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Aquatic mammal fossils in Latin America – a review of records, advances and challenges in research in the last 30 years

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Abstract

Records of aquatic mammal fossils (*e.g.* cetaceans, pinnipeds, sirenians, mustelids, and desmostylians) from Latin America (Mexico to Tierra del Fuego, including Antartica) span since the mid-1800s. Aquatic mammal fossils received little attention from the scientific community, with most of the first studies conducted by Northern Hemisphere researchers. Over the last 30 years, paleontological research in Latin America has increased considerably, with descriptions of several new species and revisions of published original records. The Latin American fossil record of marine mammals spans from the Eocene to the Pleistocene, with formations and specimens of global significance. All three main groups of cetaceans are represented in the continent (Archaeoceti, Mysticeti, and Odontoceti). Pinnipedia are represented by the families Otariidae and Phocidae, with records starting in the Middle Miocene. Both living families of Sirenia (Trichechidae and Dugongidae) are recorded. While less common, but still relevant, records of desmostylians and mustelids are known from Oligocene and Miocene deposits. This review provides a summary of the aquatic mammals known to date, with a special focus on the advances and developments of the last 30 years, since Cozzuol's (1996) review of the South American fossil record. An up-to-date complete list of species based on the literature and unpublished data is also provided. The study also provides future directions for paleontological research in Latin America, and discusses the challenges and opportunities in the field, including the emergence of a strong new generation of Latin American researchers, many of whom are women.

Keywords:
Cetacea, Pinnipedia, Sirenia, Southern Hemisphere

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Introduction

The aquatic mammal fossil record in Latin America has been known since the mid-1800s; however, it was not until the early 1900s that significant reviews of records were published, mainly concerning Argentinian specimens (Lydekker, 1893; Cabrera, 1926). Up to the 1980s, most studies on aquatic mammal fossils consisted of preliminary descriptions and re-evaluations of previous records. During the 1980s, several studies of fossil marine mammals from the South Pacific were conducted mostly by Northern Hemisphere researchers, focused on the Miocene and Pliocene deposits of Peru (*e.g.,* Muizon, 1984; Pilleri & Siber, 1989). Scattered studies of Miocene sirenians and iniids were also published in the late 1980s and early 1990s, from formations in Brazil, Argentina, and Uruguay (*e.g.,* Cozzuol, 1985). In Central America, the Caribbean, Colombia, and Mexico, research on fossil aquatic mammals is much more recent. Current aquatic mammal fossil studies in Latin America reflect the emergence of a new generation of local palaeontologists working to preserve and understand the fossil heritage of their communities. Advances in these areas of research were also in synchrony with political, geographical, and sociocultural contexts that aim to value Latin American research.

This review provides an update on new records, descriptions, and paleobiological interpretations of aquatic mammal fossils

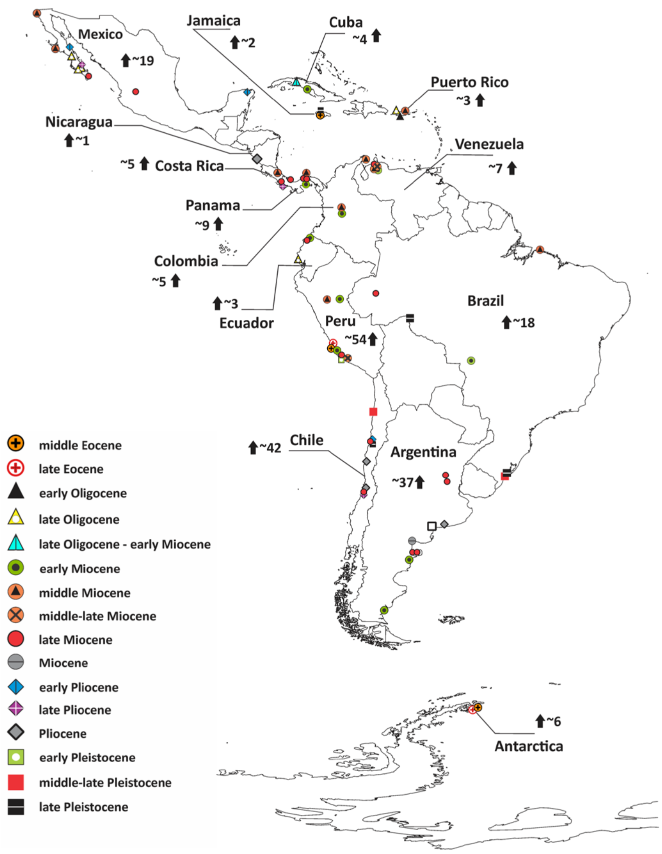

Figure 1. Aquatic mammal palaeontological research in Latin America since 1996. The map shows localities where new species, records and taxonomic reviews have been published (see Supplementary Material 1 for references). The arrow represents the number of new species, occurrences, and taxonomic updates in the Latin American aquatic mammal fossil record in each country.

in Latin America, with a special focus on the advances and developments of the last 30 years, since Cozzuol's (1996) review of the South American fossil record (Fig. 1). It also discusses future directions in aquatic mammal palaeontological research, including ethical considerations and the emergence of a new generation of women in palaeontology. Here we also discuss challenges and opportunities in the field, such as the status and accessibility of palaeontological collections, barriers facing Latin American palaeontologists, and the importance of collaborative work.

Physical drivers for the evolution of Latin American aquatic mammals

Latin America is crucial for the understanding of the evolutionary history of aquatic mammals into the Cenozoic Era's climate, oceanographic, and geological change framework (Zachos et al., 2001). These physical drivers created and modified new habitats in the region, having significant effects on the ecological succession of assemblages of fossil aquatic mammals (*e.g.,* Peru; Ochoa et al., 2021) and in their respective distributional patterns (*e.g.,* Delphinidae; do Amaral et al., 2016). Events such as sea-level fluctuations by the warm and glaciation cycles (Miller et al., 2020), the warm Equatorial Current and the origin of the Antarctic Circumpolar Current (Lyle et al., 2008), volcanism, and the origin of geographical barriers such as Gaarlandia and the Panama Isthmus (Iturralde-Vinent, 2006) were critical drivers for the evolution of aquatic mammals in Latin America.

The Fossil Record of Aquatic Mammals in Latin America

Eocene

Eocene outcrops in Latin America with aquatic mammal records are restricted to Antarctica (La Meseta and Submeseta Fm.), Peru (Otuma, Paracas, and Yumaque Fms), and Caribbean region (Jamaica, Litchfield Fm.) (Supplementary Material 1). Aquatic mammal fossils recorded from these formations include cetaceans (archaeocetes and toothed mysticetes) and sirenians (Fig. 2). The most relevant fossil records include the first protocetid whale for South America (Lambert et al., 2019), one of the oldest known basilosaurids (La Meseta Fm., Antarctica; Buono et al., 2016), the oldest toothed mysticetes (Submeseta Fm., Antarctica; Pisco Basin, Peru; Lambert et al., 2017a; Fordyce & Marx, 2018; Marx et al., 2018), and quadrupedal sirenians (Domning, 2001a, b). The Otuma Fm. in the Pisco Basin also includes a wide array of small to large well preserved archaeocetes (Uhen et al., 2011).

The Eocene fossil record of aquatic mammals from Latin America provides insight into the early evolution and paleobiogeography of cetaceans and sirenians. Protocetids from Peru, along with new records from Africa (*i.e.,* Vautrin et al., 2020; Egypt, Middle Eocene; Gohar et al., 2021) provide evidence that the cetacean transition from semiaquatic to fully aquatic forms occurred in the (sub)tropics. The fossil record of basilosaurids from Peru and Antarctica suggests a rapid spread across the Southern Hemisphere, reaching high latitudes by the Middle Eocene (Buono et al., 2019; Uhen et al., 2011). Taxonomic affinities of archaeocetes from Peru are still debatable, due to the novelty of these records. Eocene basilosaurids from Antarctica

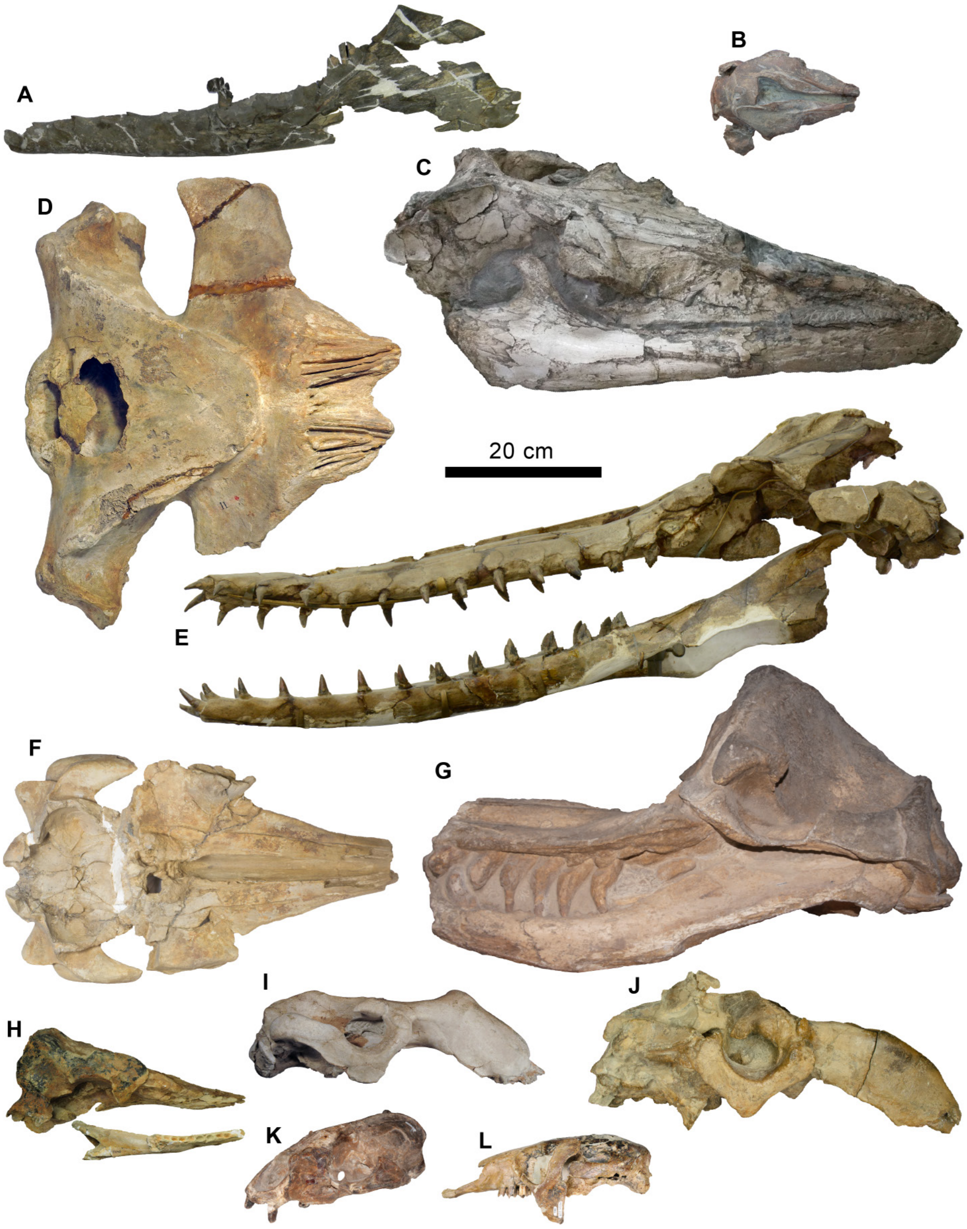

Figure 2. Examples of marine mammals from across Latin America described or redescribed within the last 30 years. (A) Basilosauridae (MLP 11-II-21-3), left mandible in lateral view; (B) *Urkudelphis chawpipacha* (MO-1), skull in dorsal view; (C) *Aetiocetus palmadentis* (MUEcSj5/24/123), skull and mandible in right dorsolateral view; (D) *Morenocetus parvus* (MLP 5-11), posterior portion of skull in dorsal view; (E) *Phoberodon arctirostris* (MLP 5-4), skull and mandibles in left lateral view; (F) *Dolgopolis kinchikafiforo* (MPEF-PV 1344), skull in dorsal view; (G) *Acrophyseter robustus* (MUSM 1399), skull and mandibles in left lateral views; (H) *Nanokogia isthmia* (UF 280000), skull and mandibles in right lateral views; (I) *Callistosiren boriquensis* (USNM 540765), skull in right lateral view; (J) *Culebratherium alemani* (UF 281000), skull in right lateral view; (K) *Hadrokirus martini* (MUSM 1662), skull in left anterolateral view; (L) *Thalassocnus antiquus* (MUSM 228), skull in left lateral view.

share more similarities with New Zealand specimens than those from Peru, providing tentative support for a dispersal route via Australasia. The earliest records of the closely related toothed mysticetes *Mystacodon* and *Llanocetus* from Antarctica and Peru provide evidence of a disparate feeding method (*i.e.,* suction-assisted raptorial feeding) in these archaic whales, compared to filter-feeding in baleen-bearing mysticetes (Lambert et al., 2017a; Marx et al., 2019). These early neocetes likely coexisted with large basilosaurids during the Late Eocene (*e.g.,* Cynthiacetus *peruvianus*; Martínez-Cáceres & Muizon, 2011; Martínez-Cáceres et al., 2017). On the other hand, Eocene sirenian records from Jamaica provide evidence for the dispersal and colonization of the Americas and Caribbean region. Such distribution reflects the distribution of seagrasses, the primary food source for sirenians (Domning, 2001a, b; Velez-Juarbe, 2014). These Caribbean Eocene sirenians mark the beginning of a long evolutionary history of the group in the region, where they diversified and dispersed toward the Atlantic and Pacific coasts of North and South America (Domning, 2001a).

Eocene records of Latin American aquatic mammals are patchy but relevant and noteworthy, adding new pieces to the complex puzzle of the evolution of cetaceans and sirenians during the Paleogene.

Oligocene

Oligocene aquatic mammals from Latin America are known from Mexico, Cuba, Puerto Rico, and Ecuador (Supplementary Material 1). However, few specimens have been formally described since 1996 and taxonomic diversity does not seem to be similar across localities. Puerto Rico and Cuba have a substantial sirenian record from San Sebastian Fm. (Early Oligocene), Lares Limestone (late Oligocene), and Colon Fm. (Late Oligocene - Early Miocene), highlighting the sirenian diversity during the Oligocene in the Caribbean (Vélez-Juarbe & Domning, 2014, 2015; Orihuela et al., 2019). By the Oligocene, sirenians had become fully aquatic and records from the Caribbean consist exclusively of Dugongidae, including multi-species assemblages which predominated in the region until the Mid-Late Pliocene (Domning, 2001a; Vélez-Juarbe, 2014; Vélez-Juarbe & Domning, 2014, 2015). On the Pacific side, the Dos Bocas Fm. from Ecuador possesses a cetacean fossil record that might provide insight into distributional patterns of Platanistoidea, as indicated by the Late Oligocene dolphin *Urkudelphis chawpipacha* (Fig. 2). This is the first record in South America and one of the few records of tropical fossil dolphins (Tanaka et al., 2017). However, other tropical Late Oligocene dolphins from Ecuador are yet to be named and described (Tanaka et al., 2017; Carrillo-Briceño et al., 2020).

The Oligocene aquatic mammal fossil record from Mexico is primarily found in Baja California Sur. So far, cetacean fossils are common in the San Gregorio and El Cien Fm., while pinnipeds and sirenians have not yet been recorded. Few fossils have been formally described, despite more than 19 taxa estimated (Barnes, 1998; Hernández-Cisneros et al., 2017). The cetacean fossil record in Mexico includes aetiocetids (*e.g., Aetiocetus palmadentis*) (Fig. 2), eomysticetids (*e.g., Eomysticetus*), stem mysticetes (*e.g., Tlaxcallicetus*), early odontocetes (simocetids) and archaeocetes such as kekenodontids (Hernández-Cisneros & Tsai, 2016; Hernández-Cisneros et al., 2017; Hernández-Cisneros, 2018; Solis-Añorve et al., 2019; Hernández-Cisneros & Nava-Sánchez, 2022). Such a record will likely increase our knowledge of the evolutionary and adaptive radiation of stem Neoceti during the Oligocene. While desmostylians are also known from the El Cien Fm. (Vanderhoof, 1942; Applegate, 1986), no additional material has been described. Research on Oligocene aquatic mammals in Latin America is still incipient, but has grown considerably over the last few years.

Miocene

Early Miocene

Aquatic mammal fossils from the Early Miocene have been reported in Cuba, Panama, Ecuador, Colombia, Argentina, Brazil, Venezuela and Peru, consisting of cetaceans and sirenians (Supplementary Material 1). The Early Miocene is a key time in the evolutionary history of cetaceans, yet a gap in the cetacean fossil record is evident in this interval, particularly 20 to 23 million years ago when assemblages dominated by archaic species were replaced by modern diverse clades due to oceanic habitat changes (Marx et al., 2019). However, factors such as research effort, lack of geochronological control, and fossil abundance in particular places likely generate bias in the Early Miocene cetacean fossil record (Uhen & Pyenson, 2007). Early Miocene outcrops in Latin America have become increasingly important. Records mainly include early-diverging lineages such as stem odontocetes, platanistoids, physeteroids, eurhinodelphinids, balaenids, and balaenopteroids (*e.g,.* Aguirre et al., 2017; Buono et al., 2017; Gaetán et al., 2018; Viglino et al., 2018, 2019; Paolucci et al., 2020, 2021a, b). Fossil physeteroids (*e.g., Diaphorocetus poucheti*) and the balaenid *Morenocetus parvus* (Fig. 2) show that some morphological adaptations observed in their extant relatives were already present since the Early Miocene (Buono et al., 2017; Paolucci et al., 2020, 2021a). The platanistoid *Notocetus vanbenedeni* was the most abundant species in the Gaiman Fm. (Cuitiño et al., 2019), with a mosaic morphology that hints to the evolution of the bizarre *Platanista* skull (Viglino et al., 2022).

The Chilcatay Fm. in Peru has become one of the most productive areas of the world in terms of odontocete diversity. Fossils from this area indicate that several Platanistoidea morphologies coexisted, including the large squalodelphinid *Macrosqualodelphis*, the small *Huaridelphis*, and the hyperlongirostrine *Ensidelphis* (Lambert et al., 2014; Bianucci et al., 2018, 2020). Taxa with specific adaptations such as the arched-rostrum of *Furcacetus* were also part of Chilcatay Fm., along with species also common in Patagonia such as *Notocetus vanbenedeni* (Bianucci et al., 2020; but see Viglino et al., 2022). This broad diversity of species with a range of ecological niches only lasted a few million years. Two other odontocetes with unknown affinities, *Chilcacetus* and *Inticetus*, indicate that early diverging odontocetes with plesiomorphic characters coexisted with highly derived taxa (Lambert et al., 2015, 2017b). Physeteroids were represented by the longirostrine *Rhaphicetus*, one of the most archaic sperm whales characterised by a restricted and low supracranial basin, and a long tooth-bearing rostrum (Lambert et al., 2020). Additional physeteroid fragments have been tentatively assigned as cf. *Diaphorocetus*. Early Miocene mysticetes are scarcely reported for Chilcatay Fm. (Di Celma et al., 2019), reflecting the sparse worldwide record of this group. In the Caribbean region, odontocetes have only been described from the Lagunitas Fm. at Domo de Zaza in Cuba, with a putative physeterid record (MacPhee et al., 2003). Early-diverging cetaceans, particularly odontocetes, were the dominant fauna in the Early Miocene southern seas. Mysticetes are mainly represented in the Southwestern Atlantic coast of Argentina.

The fossil record of Early Miocene sirenians consists of dugongines in the Lagunitas (Cuba) and Culebra (Panama) formations, and trichechids in the Pebas (Peru), Barzalosa and Castilletes (Colombia) Fms (MacPhee et al., 2003; Domning and Aguilera, 2008; Uhen et al., 2010; Antoine et al., 2016; Vélez-Juarbe & Wood, 2019; Suarez et al., 2021). These records include the first sirenians from the Pacific coast of Central America, including the dugongine *Culebratherium alemani* (Fig. 2), a close relative of *Dioplotherium allisoni* from the Middle Miocene of Baja California Sur and California (Vélez-Juarbe & Wood, 2019). Trichechids from Peru and Colombia represent the earliest records of the group in the Americas and highlight the importance and influence of the Pebas Mega-Wetland system in the evolutionary history of the group (Antoine et al., 2016; Suarez et al., 2021).

Middle Miocene

The Middle Miocene geological window in Latin America shows few new records of aquatic mammal fossils distributed in Peru, Ecuador, Colombia, Panama, Venezuela, Costa Rica, Puerto Rico, and Mexico (Supplementary Material 1). On the North Pacific coast, the Baja California Peninsula in northwestern Mexico is recognised for its rich marine mammal fossil record, although still poorly studied (Barnes, 1998). Fossils that have been described include the dugongid *Metaxytherium arctodites* as well as the dolphin *Kentriodon diusinus*, both from the Rosarito Beach Fm. (Aranda-Manteca et al., 1994; Salinas-Márquez et al., 2014), and the dwarf walrus *Nanodobenus arandai* (Tortugas Fm.; Vélez-Juarbe & Salinas-Márquez, 2018), both from Baja California. Other unnamed cetaceans, dugongids, pinnipeds, and desmostylians from the Isidro Fm. of Baja California Sur are still to be formally described. New material was assigned and described for the early manatee *Potamosiren magdalenensis*, representing the holotype of the species (La Victoria Fm., Colombia; Domning, 1997), including the designation of the type of *Metaxytherium ortegense* as a junior synonym of the former. More fragmentary fossils have been reported from Puerto Rico (Sirenia: *Metaxytherium* cf. *M. crataegense* and *Nanosiren* sp., Cibao Fm.; MacPhee & Wyss, 1990; Domning, 2001a; Domning & Aguilera, 2008), Costa Rica (Odontoceti: *Squalodon* sp., Río Banano Fm.; Laurito et al., 2011), Panama (Odontoceti indet., Gatun Fm.; Uhen et al., 2010), Colombia (Odontoceti: Platanistinae indet., Villavieja Fm.; Benites-Palomino et al., 2020b), Venezuela (Odontoceti: stem Delphinida, Caujarao Fm.; Benites-Palomino et al., 2021a) and Peru (Odontoceti: Platanistinae indet., Ipururo Fm.; Bianucci et al., 2013). The Middle Miocene represents a critical time for the marine biota due to the Middle Miocene Climate Optimum (Zachos et al., 2001; Frigola et al., 2018). The climate conditions in the Middle Miocene influenced the primary productivity of the ocean, increasing ice sheets in the poles, generating changes in the eustatic sea level, and affecting coastal environments (Zachos et al., 2001; Frigola et al., 2018; Steinthorsdottir et al., 2021). These changes in climate affected the diversity of aquatic mammals, with many lineages becoming extinct and modern lineages diversifying (*e.g.,* cetaceans and pinnipeds; Steeman et al., 2009; Marx & Fordyce, 2015; Berta et al., 2018). The diversity of Middle Miocene taxa in Latin America might increase due to additional discoveries in poorly explored localities such as Baja California Peninsula in Mexico (Barnes, 1998), refined chronostratigraphy using microfossils (*e.g.,* Salinas-Márquez et al., 2016) and description of several unnamed specimens in palaeontological collections (*e.g.,* Peru; Bianucci & Collareta, 2022).

Late Miocene

Numerous records of marine mammals have been reported in Latin American Late Miocene deposits, mainly on the Pacific coast of South America (Supplementary Material 1). Bahia Inglesa (Chile) and Pisco (Peru) formations have captured the attention of scientists worldwide. The number of well-preserved specimens and the abundance of materials have provided an unparalleled glimpse at the past proto-Humboldt diversity, illuminating our understanding of the evolution of marine communities over time. Late Miocene marine mammal assemblages from these regions show evidence of a mosaic configuration with typical, and now extinct, Miocene taxa, along with several representatives of the modern fauna.

Most of this diversity consisted of several odontocetes, including physeteroids, ziphiids, inioids, platanistoids, and delphinoids (Muizon, 1988; Gutstein et al., 2008, 2015; Buono & Cozzuol, 2013; Bianucci et al., 2016; Bosio et al., 2021). Fossil physeteroids were more diverse taxonomically and ecologically than living relatives, comprising macroraptorial sperm whales such as *Livyatan* and *Acrophyseter* (Lambert et al., 2017b) (Fig. 2), kogiids such as *Scaphokogia*, *Platyscaphokogia,* and *Koristocetus* (Benites-Palomino et al., 2020a, 2021b; Collareta et al., 2020) and other fragmentary remains of physeterids (Benites-Palomino & Urbina, 2020). Fossil inioids included marine relatives of the extant *Inia*, such as *Brujadelphis* and *Isthminia* from Panama, revealing the marine origin of this genus (Pyenson et al., 2015; Lambert et al., 2017b). Also, inioids such as *Brachydelphis* and *Samaydelphis*, related to the extant *Pontoporia*, highlighted the broad diversity of modern "river" dolphin relatives (Muizon 1988; Gutstein et al., 2009, Lambert & Muizon, 2013; Lambert et al., 2021). Porpoises such as *Piscolithax, Australithax,* and *Lomacetus* were also diverse, and their rostral morphology indicated they were feeding in a similar way to extant oceanic dolphins. Other key components of coastal Miocene environments were ziphiids which lacked adaptations for deep diving (Lambert et al., 2015b). These species include *Ninoziphius, Chavinziphius, Chimuziphius,* and *Messapicetus*, which preyed on neritic-epipelagic fishes (Bianucci et al., 2016). Other odontocetes include the first representatives of modern Delphinidae, but also bizarre taxa such as the walrus-dolphin *Odobenocetops*.

Mysticete diversity is broadly represented along the Pacific and Atlantic coasts of South America, including representatives of balaenids, cetotheriids, and balaenopterids (*e.g.,* Bouetel & Muizon, 2006; Buono, 2014; Buono et al., 2014; Pyenson et al., 2014; Gutstein et al., 2015; Marx et al., 2017). In parallel with the global modernization of the cetacean fauna which occurred during the Late Miocene, these mysticete assemblages were comprised of relicts of archaic fauna (*e.g.,* the cetotheriids *Piscobalaena*, *Herpetocetus, Tiucetus rosae*), and the first records of taxa closely related to the extant *Caperea* and *Balaenoptera* (Pilleri & Siber 1989; Bisconti, 2012; Buono et al., 2014).

Additional Late Miocene cetacean records come from the Curré Fm. in Costa Rica and the Tobabe and Chagres formations in Panama (Uhen et al., 2010; Valerio & Laurito, 2012; Vigil & Laurito, 2014; Pyenson et al., 2015; Vélez-Juarbe et al., 2015). Curré Fm. records consist of various isolated teeth assigned to several odontocetes whose affinities are still uncertain. The best material described so far consists of odontocetes from the Chagres Fm. on the Caribbean coast of Panama. These include a physeteroid, the kogiid *Nanokogia isthmia* (Fig. 2) and the inioid *Isthminia panamensis*, all of which resemble and are closely related to coeval taxa from the Pisco Fm. (Vigil & Laurito, 2014; Pyenson et al., 2015; Vélez-Juarbe et al., 2015). Additional materials awaiting description follow these patterns and may represent a case of allopatric speciation as a result of the earlier stages of the closure of the Central American Seaway. The only Late Miocene mysticete recorded for Central America and the Caribbean is a thoracic vertebra assigned to Balaenopteroidea

(Uhen et al., 2010). New balaenopteroids from the Late Miocene of Mexico have been recently studied (*Kennedycetus pericorum*; likely a junior synonym of *Norrisanima*; Solis-Añorve et al., 2021) from the Trinidad Fm., Baja California Sur.

Late Miocene sirenians have been reported from the Pisco (Peru), Bahia Inglesa (Chile), Alahuela (Panama), Urumaco (Venezuela), Paraná and Ituzaingo (Argentina) Fms (Bianucci et al., 2006; Domning & Aguilera, 2008; Vélez-Juarbe et al., 2012b; MacFadden et al., 2017). Specimens from the Pisco and Bahia Inglesa Fms. represent some of the southernmost records of sirenians in the eastern south Pacific and the only known occurrence of the dugongine *Nanosiren* outside of the Western Atlantic and Caribbean region, suggesting that seagrasses were then common along the Pacific coast of South America (Bianucci et al., 2006; Domning & Aguilera, 2008; Vélez-Juarbe, 2014). This is supported by a present relict distribution of sea grasses at Puerto Aldea, Coquimbo region, Chile (Perez-Matus et al., 2005). Materials from Alahuela Fm. consist of isolated rib fragments tentatively assigned to Dugongidae, while the Venezuelan record consist of the dwarf dugongine *Nanosiren sanchezi* (Domning & Aguilera, 2008; MacFadden et al., 2017). Material from Parana Fm. represents the southernmost records of dugongids on the Western Atlantic. These comprise at least two taxa, *Metaxytherium* and *Dioplotherium*, which are found together in other older multispecies assemblages across the region (Toledo & Domning, 1991; Domning, 2001a; Vélez-Juarbe et al., 2012a, b).

Riverine assemblages have been also reported from Solimões Fm. (Acre, Brazil) and Ituzaingó Fm. (Entre Rios, Argentina) with fragmentary remains mostly assigned to inioids and sirenians (Cozzuol, 2006, 2010). *Ischyrorhynchus vanbenedeni* is one of the best-preserved specimens from this region and has been restudied several times (Geisler et al., 2012; Pyenson et al., 2015).

Remains of phocids (seals) have been described from the Late Miocene of Puerto Madryn and Paraná (Argentina), Bahia Inglesa (Chile), and Pisco (Peru) Fms. (Cozzuol, 2001; Walsh & Naish, 2002; Soibelzon & Bond, 2013; Amson & Muizon, 2014; Pyenson et al., 2014; Valenzuela-Toro et al., 2016; Echarri et al., 2021). Remains of *Kawas benegasorum*, an early phocine seal (Cozzuol, 2001), have been reported from the Puerto Madryn Fm., constituting the only record of this subfamily in the Southern Hemisphere. Specimens from the Paraná Fm. have been identified as belonging to the poorly known *Properiptychus argentinus* and other undetermined phocids. More abundant phocid remains have been described from the Western coast of South America. Four extinct genera have been reported: *Acrophoca*, *Piscophoca* (Walsh & Naish, 2002), *Australophoca* (Muizon, 1981; Walsh & Naish, 2002; Valenzuela-Toro et al., 2013, 2016; Pyenson et al., 2014), and *Hadrokirus*, described solely from Peru (Fig. 2) (Amson & Muizon, 2014). These taxa - currently extinct - together with other extinct marine mammals from the western coast of South America such as the aquatic sloth *Thalassocnus* (Fig. 2) and the walrus-like dolphin *Odobenocetops* (Muizon et al., 1999; Canto et al., 2008; Pyenson et al., 2014), reveal that environmental conditions at the time fostered the evolution of ecological modes absent in modern marine ecosystems. This hints to a more complex ecological dynamics than that observed in this region today. Lastly, another significant Late Miocene aquatic mammal record belongs to Mustelidae (Tseng et al., 2017). *Enhydritherium terraenovae* from Miocene deposits of Juchipila Basin, Zacatecas State, Mexico, brings light to the origins of sea otters (Tseng et al., 2017).

Pliocene

The Pliocene was characterized by dramatic climate fluctuations that included glaciations and warm global conditions (Zachos et al., 2001; Robinson et al., 2008). These shifting environmental conditions likely influenced evolutive, biogeographic, and extinction events of aquatic mammals, which generated living lineages of cetaceans, pinnipeds, and sirenians (Marx & Uhen, 2010; Vélez-Juarbe et al., 2012a; Pimiento et al., 2017; Valenzuela-Toro & Pyenson, 2019). New Pliocene records have been reported in Mexico, Nicaragua, Panama, Chile, and Argentina. Many of these records belong to fragmentary or isolated specimens representing a broad range of taxa, including cetaceans such as *Protoglobicephala mexicana* (San Jose Island basin, Mexico; Aguirre-Fernández et al., 2009); the marine sloth *Thalassocnus carolomartini* (Coquimbo Fm., Chile; De Los Arcos et al., 2017), or fragmented phocid remains (Bahia Inglesa Fm. and marine sediments from Isla Guafo in southern Chile; Valenzuela-Toro et al., 2013; Valenzuela-Toro & Pyenson, 2022). The sirenian record stands out with the presence of the dugongine sirenians *Xenosiren yucateca*, *Corystosiren varguezi, Dioplotherium* sp., and *Nanosiren* cf. *N. garciae* in the Carrillo Puerto Fm., Mexico, representing the last multi-species sirenian assemblage in the region and maybe in the whole world (Domning, 1989, 1990; Vélez-Juarbe et al., 2012a). These reports suggest that during the Pliocene, the marine mammal fauna comprised a range of representatives of the once vastly diverse Miocene taxa and the early radiations of modern groups (Ochoa et al., 2021; Benites-Palomino et al., 2022). The South American fossil record shows that the Pliocene was marked by the rise of a delphinid-dominated fauna, and documents the shift from phocid-dominated to otariid-dominated pinniped assemblages. Future field excavations of poorly studied Pliocene localities (*e.g.*, Los Negros within the Bahia Inglesa Fm., and Coquimbo and Horcón Fms) and the description of new specimens deposited in collections are needed to elucidate the timing and drivers of these faunal turnovers.

Pleistocene

The fossil record of Pleistocene marine mammals from Latin America is still poorly known. These records comprise fragmentary and isolated remains of sirenians from the Falmouth Fm. in Jamaica (Domning, 2005), cetaceans and pinnipeds from the Coastal Plains of Rio Grande do Sul and sirenians and inioids from Rio Madeira Fm. in Brazil (Oliveira & Drehmer, 1997; Drehmer & Ribeiro, 1998; Rodrigues et al., 2004; Cozzuol, 2010; Perini et al., 2019; Carrasco & Buchmann, 2021), pinnipeds from the Sucesion Litoral de Mejillones and Estratos de Caldera in Chile (Valenzuela-Toro et al., 2013, 2015), and cetaceans and pinnipeds from the Caracoles and Pongo Fms in Peru (Ochoa et al., 2021). Pleistocene records of extant species suggest that many marine mammal taxa already displayed a contemporary geographical distribution. A notable exception is the Pleistocene elephant seal remains from the Antofagasta Region in Northern Chile. This record suggests that during the Pleistocene, elephant

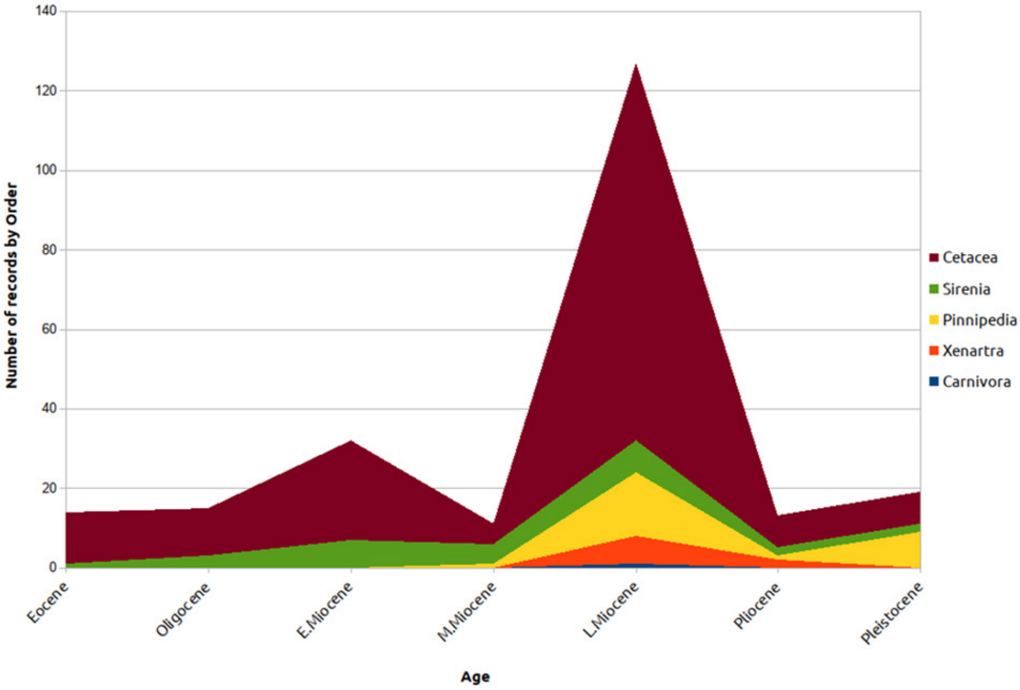

Figure 3. New records of aquatic mammal fossils in Latin America since 1996 by taxonomical order and geological epoch.

seals had a wider range in the South Pacific Ocean than today (Valenzuela-Toro et al., 2015). The scarcity of Pleistocene fossil marine mammal remains in Latin America has hampered our understanding of their recent evolutionary history, including how and when the modern fauna became established in the region (Valenzuela-Toro & Pyenson, 2019).

Biogeographical overview

The aquatic mammal fossil record in Latin America demonstrates that cetaceans and sirenians reached the New World no later than the Middle Eocene, most likely by trans-Atlantic dispersion (Fig. 3). Cetaceans are recorded in both the Atlantic and Pacific coasts, and reached high latitudes during this epoch (*e.g.,* Buono et al., 2016). The Oligocene marks the opening of the main Southern Ocean gateway (most importantly, the Drake Passage), enabling the establishment of the Antarctic Circumpolar Current which resulted in the existing global ocean circulation patterns and played a relevant role in global cooling events (Zachos et al., 2001; Steeman et al., 2009; Bohoyo et al., 2019). There was an increase in cetacean and sirenian diversity, and desmostylians first appeared (*e.g.,* VanderHoof, 1942). Dugongids originated during the Oligocene and cohabited in sympatric associations (Vélez-Juarbe & Domning, 2014), and both groups of crown cetaceans (Odontoceti and Mysticeti) radiated during this time as well. However, their true diversity remains unclear because of potential biases in rock availability and a low research effort in this interval, with many specimens in collections awaiting description (Uhen & Pyenson, 2007; Hernández-Cisneros et al., 2017).

All crown cetaceans, sirenians and pinnipeds experienced their peak diversity at some time during the Miocene (Fig. 3). This diversity is evident in both taxonomic (number of species) and functional (*e.g.*, extreme morphologies, ecological niches) richness. Newly described and recent revisions of historic species showed evidence of the high ecological and morphological diversity of cetaceans during the Early Miocene in the southwestern Atlantic. Some clades of odontocetes transitioned into freshwater environments (*e.g.,* Iniidae, Platanistidae), as sirenians also did. The Trichechidae originated in South America, which may be related to the Pebas Mega-Wetland system, an epicontinental sea that existed in the Early to Middle Miocene in parts of South America. The first records of pinnipeds are reported for the Middle and Late Miocene in localities from Mexico, Chile, Peru, and Argentina. Aquatic sloths also appear in the fossil record of Peru and Chile during the Late Miocene. Many families of extant cetaceans established by the Late Miocene, while other diverse clades (*e.g.*, longirostrine odontocetes) declined and became extinct.

The rise of the Isthmus of Panama and the concomitant closure of the Central American Seaway is a complex process that cannot be pinpointed to a single event and is probably older than the traditionally-accepted timing of 3.5 Ma (Bacon et al., 2015; Montes et al., 2015; O'Dea et al., 2016). This process undoubtedly affected the distribution and speciation of various groups of modern marine mammals, but the direct effects are difficult to point out. Lastly, the Pleistocene is characterized by repeated glacial cycles, which probably fragmented coastal habitats and resulted in the antitropical distribution of some cetaceans (Davies, 1963), with the Humboldt current and the Eastern Equatorial cold tongue probably playing important roles (do Amaral et al., 2016).

Three decades of advances, but all that glitters is not gold

"Scientific knowledge is not apolitical, neutral, nor divorced from society", as Rogers et al. (2022) stated. The advancements in the study of Latin America fossil aquatic mammals cannot be separated from the historical, social, and economic backgrounds prevailing in the region. While each country has its unique challenges, a common issue emerges: the proportionally lower government investment in STEM (science, technology, engineering, and mathematics) compared to wealthy countries (Schneegans et al., 2021). The limited investment can have a cascading effect on scientific performance. This ranges from insufficient funding, suboptimal infrastructure and equipment, and fewer opportunities to showcase local science to a global community, leading to a strong dependency on foreign support (Valenzuela-Toro & Viglino, 2021).

These constraints make Latin American aquatic mammal palaeontology vulnerable to unethical practices associated with scientific colonialism (*e.g.,* Rogers et al., 2022). Scientific colonialism is a mindset where views by colonizers have a higher status than those of the colonized, resulting in the imposition of the colonizers' perspectives and neglecting the knowledge and experience of locals. While scientific colonialism has several forms, "parachuting science" remains a widespread practice in Latin American palaeontology despite its detrimental effects on research and knowledge production. Parachuting science occurs when researchers from high-income countries conduct fieldwork in low-income/developing territories without engaging, collaborating, or acknowledging local researchers. Parachute scientists also often ignore regulations for conducting research and fieldwork in the host countries (*e.g.,* Trisos et al., 2021; Cisneros et al., 2022; Raja et al., 2022).

Scientific colonialism can also impact Latin American palaeontology by incentivising the extraction of fossil specimens with extraordinary scientific value to be permanently deposited and displayed in foreign institutions. In addition to making it difficult for Latin American researchers to study materials originally from their own countries, this practice adds extra financial burden as additional funding will be required to visit overseas collections. Requests to examine type specimens housed in overseas institutions are common during the peer review process, resulting in delayed publication for studies carried out by Latin American researchers. The unethical extraction of fossils occurs despite the efforts of several Latin American countries to safeguard their fossil heritage and promote regional research (Cisneros et al., 2022). Another dimension of scientific colonialism is linked with the lower relevance given to research produced by diverse scientists (*i.e.*, not "English-speaking white males"). Past studies have shown that gender and country of origin can negatively bias peer-review, citation rates, and indirectly, success in funding rounds (*e.g.,* Hooker et al., 2017; Astegiano et al., 2019; Salerno et al., 2019; Warnock et al., 2020). Because of this, intersectionality is so important in this context, as all these factors result in a disproportionately negative impact on Latin American researchers (Valenzuela-Toro & Viglino, 2021).

The impact of scientific colonialism on aquatic mammals' palaeontology in Latin America remains unquantified and underestimated. Here, we investigated three overarching questions: 1) where are Latin American aquatic mammal fossils deposited? 2) who publishes on the Latin American aquatic mammal fossil record? and 3) how are the citation rates of papers on Latin American fossil aquatic mammals? (See Supplementary Material 2 for details on the methods used).

Where are Latin American aquatic mammal fossils deposited?

Latin American palaeontology has a long legacy of colonial practices (*e.g.,* Raja et al., 2021; Rogers et al., 2022), including the unethical exportation of fossils to overseas institutions (Cisneros et al., 2022). Some Latin American countries such as Mexico, Brazil, Colombia, Chile, and Argentina have implemented strict regulations since the early-mid 19th century (*e.g.*, Fernández et al., 2014; Guerrero-Arenas et al., 2020; Cisneros et al., 2022). Yet, our study reveals that 20% of the published records of fossil aquatic mammals, including some holotypes, are deposited in overseas institutions. These occurrences abroad are primarily constituted by records from Peru (n=19), Chile (n=7), and Panama (n=6). We also found records of fossil aquatic mammals housed in both local and foreign institutions, primarily dominated by records from Peru (n=14) and single occurrences from Argentina and Colombia. Notably, all published records of fossil aquatic mammals from Puerto Rico are lodged in overseas institutions. This practice primarily reflects the profound colonial legacy (Puerto Rico remains an unincorporated territory of the United States), resulting in underfunded, inadequate, and understaffed scientific institutions (*e.g.,* Roldan-Hernandez et al., 2020), hampering local paleontological research. We also found that 2% of the published fossil records belong to private collections (with no guaranteed access to researchers nor appropriate housing conditions), mainly from Venezuela and one from Peru, which is currently lost. Although several holotypes of Peruvian records remain in international institutions, re-descriptions led by local scientists are consistently increasing due to their current collaborative approach.

Who publishes on the Latin American aquatic mammal fossil record?

Our analysis has revealed an increasing number of publications between 1997 and 2021, reaching a total of 130 articles (Fig. 4). Although the number of publications led by Latin America-based researchers has increased over the last decade, they still represent less than 50% of papers on fossil aquatic mammals from the region. Our analysis reveals a conspicuous increase in the number of publications led by Latin America-based researchers in 2021. This could be related to increased fieldwork by local researchers due to the travel ban imposed by the COVID-19 pandemic and increased time for the publication of backlogged projects.

The first publication led by a Latin American woman dates only from 2003 (Fostowicz-Frelik, 2003). The publication of papers led by women shows a fluctuating pattern since then, ranging from zero to no more than six articles per year (Fig. 4). Although first-author women (n = 32) were mainly based in Latin American institutions (n = 28), the first publications led by women were from researchers based in the Global North (*i.e.*, Fostowicz-Frelik, 2003; Bouetel & Muizon, 2006). Most of the publications led by Latin American women correspond to early-career researchers based in Argentina, Chile, and Mexico (many of whom are authors of this contribution), resulting from long-term mentorships established in the region. These mentorship practices have a bottom-up cascading effect, resulting in training a new generation of women palaeontologists and fostering the establishment of research groups with a growing research output. This could have a direct effect on the number of Latin American women leading research

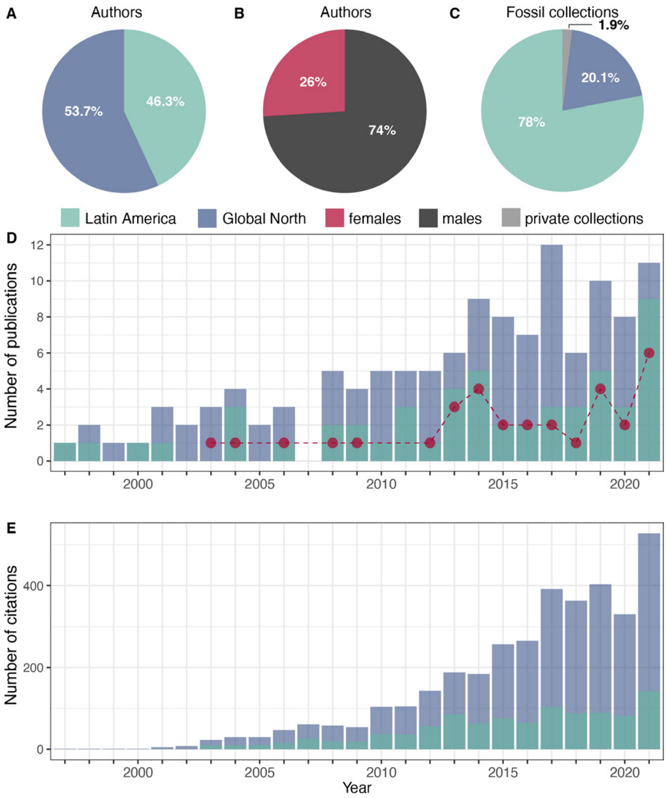

Figure 4. Impact of colonialism and gender bias in the Latin American aquatic mammal fossil record and associated publications between 1997-2021. Here, we show the geographical location, either Latin America or Global North, of the first author (A) and their gender (B), based on the references revised during the study period. We analyzed where Latin American aquatic mammal fossil specimens revised here are deposited (C). Finally, we review the number of publications (D) and their corresponding citations (E) during the study period; as in A, the colour represents the geographical location of the first author. Red dots in D represent the number of publications led by female authors. For further details on the Methods and data used, see Supplementary Material 2.

projects and articles in the near future (*e.g.,* Astegiano et al., 2019; Salerno et al., 2019), promoting a more diverse future for Latin America palaeontology.

How are the citation rates of papers on Latin American fossil aquatic mammals?

Papers on Latin American fossil aquatic mammals received the first citations in 2001, despite many papers having been published at least five years earlier (Fig. 4). An increase in the number of citations over the last two decades has been observed; however, trends are different between studies led by Latin American researchers and by those based in Global North institutions (Fig. 4). Citations of articles led by Latin American researchers were substantially lower over time, even though they represented almost half of the total number of publications during the study period (Fig. 4). Given that scientific productivity (and funding and job opportunities) in academia are directly related to publication and citation metrics, scientific outputs by Latin American scientists remain less visible within the global community. The lack of peer acknowledgment (*i.e.*, citations) generates an endless cycle, where publications by Latin American researchers result in fewer opportunities, less access to international collaborations, and less self-confidence in the quality of their work, thus perpetuating the cycle of fewer citations and poor recognition (*e.g.,* Salerno et al., 2019; Valenzuela-Toro & Viglino, 2021) experienced by Latin American scientists.

What can the scientific community do to become allies?

The abovementioned issues have resulted in a complex intersectional scenario for Latin American scientists, including palaeontologists (Raja et al., 2021; Trisos et al., 2021; Valenzuela-Toro & Viglino, 2021; Cisneros et al., 2022). Solving these issues will require a profound transformation of the academic system, including institutions, funding sources, publishers, reviewers, and individual researchers. Here we propose some small-scale actions to help us achieve a more equitable academic field:

- Scientists working in Global North museums/scientific institutions holding Latin American fossils (particularly holotypes), should support efforts to return these specimens to their countries of origin. Similarly, they should support non-traditional ways to enable access to specimens (*i.e.*, open-access 3D models, casts) for scientists from underprivileged countries;
- When working with Latin American fossils, scientists should thoroughly revise the published literature, making sure to search for articles led by regional researchers and citing them when appropriate. Diverse citations (geographical and ethnic representation, gender, etc.) generate a richer discussion of scientific results (Trisos et al., 2021; Valenzuela-Toro & Viglino, 2021);
- Museums, universities, and scientific institutions from the Global North should make sure that their staff and students are correctly informed and advised when conducting fieldwork in Latin America. This includes making sure scientists are familiar with local regulations and cultural practices (Raja et al., 2021; Trisos et al., 2021; Cisneros et al., 2022);
- Scientists from the Global North should encourage regular discussions on colonial practices in science inside their own institutions. This will help create awareness and help to prevent future issues;
- Science curricula must include ethics discussions, where "parachute science" unethical practices are questioned and discussed. This will help foster informed scientists who practice meaningful collaborations with researchers worldwide (Rogers et al., 2022);
- When scientists are doing fieldwork and/or studying Latin American fossils, they should firstly check whether local researchers are already conducting similar projects. If so, they should reach out and propose equitable collaborations. Alternatively, Global North scientists could propose research projects co-led by local researchers. The contributions of local researchers should be acknowledged appropriately, and they should be involved in every step of the project (Raja et al., 2021; Trisos et al., 2021; Cisneros et al., 2022).

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Supplementary material

Supplementary Material 1 - Records of Latin American aquatic mammal fossils since 1996.

Supplementary Material 2 - Literature search methods used to investigate the impact of scientific colonialism in Latin American Paleontology.


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