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The ichthyofaunistic colonization and complex biogeographic history of the southern portion of the Southwest Atlantic Ocean

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Abstract

Here, we highlight the geological processes that resulted in the current conformation of the southern Southwest Atlantic Ocean, and explore the heterogeneous composition of the marine ichthyofauna found between 33° and 56° from a paleobiological perspective. During the early Cretaceous (140 Mya), the South Atlantic was still not formed, and Gondwana was probably a set of united plates with shallow continental waters. In the middle Cretaceous (112 Mya), the major Gondwanan plates started diverging from each other, allowing shallow marine intrusions and the diversification of an endemic fish fauna. By the end of the Mesozoic (66 Mya), the proto-South Atlantic connected with the North Atlantic, which was still part of the Tethys Sea, allowing its ichthyofauna to colonize the south and reach the Antarctic region. The opening of the Drake Passage in the Oligocene (33 Mya) enabled the cold waters of the Pacific Ocean to reach the South Atlantic, causing drastic effects on the thermophilic fauna and favoring the dispersion of cold-water species. Successive glaciations during the Quaternary (2 Myr to 10,000 years ago) resulted in the prevalence of Antarctic climatic conditions in the southern Southwest Atlantic. The long history of changing scenarios in the constitution of the southern Southwest Atlantic is reflected in the heterogeneous composition of the marine ichthyofauna between 33° and 56°S, which is characterized by a mixture of cosmopolitan, Tethyan, Pacific, Gondwanan, Antarctic, and endemic origins.

KEYWORDS
Drake Passage, endemism, evolutionary history, ichthyofauna, phylogeography, Weddellian Province

1 | OVERVIEW

The supercontinent Gondwana started to break up by the early Cretaceous (140 to 130 Mya), resulting in the formation of South America, Africa, Madagascar, Peninsular India, Australia, New Zealand, New Guinea, and New Caledonia, which drifted northwards, and Antarctica (Jolivet & Verma, 2010). The breakup of the Gondwanan plate also resulted in the formation of the South Atlantic and Southern oceans. However, the opening of the South Atlantic was probably not synchronous along the line of rifting (135–130 to 119–105 Mya) as the African and South American landmasses drifted from each other. The subsidence in the Powell Basin between West Antarctica and South America likely led to the creation of mid and deep-water passages, before the Scotia Sea underwent the seafloor spreading and established the deep marine Drake Passage during the Oligocene (32–28 Mya) (McLoughlin, 2001). As a consequence, the geological changes involving Africa, South America and Antarctica allowed marine water mass intrusions with different physical parameters and biota. These biogeographic processes took place in about 100 Mya and are reflected in today's complex ichthyofaunistic composition of the southern portion of the Southwest Atlantic Ocean (SSWA).

2 | SOUTHERN SOUTHWEST ATLANTIC OCEAN

The SSWA reached its current configuration after the end of the last Pleistocene glaciation period *c*. 11,000 years ago (Ponce & Rabassa, 2012). At present, it is characterized by open and extensive coasts, as opposed to continental bounded seas with little or no connection to the ocean, such as the Mediterranean and the Caspian. The SSWA spreads over a large continental shelf with a gradual slope, which is an extension of the northern Pampas plain and southern Patagonian plateau; this continental shelf is considered one of the largest in the world (Violante et al., 2014). Around 65% of the continental shelf seafloor in the SSWA is sandy, with a north to south and deep to shallow increase in grain size (Ponce et al., 2011). A series of underwater canyons are present at the eastern limits of the Argentinian shelf up to about 48°S, and hard bottoms are present in the southeastern Malvinas/Falkland Islands and Burdwood Bank areas (Violante et al., 2017). The western limit of the Argentinian shelf is characterized by bands of hard bottoms, which are narrow from the south of Buenos Aires Province (39°S) to the north of San Jorge Gulf (45°S), and wider from Santa Cruz to Tierra del Fuego provinces (Cousseau & Perrotta, 2013).

The SSWA waters have a sub-Antarctic origin and are gradually modified by continental runoff, water mass convection and heat exchange with the atmosphere (Guerrero & Piola, 1997). These waters drift from the Antarctic Circumpolar Current and penetrate the Argentinian shelf through a passage between the Malvinas Islands and Tierra del Fuego (Piola & Gordon, 1989). Another branch of this current drifts to the north along the continental slope (500–600 m depth range) originating the cold Malvinas Current. Between 36° and 38°S, the Malvinas Current meets the warm Brazil Current at the subtropical confluence, which drifts southward, resulting in the anticyclonic vortex of the SSWA (Piola & Matano, 2001). One part of the Malvinas Current flows northwards below the Brazil Current (García, 1997), whereas the other portion turns southward (Franco et al., 2009). The sub-Antarctic waters in the Patagonian shelf mix with meltwater from a series of coastal channels in the Tierra del Fuego, Magallanes strait and Patagonian rivers (41°–55°S). The north-northeastward flow of these waters receives the name Patagonian Current (Piola & Rivas, 1997). In addition, the northern area of the SSWA receives a considerable freshwater discharge from several rivers (Pasquini & Depetris, 2007). For example, the Río de la Plata discharges a considerable amount of freshwater into the northern SSWA (Nagy et al., 2002), inducing a large-scale buoyant plume that in winter extends beyond 1000 km from the estuary (Piola et al., 2008). As a result of the freshwater discharge to the open sea, topography, and water masses, diverse forces generate frontal areas along the SSWA, which are characterized by high biological productivity (Acha et al., 2015).

The SSWA is characterized by a transitional system between the warm-temperate and cold-temperate zoogeographic areas (Cousseau & Figueroa, 2010). Two biogeographic provinces are distinguished considering their ichthyofauna, the Argentine and Magellanic, which comprise the subtropical and sub-Antarctic regions (Balech & Ehrlich, 2008; Cousseau et al., 2019). The Argentine Province extends across southern Brazil (state of Rio Grande do Sul), Uruguay, Buenos Aires and North Patagonian coasts up to the middle continental shelf (Balech & Ehrlich, 2008; Pinheiro et al., 2018); its ichthyofaunistic composition corresponds to the southern extreme of an impoverished fauna from Brazil (Figueroa, 2019; Menezes et al., 2003). The Magellanic Province extends over the Patagonian continental shelf and northeastern areas of the SSWA, following the Malvinas Current drift along the continental slope (Balech & Ehrlich, 2008); its ichthyofaunistic composition is characterized by a combination of cosmopolitan, Pacific, Gondwanan, Antarctic, and endemic origins.

3 | GEOLOGICAL EVOLUTION

The SSWA is one of the youngest major oceanic portions of the world. The region underwent several changing scenarios, considering its short chronology from a geological standpoint (*c*. 11,000 years). In the early Cretaceous (about 140 Mya), the South Atlantic was not yet formed since the South American and African plates were still joined in a single landmass (Figure 1a). During the middle Cretaceous (120–105 Mya), these plates started to diverge, with the consequent formation of the proto-South Atlantic (Figure 1b). The water masses that started to occupy the proto-South Atlantic corridor were hypersaline and characterized by low oxygen concentration (Compagnucci, 2014). The ichthyofauna was then entirely endemic and different from that inhabiting the region today. During the late Cretaceous (about 66 Mya), the two plates reached a level of divergence that favored a markedly increase in water circulation from the western Tethys Sea (i.e., part of the current North Atlantic, Figure 1c). At this time, oxygen levels and salinity started to resemble the conditions today, facilitating the ichthyofaunistic colonization of the region (Maisey, 2000; Prámparo et al., 2013). The disposition of the tectonic plates prevented deep and colder waters from the Pacific to access the South Atlantic (De Wit, 1977). As a result, the warm current of Brazil, as is known today, extended further south, reaching Antarctica and possibly some areas of Oceania (Cione et al., 2011; Dolganov, 2002). This situation resulted in a greenhouse effect in

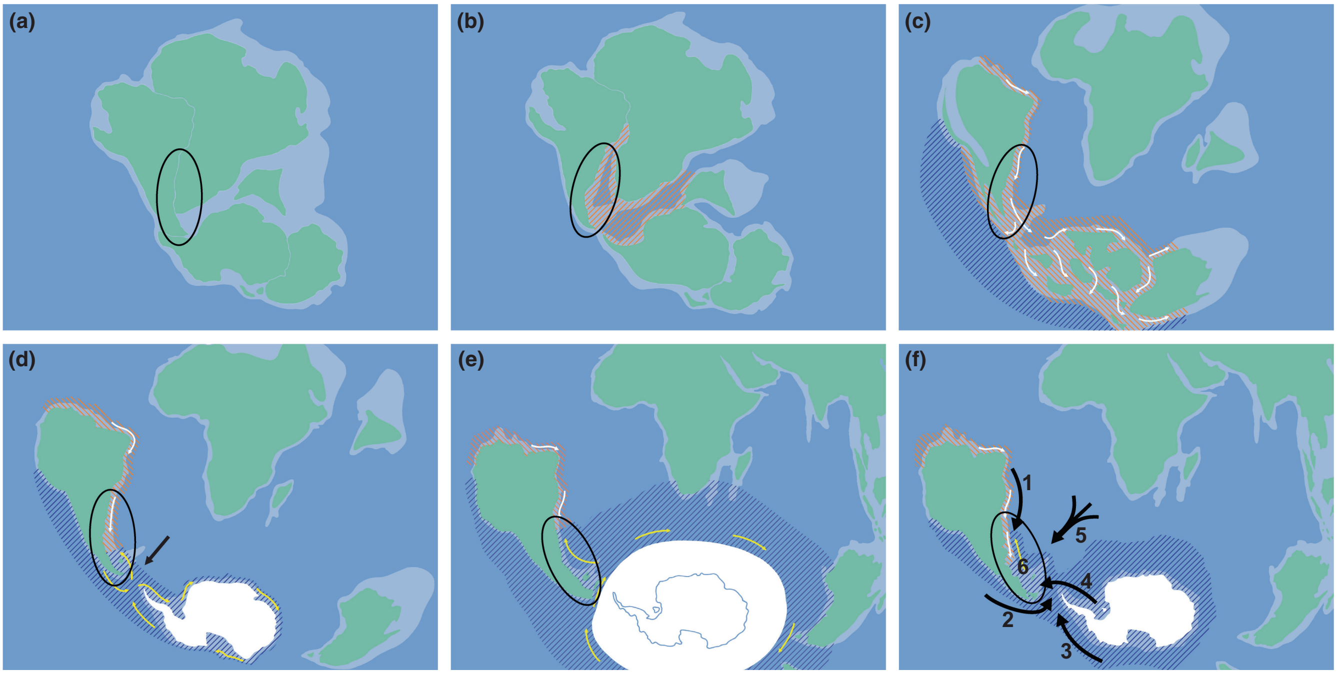

FIGURE 1 Paleogeological reconstruction of the main events in the formation of the southern Southwest Atlantic Ocean (SSWA). (a) Gondwana supercontinent during the early Cretaceous (140 Mya); (b) Gondwana supercontinent during the middle Cretaceous (120–105 Mya), with South America and Africa drifting away and originating the proto-South Atlantic Ocean (within red shaded area); (c) Weddellian Province (South America, Antarctica and Australasia) surrounded by warm-temperate (red shaded area) and cold (blue shaded area) waters during the late Cretaceous (66 Mya), when the South American and African plates diverged more and the SSWA corridor was stablished; (d) American, African, Australasian, and Antarctic continents during the Oligocene (Tertiary, 30 Mya) when the Scotia Arc (black arrow) opened, allowing the penetration of cold Pacific currents through the Drake Passage; (e) American, African, Australasian, and Antarctic continents during the Pleistocene (Quaternary, 18,000 years; polar ice cap in white); (f) current configuration of American, African, Australasian, and Antarctic continents, and the hypothetical fish paths reaching the SSWA: (1) Tethyan (e.g., Carangidae, Sciaenidae), (2) Pacific (e.g., Zoarcidae, Rajidae: *Bathyraja* genus), (3) Gondwanan (e.g., Rajidae: genus *Zearaja*), (4) Antarctic (e.g., Nototheniidae, with the exception of *Patagonotothen*), (5) cosmopolitan (e.g., Myctophidae, Stomiidae, Macrouridae), and (6) endemic (Rajidae: Arhynchobatinae, Nototheniidae: genus *Patagonotothen*, Serranidae: genus *Dules*, Clupeidae: genus *Platanichthys*). Red and blue shaded areas indicate warm-temperate and cold waters, respectively. White and yellow arrows indicate thermophilic and cryophilic colonizing fish currents, respectively. The black oval indicates the location of the SSWA across time. Modified from Figueroa et al. (2013).

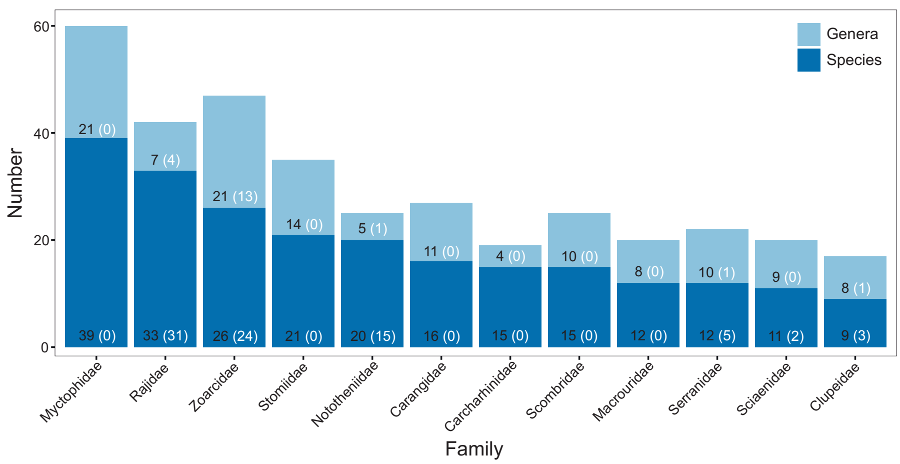

FIGURE 2 Marine fish families with the largest number of species present in the southern Southwest Atlantic Ocean between 33° and 56°. Total and endemic (in parenthesis) number of genera and species are shown for each family.

the region, which led to what is known as the Weddellian Province (i.e., southern South America, Antarctica and Australasia, Figure 1c) (Anderson, 1990; Cione et al., 2007; Eastman, 1993; Long, 1994; Zinsmeister, 1979, 1982).

During the Oligocene (about 30 Mya), the opening of the Drake Passage (i.e., Scotia Arc) enabled the intrusion of cold- and deep-water currents carrying a cryophilic ichthyofauna from the Pacific to the South Atlantic. The opening of the Drake Passage also resulted in the development of the Antarctic Circumpolar Current, which had a global effect on climate and was responsible for the climatic isolation of Antarctica (Clarke & Johnston, 1996; Eastman, 1991a, 2000; Kock, 1992), also contributing to drastic changes in the biota of South America (Cione & Reguero, 1994; Figure 1d). During the Pleistocene (about 2.5 Mya), several glaciation events occurred, among which the greatest at about 18,000 years ago (Mercer, 1976). The magnitude of the polar ice caps decreased the sea level by more than 100 m below the current level, whereas the Antarctic Polar Front shifted towards northern latitudes, leaving the SSWA fully under the Antarctic influence (Figure 1e). After this period, the temperature started to rise gradually and the ice retreated, and as a result the Antarctic Polar Front retracted to near its current location, stabilizing the climate of the SSWA as it is today (Figure 1f) (Cione et al., 2011; Ponce & Rabassa, 2012).

4 | ICHTHYOFAUNISTIC COMPOSITION

A total of 601 species of fish belonging to 182 families are recorded in the SSWA between 33° and 56°S (Figueroa, 2019). Among these families, 12 are the most diverse comprising nine or more species (Figure 2). The analysis of the composition and distribution of these families reflects the complex biogeographic history of the young SSWA.

4.1 | Myctophidae

The Myctophidae is a cosmopolitan family composed of meso- and bathypelagic fishes. It is the largest family within the SSWA, with 39 species (Figueroa, 2019). Myctophids are important prey items to the Argentine hake *Merluccius hubbsi*, one of the most important demersal fish resources in the SSWA (Angelescu & Cousseau, 1969). They also represent the main prey item for upper trophic predators such as seabirds and marine mammals (Palomares et al., 2005).

4.2 | Rajidae (sensu Nelson et al., 2016)

The Rajidae is an ideal candidate for biogeographic analyses because of its cosmopolitan distribution and the life history characteristics of the species of the group. The most particular traits among those fishes include a non-migratory life mode, bottom-dwelling behavior at all ages, and most species inhabiting the shelf and upper slopes up to 1000 m of depth but not moving across deeper marine regions (Dolganov, 2002; Last et al., 2016). It may be one of the first fish families to colonize the SSWA, as there are old fossil records of skate-like teeth across the eastern South American coast, in particular in Las Colonias rock formations (Chubut Province, Argentina), from late Cretaceous, *c*. 66 Mya (Figueroa et al., 2013). The species composition of the Rajidae in the SSWA synthesizes the changes that occurred in this region since its origin. Four endemic genera (*Atlantoraja*, *Psammobatis*, *Rioraja* and *Sympterygia*, all in the Arhynchobatinae) with 12 species are found across the Argentine and Magellanic biogeographic provinces, with ancestors probably originating in the western Tethys Sea. Such a degree of endemism is only similar to that found in Australasia (Last & Yearsley, 2002). Two cosmopolitan genera, *Amblyraja* and *Bathyraja*, in turn, are found in the Magellanic Province. Their ancestors probably dispersed from the Pacific after the opening of the Drake Passage (Oligocene *c*. 32–28 Mya) (McLoughlin, 2001). According to Stehmann (1986), the Magellanic Province constitutes a radiation center for *Bathyraja* (with more than ten species), a situation also found in the North Pacific where more than 50% of the species of this genus are recorded (Last et al., 2016). Another interesting case is the yellownose skate *Zearaja brevicaudata*, which belongs to a genus considered Gondwanan (Awruch et al., 2021; Concha et al., 2019; Figueroa, 2019; Last & Gledhill, 2007; Last & Yearsley, 2002). Ancestors of this genus may have entered the SSWA via the Drake Passage opening and evolved from species inhabiting the eastern Gondwanan sea.

4.3 | Zoarcidae

The Zoarcidae is notably diverse, comprising 19 genera of which 13 are endemic to the Magellanic Province and adjacent waters (Figueroa, 2019). Anderson (1994) indicated a possible origin of this group during the Eocene *c*. 58–37 Mya, which was successful in occupying the continental slopes of the boreal regions. Based on fossil evidence, Anderson (1994) also discussed the possibility of dispersal of zoarcids to the Southern Hemisphere during the Miocene *c*. 24–5 Mya (Anderson, 1994). Accordingly, Gosztonyi (1977) considered the SSWA as a secondary distribution center for zoarcids. The ancestral species of the Zoarcidae that colonized the Magellanic Province after the opening of the Drake Passage during the Oligocene *c*. 32–28 Mya (McLoughlin, 2001) probably dispersed from the North Pacific. In the early Oligocene (32 Mya), new opportunities for diversification of this group may have emerged as a consequence of the biogeographical changes in the Patagonian shelf. Anderson (1994) suggested that the recent species, which settled off the Patagonian coast evolved from ancestral species that inhabited deep waters.

4.4 | Nototheniidae

The Nototheniidae diversified in the Antarctic region after the opening of the Drake Passage. This family belongs to the "cryonotothenioids," the group of notothenioids that radiated in Antarctica (Eastman & Eakin, 2021). This radiation is probably related to events that occurred in the Antarctic continent during the Tertiary (about 32 Mya), including the isolation of the Antarctic shelf waters, the variation in the current patterns of the region, the formation of ice caps, the temperature and seasonality fluctuations, and changes in trophic conditions. These geological and climatic changes were unsuitable for the thermophilic biota of the Weddellian Province, but represented new opportunities for ancestral species that could adapt and thrive in this new environment, such as notothenioids (Anderson, 1990; Clarke & Johnston, 1996; Eastman, 1991a, 1993, 2000; Kock, 1992). Similar changes also occurred in the Patagonian waters (i.e., Argentina and Chile) during that period, where members of the family are also found.

Among the five extant genera of Nototheniidae found in the SSWA, *Patagonotothen* includes more than ten species (Eastman & Eakin, 2021; Figueroa, 2019). Such a relatively high number of species is uncommon among Antarctic "cryonotothenioids" genera. The ancestral species of this non-Antarctic endemic genus may have reached the region during glaciations, at times when the Argentinian shelf or part of it remained within the Polar Front. Following the retreat of the front during the interglacial period, the environmental conditions became less adverse, and a vacant ecosystem may have represented new opportunities for *Patagonotothen* to diversify.

4.5 | Other fish families

The remaining fish families with nine or more species in the SSWA are cosmopolitan or have a wide distribution throughout the world (Figueroa, 2019; Menezes et al., 2003; Nelson et al., 2016). Members of the Stomiidae inhabit meso- and bathypelagic environments. The Carangidae is distributed in warm and temperate seas and probably has a Tethyan origin (Cowman & Bellwood, 2013; Friedman & Carnevale, 2018; Pinheiro et al., 2018). The Carcharhinidae includes sharks of broad distribution, from the coast to oceanic waters. Members of the Scombridae inhabit epipelagic zones in tropical and temperate seas. The Macrouridae is comprised of grenadiers with an antitropical distribution, occupying demersal and benthic depths. The Serranidae is diverse and found in tropical, subtropical and temperate regions, reaching depths of up to 200 m; its origin is probably Tethyan (Cowman & Bellwood, 2013; Friedman & Carnevale, 2018; Pinheiro et al., 2018). In this family, *Dules* represents an endemic monotypic genus in the Southwest Atlantic (Figueiredo & Menezes, 1980; Menezes et al., 2003), also inhabiting the Argentine Province. The Clupeidae comprises sardines with neritic pelagic habits, with *Platanichthys* representing an endemic monotypic genus in the Southwest Atlantic (Menezes et al., 2003; Whitehead, 1985), including the Argentine Province. Fishes of the Sciaenidae are found in demersal-benthic regions on the coasts of tropical, subtropical and temperate seas, including estuarine and freshwater environments; its origin is Tethyan (Sasaki, 1989).

5 | DISCUSSION

Only a few oceanic regions of the world experienced complex changes like the ones the SSWA have undergone in its geologic history. The SSWA did not exist 120 Mya, but became one of the regions of the world with the greatest fish complexity and biodiversity. Since the Atlantic was the last ocean of the world to form, in a process that began in the northern hemisphere and continued into the south during the Cretaceous (150–120 Mya, Figure 1a) (Benedetto, 2010; Levin, 1999), the SSWA can be considered one of the most recently formed oceanic regions of the world.

The opening of the South Atlantic began in the south during the middle to late Cretaceous (135–130 Mya) and progressed northwards (McLoughlin, 2001). The early aquatic environments of the region were different to the ones found today and were inhabited by an endemic ichthyofauna (Maisey, 1991). For example, the coelacanth *Mawsonia* has been found in fossil deposits of Araripe in Brazil and Benue in Nigeria (Maisey, 1991, 2000; Martill, 1993) (Figure 1b). As oxygen and salinity levels settled and surface water exchange began in the equatorial Atlantic during the middle and late Albian (106–101 Mya), a more widespread marine invasion (probably from Caribbean Tethys) occurred (Maisey, 2000). This gradual opening resulted in an oceanic circulation system in the South Atlantic, where the warm current from Brazil influenced the Patagonian and Antarctic coasts via the Scotia Arc (late Cretaceous to Eocene, Dolganov, 2002), leading to the colonization of the ichthyofauna from the Tethys Sea to the Weddellian Province (Figure 1c). Teleost families that inhabited the western Tethys Sea gradually colonized the eastern American coasts while the North and South Atlantic formed. For this reason, representatives of the Carangidae, Serranidae and Sciaenidae, among other families, are found today with a wide latitudinal distribution across both hemispheres (Figueroa, 2019; Menezes et al., 2003). Batoids, however, underwent a different situation. The Myliobatoidei (eagle rays and related groups) originated in the eastern Tethys Sea, likely representing a major competition for skates (Rajidae) to occupy ecological niches across shallow tropical waters (Dolganov, 2002). This situation could have forced skates to colonize colder areas at higher latitudes, diverging from the species in the North Atlantic.

Towards the end of the Paleocene and the beginning of the Eocene (60–50 Mya), the world underwent the Paleocene-Eocene Thermal Maximum (Benedetto, 2010). During this period, sea temperature increased between 4°C and 8°C across shallower waters and around 5°C in deeper waters. These warmer conditions in the Weddellian Province allowed a cosmopolitan and diverse ichthyofauna to inhabit and probably diversify in Antarctica (Eastman, 2005). However, the Oligocene (about 33 Mya) marked the beginning of one of the most abrupt global cooling during the Phanerozoic (Benedetto, 2010). In a few million years, the average global temperature decreased by 10°C and the Earth shifted from a "warm greenhouse" climatic state to an "icehouse" state (Benedetto, 2010). This climatic shift also marked the beginning of glaciations, the thickening of the polar ice caps, and the presence of strong thermal gradients between the poles and the Equator, following a drastic change in the deep oceanic circulation after the Gondwanan fragmentations (Benedetto, 2010). These fragmentations included the formation of Australia and Antarctica (38–32 Mya) and the opening of the Drake Passage (25 Mya), which led to the full isolation of Antarctica and the full development of the Circumpolar Antarctic Current (Benedetto, 2010; McLoughlin, 2001; Sanmartín

& Ronquist, 2004). By separating warm subtropical gyres from the continent, this current served as a barrier to heat flow and thermally isolated the Antarctic continent (Eastman, 1991b) (Figure 1d). In Australasia, for example, the Antarctic Polar front advanced 300 km to the north during the late Miocene (6.5–5 Mya) and cold water reached as far north as New Zealand (Eastman & McCune, 2000). The process resulted in the end of the Weddellian Province, causing the extinction of the thermophilic ichthyofauna that inhabited the Antarctic coasts (Eastman, 2005; Eastman & McCune, 2000). This also forced the thermophilic ichthyofauna in Australasia and South America to migrate towards lower latitudes. Dolganov (2002) argued that this process represented a favorable scenario for the origin of *Bathyraja*-like skates.

With the isolation between Africa and South America, the Southwest Atlantic corridor opened, favoring the ichthyofaunistic colonization of the Weddellian Province from the Western Tethys Sea. Evidence of this may be the evolution and diversification of skates of the subfamily Arhynchobatinae. This group of skates from the SSWA became isolated when the Antarctic bridge was lost with the formation of the Circumpolar Current, along with their Australasian counterpart, giving rise to remarkable endemism at the generic level (Figueroa et al., 2013; Last & Yearsley, 2002). Another example highlighting the relevance of the opening of the Southwest Atlantic corridor is presented by Near et al. (2015). They proposed a new phylogeny for notothenioids with an origin in the western portion of the Weddellian Province, particularly in South America. Based on phylogenetic analysis of DNA sequences, the authors provided strong support for a *Percophis brasiliensis* sister-group relationship with other notothenioids. *Percophis* is an endemic monotypic genus of the Southwest Atlantic (Menezes et al., 2003), inhabiting the Argentine Province. These examples of endemism, such as the ones mentioned for the Serranidae and Clupeidae, could represent evidence supporting the Argentine and Paulista Biogeographic Provinces (Balech & Ehrlich, 2008) as partial remnants of the former Weddellian Province.

The opening of the Drake Passage allowed the intrusion of deep and cold waters from the Pacific that drastically changed the oceanographic conditions in the SSWA. Firstly, it originated the Malvinas Current and what is currently known as the Magellanic Province (Balech & Ehrlich, 2008), while limiting at the same time the southward extent of the warm Brazil Current. This novel water mass dynamic and other factors such as topography, winds, tides and freshwater discharge, resulted in a complex system of marine fronts of greater biological production (Acha et al., 2004). As a consequence, the new ecological niches (continental shelf and slope) in the SSWA favored the establishment and rapid diversification of a cryophilic ichthyofauna (i.e., batoids in the Patagonian Slope Province) (Sabadin et al., 2020).

The beginning of glaciations in the Oligocene (33 Mya) marked a new climatic regime in the SSWA. The SSWA has one of the largest continental shelves in the world, which expands nearly 1,000,000 km^2 (Cousseau & Perrotta, 2013). Using a paleogeographic evolution model, Ponce and Rabassa (2012) concluded that the last ice age began in the Pleistocene 115,000 years ago, with its coldest period, known as the Last Glacial Maximum, occurring between 24,000 and 22,000 years ago. During this Last Glacial Maximum, the accumulated volume of ice over the continents reached its maximum value. The sea level oscillated between 120 and 140 m below the current level, leaving most of the Argentinian continental shelf exposed. The model indicated that during this period the Malvinas islands (Gran Malvina and Soledad) formed a sole island with an approximate surface of 45,880 km^2, which is four times larger than the current size of the archipelago. This ancient island was separated from the continent by a strait only 220 km wide. Nearly 120 km south of the Malvinas Archipelago, another large island formed, as a result of the emerged Burdwood Bank. This paleo island existed as much as *c*. 15,500 years ago and was located 150 km east of the continent, with an exposed surface of ~13,600 km^2 (slightly larger than the Malvinas Archipelago today). In addition, the Isla de los Estados was connected to the rest of the continent along with Tierra de Fuego's Isla Grande. Under these circumstances, the southern limit of the continental sector of Patagonia extended some 450 km further south from its current position (Figure 1e).

Eastman (1997) proposed an interesting analogy when comparing Antarctica and the Arctic concerning their fish faunas. The author used a protocol in experimental biology as an analogy, in which fish fauna in the polar regions can be considered the result of two evolutionary experiments. As mentioned in Eastman (1997: pp. 348–349), "The experiments began during the late Cretaceous/early Tertiary when the fish of the world ocean had a cosmopolitan distribution and distinct polar biotas did not exist. The experiments ran for tens of millions of years during which geologic and climatic changes (vicariant events) led to different degrees of continental isolation, to cooling of the oceans and to cycles of glaciation and deglaciation". These vicariant events represented uncontrolled variables, likely leading to a differing taxonomic composition and biology of the faunas. Considering Eastman's analogy, its recent conformation, complex biogeographic history, and the diverse colonizing fish pathways (Figure 1f) that settled and diversified, the SSWA can be considered another "evolutionary experiment."

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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