

Marine vertebrate assemblages in the southwest Atlantic during the Miocene

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Two biogeographical units are generally recognized in the present shelf area of Argentina: the Magellanian and Argentinian Provinces. The two provinces differ in their fossil record. The evolution of these provinces has been characterized by migrations, extinctions, pseudoextinctions and, perhaps, even speciation events. Marine vertebrate assemblages with some similarities to the Argentinian fauna were already present in the Miocene, whereas no associations similar to those of the Magellanian fauna have been found in South America before the Pleistocene. Two successive major marine transgressions flooded northern Patagonia during the Miocene: the ‘Patagoniense’ (Early Miocene) and the ‘Entrerriense’ (Middle to Late Miocene). We analyse three rich fossil assemblages that were formed during these transgressions. The absence of Magellanian Miocene vertebrate assemblages is consistent with the hypothesis of a more southern distribution of the cold-temperate fauna at that time. In Patagonia, as in other regions, an increased number of living groups appeared from the Lower to Upper Miocene. The Late Miocene aquatic mammals had a modern aspect, and some of the fish species are still living in the South Atlantic Ocean. In this contribution, we stress that warm-temperate fishes and a high diversity of penguins are found together at the base of the Gaiman Formation. We hypothesize that penguins were adapted to live in warmer waters than those of the latest Cenozoic and the Recent. Finally, we recall that many taxa became extirpated because of the global temperature drops of the late Cenozoic. However, some fishes and pinnipeds which were extirpated only in the Atlantic Ocean are discussed here. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 423–440.

ADDITIONAL KEYWORDS: Actinopterygii – Aves – biogeography – Elasmobranchii – Mammalia – shelf.

Actualmente se reconocen dos provincias biogeográficas en la plataforma marina argentina actual: la Magallánica y la Argentina. Las dos unidades difieren en su registro fósil. Se sugiere aquí que la evolución de las provincias fue compleja y caracterizada por migraciones, eventos de especiación, extinciones, pseudoextinciones. Durante el Mioceno ya había asociaciones de vertebrados marinos con similitudes taxonómicas con los de la Provincia Argentina pero no se detectaron hasta ahora asociaciones fósiles similares a las de la Magallánica hasta el Pleistoceno. Aquí describimos tres ricas asociaciones faunísticas marinas del Mioceno que se depositaron durante dos grandes transgresiones atlánticas: el ‘Patagoniense’ (Mioceno Temprano) y el ‘Entrerriense’ (Mioceno Medio a Tardío). La ausencia de asociaciones de tipo magallánicas en el Mioceno confirma la hipótesis de que la fauna templado-fría se distribuía más al sur en ese tiempo. En Patagonia, tal como en otras áreas, se registra un número mayor de formas actuales desde el Mioceno Temprano al Tardío. Los mamíferos acuáticos del Mioceno

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Tardío tenían un aspecto moderno; incluso alguna de las especies de peces perdura en la actualidad. Asimismo, en este trabajo llamamos la atención sobre la coexistencia de una diversidad muy alta de pingüinos con tiburones de ambientes templado-cálidos en la base de la Formación Gaiman. Interpretamos que estos pingüinos estaban habituados a soportar aguas más cálidas que los actuales. Finalmente, discutimos la pseudoextinción de vertebrados en el Océano Atlántico.

PALABRAS CLAVE: Actinopterygii – Aves – biogeografía – Elasmobranchii – Mammalia – plataforma continental.

INTRODUCTION

The Recent vertebrate biogeography of the southwest Atlantic has been relatively well studied (Menni, Ringuelet & Arámburu, 1984; Cousseau & Perrotta, 1998; Menni & Stehmann, 2000; Acosta Hospitaleche, 2006; Acosta Hospitaleche *et al.*, 2007a; Jefferson, Weber & Pitman, 2008). Cold- and warm-temperate associations coexist on the shelf off Patagonia and central Argentina (Menni *et al.*, 2010). These associations include many modern marine vertebrate families which have been reported since the Miocene, but also some extant Miocene species, at least among fishes. A knowledge of the Miocene vertebrates and their distribution is relevant for a proper understanding of extant biocenoses and biogeographical patterns. Miocene marine vertebrates are relatively well documented in southern South America (Cione, 1988; Cozzuol, 1993, 1996, 2001; Arratia & Cione, 1996; Acosta Hospitaleche, 2003, 2004, 2006; Cione & Báez, 2007). Here, we describe the vertebrate fauna from two lithostratigraphic units of early and middle–early late Miocene age from Patagonia (Gaiman and Puerto Madryn), and a formation of late Miocene age from central-eastern Argentina (Paraná), rich in fossil vertebrates and thus relevant to our evolutionary and biogeographical discussion. The aim of this contribution is to synthesize knowledge about the successive changes in the composition of marine vertebrate faunas from the southwest Atlantic Ocean during the Miocene, and to interpret it in relation to known or inferred modifications in the environment and to the evolution of the different clades in which the Recent biota is rooted.

GEOLOGICAL CONTEXT

During late Palaeogene and early Neogene times, southern South America east of the Andes experienced stable tectonic conditions and the dominant sedimentary accumulations are fine grained (Uliana & Biddle, 1988; Malumián, 2002). Remarkably, on many areas of continental Argentina, the late Palaeogene and early Neogene are missing because of a

regional unconformity, largely caused by reduced accommodation (erosional beveling plus nondeposition) around the 29–30 Ma eustatic drop (Uliana & Biddle, 1988). However, rocks corresponding to this lapse seem to be well represented in Patagonia. Late Palaeogene and Neogene marine inundation occurred in the same general areas as those in which Late Cretaceous flooding occurred; the large areal extent of the marine deposits reveals that the mean freeboard of the plate interior was still consistently low during this period (Uliana & Biddle, 1988). The end of the extensive marine encroachment that lasted from the late Oligocene to the late Miocene (Mid-Tertiary Transgressive Onlap Sequence) was parallel to the early Neogene trend of global eustatic rise (Haq, Handberg & Vail, 1987; Uliana & Biddle, 1988; del Río, 1991). The early Miocene transgression was limited to Patagonia and is known as the ‘Patagoniense’ (Figs 1A, 2). The marine deposits of middle and late Miocene age are restricted to northeastern Patagonia and the Chaco-Pampean area. These transgressions are known as the ‘Entrerriense’ or ‘Paranense’ (Figs 1B, 2). The Miocene marine influence supposedly reached up to Bolivia (Marshall, Sempere & Gayet, 1993). Some authors have proposed that a sea branch crossed South America reaching even the Caribbean Sea (Räsänen *et al.*, 1995; Aceñolaza, 2000; for a different view, see Hernández *et al.*, 2005; Cozzuol, 2006). This depositional pattern was controlled by tectonics in a context of high sea level (Yrigoyen, 1975; Haq *et al.*, 1987; Uliana & Biddle, 1988; Marshall *et al.*, 1993). After the Miocene, no important transgressions are known in the area, and there are no certain records of early and middle Pleistocene marine vertebrates.

The Gaiman Formation crops out extensively in northeastern Patagonia (Mendía & Bayarski, 1981; Cione, 1988). This formation was deposited during the ‘Patagoniense’ and most of the early Miocene marine vertebrates known for northern Patagonia were obtained there. Vertebrate remains were found in two reworked and winnowed lags associated with transgressive surfaces, which display a concentration of phosphatic concretions, ooids, bones and teeth,

decapod remains, and some large shells, collectively constituting condensed deposits (lower and upper T2 levels of Scasso & Castro, 1999). The beds of the 'Entrerriense' overlying the Gaiman Formation in the Península Valdés area were included in the Puerto Madryn Formation (Haller, 1979). The strata of the Puerto Madryn Formation have been correlated with the Paraná Formation of the base of the Río Paraná cliffs (near Paraná, Entre Ríos Province, eastern Argentina). Vertebrate evidence suggests that the lower beds of the Puerto Madryn Formation could be older than the strata cropping out in the Río Paraná cliffs (Cozzuol, 1993, 1996; Cione *et al.*, 2000). Sections of more than 100 m crop out in the Península Valdés area over the Gaiman Formation. Most of the marine vertebrate fossils were collected in the lower and middle levels, of probable middle Miocene age. In the Paraná region, instead, only the uppermost 20 m of the Paraná Formation crop out. The total thickness of this unit is about 100 m. Vertebrates were thus collected solely in the upper section of the Paraná Formation, of confirmed late Miocene age (Cione *et al.*, 2000, 2005a).

The radiometric ages of the different units are discussed in Zinsmeister *et al.* (1981), Scasso *et al.* (2001), Schultz *et al.* (2004), Cione *et al.* (2005b) and Hernández *et al.* (2005).

RECENT OCEANOGRAPHY

The marine biogeography of the southwestern Atlantic South American shelf is greatly constrained by the current pattern. The Recent Patagonian shelf is the largest in South America. The bottom is flat and with a gentle slope (Parker, Paterlini & Violante, 1997; see also Cavallotto, Violante & Hernández Molina, 2011, Ponce *et al.*, 2011). The dominant feature of the current system of the southern region is the Antarctic Circumpolar Current which influences the greatest part of the Antarctic oceanic region and the entire temperate oceanic region (Knox, 1960; Fig. 3). It branches into currents flowing northerly off the coast of the major land masses. On the western part of South America, it becomes the Humboldt Current (also Perú Current). In the Drake Passage, the Ant-

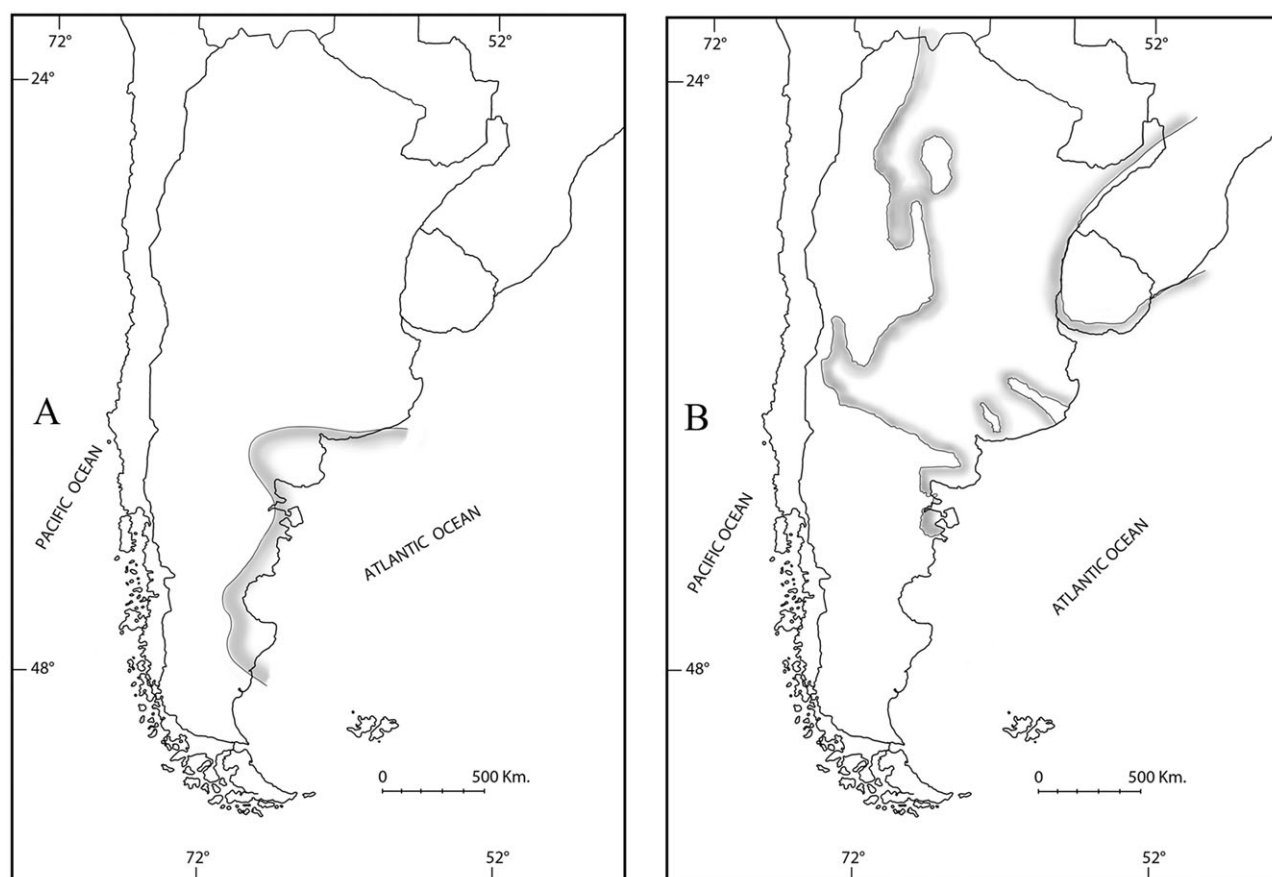


Figure 1. A, Flooded area during the deposition of the Gaiman Formation. B, Flooded area during the 'Entrerriense' (modified from Uliana & Biddle, 1988).

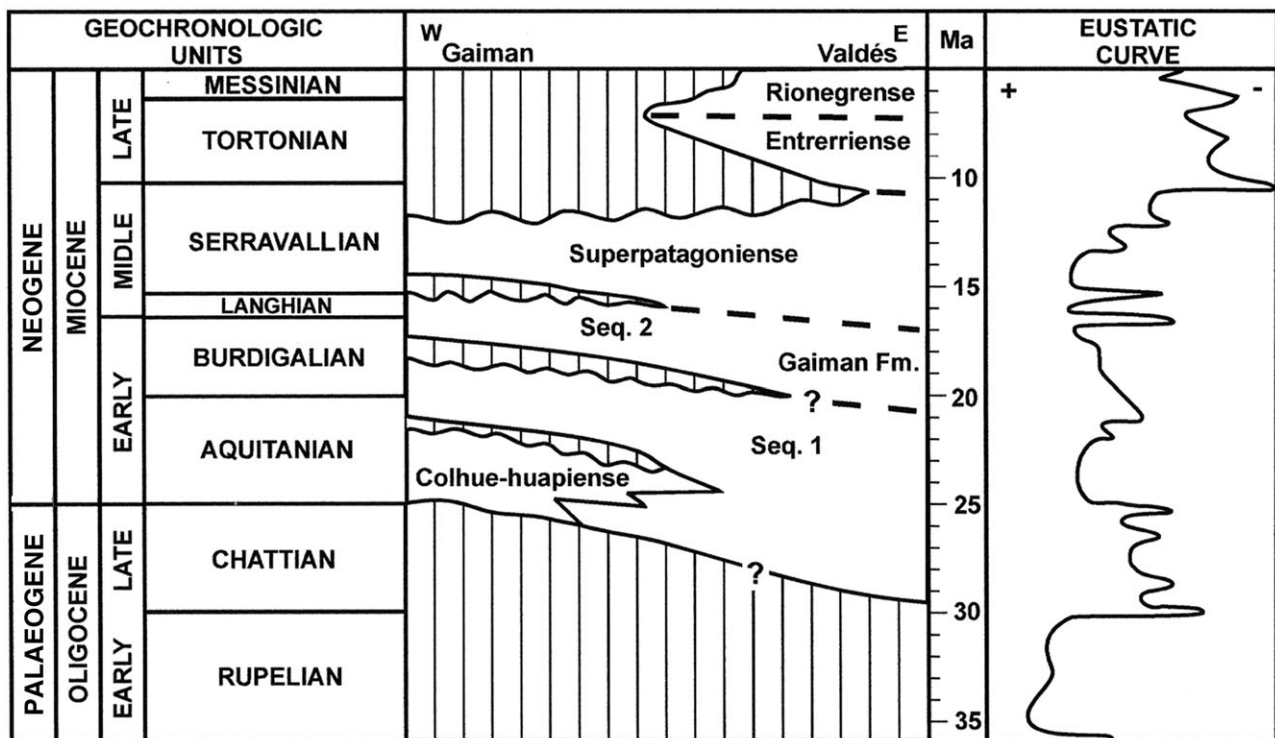


Figure 2. Stratigraphy of Miocene units in northeastern Chubut (modified from Scasso & Castro, 1999).

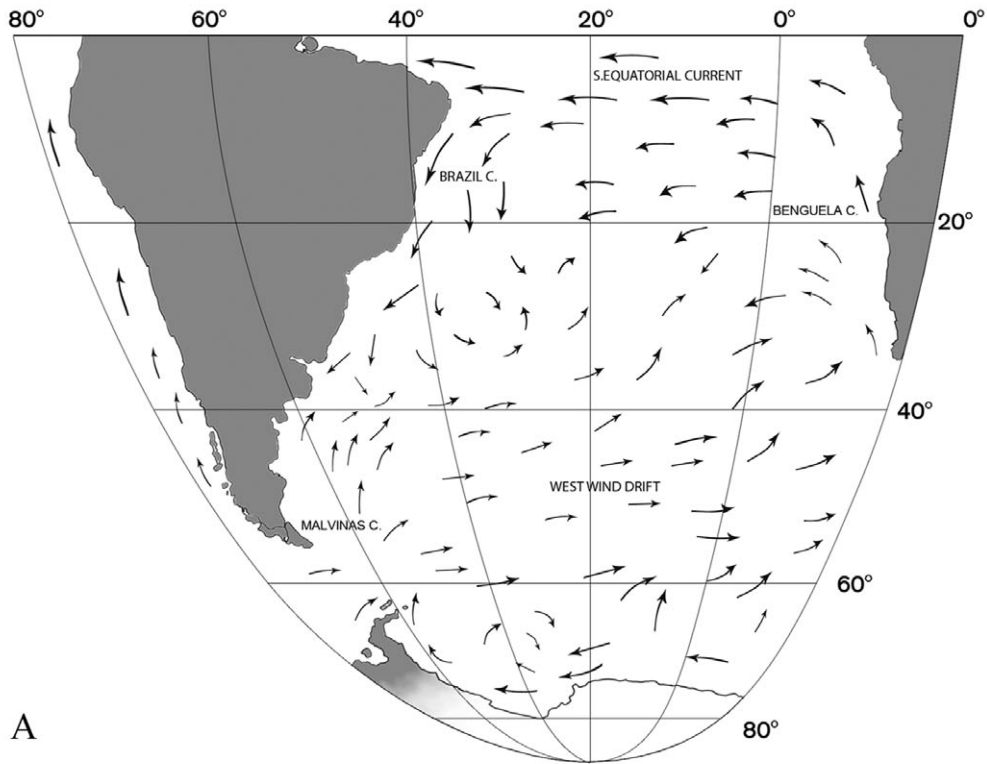
arctic Circumpolar Current is known as the Cape Horn Current which, after passing the southern tip of the continent, divides into two branches. The west branch passes on both sides of the Malvinas-Falkland Archipelago and is called the Malvinas-Falklands Current. It collides with the warm southward Brazil Current and turns east (Olson *et al.*, 1988). The Humboldt Current is much stronger than the Malvinas-Falklands Current and its influence extends to near the equator (Sverdrup, Johnson & Fleming, 1964; Thiel *et al.*, 2007).

RECENT MARINE BIOGEOGRAPHY OF SOUTHERN SOUTH AMERICA

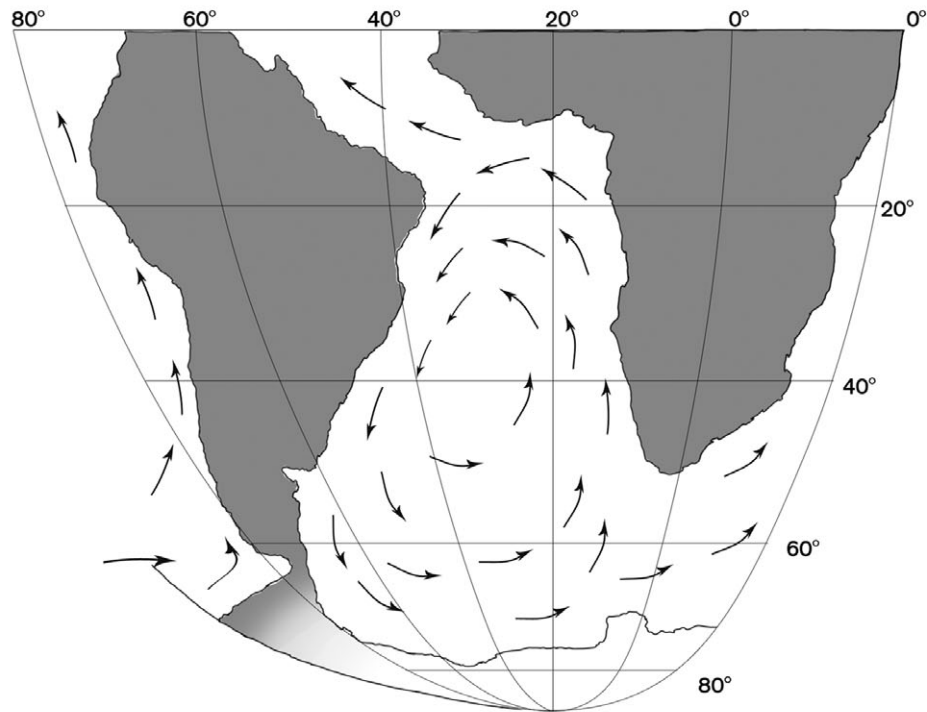
Different authors have divided the coastal marine waters of South America into biogeographical units (see Menni, 1981; Menni *et al.*, 2010). López (1964) considered the following biogeographical units (Fig. 4): Magellanian Province (of cold-temperate waters) with two districts, South Chilean and Patagonian; Argentinian Province (of warm-temperate waters) with two districts, Bonarian and South Brazilian; West Indian Province (of warm waters) with three districts, Gulf of Mexico and Caribbean, Antillean, and Brazilian. Balech (1964) proposed a rather different scheme. The Magellanian Province occupies

the southernmost part of South America. According to López (1964) and Menni *et al.* (2010), it reaches 42°S in the Atlantic coast and 40–41°S in the Pacific Ocean (Fig. 2). According to Balech (1964), it reaches up to 43°S and 40°S, respectively. However, in the outer shelf and slope, the Magellanian Province reaches further north to approximately 34°S, separating from the coast at the latitude of 43–45°S. The Argentinian Province ranges from about 42°S to 23°S according to López (1964). Boundaries between the Argentinian and Magellanian Provinces could be presently changing as a result of global temperature changes (see Góngora *et al.*, 2003). Penguins are characteristic of the Magellanian Province. Although some individuals reach the Argentinian Province (mostly *Spheniscus magellanicus*), no penguin breeds in this area. Typical fish taxa of the Argentinian Province (with fossil record in the area) are the squatinid *Squatina*, the myliobatids *Myliobatis*, the carcharhinids *Carcharinus* and *Galeocerdo*, the sphyrid *Sphyrna*, the odontaspidae *Carcharias taurus*, labrids, sciaenids and others. Some fishes with fossil records, such as the squalid *Squalus*, are present in both provinces.

Northern Patagonian Miocene outcrops are located near the latitude of the boundary between both provinces. Paraná localities are at the latitude of the current Argentinian Province.



A



B

Figure 3. A, Recent marine circulation in the southern Atlantic Ocean (modified from Sverdrup *et al.*, 1964). B, A model of marine circulation during Eocene times previous to the establishment of the Antarctic Circumpolar Current (modified from Cione *et al.*, 2007a).

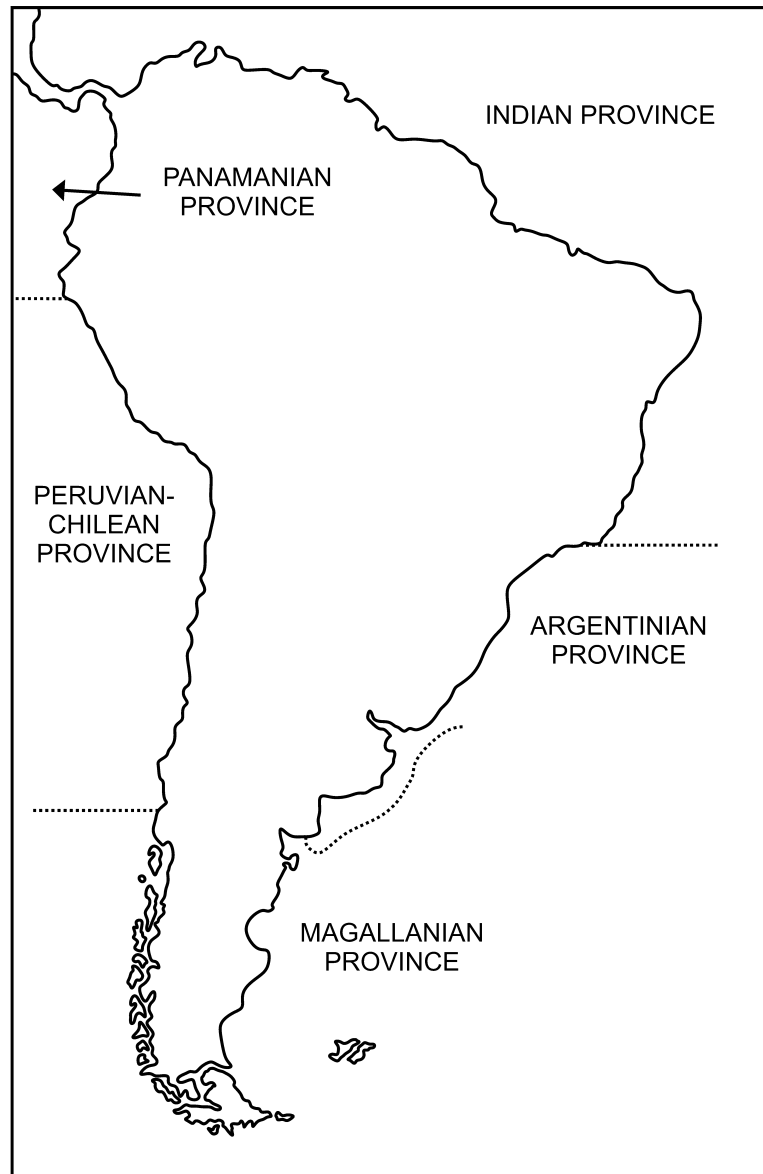


Figure 4. Biogeographical shelf provinces (modified from López, 1964; Menni, 1981).

VERTEBRATES OF ARGENTINIAN FORMATIONS OF MIOCENE AGE GAIMAN FORMATION (EARLY MIOCENE)

During the early Miocene, marine mammals are only represented by cetaceans, both Odontoceti and Mysticeti. At this moment, some living families are already recognizable (Cozzuol *et al.*, 1990; Cozzuol, 1996). Mysticeti are represented by the earliest Balaenidae (*Morenocetus parvus*; Buono, Dozo & Cozzuol, 2009) and the extinct Cetotheriidae. Cetotherids are a primitive, paraphyletic group, probably related to Balaenopteridae, with two species in the Gaiman Formation. The best known is *Aglocetus moreni*, with

several well-preserved skulls and associated postcranial skeleton (Cozzuol, 1996). The other species, *Plecicetus dyticus*, is only known by the posterior part of a skull. Odontoceti are represented by several extinct families: Squalodelfidae, Eurhinodelfidae, Squalodontidae, Prosqualodontidae and Kentriodontidae and the earliest Physeteridae (cachalots). This latter family includes two species from different genera: *Diaphorocetus poucheti* and *Idiorophus patagonicus*. The most abundant cetacean in this formation is the squalodelfid *Notocetus vanbenedeni*, a dolphin about 3 m long and with a relatively long rostrum (Cozzuol, 1996). The family Eurhinodelfidae was distributed worldwide during the early and middle Miocene and

became extinct during the late Miocene. In Patagonia, it is represented by *Argyrosetus patagonicus*. The squalodontid *Phoberodon arctirostris* is one of the most primitive platanistoids. The prosqualodontid *Prosqualodon australis* is a brevirostrid odontocetid recently removed from the family Squalodontidae. Another species of this genus was described for Australia and New Zealand, and it is possible that it would be a synonym of *P. australis*. In any case, the genus had a circumpolar distribution and it would be the first fossil cetacean species shared with these areas (Cozzuol *et al.*, 1990). The oldest kentriodontids (Delphinoidea) are known from the Gaiman Formation. The best specimen is a partial skull of a small species of *Kentriodon* (Cione & Cozzuol, 1990). Undescribed periotic bones from the same unit belonging to Kentriodontidae indicate that the diversity of families was greater than expected for that period.

Most marine birds in the Gaiman Formation are penguins. Spheniscids include four sympatric species represented by disarticulated bones: *Eretiscus tonni*, *Palaeospheniscus bergi*, *P. patagonicus* (Fig. 5) and *P. biloculata*. There are small- and medium-sized species. Although penguin diversity was high, it has been overestimated (Acosta Hospitaleche, Tambussi & Cozzuol, 2004; Acosta Hospitaleche, 2007, 2009, 2010). Articulated or associated skeletons were found only in a few cases (Acosta Hospitaleche *et al.*, 2008). Further south, in the Monte León Formation of Santa Cruz, a partially articulated specimen of *Paraptenodytes antarctica* was found (Acosta Hospitaleche, 2005), and unidentifiable isolated bones of penguins occur in the Chenque Formation of southern Chubut. The largest numbers of penguin bones come from the Gaiman Formation outcrops, where penguins are represented mainly by disarticulated bones, many of which show predation marks (Cione *et al.*, 2010). This assemblage may belong to a long-lasting breeding colony. When the sea transgressed onto the continent, the penguin bones deposited in subaerial conditions would have been buried into the marine sediments. An anseriform related to a living African form was also recorded. This is the oldest record of a nonflying anseriform (Noriega, Tambussi & Cozzuol, 2008).

The better known fishes from the early Miocene beds are elasmobranchs. The dearth of actinopterygians can probably be attributed to taphonomic reasons (Cione, 1988; Cione *et al.*, 2010). Several shark taxa of the early Miocene of Patagonia are cosmopolitan in temperate or warmer seas: *Isurus hastalis* (very abundant), *Carcharocles chubutensis*, *Hemipristis serra*, *Galeocerdo aduncus* (Fig. 6; Cione, 1978, 1986, 1988; Arratia & Cione, 1996). The shark genus and species *Carcharoides totuserratus* (very abundant) was resurrected by Cappetta (1987) and Cione (1988). *Carcharoides totuserratus* is the vicari-

ant species of the northern *C. cattica*. *Carcharoides* has a bipolar geographical distribution (Cione, 1988). Two endemic species are the echinorhinid *Echinorhinus pozzii* (Fig. 6) and the carcharhiniform *Megascyliorhinus trelewensis* (Cione, 1986).

Other fishes from the Gaiman Formation have been identified at the generic or higher level; for instance, the squalid *Squalus*, the pristiophorid *Pristiophorus*, the heterodontid *Heterodontus*, the odontaspidid *Odontaspis*, myliobatid batoids (abundant), holocephalans, *Oplegnathus*, labrid and molid teleosts (Cione & Expósito, 1980; Cione & Pandolfi, 1984; Cione, 1988; Arratia & Cione, 1996; Cione & Azpelicueta, 2002).

PUERTO MADRYN FORMATION (MIDDLE-LATE MIOCENE)

Most of the material collected from this formation came from the lower-middle beds, of probable middle Miocene age. Vertebrates are not common in the Puerto Madryn Formation, but they are remarkable because of their fine preservation; many specimens are even known by complete skeletons. The extraordinary preservation of vertebrates and invertebrates (Cozzuol, 1993, 2001; Riva Rossi, Gosztanyi & Cozzuol, 2000; del Río, 2001; Casadío, Feldmann & Schweitzer, 2005; Acosta Hospitaleche *et al.*, 2007) may, in part, be a result of rapid burial after storms, which deposited a large volume of sediment in a short time. A series of storm deposits along the sequence was described by Scasso & del Río (1987), Scasso *et al.* (2001) and del Río (2001). The best specimens are normally found at the top of massive layers of fine, silty sandstones less than a metre thick. No evidence of postburial predation/scavenging was observed.

The Puerto Madryn Formation includes more modern cetaceans than does the Gaiman Formation and the oldest Southern Hemisphere pinnipeds (Cozzuol, 1996, 2001; Buono & Cozzuol, 2010). Odontoceti, which predominated during the early Miocene (Squalodontidae, Eurhinodelphidae and Kentriodontidae) became extinct, whilst modern families diversified (Physeteridae, Delphinidae, Phocoenidae, Ziphiidae, Pontoporidae). Mysticeti are represented by the Cetotheriidae and new Balaenidae. A new species of a primitive small balaenid, 4 m long, is known by four specimens, filling the gap between the early Miocene *Morenocetus parvus* and the late Miocene balaenids recorded elsewhere. Stratigraphic and geographical evidence suggests that the origin and early evolution of the Balaenidae occurred along the eastern coasts of South America (Buono *et al.*, 2009). The oldest pinnipeds in the Southern Hemisphere surprisingly appear to correspond to the Phocinae, otherwise restricted to the Northern Hemisphere (Cozzuol, 1996, 2001).

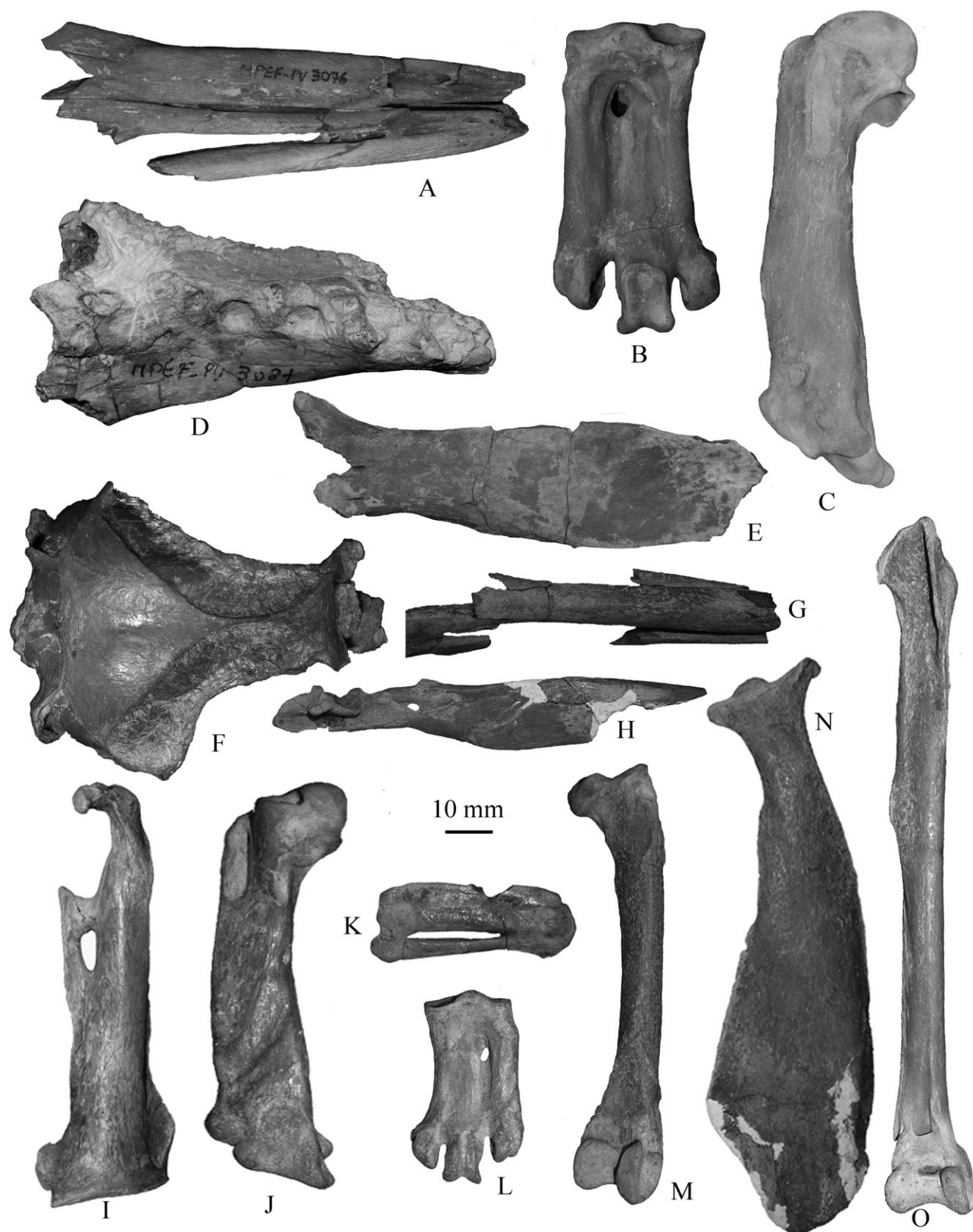


Figure 5. Miocene birds from the Miocene marine beds of Patagonia. A–E, *Palaeospheniscus patagonicus* (MEF-PV 3069–3082) from about 6 km to the south of Playa Santa Isabel, Chubut Province, Argentina (Gaiman Formation, early Miocene). A, Rostrum in lateral view. B, Right tarsometatarsus in anterior view. C, Left humerus in posterior view. D, Synsacrum in lateral view. E, Fragmentary left scapula in anterior view. F–O, *Madrynornis mirandus* (MEF-PV 100) from Playa Villarino, Península Valdés, Chubut Province, Argentina (Puerto Madryn Formation, early late Miocene). F, Skull in dorsal view. G, Rostrum in dorsal view. H, Mandible in internal view. I, Coracoids in anterior view. J, Humerus in anterior view. K, Carpometacarpus in anterior view. L, Tarsometatarsus in cranial view. M, Femur in posterior view. N, Scapula in anterior view. O, Tibiotarsus in anterior view. The fossil material is deposited in the Museo Egidio Feruglio, Trelew, Argentina. Scale bar: 1 cm.

Spheniscids are scarcer than in the early Miocene. A few isolated remains are known from this unit from different localities (Acosta Hospitaleche, 2003, and references cited therein). However, a remarkable penguin specimen (Acosta Hospitaleche *et al.*, 2007a) constitutes the most complete skeleton known for a fossil penguin (Fig. 5). Phylogenetic studies suggest that *Madrynornis mirandus* was closely related to modern penguins living in the area today (Acosta Hospitaleche *et al.*, 2007a). In addition, an isolated remain assigned to *Dendrocygna* (Anseriformes) was found in the upper levels (Acosta Hospitaleche, Tambussi & Dozo, 2007b), as well as the first record of a Ciconiidae with a new species (Noriega & Cladera, 2008).

Elasmobranchs are not abundant. Only the otodontid *Carcharocles megalodon*, the lamnid '*Isurus*' *xiphodon*, the odontaspideid *Carcharias* sp., the squatinid *Squatina* sp. and the myliobatid *Myliobatis* sp. were reported (Cione, 1978, 1988; Arratia & Cione, 1996). Osteichthyans are more abundant and frequently preserved as articulated skeletons. They include siluriforms, ophidiiforms, escorpaeniformes, perciforms (Pinguipedidae, Pomadasidae), pleuronectiformes and gadiforms (Cozzuol *et al.*, 1990; Cione, Azpelicueta & Caille, 1996; Riva Rossi, 1997; Riva Rossi *et al.*, 2000).

PARANÁ FORMATION (LATE MIOCENE IN THE OUTCROPPING BEDS)

The fossils occur in the uppermost, outcropping beds of the formation. The vertebrate fauna of the late Miocene beds of the Paraná Formation (near the city of Paraná, Entre Ríos, 31°43'S, 60°31'W) is more similar to the Recent fauna than is that in Patagonia. The first balaenopterids occur, and physeterids and balaenids have a modern aspect (Cozzuol, 1993, 1996). In addition, pontoporiids (*Pontistes rectifrons*), together with dugongid (*Metaxitherium* or *Dioplotherium*) and trichechid sirenians, appear for the first time in South America (Cozzuol, 1993, 1996). Phocids are represented by the Monachinae *Properiptychus argentinus* (Muizon & Bond, 1992). Neither cethotheriid cetaceans nor marine birds are known from the Paraná Formation.

The marine elasmobranch fauna found in the Paraná Formation comprises the still living odontaspideid *Carcharias taurus* (very abundant), the carcharhinids *Carcharhinus* spp. (very abundant) and *Galeocerdo aduncus*, the sphyrnid *Sphyrna*, the scyliorhinid *Megascyliorhinus trelewensis*, the heterodontid *Heterodontus*, the squatinid *Squatina*, the lamnid '*Isurus*' *xiphodon* and *Carcharodon* sp., the otodontid *Carcharocles megalodon*, the hemigaleid *Hemipristis serra*, the squalid *Squalus*, and batomorphs Dasyatidae and Myliobatoidei (including *Rhinoptera*) (abundant) (Cione, 1978, 1988; Arratia & Cione, 1996; Cione *et al.*, 2000; 2005a, 2008, Noriega, Cione & Aceñolaza, 2007, and references cited therein). Teleosteans described from the Paraná Formation near the city of Paraná belong to the Sparidae and Sciaenidae (Cione *et al.*, 2000). Elasmobranchs and osteichthyans suggest warm-temperate waters, probably similar to or warmer than present sea water at the same latitude. There are no tropical associations.

VERTEBRATE BIOGEOGRAPHY

The present oceanic current pattern began to be established when the Drake Passage was fully open (Fig. 3). The exact moment is still a matter of debate, but, by the Miocene, the West Wind Drift was already established (Cione, Reguero & Acosta Hospitaleche, 2007a). In this oceanographic context, an equivalent of the Malvinas-Falklands Current was probably present on the southwest Atlantic Ocean shelf. However, the temperatures of this current would have been higher than those of the present Malvinas-Falklands Current because global temperatures were higher than they are today (Zachos *et al.*, 2001; Fig. 7). In addition, considering the major inundated area, the shelf was much wider than today and the coastal waters were probably located further away from the Malvinas-Falklands Current influence (Fig. 1).

The Miocene appears as a lapse when marine vertebrate groups radiated, many important living vertebrate groups appeared and present marine bio-

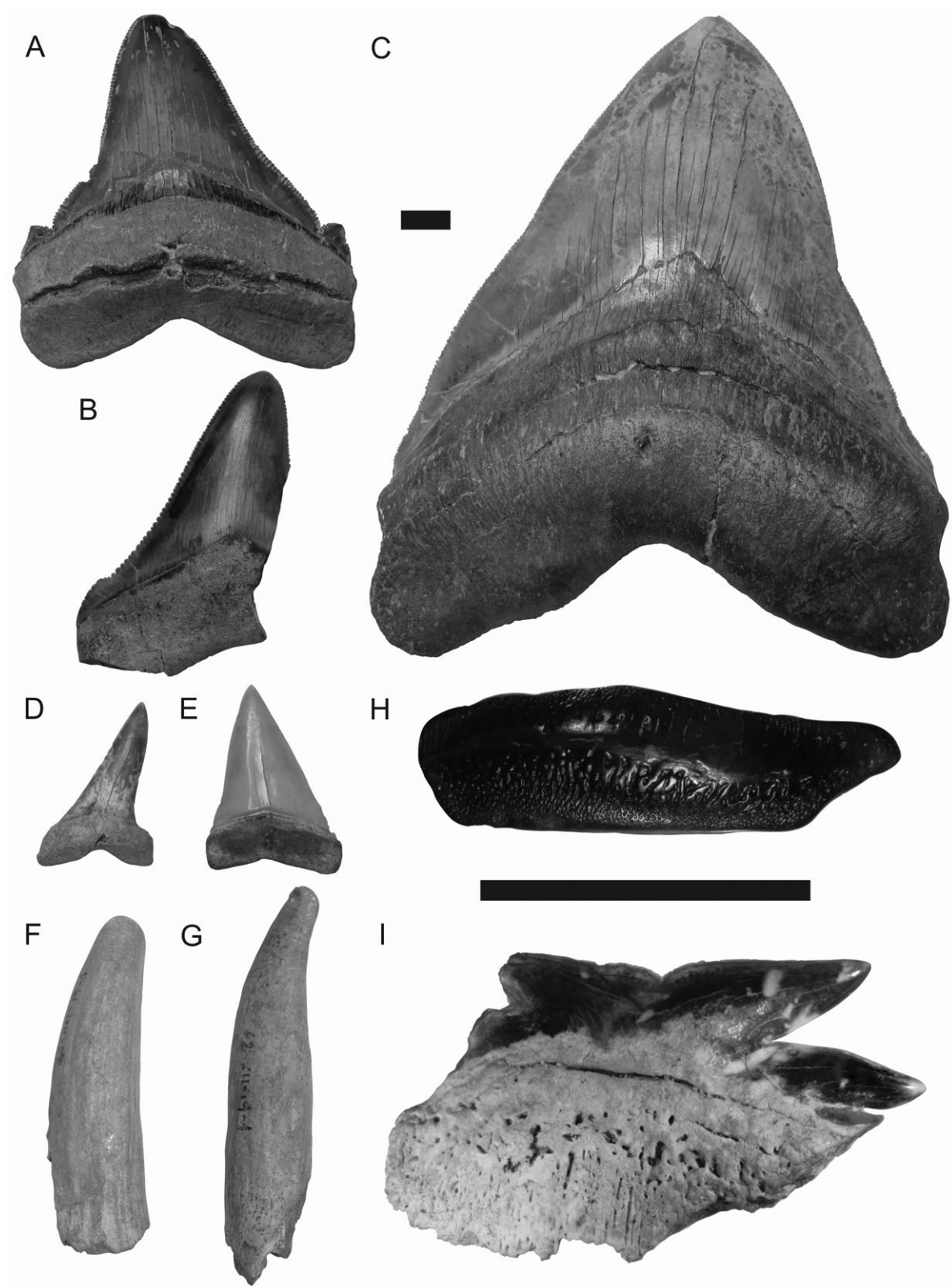


Figure 6. Miocene fishes and cetaceans from Miocene marine beds of Patagonia and Paraná. A, B, *Carcharocles chubutensis* (MLP 86-II-25-9, MLP 86-II-25-10), Bryn Gwyn, Chubut, Argentina (Gaiman Formation, early Miocene). C, *Carcharocles megalodon* (MLP 86-V-1-159), Paraná, Entre Ríos, Argentina (upper Paraná Formation, late Miocene). D, *Isurus hastalis* (MLP 49-XII-6-29), Bryn Gwyn. E, *Isurus xiphodon* (MLP 21-589) (upper Paraná Formation, late Miocene). F, G, *Aulophyseter* (MLP 62-XII-19-1), Rio Negro, Argentina ('Entrerriense', late Miocene). H, *Heterodontus* sp. (MLP 77-XII-22-144), Bryn Gwyn (Gaiman Formation, early Miocene). I, *Echinorhinus pozzii* (MLP 77-XII-22-212), Bryn Gwyn. The material is deposited in the Museo de La Plata, La Plata, Argentina. Scale bar: 1 cm.

geographical patterns began to be established. The radiation is in agreement with a polytaxic period, according to the nomenclature of Fischer & Arthur (1977). High diversity of marine vertebrates, at least in the Southern Hemisphere, would be a consequence of the availability of resources that occurred when the West Wind Drift became established. From the early Miocene to the late Miocene, there was a faunal turnover, with the new taxa becoming more similar to their Recent counterparts.

The vertebrate assemblages present in the Gaiman, Puerto Madryn and Paraná Formations correspond to

a sea of normal marine salinity (Cione, 1978; Cione *et al.*, 2000). The fish fauna included shelf and some oceanic forms.

Marine Miocene faunas in Argentina do not include cold-temperate fish associations (as found in the uppermost, latest Eocene, levels of La Meseta Formation of Antarctica; Cione *et al.*, 2007a) or the present Magellanian fishes, nor tropical fish assemblages (such as those of the Miocene Pirabas Formation of tropical Brazil; Reis, 2005). Recent species of the fish genera occurring in the Gaiman, Puerto Madryn and Paraná Formations either mostly live in marine waters located to the north of the present latitude of Gaiman, in the Argentinian Province, are extinct or have become locally extirpated. However, it is important to recall that most of the fish record is restricted to chondrichthyans and little is known about the bony fish. Most of the present Patagonian shelf corresponds to the Magellanian Province. Yet, no exclusive Magellanian fish occurs in the Miocene units of the area, and it appears that the present Magellanian Province is relatively new in the region. Notably, fish in the Gaiman Formation occur at the same locations and levels as those in which the largest spheniscid diversity is known (see discussion below).

Early Miocene marine tetrapods share genera and even species with other Southern Hemisphere areas, such as Australia and New Zealand. The only exception is the kentriodontid odontocetes. Unfortunately, we have no coeval information from Africa.

The fish and cetacean assemblages from the Paraná Formation are different from those found in the partially coeval Puerto Madryn Formation, but similar to those present in the northern part of the Argentinian Province (Cione, 1978). Although, at Paraná, carcharhinids, hemigaleids and odontaspids dominated, Patagonian ichthyofaunas were dominated by lamnids. However, the sirenian and the pinnipeds found in the Patagonian Formation suggest warmer waters than those of the Argentinian Province for Paraná. Pontoporiid cetaceans (including the recently excluded Brachydelphidae; Cozzuol, 2010) were also common in northern Chile and southern Peru (Cozzuol, 1996, 2010), and the North Atlantic Ocean (Lambert & Post, 2005; Pyenson & Hoch, 2007; Godfrey & Barnes, 2008). The occurrence of ponto-

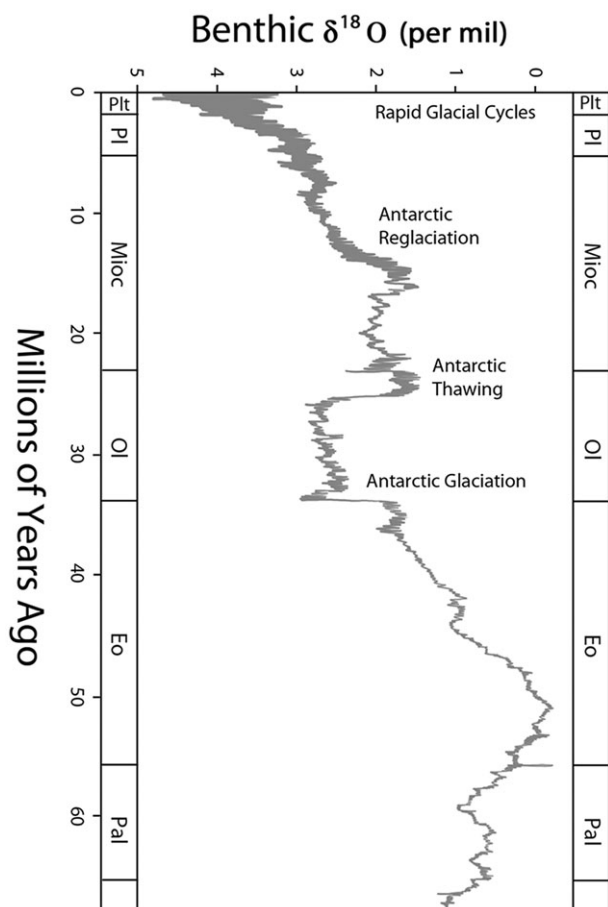


Figure 7. Cenozoic marine temperatures (modified from Zachos *et al.*, 2001).

poriids in the Paraná Formation suggests a biogeographical connection with these regions, at a time when the Central American seaway was still open. *Dioplotherium*, apparently present in these deposits, was also found in northern Brazil (Pirabas Formation of Toledo & Domning, 1991) and in the North Atlantic and Pacific Oceans (Domning, 1989). Balaenopterids have been proposed to have originated in the tropical Atlantic Ocean not before the late middle Miocene, but they appear in the records worldwide by the late Miocene, as is the case of the Paraná Formation. If the *Monachus* affinities of *Poperiptychus argentinus* are confirmed, this group is also known to have a tropical distribution. Consequently, the marine mammals in these formations indicate a stronger south–north connection than, alternatively, connections with other localities in the Southern Hemisphere.

CO-OCCURRENCE OF WARM-TEMPERATE FISHES AND HIGH PENGUIN DIVERSITY IN THE GAIMAN FORMATION BASE

Marine mammals, birds and fishes supposedly having different temperature optima are found together at the base of the Gaiman Formation and this requires an explanation. Four hypotheses can be proposed to explain these associations.

TWO MASSES OF WATER OF DIFFERENT TEMPERATURE EXISTED IN THE AREA

In some areas, two masses of water with different temperature are close or converge. The Malvinas–Falklands current was probably established at the time of the sedimentation of the Gaiman Formation. However, assuming that the breeding biology of the four different fossil penguin species was not different from that of extant penguin species, it seems unlikely that the four species would have had breeding areas in the proximity of warmer waters. Moreover, no fishes of cold-temperate or cold water have been reported from the Gaiman Formation.

SEASONALITY

Many marine vertebrates migrate. Although there is probably a mixture of fishes adapted to rather different temperatures that can be explained by seasonal changes in temperature, there is no present example of such a dramatic change in one year.

PENGUINS WERE NOT EXACTLY COEVAL WITH FISHES
Flooding of the region was caused by rising temperature (Fig. 7). The abundant penguin bones from the

base of the Gaiman Formation appear to correspond to breeding areas (Cione *et al.*, 2010). Fish remains could have corresponded to warmer conditions than those corresponding to the period when penguins were breeding on the coast, before sea level rose.

PENGUINS CHANGED THEIR ECOLOGICAL CONSTRAINTS

Penguins are confined to southern high latitudes. However, *Spheniscus mendiculus* breeds in the Galápagos Islands (near the equator) because of the influence of the cold Humboldt Current (Martínez, 1992; Fig. 4). The four species whose remains are found in this formation could therefore have been adapted to breeding in warmer waters.

Penguins certainly developed tolerance to very low temperatures because they adapted to breed in polar areas in spite of the extreme conditions of the late Cenozoic and the Recent (e.g. emperor penguin, *Aptenodytes patagonica*; see Cione & Tonni, 1981; Martínez, 1992). The high diversity of penguins recorded in the Gaiman Formation is not observed today at this latitude, where only one species (*Spheniscus magellanicus*) breeds. Taking into account the high temperatures that characterized the early and middle Miocene (Fig. 7), the occurrence of four species breeding at this latitude does not appear to be likely. However, taxa occurring in the early Miocene of Patagonia did not belong to Recent genera. The oldest representatives of Recent genera occur in the middle Miocene and Pliocene of the Pacific (Acosta Hospitaleche, 2006; Göhlich, 2007).

We favour the hypothesis that penguins changed their ecological requirements for the following reasons: (1) taxa found in the base of the Gaiman Formation are not related to the Recent ones; (2) there were four species breeding in the area; (3) the global temperatures were higher; and (4) both the terrestrial vegetation and the marine fishes suggest locally higher temperatures.

EXTIRPATION OF SEVERAL MARINE VERTEBRATE TAXA

A well-known feature of Cenozoic history is the worldwide retraction of faunas because of global drops in temperature (Fig. 7). These changes caused extirpations in high latitudes. The modification in composition of the Antarctic faunas during the Cenozoic constitutes a remarkable example (Cione & Reguero, 1994). However, there are other pseudoextinctions that cannot be related to these global processes. In the southwest Atlantic, these include the shark families Heterodontidae, Pristiophoridae and the carcharhinid genus *Hemipristis*. In addition, the teleostean

genus *Oplegnathus* and the mammalian Dugongidae and Phocinae became locally extirpated. These living taxa have been recorded as fossils in many different locations around the world, some since the Jurassic. We summarize the stratigraphic and geographical distribution and some ecological information in Table 1.

The extirpation of high-latitude biota was directly related to global and local cooling (Cione, 1988; Cione & Reguero, 1994, 1998). However, the extirpations of some sharks and teleosts (and some marine mammals) from the Atlantic Ocean are not explained by temperature changes because these fishes persisted in similar environments with similar temperatures in the Pacific and Indian Oceans. The Patagonian extirpated taxa were found along with a temperate fish assemblage (see Table 1). Marine recent representatives of the genera recorded in the Miocene of Argentina that did not become totally extinct or extirpated occur in the Argentinian Biogeographic Province in Recent times (Figs 1, 4). *Pristiophorus*, *Heterodontus* and oplegnathids involve bottom dwellers. Yet, other bottom dwellers, such as *Squatina*, persisted. Certainly, geological events during the late Cenozoic provoked extended environmental perturbations. These events included the restriction of the Mediterranean, the separation of the Pacific and Atlantic Oceans by the rise of the Panama Isthmus, and strong fluctuations in sea level related to global climatic cooling. Shelf areas became greatly reduced during Pleistocene glacial episodes. The latter resulted in the extirpation of the shark *Carcharias taurus* along western South America (Cione *et al.*, 2007b). These events cannot explain the extirpation of the fishes and mammals mentioned above for the Atlantic Ocean.

CONCLUSIONS

The Recent distribution of marine vertebrates in the southwest Atlantic Ocean is ecologically determined by water temperature, topography, salinity, currents and areas of upwelling. Two biogeographical units are generally recognized in the present shelf area of Argentina based on fishes and invertebrates: the Magellanian and Argentinian Provinces. The two provinces differ in their fossil record. We suggest that the evolution of these provinces was complex, characterized by migrations, speciation events, extinctions and pseudoextinctions. Marine vertebrate assemblages with some similarities to the Argentinian fauna were already present in the Miocene, whereas no associations similar to those of the Magellanian fauna have been found in South America before the Pleistocene. During the Miocene, two successive major marine transgressions flooded northern

Patagonia: the 'Patagoniense' (early Miocene) and the 'Entrerriense' (middle to late Miocene). We analysed here the rich assemblages present in three lithostratigraphic units deposited during these transgressions: the Gaiman Formation (early Miocene, Patagonia), the Puerto Madryn Formation (middle-late Miocene, Patagonia) and the Paraná Formation (late Miocene of central-eastern Argentina).

The absence of Magellanian Miocene vertebrate assemblages is consistent with the hypothesis of a more southern distribution of the cold-temperate fauna at that time. In addition, neither tropical nor cold assemblages were recorded.

In Patagonia, as in other areas, an increased number of living groups appeared from the early to late Miocene. Cetaceans belonging to modern families began to be recorded in latest Oligocene-early Miocene rocks. Marine bird and fish assemblages of that age were dominated by diversified penguins and elasmobranchs, probably for taphonomic reasons. Lamnid, otodontids, heterodontids and batomorphs dominated. A major turnover is recorded in marine vertebrates between the early Miocene and middle-late Miocene. By the middle Miocene, aquatic mammals included more modern taxa: balaenids, ziphiids and also the oldest Southern Hemisphere pinnipeds. Spheniscids showed less diversity and abundance than in the early Miocene. Some osteichthyans and elasmobranchs were very similar to recent ones. The late Miocene aquatic mammals had a modern aspect, and pontoporid, together with dugongid and trichechid, sirenians occurred for the first time in South America. Late Miocene elasmobranch associations still included lamnids, otodontids, heterodontids and batomorphs, but odontapids and carcharhiniforms were extremely abundant. Some of these fish species are still living in the South Atlantic Ocean. In this article, we also stress that warm-temperate fishes and a high diversity of penguins are found together at the base of the Gaiman Formation. This high penguin diversity is not present in the area today. We interpret that these penguins were adapted to live in warmer waters than those of the latest Cenozoic and the Recent. Finally, many taxa become extirpated because of the global temperature drops of the late Cenozoic. However, some fishes and pinnipeds were extirpated only in the Atlantic Ocean. We have not yet found a suitable explanation for these pseudoextinctions.

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Table 1. Stratigraphic and geographical distribution and ecological information on some fish and mammals present in the southwestern Atlantic Ocean during the Miocene

Taxon	Some ecological observations	Present distribution	Stratigraphic and geographical distribution
<i>Heterodontus</i> (Heterodontidae)	Small, sluggish bottom feeders inhabiting shallow, warm-temperate and tropical waters (Springer & Gold, 1989; Compagno, Dando & Fowler, 2005)	Pacific and western Indian Oceans (Compagno, 1984; Compagno <i>et al.</i> , 2005)	Jurassic of Germany; Cretaceous of England, France, Lithuania, Belgium and Texas, USA; Palaeocene of Denmark, England, Belgium and Morocco; Eocene of Georgia, USA, England, Belgium and Morocco (Cappetta, 1987; Kriwet, 2008); Oligocene and Miocene of Patagonia (Cione, 1978; Cione & Pandolfi, 1984); late Miocene of eastern Argentina (Paraná Formation; Cione <i>et al.</i> , 2000)
<i>Pristiophorus</i> (Pristiophoridae)	Bottom dwellers in temperate and tropical continental and insular shelves (Springer & Gold, 1989). In the Atlantic Ocean, they are known only from relatively deep water (438–952 m; Compagno <i>et al.</i> , 2005). Outside the Atlantic, they may occur in depths as shallow as 30–40 m (Springer & Gold, 1989)	An endemic species, <i>P. schroederi</i> , persists in Cuba, Florida and the Bahamas (Compagno, 1984). The other species are distributed in the western Pacific off Japan, Korea, China, the Philippines, Australia and Arabian Sea (Compagno <i>et al.</i> , 2005)	Palaeocene of Morocco; Eocene of Seymour Island, Antarctica (Grande & Eastman, 1986); Oligocene of Belgium and Holland; Miocene of Germany, France and Portugal; Pliocene of France (Cappetta, 1987); Oligocene and Miocene of Patagonia (Cione & Expósito, 1980; Cione, 1988); Pliocene of Belgium (Cappetta, 1987)
<i>Hemipristis</i> (Carcharhinidae)	Warm and temperate seas	The Recent species <i>Hemipristis elongatus</i> occurs in Australia, southern Asia, Red Sea, east Africa, Madagascar and the western coast of Africa (Compagno <i>et al.</i> , 2005)	Eocene of Egypt, USA, Guinea Bissau and Peru; Miocene of eastern USA, Argentina, Germany, France, Belgium, Italy, Cabinda and Zaire, Java, India, Japan and Australia; Pliocene of Angola, Zanzibar; Pleistocene of Celebes (Cappetta, 1987; Cione, 1988)
<i>Oplegnathus</i> (Oplegnathidae)	Oplegnathid fishes inhabit the fringe of the tropics and seem to be mostly limited by the summer isotherm of surficial waters of about 20 °C (Cione & Azpelicueta, 2002)	Recent species are patchily distributed in western Australia, Tasmania, Japan, Hawaii, northern Chile, Galápagos and Easter Islands, and the east coast of South Africa (Cione & Reguero, 1994; Cione & Azpelicueta, 2002)	Eocene of Antarctica, Oligocene of Europe and Miocene of Chubut, Australia and western North America (Cione & Reguero, 1994; Cione & Azpelicueta, 2002). The family was extirpated from Antarctica after the middle Eocene and from the Atlantic Ocean after the early Miocene

<i>Metaxytherium</i> and <i>Diplotherium</i> (Dugongidae)	Dugongids are presently distributed in the Red Sea, Indian Ocean and western Pacific (Paula Couto, 1979). Hydrodamalin dugongs inhabited the northern Pacific until recently, but are extinct as a result of hunting	Miocene Pirabas Formation (Brazil; Paula Couto, 1979; Toledo & Domning, 1991) and the late Miocene outcrops of the Paraná Formation (Argentina; Reinhart, 1976; Cozzuol, 1993, 1996)
Monachin seals (Phocidae)	Presently restricted to the Mediterranean and eastern North Atlantic, Caribbean and Hawaii (Cozzuol, 1993)	Late Miocene outcrops of Paraná and Ituzaingó Formations of Argentina and Pliocene units of South Africa (Barnes, Domning & Ray, 1985; Muizon & Bond, 1992; Cozzuol, 1993)

la Patagonia: sus efectos sobre la diversidad', held at the La Plata Museum in May 2009. We also thank José Orensanz who invited the senior author to a former symposium on 'Biogeografía del Atlántico Sudoccidental', held some years ago in Puerto Madryn, northern Patagonia. A special acknowledgement is given to Daniel Ruzzante and José Orensanz, who greatly collaborated in improving this article. Our research was partially supported by the Agencia Nacional de Promoción Científica y Tecnológica, Consejo Nacional de Investigaciones Científicas y Técnicas and Universidad Nacional de La Plata. Luciano Rasia and Pablo Motta assisted us with some drawings.

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