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Late Miocene continental biota in Northeastern Patagonia (Península Valdés, Chubut, Argentina)

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ABSTRACT

A new vertebrate faunal assemblage was recently discovered from the uppermost part of the late Miocene Puerto Madryn Formation. These deposits crop out along the southwestern coast of the Península Valdés area near Punta Delgada (Chubut Province, Argentina). The exhumed vertebrate fauna includes a range of fish, bird and mammal taxa, of which the latter are most varied and abundant. The new findings represent the first record of continental fossil vertebrates in the Puerto Madryn Formation and this is the first assemblage of late Miocene continental vertebrates recorded to the south of Río Negro Province. It also includes the southernmost record of Hydrochoeridae rodents, Dendrocygninae birds and Loricariidae fishes. The mammals suggest that the fossil-bearing sediments are Huayquerian in age. The climate during the accumulation of late Miocene deposits in this region is inferred to have been warmer and seasonally drier than that of today.

1. Introduction

The clastic sedimentary succession of the Puerto Madryn Formation at Península Valdés (northeastern Patagonia) is well known for its abundant content of late Miocene marine invertebrates and well preserved vertebrate remains including teleost fishes (Riva Rossi, 1997; Riva Rossi et al., 2000), marine tetrapods such as Sheniciformes birds (Cozzuol et al., 1993, Acosta Hospitaleche et al., 2007) and marine mammals (Cozzuol, 1996, 2001). Many of these specimens are found in an excellent state of preservation, with complete and even articulated skeletons. These levels have also yielded the first record of a new species of Ciconiidae Leptoptilini (Noriega and Cladera, 2008), abundant marine invertebrates such as pectinids, oysters, bryozoans, brachiopods, echinoderms (del Río, 2004 and references therein) and crustaceans (Casadio et al., 2005). These analyses include not only systematic and biogeographic but also taphonomic aspects for reference.

A new vertebrate faunal assemblage was recently discovered from the uppermost part of the late Miocene Puerto Madryn Formation (Dozo et al., 2002, 2007, 2008). These deposits crop out in the Península Valdés area nearby Punta Delgada (Rincón Chico and La Pastosa paleontological sites). In this study, we gather all the available fossil information with the aim of discussing the systematic aspects, stratigraphical location, and biochronological and paleobiogeographical implications of this faunal assemblage. In addition, the major floristic associations are discussed to achieve an approximate reconstruction of the northeastern Patagonian landscape during the late Miocene.

The exhumed vertebrate fauna includes taxa typical of continental or freshwater environments, such as fishes, birds and mammals, of which the latter are most varied and abundant. The new findings represent the first record of continental fossil vertebrates in the Puerto Madryn Formation.

2. Materials and methods

The search, detection, and *in situ* extraction of the fossil remains from Puerto Madryn Formation were made by direct collection and exhumation of specimens exposed on the surface. The specimens are deposited in the Museo Paleontológico "Egidio Feruglio" (MPEF-PV, Trelew, Chubut, Argentina).

The supporting geological field work, which was performed alongside the paleontological work, consisted of the description of

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the local stratigraphic section at the La Pastosa and Rincón Chico sites in order to analyze the lithofacies and to collect rock samples for the sedimentological studies.

The identification of the collected material was done through anatomic comparisons with specimens belonging to the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN, Ciudad Autónoma de Buenos Aires, Argentina), the Museo de La Plata (MLP, La Plata, Provincia de Buenos Aires, Argentina) and the Museo Paleontológico "Egidio Feruglio". The geochronological correlation of the Mammal Ages follows Flynn and Swisher (1995) and Fleagle et al. (1995). The description of bird remains follows the terminology of Baumel and Witmer (1993).

3. Geographic and stratigraphic context

The new continental vertebrate faunal association comes from the Rincón Chico and La Pastosa sites, in the southwestern coast of Península Valdés (Fig. 1). Stratigraphically, these outcrops correspond to the so-called "Rionegrense" (uppermost levels of the Puerto Madryn Formation or Río Negro Formation, according to different authors) (Fig. 2).

La Pastosa site is located 15 km southwest of Punta Delgada, near the farming ranch of the same name, at approximately 42°49.357′S and 63°48.897′ W (Fig. 1.1). The section surveyed at this site is 26 m thick and consists of interstratified sandstones and shales forming hetherolithic facies, with intercalated coquinas and conglomerates. The coquinas bear disarticulated oyster and pectinid valves in a sandy matrix. The conglomerate bearing vertebrate remains is a 0.5 m thick oligomictic, intraformational conglomerate with matrix-supported texture and mud intraclasts.

Rincón Chico site is located 5 km southwest of Punta Delgada, at 42°47.503′S and 63°41.005′ W (Fig. 1.2). In this sector, the sedimentary section is exposed at a 40 m high inactive cliff. Part of the section is covered by recent eolian or mass-transported deposits located primarily in the basal section. Sandstones with shale intercalations or shale lenses dominate the profile. Part of the sequence also includes some conglomerate lenses and coquina levels similar to those in La Pastosa.

According to Scasso and del Río (1987) the upper part of the Puerto Madryn Formation was accumulated in a shallow shelf paleoenvironment. In the studied interval the coquinas represent deposits of the shoreface, the heterolithic facies deposits of tidal flats and the large scale cross-stratified sandstones and intraformational conglomerates deposits of tidal channels.

4. Systematic paleontology

The collected fossils include Siluriformes and Percomorpha fishes, Gruiformes, Anseriformes and Falconiformes birds, and Xenarthra, Rodentia and Litopterna mammals. Although most were collected at the Rincón Chico and La Pastosa sites, additional individuals described here correspond to isolated findings in other parts of Península

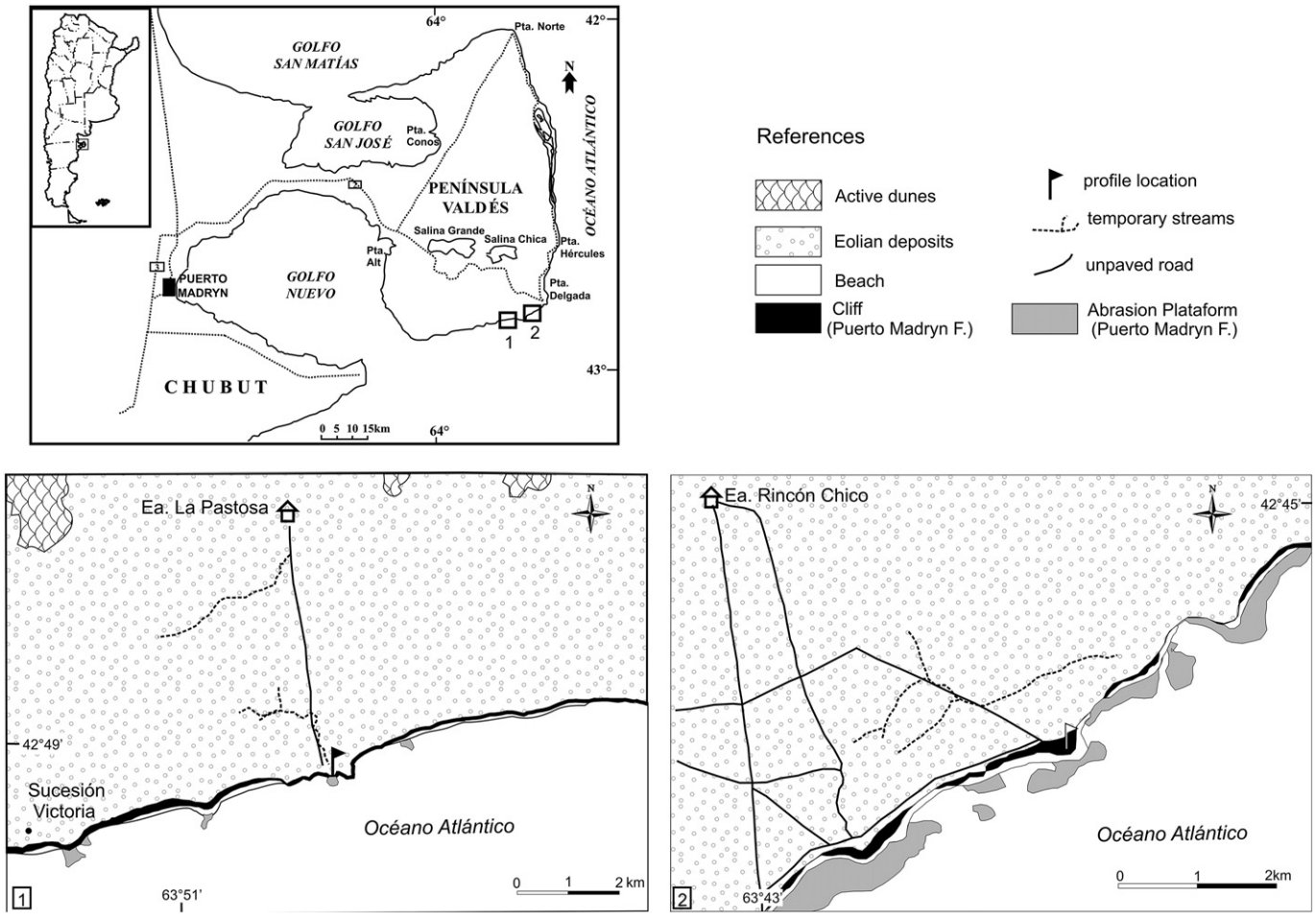

Fig. 1. General location map and geological maps of La Pastosa and Rincón Chico localities (1 and 2), Península Valdés, Chubut Province, Argentina, where the specimens described were found.

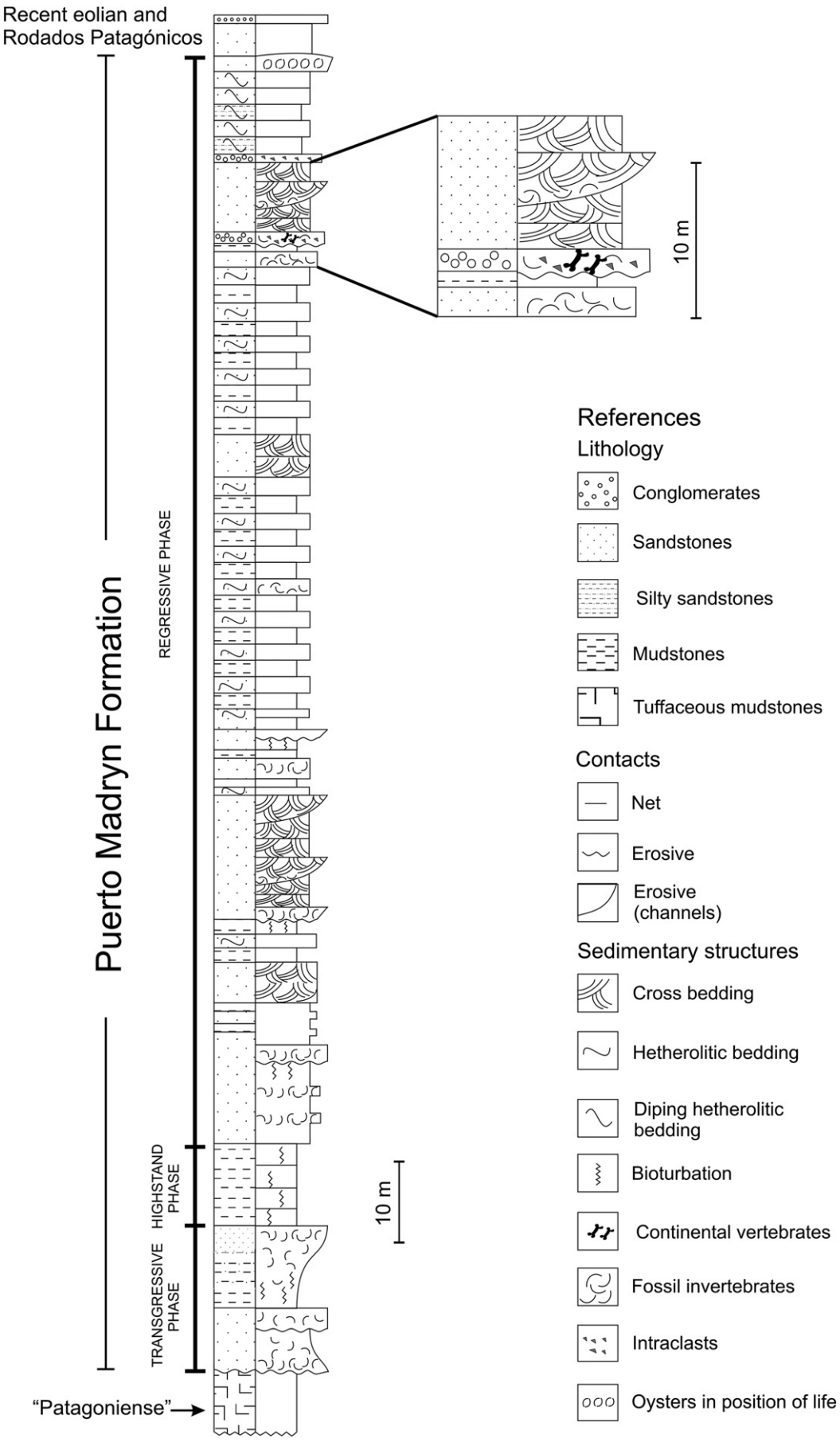

Fig. 2. Integrated sedimentary section of Puerto Madryn Formation in Península Valdés.

Valdés: one in Punta Delgada, another in the vicinity of Punta Conos, in San José Gulf, and another in the area of Punta Alt, in the vicinity of Estancia San Pablo, in Nuevo Gulf (Fig. 1).

OSTEICHTHYES Howes, 1894
SILURIFORMES sensu Grande, 1987
Siluriformes *indet.*

Referred material. MPEF-PV 2500-2503: Fragments of pectoral spines.

Provenance. Rincón Chico site, Península Valdés, Chubut.

LORICARIOIDEI
LORICARIIDAE Gill, 1872
Loricariidae indet.

Referred material. MPEF-PV 2504 and MPEF-PV 2505: Fragments of pectoral and dorsal spines. MPEF-PV 2506: Cleithrum; MPEF-PV 2507–2511: Plates; MPEF-PV 2512: undetermined bone from skull roof.

Provenance. Rincón Chico site, Península Valdés, Chubut.

ACANTHOPTERYGII
PERCOMORPHA
Percomorpha indet.

Referred material. All material is fragmentary. MPEF-PV 2513-2514: Fin rays; MPEF-PV 2515, MPEF-PV 2516, MPEF-PV 2518: Dentary; MPEF-PV 2519: Premaxilla; MPEF-PV 2517: Opercle.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Comments. A detailed description of these fishes was presented by Cione et al. (2005). Freshwater loricariid siluriforms are described for the first time from Patagonia. The fossil material consists of fragments of spines and plates.

AVES Linnaeus, 1758
NEOGNATHAE Pycraft, 1900
ORDER *incertae sedis*
CARIAMAE Fürbringer 1888
PHORUSRHACIDAE Ameghino, 1889
PSILOPTERINAE Dolgopol de Saez, 1927
Psilopterinae indet.

Referred material 1. MPEF-PV 2525: cervical vertebra corresponding to the most distal region of the neck; preserves the *arcus vertebrae*, both *laminae arcocostalis* and the left *ansa costotransversalis;* the *procesus ventralis* is eroded. Fig. 3A–C.

Provenance. La Pastosa site, Península Valdés, Chubut.

Description. The presence of strongly marked striae on the *ansa costotransversalis* (typical of Phorusrhacidae) and the size of this material allow assigning it to Psilopterinae. The vertebrae presents *torus dorsalis* slightly visible, *laguna interzigoapofisiaria* laterally wide but anterior-caudally shallow and *facies articularis caudalis* quadrangular in shape.

Comments. Psilopterinae includes six species distributed from the Paleocene to the Pliocene of Brazil and Argentina. The phorusrhacids (Phorusrhacidae) classically have been associated with predatory habits. Within these, psilopterids are the smaller and more gracile; some may even have retained limited flying ability (Tambussi and Noriega, 1996).

Referred material 2. MPEF-PV 2526: Ungual phalanx. Fig. 3D.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Description. Curved phalanx with characteristic proximodistal lateral grooves typical of the Phorusrhacidae and Cathartidae (Ciconiiformes). Transverse section dorsally concave; ventral surface not excavated without evident ridges in the limit between lateral and ventral surfaces. The flexor tuberosity, though eroded, is poorly developed; simple and directed posteriorly (it is double in Brontornithinae and Patagornithinae, Mosto et al., 2007). The joint facet is concave, subdivided into two subequal areas more excavated ventrally than dorsally.

FALCONIFORMES Sharpe, 1874
ACCIPITRIDAE Vieillot, 1816
Indeterminate genus and species

Referred material. MPEF-PV 2523: Partial skull roof and remains of lateral, occipital, orbital regions, cavum tympanicum and cavum cranii. Fig. 3E–F.

Provenance. La Pastosa site, Península Valdés, Chubut.

Description. The conservation of the internal cranial cavity (*cavum cranii*), which reflects much of the brain anatomy and the partial conservation of both middle ears, is remarkable. The flat skull, triangular with rounded base and bulky parietals separated by a thin groove allows assignment of this skull to Accipitridae.

Comments. This is a significant finding, as it is the first fossil record of a cranial element of this family. It corresponds to a large-sized adult eagle. A detailed description of this fossil and its endocranial cast can be found in Picasso et al. (2009). Accipitridae was traditionally included in the order Falconiformes but it has been recently removed from the group (Hackett et al., 2008).

ANSERIFORMES Wagler, 1831
ANATIDAE Vigors, 1825
DENDROCYGNINAE Reichenbach, 1850
Dendrocygninae indet.

Referred material 1. MPEF-PV 2522: synsacrum formed by six preacetabular and nine postacetabular anquilosed vertebrae with partially preserved ilia, Fig. 3G–H–I.

Provenance. La Pastosa site, Península Valdés, Chubut.

Comments. This material was preliminarily described and assigned to *Dendrocygna* sp. (Acosta Hospitaleche et al., 2007). Here, after re-examination of the material, we prefer to keep the subfamily level allocation, and refrain from referring it to a specific genus.

Referred material 2. MPEF-PV 2527: left coracoid, with eroded distal epiphysis, tip of procoracoid process and acrocoracoid process. Fig. 3J.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Description. The coracoid presents striated muscle scars on its dorsal surface; the procoracoid foramen is absent. The scapular cotyla is deep, with subcircular contour. In transverse section, the coracoid body is slightly convex. It shares with *Dendrocygna* Swainson, 1837 (Anatidae Dendrocygninae) the following characters: a narrow crest between the acrocoracoid process and the humeral articular surface that forms an angle of less than 30° with the diaphyseal axis; weak and curved scar of the acrocoracoid ligament; slightly marked supracoracoid sulcus; humeral articular surface not delimiting a ridge and not completely covering the underlying coracoid body.

Referred material 3. MPEF-PV 2528: distal fragment of left humerus. Fig. 3K–L.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Description. The shape of the *fossa brachialis* and t*uberculum supracondylare ventrale* and the equal extension of the *epycondylus ventralis* and *condylus ventralis* are similar to *Dendrocygna.* The material differs from *Dendrocygna* in that the incisura intercondylaris is sub parallel to the sagittal plane of the diaphysis, the medial ridge of the *sulcus scapularis tricepitalis* is less extended proximodistally. Additionally, the material is relatively larger than the individuals of D. *viduata*, D. a*rcuata* and D. *bicolour* available for comparison.

Comments. The coracoid was originally referred to Dendrocygnidae (sic) by Dozo et al. (2002); we agree with this allocation. It is worth noting that in the above mentioned publication, Dendrocyninae was used in reference to the classificatory schemes of the time (Eduardo Tonni pers. comm.) and did not include the Thalossornithinae. The fossil is appreciably larger than the specimens of *D. viduata* (Linnaeus 1758), *D. arcuata* Horsfield 1824 and *D. arcuata bicolour* Vieillot 1816 with which it was compared. Also in that same work, the distal humeral end is assigned to "Dendrocygnidae"; we agree with this allocation with the same comments as for its familial status. The latter specimen undoubtedly shows considerable similarities with *Dendrocygna*. However, the most diagnostic characters that can

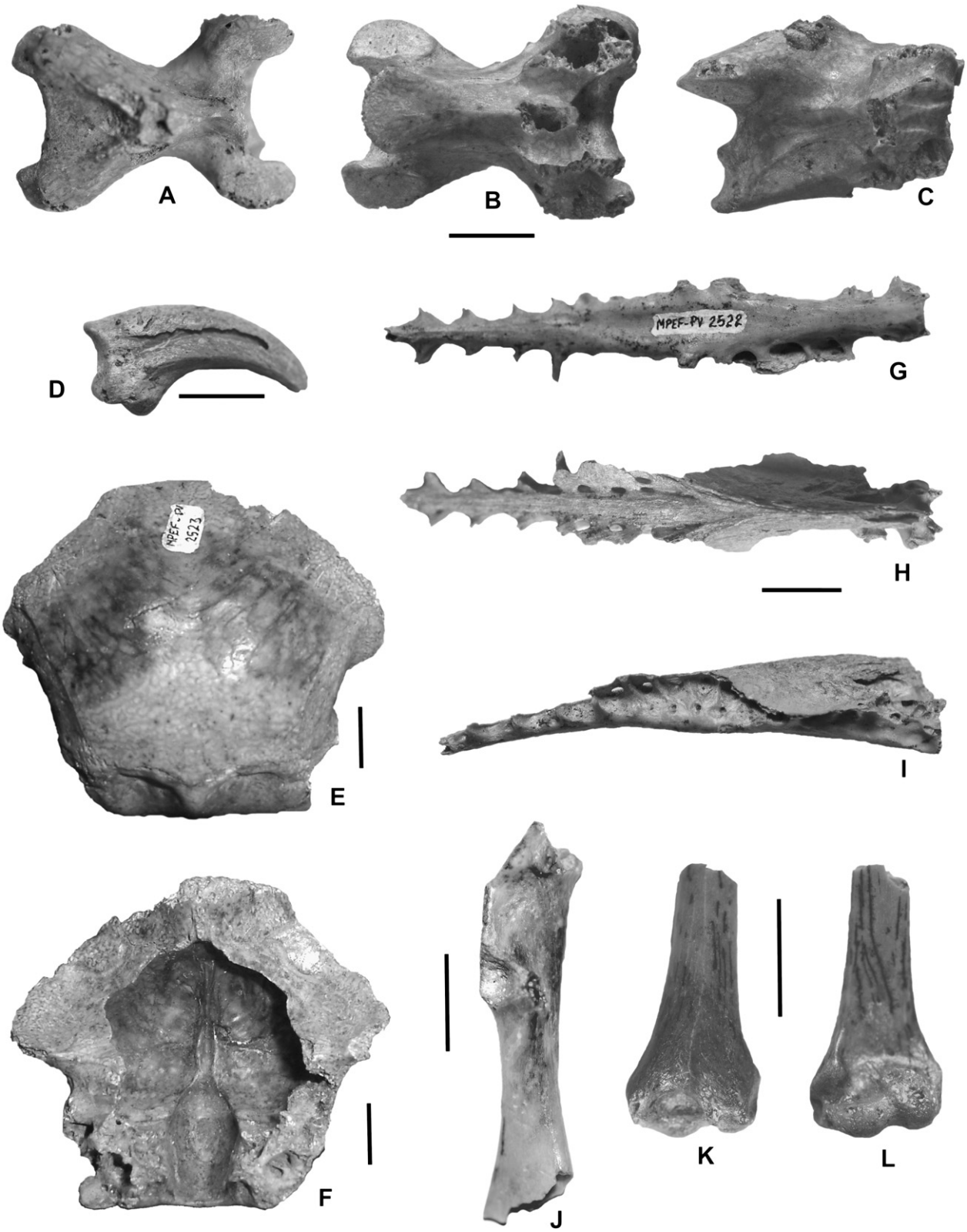

Fig. 3. Fossil birds from La Pastosa and Rincón Chico localities. Psilopterinae indet. (MPEF-PV 2525), cervical vertebra corresponding to distalmost region of the neck: (A) dorsal view, (B) ventral view and (C) lateral view ; (MPEF-PV 2526) ungual phalanx (D) lateral view; Accipitridae indet. (MPEF-PV 2523) partial skull roof and remains of lateral, occipital, orbital regions, cavum tympanicum and cavum cranii: (E) dorsal view, (F) ventral view; Dendrocygninae indet. (MPEF-PV 2522) synsacrum with partially preserved ilia: (G) ventral view, (H) dorsal view, (I) lateral view; (MPEF-PV 2527) left coracoid, with eroded distal epiphysis, tip of procoracoid process and acrocoracoid process: (J) dorsal view; (MPEF-PV 2528) distal fragment of left humerus: (K) posterior view, (L) anconal view. Scale bar equals 10 mm.

be used for systematic assignation of this genus are located in the proximal sector of the humerus, which is not preserved. For this reason we prefer to keep the allocation at the subfamilial level.

The Dendrocygninae are aquatic birds that occur in lentic environments with dense surface vegetation, feeding mainly on the fruits of aquatic plants. The earliest records for the subfamily correspond to

the lower Miocene of Europe and North America. Currently, one specimen from early-middle Miocene sediments of Santa Cruz (Santacrucian, Argentina) that was originally assigned to the subfamily is being re-studied (Cenizo et al., 2006). While this material shares some common characters with *Dendrocygna*, other presumably derived features would exclude it from the subfamily Dendrocygninae (Cenizo pers. comm. to CPT, February 2009). If this were the case, then the material included here would represent the oldest and southernmost record of a Dendrocygninae.

MAMMALIA Linnaeus, 1758
XENARTHRA Cope, 1889
CINGULATA Illiger, 1811
GLYPTODONTOIDEA Gray, 1869
PAMPATHERIIDAE Ameghino, 1875
Scirrotherium Edmund and Theodor, 1997
Scirrotherium sp.

Referred material. MPEF-PV 2529/1–11: Dorsal carapace osteoderms: 1–8: eight fixed osteoderms and 9–11: three mobile elements. Fig. 4A–H.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Description. The approximately hexagonal shape, size and central figure of the fixed and mobile osteoderms are very similar to those of the pampatherid genus *Scirrotherium* from the middle Miocene of Colombia.

Comments. This is a small pampatheriid, smaller than *Kraglievichia paranensis.* Until recently, the genus was only recorded in the middle Miocene of Colombia, in the Honda Group (Edmund and Theodor, 1997). Recently, Scillato-Yané and Carlini (in Cione et al., 2000) mentioned it for the "Conglomerado osífero" of the Ituzaingó Formation (Huayquerian, late Miocene, Entre Ríos, Argentina), with a new species not yet named nor described. Consequently, the presence of *Scirrotherium* sp. in the Patagonian Neogene is of particular paleobiogeographical interest.

TARDIGRADA Latham and Davies, 1795
MYLODONTOIDEA Gill, 1872
MYLODONTIDAE Gill, 1872
MYLODONTINAE Gill, 1872
Mylodontinae indet.

Referred material. MEFP-PV 2530: upper left second or third molariform. Fig. 4I–J.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Comments. A large mylodontid, comparable to *Glossotherium robustum*. Unfortunately, it cannot confidently be referred to a specific genus due to the lack of homologous materials, but based on general comparisons with lower molariforms (degree of lobulation, depth of the grooves, size, etc.) this specimen likely corresponds to *Ranculcus* Ameghino 1891 or *Megabradys* Scillato-Yané 1981. The former is present at the base of Ituzaingó Formation ("Mesopotamian"), at the base of Raigon Formation (Huayquerian Age, late Miocene) (Perea and Scillato-Yané, 1990; Perea et al., 1994) and in the Solimões Formation (late Miocene–Pliocene) of Acre State, Brazil (Latrubesse and Rancy, 1994). The latter only occurs in the "Conglomerado osífero" ("Mesopotamian", Ituzaingó Formation) (Scillato-Yané, 1981, Cione et al., 2000).

GLYPTODONTIDAE Gray, 1869
HOPLOPHORINAE Huxley, 1864
PALAEHOPLOPHORINI Hoffstetter, 1958
Palaehoplophorini indet.

Referred material 1. MPEF-PV 2531**:** Articulated osteoderms from caudal ring. Fig. 4K.

Provenance. Punta Conos, Golfo San José, Península Valdés, Chubut**.**

Referred material 2. MPEF-PV 2532: Isolated osteoderm from the dorsal carapace. Fig. 4L.

Provenance. Punta Alt, Estancia Don Pablo, Golfo Nuevo, Península Valdés, Chubut.

Description. The osteoderms present a central figure surrounded by moderately developed peripheral figures (some of which form rugose tuberosities), with large foramina surrounding the central figure.

Comments. The Palaehoplophorini were the most abundant Glyptodontidae both during the Chasicoan Age, in the southern Pampas, and during the Huayquerian Age. In this respect, they are the predominant tribe in the "Mesopotamian" (Ituzaingó Formation, late Miocene) of Entre Ríos and Corrientes provinces, both in number of occurrences (i.e., abundance) and in degree of diversification reached (i.e., taxonomic diversity; Cione et al., 2000; Zurita, 2007; Zurita and Aramayo, 2007). The specimens described here would represent the first record for Patagonia.

NEURYURINI Hoffstetter, 1958
Neuryurini indet.

Referred material. MPEF-PV 2533: isolated osteoderm from the dorsal carapace. Fig. 4LL.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Description. The osteoderm is pentagonal, rugose and with evenly distributed small foramina.

Comments: The Neuryurini glyptodontids, originally recorded since the Huayquerian Age (Ituzaingó Formation) (Cione et al., 2000), are one of the least known groups of cingulates. This record, along with another one of Santacrucian Age from Santa Cruz province, are the first records of these glyptodonts for Patagonia, and the latter would be the oldest known Neuryurini (González Ruiz et al., submitted for publication).

RODENTIA Bowdich, 1821
HYSTRICOGNATHI Tullberg, 1899
HYDROCHOERIDAE Gill, 1872
CARDIATHERIINAE (Kraglievich, 1930) Simpson, 1945
Cardiatherium patagonicum Vucetich, Deschamps, Olivares and Dozo, 2005.

Referred material. MPEF-PV 740/1: right mandibular fragment with m1–m2; 2, 3, 4, 5, 24 and 25: isolated right m1 or m2; 6: small right mandibular fragment with m2; 7: fragment of left m3?; 8: damaged right M1 or M2; 9 and 26: left p4; 10: anterior fragment of right p4; 11 and 12: anterior fragment of left p4; 13: isolated right P4, M1 or M2; 14, right P4; 15 and 16, left M1 or M2; 17: small fragment of left palate with M1; 18: isolated right M3, upper incisor fragment; 20: m3 fragment ?; 22: fragment of palate with left P4; 23: isolated left M1 or M2 ; 27: right p4; fragment of left M3.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Referred material. MPEF-PV 2520: incomplete skull of a young individual and MPEF-PV 2521: complete skull. Fig. 4M–N.

Provenance. La Pastosa site, Península Valdés, Chubut.

Comments. Numerous teeth of different sizes corresponding to different ontogenetic stages of the new species *Cardiatherium patagonicum* were collected at the site Rincón Chico (Vucetich et al., 2005). One remarkable find in La Pastosa site was the discovery of two nearly complete skulls of hydrochoerid rodents. Based on morphological and morphometric characters of the molariforms, including the presence of 9 or 10 plates in the M3, these are also assigned to *C. patagonicum*. A detailed study of these specimens, along with endocranial casts, is currently underway (Dozo, in prep.).

CHINCHILLIDAE Bennett, 1833.
Lagostomopsis ?

Referred material. MPEF-PV 742, left P4.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Comments. This tooth is identified as a P4 based on the absence of an interdental contact facet. Its lobes are of similar length. The outer portion of the hypoflex is slightly recurved posteriorly.

CAVIIDAE Gray, 1821
Dolichotinae indet.

Referred material. MPEF-PV 743/1 and 2. Two isolated teeth of different sizes.

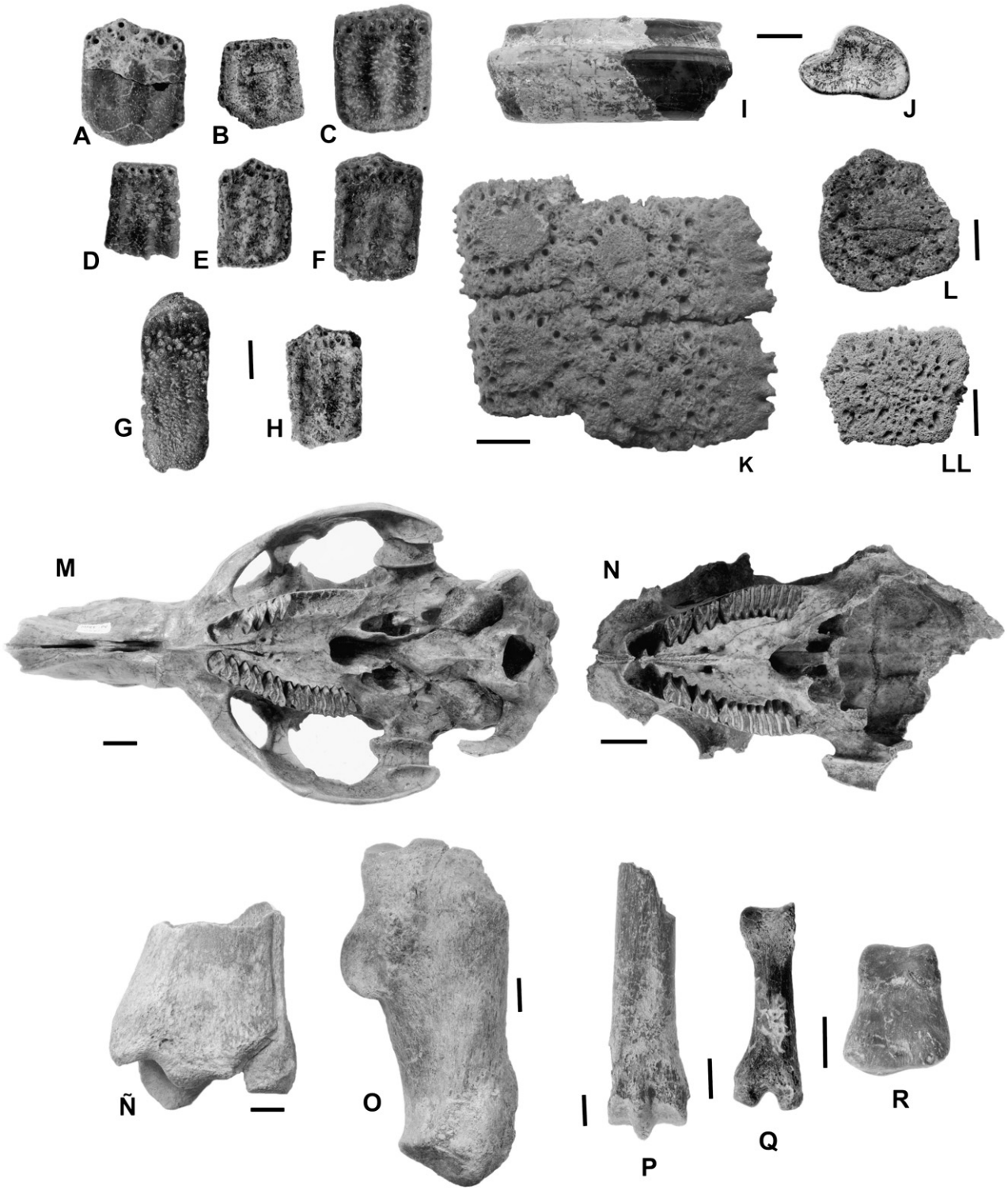

Fig. 4. Fossil mammals from La Pastosa and Rincón Chico Localities. *Scirrotherium* sp. (MPEF-PV 2529) dorsal carapace osteoderms (A–H); Mylodontinae indet. (MPEF-PV 2530) upper left second or third molariform: (I) lateral view, (J) occlusal view; Palaehoplophorini indet. (MPEF-PV 2531) articulated osteoderms from caudal ring (K); (MPEF-PV 2532) isolated osteoderm from the dorsal carapace (L); Neuryunini indet. (MPEF-PV 2533) isolated osteoderm from the dorsal carapace (LL); *Cardiatherium patagonicum* (MPEF-PV 2521) complete skull (M); (MPEF-PV 2520) incomplete skull of a young individual (N); Macraucheniidae indet. (MPEF-PV 2534) distal end of tibia y fibula (Ñ); (MPEF-PV 2536) calcaneus (O); (MPEF-PV 2535) metapodial (P), two phalanges (Q–R). Scale bar equals 10 mm.

Provenance. Rincón Chico site, Península Valdés, Chubut.

LITOPTERNA Ameghino, 1889.

MACRAUCHENIIDAE Gervais, 1855.

Macraucheniidae indet.

Referred material 1. MPEF-PV 2534, distal end of tibia and fibula. Fig. 4Ñ.

Provenance. La Pastosa site, Península Valdés, Chubut.

Referred material 2. MPEF-PV 2536, calcaneus. Fig. 4O.

Provenance. Punta Delgada, Península Valdés, Chubut.

Referred material 3. MPEF-PV 2535 2 phalanges, 1 metapodial, 1 incisor. Fig. 4P–R.

Provenance. Rincón Chico site, Península Valdés, Chubut.

Comments. Although a more precise determination is not possible, these specimens show the presence of endemic South American ungulates in the Puerto Madryn Formation.

5. Discussion

5.1. Stratigraphic location of the sequences

Feruglio (1949) mentions two main marine units for Península Valdés, the "Patagoniense" and the "Entrerriense", and a third transitional unit designated as "Rionegrense". These are informal chronostratigraphic units, recognized by the nature of the rocks, their stratigraphic relationships and fauna (Cione and Tonni, 1995). The contact between the "Patagoniense" and the "Entrerriense" is clear, whereas Feruglio (1949:199) stated that the transition between the "Entrerriense" and the marine "Rionegrense" was gradual, and consequently the boundary is conventional. Scasso and del Río (1987) defined a single major regressive marine sedimentary cycle for the area of Puerto Madryn and Península Valdés that includes minor transgressive–regressive oscillations. The main cycle included the chronoestratigraphical units "Patagoniense" and "Entrerriense", and the "Rionegrense" was considered as the upper part of the "Entrerriense", mostly characterized by the grey hue of its sediments.

Haller (1979) and Haller et al. (2001) grouped the "Entrerriense" and "Rionegrense" under the name Puerto Madryn Formation, a lithostratigraphic unit formed mainly by sandstones, siltstones and coquinas. At the mouth of the Río Negro, the "Rionegrense" was designated as the Río Negro Formation (Andreis, 1965). Later, Malumián (1999:575) assigned the sediments in the upper levels of Puerto Madryn Formation at Península Valdés to the Río Negro Formation, considering them to represent the regressive phases of the "Entrerriense" transgression. Thus, the sections studied here are assigned to the upper levels of the Puerto Madryn Formation, including the upper part of the "Entrerriense" and the "Rionegrense" chronostratigraphic units.

5.2. Biochronological and paleobiogeographical implications

From an ichthyogeographical point of view, the Neotropical region has been subdivided into two main subunits: the Austral and the Brazilian Subregions. Most of the diversity is concentrated in the latter subunit, which also represents the southern geographical limit for the loricariids, one of the most diverse families of America. These fishes are confined to tropical and subtropical climates and their diversity drops abruptly southward of South America. The occurrence of loricariids in Península Valdés (Cione et al., 2005) suggests that the climate was much warmer than today, and is consistent with Cione's hypothesis that the range of Brazilian fish fauna extended much more southwards during the Cenozoic. The local extinction of Loricariidae in the southern part of South America may have been related to climatic changes due to the rise of the Patagonian Andes. According to Pascual et al. (1996) the Patagonian climate already had been affected by the Quechua Phase since the middle Miocene.

Several of the recorded mammal taxa are good temporal indicators. The pampatheriid *Scirrotherium* has been recorded in the Honda Group of Colombia (late middle Miocene) and in the "Conglomerado osífero" of the Ituzaingó Formation (Entre Ríos province, Argentina), assigned to the Huayquerian Age (Cione et al., 2000). The Neuryurini glyptodonts are known from the Huayquerian to the Lujanian age (in the "Conglomerado osífero" and also in Buenos Aires, Catamarca and Tucumán provinces). The mylodontids *Ranculcus* and *Megabradys* are known from the "Conglomerado osífero" (Cione et al., 2000) and the former also occurs in the Raigon Formation (Uruguay) and Solimões Formation (Brazil), also assigned to the Huayquerian age (Perea and Scillato-Yané, 1990). The Hydrochoeridae are known since the Chasicoan, but the greatest species diversity of the genus *Cardiatherium* occurs during the Huayquerian Age ("Conglomerado osífero", Ituzaingó Formation, Entre Ríos Province; Puerta de Corral Quemado, Catamarca Province; Cerro Azul Formation, La Pampa Province, Río Negro Formation, Río Negro Province; Loma de las Tapias Formation, San Juan Province; Puerto Madryn Formation, Chubut Province; Deschamps et al., 2009; and Kiyú and San José Formation, Uruguay; Urumaco Formation, Venezuela; Solimões Formation, Brasil; Cozzuol, 2006 and included references). The hydrochoerid rodents from Península Valdés in particular represent the southernmost record known for this family. The chinchillid *Lagostomopsis* is known since the Chasicoan Age. The Caviidae are recorded with doubts since the Colloncuran, and the Dolichotinae, since the Laventan (Walton, 1997). Summarizing, the temporal ranges of the recorded taxa together span the middle Miocene to the Pliocene, with the Huayquerian age common to all (Dozo et al., 2002).

5.3. The Huayquerian age and radiometric datings in Península Valdés

The age of the Puerto Madryn Formation has been extensively debated. In recent years, it had been referred to the middle Miocene on the basis of the record of "Entrerriense" malacofauna, but recently it was assigned to the late Miocene (Martínez and del Río, 2002; del Río, 2004). The main argument used by del Río (1988) to assign the "Entrerriense" to the late middle Miocene were the peaks of rising temperatures recorded globally between 14 and 13.6 Ma, and between 12.5 and 12.25 Ma. However, subsequent studies have indicated the existence of three pulses of temperature peaks in the Southern Hemisphere: 9.7–8.8 Ma, 7.8–7.2 Ma, and 6.1–6.5 Ma; consequently, the warm-water mollusc fauna of this formation could have been established during any of these lapses (Martínez, 1994). A recent palynological study also assigned the sediments of the Puerto Madryn Formation to the late Miocene (Palazzesi and Barreda, 2004).

The Huayquerian Age attributed to the fossil-bearing sediments of the new site, on the basis of its fossil mammal content, agrees also with the radiometric ages obtained for Península Valdés in three glass concentrates from a tuff in the upper layer of the marine "Rionegrense" from Bahía Cracker (southern coast of the Nuevo Gulf, Chubut Province), which were dated by $^{40}K/^{39}Ar$, yielding an average Tortonian age of 9.41 Ma (Zinsmeister et al., 1981). Scasso et al. (2001) presented numerous datings obtained by $^{87}Sr/^{86}Sr$ techniques from Pectinidae and oyster shells, which yielded a mean age of 10.1 Ma (middle Tortonian). It is worth noting that these dates span a range of 18.4 to 8.7 Ma, but Scasso et al. (2001) discarded the oldest ages and retained those spanning 10.8 to 8.7 Ma because the latter were considered more reliable. Both the calculated radiometric ages and the above mentioned mollusc fauna allow inferring that this could represent the first warm pulse of the Tortonian (del Río, 2000).

5.4. Paleofloristic context based on terrestrial and marine palynomorphs

The palynological records from the Puerto Madryn Formation provide some significant insights into the floristic context, paleoenvironment and paleoclimate in northeastern Patagonia during late Miocene times. The history of Miocene vegetation in northeastern Patagonia is related to the progressive replacement of forest types (early Miocene) by more open and xerophytic types (late Miocene) according to Barreda and Palazzesi (2007). Major turnovers in community composition appear to reflect mainly the effects of Andean uplift and step-wise decreases of sea-surface temperatures (SST) associated with the establishment of the circum-Antarctic current and Antarctic ice cap. Other forces such as volcanism may have directly influenced the development of vegetation in non-Andean Patagonia. Whether or not all of these forcing factors promoted the spread of xerophytic taxa to lowland regions in the late Miocene remains to be tested. The progressive eastward migration and disappearance of

Nothofagus forests in eastern Patagonia likely reflects the repeated loss of closed forest habitats due to aridity during late Neogene (Blisniuk et al., 2005; Barreda et al., 2008).

In the Valdés Basin, in particular, terrestrial palynomorphs (mostly pollen grains) suggest the presence of low xerophytic open forests formed by *Schinus* (pepper trees), *Prosopis* (Calden family), *Celtis* (hackberry) and several shrubs belonging to the Asteraceae (sunflower family), currently extinct in the region (e.g. *Schlechtendalia*). In some cases, halophytic shrubs with Chenopodiaceae (glasswort family), Ephedraceae (joint-pine) and Convolvulaceae *Cressa*-type (morning glory family) dominate the assemblages, indicating tidal salt-marshes in the vicinity of the basin (Palazzesi and Barreda, 2004). The constant record of Cyperaceae (sedges) and Typhaceae (bur-reed family) may indicate ponds or permanently saturated soils in which freshwater algae (e.g. *Botryococcus*, *Pediastrum*) and aquatic ferns (*Azolla*) could have also developed (Palazzesi, 2008; Palazzesi and Barreda, 2004). The presumed living representatives of the woody taxa recorded in Puerto Madryn Formation occur today in a number of structurally distinct plant communities distributed in central and eastern Argentina (Espinal District; Córdoba and Entre Ríos Provinces). The constant record of terrestrial, aquatic and marine palynomorphs strongly suggests that the marine accumulation of the Puerto Madryn Formation took place on the inner continental shelf. Seasonal swamps and ponds may have developed nearby the coast, particularly in the uppermost levels of this unit, without any marine influence under warm and calm conditions, according to the abundance of floating plants (e.g. *Azolla*). This is supported by the presence of semi-aquatic mammals (e.g. capybaras) and freshwater fishes reported in this study.

Marine palynomorphs indicate high summer sea-surface temperatures (SST) according to the presence of *Tuberculodinium vancampoae*, the cyst of *Pyrophacus steinii* which currently occurs in warm-temperate to tropical environments (Faust, 1998; Zonneveld and Susek, 2007). High abundances of this species in modern North Atlantic sediments are found where summer SST are around 27 °C and water depths are less than 60 m (Edwards and Andrle, 1992).

6. Conclusions

This is the first assemblage of late Miocene continental vertebrates recorded south of Río Negro Province; it also includes the southernmost record of hydrochoerid rodents, dendrocygnine birds and loricariid fishes.

The mammals are correlated with the Mesopotamian assemblage in the "Conglomerado osífero" of Ituzaingó Formation (Entre Ríos province, Argentina) and they suggest that fossil-producing levels are Huayquerian in age. The chronological position of the Huayquerian Age, 9 Ma at its base and 6.8 Ma at the top, agrees well with the radiometric dates previously performed in beds closely underlying the fossiliferous intraformational conglomerate.

At the admittedly early present early state of knowledge the only carnivores registered in these environments are psilopterines and accipitrids birds.

The climate during the accumulation of late Miocene deposits in this region is inferred to have been warm and probably seasonally dry, according to the present-day distribution of the nearest living relatives of most angiosperm groups that occur in the fossil record.

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