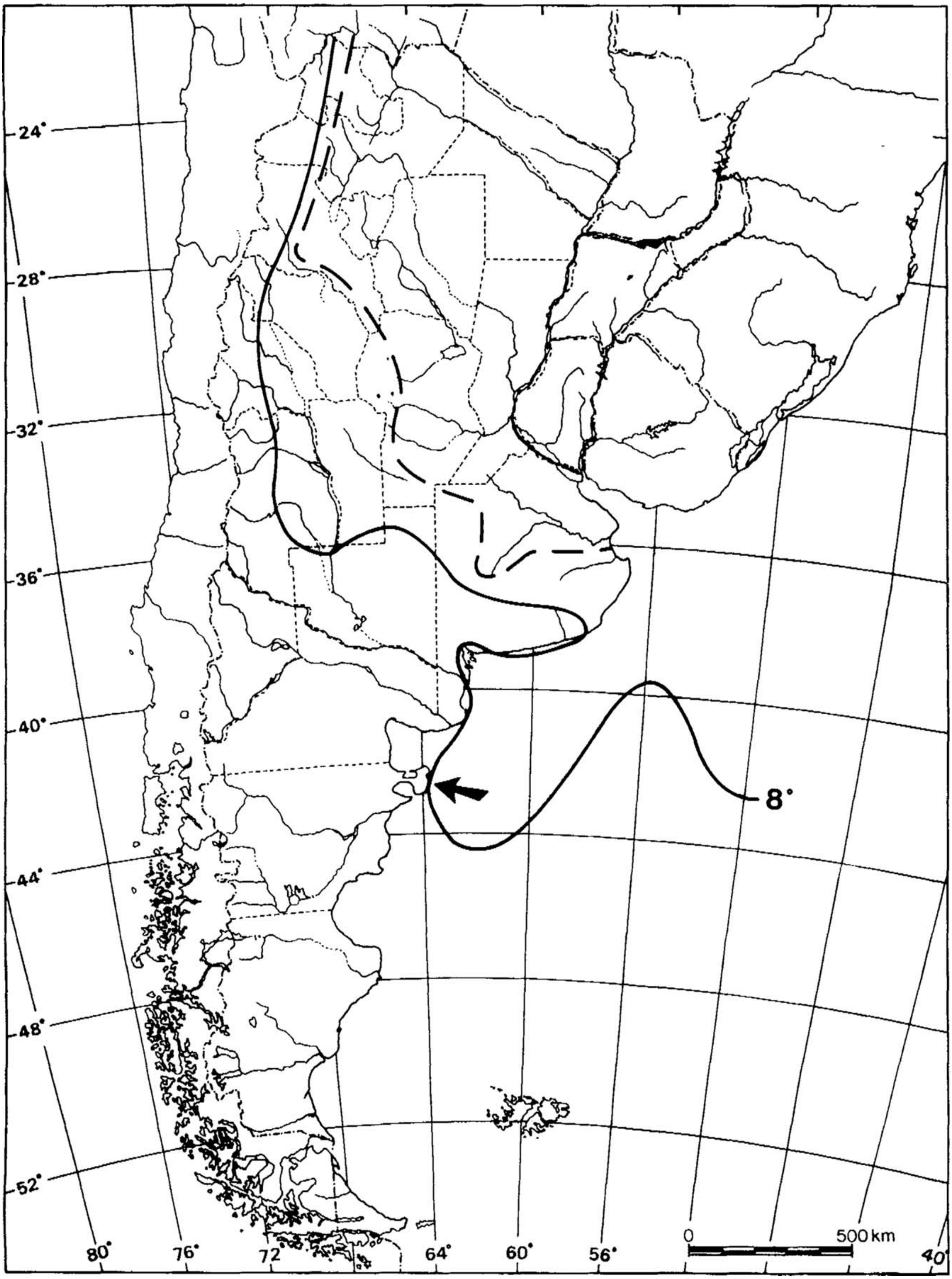

Fig. 9. Broad line indicates the boundary between Brazilian and Austral subregions. Dashed line indicates the present distribution of Loricariidae. The arrow indicates Península Valdés. The isotherm of 8 °C in winter is depicted according to García (1992).

north and east from about the June mean isotherm of 8 °C (García, 1992; Fig. 9). Globally higher temperatures than present have been proposed for the late Miocene (Crowley and North, 1991; Naish et al., 2001). In fact, climate was much warmer (and wetter) than present during the Miocene in southern South America and tropical terrestrial mammals occurred even in southernmost South America (e.g. Primates, Marshall et al., 1983). Sharks, teleosts, mammals, and mollusks present in the Puerto Madryn Formation also indicate warmer marine temperatures in the area (Cione, 1978,1988; Cione and Tonni, 1981; Del Río, 1990; Cione et al., 1996; Del Río et al., 2001; Dozo et al., 2002). Temperature conditions were adequate as well for the presence of loricariid fishes. According to global evidence, suitable temperatures probably prevailed in central Patagonia until early Pliocene (see, Cronin et al., 1992). Additionally, in late Miocene times the Andean rain shadow probably was not as important as today (Marshall et al., 1983).

Characiformes were recorded in the Eocene of Golfo de San Jorge area (Cione, 1986) and in the Miocene of south central Chile (Rubilar, 1994). These findings, along with the present record of a loricariid and a possible pimelodid, demonstrate that tropical fauna was distributed in Patagonia and Chile at least off and on since the Eocene. The rivers where fishes lived at Punta Delgada must have been hydrographically connected with more northern basins at some point. However, tropical taxa present in the Patagonian Miocene inhabited the region along with Austral taxa such us the southern perchs Percichthyidae and the endemic catfish *Nematogenys*, thus forming associations with living analogies (sensu Barnosky, 1993; Wood and Barnosky, 1994). In other continents, many late Pleistocene vertebrate communities contain associations of extant species that do not occur together today. These fossils clearly show that many community relationships are ephemeral (Graham et al., 1996; Wilson and Williams, 1993). We have found several vertebrate associations without modern analogies in the Pleistocene of the Pampean area (Pardiñas et al., 1996, 2001). Loricariid catfishes surely could have inhabited not only the Península Valdés area but a wide area of Patagonia because the hydrography, topography and climate were suitable for this group.

The Península Valdés is located in the present Austral Subregion although there are no permanent streams in the area and the climate is semidesert (García, 1992). The closest river is the río Chubut, some 100 km to the south (Fig. 9). The río Chubut has an allochthonous course, as all the other rivers that outwash in the Patagonian Atlantic coast. These rivers originate in the Patagonian Andes located in the west of South America, where Westerlies cause high precipitation to occur. The río Chubut is isolated from the north Patagonian watersheds such as the ríos Colorado and Negro, and from the Pampean lakes and rivers where loricariids have their present southernmost distribution. However, the area where these fishes occur is not separated from the Península Valdés by mountain ranges.

The type “Rionegrense” was considered to be related with the establishment of the Colorado and Negro river basins (Pascual and Bondesio, 1985), which are the closest permanent streams to the north of Península Valdés. Yet, the supposedly fluvial sands of the type “Rionegrense” seems to have been deposited under an eolian regime and the fluvial income would have been minor (Zavala and Freije, 2001). Consequently, we know nothing about the hydrographic connections of the Península Valdés with more northern basins.

8. Loricariid fossil record

The most ancient loricarioidei come from the Maíz Gordo Formation of Salta, Argentina (the callichthyid *Corydoras revelatus* was found in the locality Arroyo Abra del Trigo according to Giudici and Oliver Gascón, 1982, and “Sunchal” according to Cockerell, 1925; see also Arratia and Cione, 1996). Remarkably, the Maíz Gordo Formation is considered Paleocene in age that seems rather old for an advanced group such callichthyids. The most ancient remains of loricariid fishes were found in late Oligocene sediments of Brazil (Malabarba, 1988; Bergqvist and Ribeiro, 1998). Other loricariid remains occur in the Honda Group of Colombia (Serravallian, late middle Miocene; Lundberg, 1997), Ituzaingó Formation of central Argentina (Tortonian, early late Miocene; Cione and Casciotta, 1997; Cione et al., 2000). Paleogene and early Neogene climatic conditions (precipitations, temperature) were certainly adequate for the presence of loricariid fishes in Patagonia. Consequently, loricariids could be there at least since Oligocene times.

The local extinction of Loricariidae in southern South America might be related to the climatic changes that were generated by the elevation of the Patagonian Andes (Quechua Phase, according to Marshall et al., 1983, since the middle Miocene). However, global climate was still warm until early and possibly late Pliocene and probably temperatures were fit for loricariids during this time (see above). We have almost no vertebrate record in Patagonia after the “Rionegrense” (i.e. Huayquerian, Tortonian) times. It is possible that several Brazilic fishes (including loricariids) could cope with environmental changes until glacial times. Certainly, when temperatures dropped abruptly since late Pliocene and especially since middle Pleistocene, only some Brazilic fishes succeeded in surviving in northern Patagonia (e.g. the characid *Gymnocharacinus bergi*, in a special habitat of thermal waters or the characid *Cheirodon interrupts* Ringuelet, 1961; Menni and Gómez, 1995; Almirón et al., 1997; Escalante and Menni, 1999), *Oligosarcus jenynsii*, and *Astyanax eigenmanniorum* in the río Colorado (Almirón et al., 1997).

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Appendix

Vertebrates found in levels 3–5 at Punta Delgada: Osteichthyes, Siluriformes: Loricariidae indet.; Percomorpha indet.; Aves, Ciconiiformes: Threskiornitidae indet.; Anseriformes: Dendrocygnidae indet.; Mammalia, Xenarthra, Cingulata, Pampatheriidae: *Scirrotherium* sp.; Glyptodontidae: Neuryurini indet.; Tardigrada, Mylodontidae, Mylodontinae: *Ranculcus* or *Megabradys*; Rodentia, Caviomorpha, Hydrochoeridae, Cardiatheriinae: cf. *Kiyutherium*; Chinchillidae: cf. *Lagostomopsis*; Caviidae: Dolichotinae indet.; Litopterna: Macrauchenidae indet.

References

Aceñolaza, F.G., 2000. La Formación Paraná (Mioceno medio): estratigrafía, distribución regional y unidades equivalentes. Serie de Correlación Geológica 14, 9–28.

Almirón, A., Azpelicueta, M. de las, M., Casciotta, J., López Cazorla, A., 1997. Ichthyogeographic boundary between the Brazilian and Austral subregions in South America, Argentina. Biogeographica 73, 23–30.

Ambruster, J.W., Provenzano, F., 2000. Four new species of the suckermouth armored catfish genus *Lasiancistrus* (Loricariidae: Ancistrinae). Ichthyological Exploration of Freshwaters 11, 241–254.

Ameghino, F., 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonia, avec un paralèlle entre leurs faunes mammalogiques et celles de l'ancien continent. Anales del Museo Nacional de Buenos Aires 15, 1–568.

Ameghino, F., Woodward, A.S., 1897. Geology and Paleontology of Argentine (translated with supplementary observations). Geological Magazine 4, 4–9.

Anaya, F., MacFadden, B., 1995. Pliocene mammals from Inchasi, Bolivia: the endemic fauna just before the Great American Interchange. Bulletin of the Florida Museum of Natural History 39, 87–140.

Andreis, R., 1965. Petrografía y paleocorrientes de la Formación Río Negro. Revista del Museo de La Plata 36, 1–25.

Angulo, R., Casamiquela, R., 1982. Estudio estratigráfico de las unidades aflorantes en los acantilados de la costa norte del Golfo San Matías (Provincia de Río Negro y extremo austral de la Provincia de Buenos Aires) entre los meridianos 62°30′ y 64°30′ O. Mundo Ameghiniano 2, 20–73.

Arratia, G., 1997. Brazilian and Austral freshwater fish faunas of South America. A contrast. In: Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems. pp. 179–187.

Arratia, G., Cione, A.L., 1996. The fish fossil record of southern South America. Münchener Geowissenschaft Abhanlungen 30A, 9–72.

Arratia, G., Peñafort, M.B., Menu-Marque, S., 1983. Peces de la región sureste de los Andes y sus probables relaciones biogeográficas actuales. Deserta 7, 48–107.

Barnosky, A.D., 1993. Faunal response to glacial-interglatial transitions in the western United States. Abstracts of the Sixth International Theriological Congress, pp. 14.

Berggren, W.A., Hilgen, F.J., Langereis, C.G., Kent, D., Obradovich, J., Raffi, I., et al., 1997. Late Neogene chronology: new perspectives in high-resolution stratigraphy. Bulletin of the Geological Society of America 107, 1272–1287.

Bergqvist, L.P., Ribeiro, A.M., 1998. A Paleomastofauna das Bacias Eoterciárias Brasileiras e sua importancia na dataçao das Bacias de Itaboraí e Taubaté. In: Casadío, S. (Ed.), Paleógeno de América del Sur y de la Península Antártica. Asociación Paleontológica Argentina, pp. 19–34.

Berra, T.M., 2001. Freshwater Fish Distribution. Academic Press, San Diego p. 1–604.

Cande, S.C., Kent, D., 1995. Revised calibration of the Geomagnetic polarity time scale for the Late Cretaceous and Cenozoic. Journal of Geophysical Research 100, 6093–6096.

Casciotta, J., Almirón, A., Cione, A., Azpelicueta, M. de las, M., 1999. Brazilian freshwater fish assemblages from southern Pampean area, Argentina. Biogeographica 75, 67–78.

Castro, L.N., 1981. Estudio sedimentológico de las psamitas, pelitas y calizas de la Formación Puerto Madryn, correspondiente a las localidades de Puerto Pirámide y Punta Delgada, península de Valdés, provincia del Chubut. Grade (Licenciatura) dissertation, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, p. 1–199.

Cione, A.L., 1978. Aportes paleoictiológicos al conocimiento de la evolución de las paleotemperaturas en el área austral de América del Sur durante el Cenozoico. Aspectos zoogeográficos y ecológicos conexos. Ameghiniana 15, 183–208.

Cione, A.L., 1986. A new *Megascyliorhinus* (Chondrichthyes, Galeomorphii) from the middle Tertiary of Patagonia. Journal of Vertebrate Paleontology 6, 105–112.

Cione, A.L., 1988. Los peces de las formaciones marinas del Cenozoico de Patagonia. Doctoral dissertation. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, p. 1–536.

Cione, A.L., Azpelicueta, M. de las, M., Caille, G., 1996. An ariid catfish (Osteichthyes: Siluriformes) from marine middle Miocene beds of Patagonia. Recent ariid biogeography in southern South America. Revista Española de Paleontología 11, 11–17.

Cione, A.L., Casciotta, J.R., 1997. Miocene cynodontids (Osteichthyes: Characiformes) from Paraná, central eastern Argentina. Journal of Vertebrate Paleontology 17, 616–619.

Cione, A.L., López Arbarello, A., 1995. Los peces fósiles del Cenozoico tardío de la región pampeana. In: Alberdi, M.T., Leone, G., Tonni, E.P. (Eds.), Registro continental de la evolución climática y biológica de los últimos 5 millones de años en el Hemisferio Norte (SO de Europa) y el Hemisferio Sur. Monografías CSIC, Argentina, pp. 129–142 vol. 12.

Cione, A.L., Tonni, E.P., 1981. Un pingüino (Aves, Spheniscidae) de la Formación Puerto Madryn (Mioceno tardío) de Chubut, Argentina. Comentarios acerca del origen, la paleoecología y zoogeografía de los Spheniscidae. Annais do II Congreso Latinoamericano de Paleontología 2. pp. 591-604.

Cione, A.L., Tonni, E.P., 1995a. Chronostratigraphy and "Land mammalages" in the Cenozoic of southern South America: principles, practices and the "Uquian" problem. Journal of Paleontology 69, 135–159.

Cione, A.L., Tonni, E.P., 1995b. Los estratotipos de los pisos Montehermosense y Chapadmalalense (Plioceno) del esquema cronológico sudameircano. Ameghiniana 32, 369–374.

Cione, A.L., Tonni, E.P., 1996. Inchasi, a Chapadmalalan (Pliocene) locality in Bolivia. Comments on the Pliocene–Pleistocene continental scale of southern South America. Journal of South American Earth Sciences 9, 221–236.

Cione, A.L., Tonni, E.P., 1999. Biostratigraphy and chronological scale of the uppermost Cenozoic of the Pampean area, Argentina. In: Tonni, E.P., Cione, A.L. (Eds.), Quaternary Vertebrates of South America. Quaternary of South America and Antarctic Peninsula 12, pp. 23–51.

Cione, A.L., Tonni, E.P., 2001. Correlation of Pliocene to Holocene southern South American and European mammal-bearing units. Bolettino della Societá Paleontologica Italiana 40, 167–174.

Cione, A.L., Azpelicueta, M. de las, M., Bond, M., Carlini, A.A., Casciotta, J.R., Cozzuol, M.A., De la Funte, M., Gasparini, Z., Goin, F.J., Noriega, J.I., Scillato-Yané, G.J., Soibelzon, L., Tonni, E.P., Verzi, D.H., Vucetich, M.G., 2000. The Miocene vertebrates from Paraná, eastern Argentina. In: Aceñolaza, F.G., Herbst, R. (Eds.), El Neógeno de Argentina. Serie Correlación Geológica 14. pp. 191–237.

Cockerell, T.D., 1925. A fossil fish of the family Callichthyidae. Science 62, 317–322.

Codigo Argentino de Estratigrafía, 1992. Asociación Geológica Argentina, Serie "B" 20, 1–64.

Cronin, T.M., Dowsett, H.J., Ishman, S.E., Litwin, R.J., Poore, R.Z., Thomson, R.S., et al., 1992. Pliocene research interpretation and synoptic mapping (prism). North Atlantic paleoclimates and thermal gradients at 3.0 Ma. In: First Congress RCANS, Lisboa. pp. 91–92.

Crowley, T., North, G., 1991. Paleoclimatology. Oxford University Press, New York p. 339.

Darwin, C., 1846. Geological observations. D. Appleton Co., London p. 648.

Del Río, C.J., 1988. Bioestratigrafía y cronoestratigrafía de la Formación Puerto Madryn (Mioceno medio), Provincia del Chubut, Argentina. Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales 40, 231–254.

Del Río, C.J., 1990. Composición, origen y significado paleoclimático de la malacofauna "Entrerriense" (Mioceno medio) de la Argentina. Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales 42, 207–226.

Del Río, C.J., Martínez, S., Scasso, R., 2001. Nature and origin of spectacular marine Miocene shell beds of northeastern Patagonia (Argentina): paleoecological and bathymetric significance. Palaios 16, 3–25.

Doering, A., 1882. Informe oficial de la Comisión científica agregada al Estado Mayor General de la expedición al Río Negro. Geología, Buenos Aires, pp. 299–530.

Dozo, M.T., Monti, A., Bouza, P., Vucetich, M.G., Cione, A.L., Tonni, E.P., et al., 2002. Geología y vertebrados continentales en cercanías de Punta Delgada (Neógeno de Península Valdés, Chubut, Argentina). In: Cabaleri, N., Cingolani, C.A., Linares, E., López de Luchi, M.G., Ostera, H.O., Panarello, H.O. (Eds.), Actas del XV Congreso Geológico Argentino CD-ROM, Artículo No. 118, p. 1–6.

Escalante, A., Menni, R.C., 1999. Feeding ecology of the relict fish *Gymnocharacinus bergi*, a characid from southern South America. Water SA 25, 529–532.

Feruglio, E., 1949. Descripción geológica de la Patagonia 2. Yacimientos Petrolíferos Fiscales, Buenos Aires, 1–349.

Flynn, J.J., Swisher, C.C., 1995. Cenozoic South American Land-mammal ages: correlation to global geochronologies. In: Berggren, W.A., Kent, D.V., Handerbol, J. (Eds.), Geochronology, Time scales, and Correlation: Framework for a Historical Geology. SEPM Special Publication, pp. 317–333.

Frenguelli, G., 1926. El Entrerriense en el Golfo Nuevo del Chubut. Boletín de la Academia Nacional de Ciencias de Córdoba 29, 191–270.

García, O.N., 1992. Síntesis climatográfica de la República Argentina. In: Iriondo, I. (Ed.), El Holoceno en la Argentina I. Cadinqua, pp. 79–103.

Giudici, A., Oliver Gascón, J., 1982. Algunas localidades fosilíferas del Grupo Salta en la Sierra de Santa Bárbara, provincia de Jujuy. Revista de la Asociación Geológica Argentina 37, 480–482.

Gosline, W.A., 1975. The palatine-maxillary mechanism in catfishes, with comments on the evolution and zoogeography of modern siluroids. Occasional Papers of the California Academy of Sciences 120, 1–31.

Graham, R.W., Lundelius, E.L., Graham, M., Schroeder, E.K., Toomey III, R.S., Anderson, E., et al., 1996. Spatial response of mammals to Late Quaternary environmental fluctuations. Science 2772, 1601–1606.

Grande, L., 1987. Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. Journal of Vertebrate Paleontology 7, 24–54.

Guler, M.V., Guerstein, G., Malumián, N., 2002. Bioestratigrafía de la Formación Barranca Final, Neógeno de la Cuenca del Colorado Argentina. Ameghiniana 39, 103–110.

Haller, M., 1979. Estratigrafía de la región al poniente de Puerto Madryn, Provincia de Chubut, República Argentina. Actas del VI Congreso Geológico Argentino 1. pp. 285–297.

Haller, M., 1981. Descripción geológica de la Hoja 43h, Puerto Madryn. Boletín del Servicio de Geología y Minería Nacional 184, 1–41.

Handerbol, J., Thierry, J., Farley, M.B., Jacquin, T., Graciansky, P.-C., Vail, P.R., 1998. Mesozoic and Cenozoic sequence chronostratigraphic chart. In: Graciansky, P.C., Handerbol, J., Jacquin, T., Vail, P.R. (Eds.), Mesozoic and Cenozoic Sequence Stratigraphy of European Basins. Society for Sedimentary Geology (Special Publication 60).

Kaaschieter, J.P.H., 1965. Geología de la Cuenca del Colorado. Actas de las Segundas Jornadas Geológicas Argentinas 7, 251–269.

Latrubesse, E., Rancy, A., 1994. La Formación Solimões (Mioceno superior-Pleistoceno) de Amazonia sudoccidental; implicaciones paleoclimáticas y estratigráficas. Revista del Museo de Historia Natural de San Rafael 12, 212.

Lauder, G.V., Liem, K.F., 1983. The evolution and interrelationships of the Actinopterygian fishes. Bulletin of the Museum of Comparative Zoology 150, 95–197.

Lundberg, J., Mago-Leccia, F., Nass, P., 1991. Exallodontus aguanai, a new genus and species of Pimelodidae (Pisces: Siluriformes) from deep river channels of South America, and delimitation of the subfamily Pimelodidae. Proc. Biol. Soc. Washington 104, 840–869.

Lundberg, J.G., 1997. Fishes of the La Venta fauna: additional taxa, biotic and paleoenviromental implications. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), Vertebrate Paleontology in the Neotropics. The Miocene fauna of La Venta. Smithsonian Institution Press, Colombia, pp. 67–91.

Madden, R.H., Guerrero, J., Kay, R.F., Flynn, J.J., Swisher, C.C., Walton, A.H., 1995. The Laventan stage and age. In: Kay, R.F., Madden, R.H., Cifelli, R.L., Flynn, J.J. (Eds.), Vertebrate Paleontology in the Neotropics. The Miocene fauna of La Venta Colombia. Smithsonian Institution Press, pp. 499–550.

Malabarba, M.C., 1988. Loricariid dermal plate and pectoral fin spines from the Tertiary of Sao Paulo, Brazil (Osteichthyes, Siluriformes). Comuniçacões Museu de Ciências, PUCRS, Zoologia 1, 5–12.

Malumián, N., 1999. La sedimentación en la Patagonia extraandina. In Geología Argentina. Anales del Instituto de Geología y Recursos Minerales 29, 557–578.

Marengo, H., 2000. Rasgos micropaleontológicos de los depósitos de la transgresión Entrerriense-Paranense en la cuenca Chaco-Paranense y noroeste argentino. Serie de Correlación Geológica 14, 29–45.

Markwick, P.J., 1998. Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. Palaeogeography, Palaeoclimatology, Palaeoecology 137, 205–271.

Marshall, L., Hoffstetter, R., Pascual, R., 1983. Mammals and stratigraphy: geochronology of the continental mammal-bearing Tertiary of South America. Palaeovertebrata, Mémoire Extraordinaire, 1–93.

Mendía, J., Bayarsky, A., 1981. Estratigrafía del Terciario en el valle inferior del río Chubut. Actas del VIII Congreso Geológico Argentino 3, pp. 593–606.

Menni, R.C., Gómez, S.E., 1995. On the habitat and isolation of *Gymnocharacinus bergi* (Osteichthyes: Characidae). Environmental Biology of Fishes 42, 15–23.

Miquelarena, A.A., López, H.L., 1995. Fishes of the lagunas Encadenadas (Province of Buenos Aires, Argentina), a wetland of international importance. Freshwater Forum 5, 48–53.

Naish, T., Woolfe, K., Barrett, P., Wilson, G., Atkins, C., Bohaty, S., et al., 2001. Orbitally induced oscillations in the East Antarctic ice sheet at the Oligocene/Miocene boundary. Nature 413, 719–723.

Orbigny d', A., 1842. Voyage dans l'Amérique méridionale. P. Bertrand, Paris p. 188.

Pardiñas, U.F.J., Gelfo, J., San Cristóbal, J., Cione, A.L., Tonni, E.P., 1996. Una tafocenosis de organismos marinos y continentales en el Pleistoceno superior en el sur de la provincia de Buenos Aires. Actas del XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos 5. pp. 95–111.

Pardiñas, U.F.J., San Cristóbal, J., Cione, A.L., Verzi, D.H., Taglioretti, M., Tonni, E.P., 2001. Vertebrados indicadores de condiciones interglaciales en el sudeste de la provincia de Buenos Aires. Reunión Anual de Comunicaciones, Asociación Paleontológica Argentina, Mar del Plata, Ameghiniana Resúmenes 37, 76R–77R.

Pascual, R., Bondesio, P., 1985. Mamíferos terrestres del Mioceno mediotardío de las cuencas de los ríos Colorado y Negro (Argentina): evolución ambiental. Ameghiniana 22, 133–145.

Pascual, R., Ortega Hinojosa, E.J., Gondar, D., Tonni, E.P., 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquéllas del territorio bonarense. Anales Comisión Investigaciones Científicas Buenos Aires 6, 165–193.

Patterson, C., 1975. The distribution of Mesozoic freshwater fishes. Mémoires du Muséum nationale d'Histoire naturelle. Paris 88, 156–173.

Perea, D., Scillato-Yané, G.J., 1990. *Ranculcus* Amegh. (Xenarthra: Mylodontinae) en el Mioceno superior del Uruguay. Primer Congreso Uruguayo de Geología (Montevideo, abril de 1990), Resúmenes Ampliados 2. pp. 1–4.

Perea, D., Ubilla, M., Martínez, S., Piñeiro, G., Verde, M., 1994. Mamíferos neógenos del Uruguay: la edad Mamífero Huayqueriense en el "Mesopotamiense". Acta Geológica Leopoldiense 17, 375–389.

Ringuelet, R.A., 1961. Rasgos fundamentales de la zoogeografía de la Argentina. Physis 22, 151–170.

Ringuelet, R.A., 1975. Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. Ecosur 2, 1–122.

Rovereto, G., 1921. Studi di geomorfologia argentina: la peninsola Valdéz. Bolletino della Società di Geologia Italiana 40, 1–47.

Rubilar, A., 1994. Diversidad ictiologica en depositos continentales miocenos de la Formación Cura-Mallin, Chile (37–39 S): implicancias paleogeograficas. Revista Geológica de Chile 21, 3–29.

Sasaki, K., 1989. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). Memoirs of the Faculty of Fisheries Hokkaido University 36, 1–134.

Scasso, R., Del Río, C., 1987. Ambientes de sedimentación, bioestratigrafía y proveniencia de la secuencia marina del Terciario superior de la región de Península Valdés, Chubut. Revista de la Asociación Geológica Argentina 42, 291–321.

Scasso, R.A., Mc Arthur, J.M., Del Río, C., Martínez, S., Thirlwall, M.F., 2001. 87 SR/86 SR Late Miocene age of fossil molluscs in the "Entrerriense" of the Valdés Peninsula (Chubut, Argentina). Journal of South American Earth Sciences 14, 319–329.

Schultz, P.H., Zárate, M., Hames, W., Camilión, C., 1998. Impact-generated escorias as benchmarks for Argentine loess chronostratigraphy. Resúmenes del VII Congreso Argentino de Paleontología y Bioestratigrafía, p. 133.

Tonni, E.P., Cione, A.L., Figini, A., 1999. Predominance of arid climates indicated by mammals in the pampas of Argentina during the late Pleistocene and Holocene. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 257–281.

Uliana, M.A., Biddle, K.T., 1988. Mesozoic–Cenozoic paleogeographic and geodynamic evolution of southern South America. Revista Brasileira de Geociências 18, 172–190.

Vari, R.P., Malabarba, L.R., 1998. Neotropical ichthyology: an overview. In: Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, Z.M., Lucena, C.A.S. (Eds.), Phylogeny and Classification of Neotropical Fishes. Edipucrs, Porto Alegre, pp. 1–11.

Wilson, M.V., Williams, R.R., 1993. Phylogenetic, biogeographic, and ecological significance of early fossil records of North American freshwater teleostean fishes. In: Mayden, R.L. (Ed.), Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford University Press, pp. 224–244.

Wood, D.L., Barnosky, A.D., 1994. Middle Pleistocene climate change in the Colorado Rocky Mountains indicated by fossil mammals from Porcupine Cave. Quaternary Research 41, 366–375.

Yrigoyen, M., 1975. Geología del Subsuelo y Plataforma continental. Relatorio del VI Congreso Geológico Argentino, pp. 139–168.

Zambrano, J.J., 1980. Comarca de la cuenca cretácica del Colorado. In: II Simposio de Geología Regional Argentina. Academia Nacional de Ciencias, Córdoba, pp. 1032–1070.

Zavala, C., Freije, R.H., 2001. On the understanding of aeolian sequence stratigraphy: an example from Miocene–Pliocene deposits in Patagonia, Argentina. Rivista Italiana de Paleontologia e Stratigrafia 107, 251–264.

Zinsmeister, W., Marshall, L.G., Drake, R., Curtis, G., 1981. First radioisotope (potassium-argon) age of marine Neogen Río Negro Beds in northeastern Patagonia, Argentina. Science 212, 440.