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THE ORIGIN OF BIOGEOGRAPHIC SEGREGATION IN THE COPPER SHARK (*CARCHARHINUS BRACHYURUS*): AN INTEGRATIVE RECONSTRUCTION BASED ON NEONTOLOGICAL AND PALEONTOLOGICAL DATA

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BRONZE WHALER
CALOOSAHATCHIAN PROVINCE
CARCHARHINIDAE
CENTER OF ORIGIN
DISPERSAL
ANTITROPICAL DISTRIBUTION
GATUNIAN PROVINCE
PALEOBIOGEOGRAPHY

ABSTRACT. – Nowadays, the copper shark *Carcharhinus brachyurus* Günther, 1870 displays an antitropical, disjunct distribution in marginal-marine environments of both the hemispheres. Differing from other species of *Carcharhinus*, *C. brachyurus* inhabits temperate rather than tropical coastal waters, and its dispersal abilities are strongly conditioned by the presence of habitats suitable as nursery grounds. Here we analyze, through well-defined geological time-slices, the global fossil record of *C. brachyurus* in order to identify the main biogeographic dynamics that led to the present-day biogeographic segregation pattern of this requiem shark species. By integrating a thorough review of the paleontological literature with the results of recent phylogeographic analyses on extant copper shark populations, our study provides a first integrated reconstruction of the historical distributional patterns of this shark species that allows for proposing the identification of some dispersal trajectories as well as of a number of key events in the paleobiogeographic history of *C. brachyurus*. Our research supports the notion that the present-day distributional pattern of *C. brachyurus* is the product of historical biogeographic processes and events that might be traced back to an early Miocene East Pacific-central West Atlantic center of origin and likely reflect major changes in the global ocean system (including the closure of major seaways and the emergence of new oceanic circulation patterns).

INTRODUCTION

Extant species belonging to the genus *Carcharhinus* Blainville, 1816 mostly live in tropical and warm-temperate waters and are distributed worldwide (*e.g.*, Garrick 1982). The copper shark, *Carcharhinus brachyurus* Günther, 1870, is the unique species in this genus to inhabit temperate rather than tropical coastal waters (Garrick 1982, Compagno *et al.* 2005, Benavides *et al.* 2011). This antitropical, coastal shark (also known as the bronze whaler) is distributed in the West Atlantic (in the Gulf of Mexico), in the western South Atlantic (from southern Brazil to northern Argentina), and in the East Atlantic (off France and North Africa, in the Mediterranean Sea, and along the southwestern coasts of South Africa) (Compagno 1984, Walter & Ebert 1991, Last & Stevens 1994, Froese & Pauly 2019). Its range also extends to the Indian Ocean off southeastern South Africa (Cliff & Dudley 1992), the western Pacific off Australia, New Zealand and Japan, whereas the occurrence of copper sharks in the Gulf of Thailand and the Seychelles has still to be confirmed (Duffy & Gordon 2003, and references therein). In the East Pacific, the distribution of *C. brachyurus* appears to be disjunct, this species having been recorded along the North American coasts from southern California to Baja California and along the South American coasts off Peru (Garrick 1982, Compagno 1984); however, the exact range and size of East Pacific populations of *C. brachyurus* are still poorly known (Duffy & Gordon 2003). The presence of the copper shark in the Ecuadorian and Colombian Pacific waters has been recently supported by Bearez (1996), Martínez-Ortiz *et al.* (2007), Jacquet *et al.* (2008) and Mejía-Falla *et al.* (2019). Surprisingly, in the East Atlantic, *C. brachyurus* also occurs off Equatorial Guinea – a location that contrasts with the otherwise antitropical distributional pattern of this species (Garrick 1982, Compagno 1984, Duffy & Gordon 2003).

Dispersal abilities of the copper shark appear to be strongly conditioned by the presence of habitats suitable as nursery grounds. Crucially, unlike most other congeneric species, the nursery grounds of *C. brachyurus* are located in temperate waters and occur at the highest latitudes available within the regional distributional ranges of this species (Lucifora *et al.* 2005). These critical areas tend to be large and poorly defined, and include shallow bays and inlets as well as more open coastal habitats (Duffy & Gordon 2003). The copper shark is also characterized by life-history traits such as a long lifespan, the production of relatively few offspring, a delayed age of sexual maturity (13-20 years; males mature earlier than females), and a strong tendency of females to return to their discrete nursery areas for giving birth (Smith *et al.* 1998, Lucifora *et al.* 2005, Benavides *et al.* 2011). The ability, shown by *C. brachyurus*, to cover long distances along continental coastlines has been documented by various authors (*e.g.*, Cliff & Dudley 1992, Compagno *et al.*

2005). Further highlighting this attitude, Benavides *et al.* (2011) recovered no differences in the genetic structure of populations of *C. brachyurus* found across South Africa and Namibia (*i.e.*, along a 2700 km-long coastline), and the same authors also recognized a high degree of biological connectivity in the copper shark populations distributed along the coasts of Australia and New Zealand. The strong degree of female reproductive philopatry and the unavailability of habitats suitable as nurseries at the warm, low latitudes of the global ocean inhibit the dispersal abilities of female copper sharks through the tropical thermal barrier. Copper shark males do not show the same level of fidelity to the mating areas as females (Feldheim *et al.* 2004); therefore, male-mediated gene flow often occurs over wider geographic areas (Schultz *et al.* 2008, Portnoy *et al.* 2010, Benavides *et al.* 2011). The cool waters that usually restrict the gene flow in subtropical and tropical carcharhiniforms act as less limiting factors in structuring the copper shark populations (Lucifora *et al.* 2005, Benavides *et al.* 2011).

The phylogeography of the copper shark was recently examined by Benavides *et al.* (2011) with particular reference to the Southern Hemisphere. Based on the distribution of genetic diversity and the evolutionary relationships among mtCR haplotypes, these authors identified two major, highly divergent mtCR clades: the first includes the *C. brachyurus* populations from South Africa, Namibia, Brazil, and Spain, whereas the second gathers the copper shark communities from Australia, New Zealand, Peru, and the Pacific Mexico. Benavides *et al.* (2011) proposed a East Pacific-central West Atlantic (*i.e.*, Gatunian) center of origin for this species that predated the separation of these oceanic basins. After the closure of the Panamanian Seaway, the Pacific and Atlantic lineages of *C. brachyurus* experienced vicariant isolation.

Based on thousands of fossil teeth of *C. brachyurus*, mostly belonging to immature individuals, from both the early Miocene Chilcatay Formation and the late Miocene Pisco Formation of Peru, Landini *et al.* (2017 a, b, 2019) identified the coastal East Pisco Basin as a fossil copper shark nursery area. This critical area is thus highly suggestive of having played a key role in the recruitment of the Pacific South American population of *C. brachyurus* during the Miocene at least. As the fossil record of *C. brachyurus* is nowadays relatively conspicuous, the discovery of the East Pisco Basin paleonurseries encouraged us to build up an integrated analysis of the paleobiogeographic patterns of this shark species. The aim of this work is thus to analyze, through well-defined geological time-slices, the global fossil record of *C. brachyurus* in order to identify the main biogeographic dynamics that, starting from the origination of this shark species, led to the colonization of new geographical districts, as well as to changes in the latitudinal and longitudinal ranges and regional extinctions. By integrating a thorough review of the paleontological literature with the results of the aforementioned phylogeographic study on the extant copper shark populations by Benavides *et al.* (2011), our meta-analysis results in the proposal of some paleobiogeographic trajectories, as well as in the identification of some major episodes (including *e.g.* the closure of major seaways and the emergence of new oceanic circulation patterns) that were likely crucial in shaping the biological connectivity potential of the past copper shark populations, thus contributing to explain its currently disjunct antitropical distribution.

MATERIALS AND METHODS

The paleobiogeographic dataset: We compiled a geographical and temporal distributional database for the fossil occurrences of *C. brachyurus* using previously published data as well as new (i.e., as yet unpublished) records from Ecuador and Peru. We categorized the fossil data into five geological time-slices (early, middle, and late Miocene; Pliocene; and Pleistocene) and eight geographic districts (Northern and Southern West Pacific; Northern, Central, and Southern East Pacific; Central and Northern West Atlantic; and Central East Atlantic, including the Mediterranean Sea). During the collection of data from paleontological literature, a rigorous and selective validation process was performed in order to discard incorrect or unreliable records of this species. This was done by checking all the illustrations of fossil teeth attributed to *C. brachyurus* and, in some cases, even the fossil specimens themselves. In addition, and following a similar approach, we searched the paleontological literature for illustrations of fossil teeth that have been assigned to the problematic species *Carcharhinus egertoni* (Agassiz, 1843) and *Carcharhinus priscus* (Agassiz, 1843).

Cappetta (1987) included the dubious Neogene species *C. egertoni* in the "bull-group", named after the bull shark *Carcharhinus leucas* (Valenciennes, 1839) and consisting of all the extant species of *Carcharhinus* having broadly triangular upper teeth with erect or semi-oblique cusps, no mesial heels, weakly to moderately incised distal edges, and both cutting edges fully serrated. A different opinion was expressed by Purdy *et al.* (2001) and Marsili (2007): according to these authors, one of the two syntypes of *Corax egertoni* figured by Agassiz (1843: pl. 36, fig. 6) is identical to the upper teeth of the extant *C. brachyurus*, whereas the other one (Agassiz 1843: pl. 36, fig. 7) is similar to the lateral teeth of *C. leucas*. Adnet *et al.* (2007) argued instead that the syntype figured by Agassiz (1843) in his plate 36, figure 6, differs from the upper teeth of the extant copper shark by the aspect ratio of the main cusp (length/height < 1 in *C. brachyurus*; length/height > 1 in Agassiz's specimen), the morphology of the mesial edge, and the serration pattern of the cutting edge. Adnet *et al.* (2007) regarded the aspect of this specimen as consistent with teeth belonging to the *C. leucas*-group (*sensu* Compagno 1988). *Carcharhinus brachyurus* exhibits a gynandric, dignathic dentition: teeth of adult males are generally distinctly hooked, longer, narrower, and more curved laterally than those of adult females (Bass *et al.*

1973, Garrick 1982, Purdy *et al*. 2001, Psomadakis *et al*. 2009, Landini *et al*. 2017b). Based on our personal observations, the length/height ratio calculated on extant jaws of *C. brachyurus* kept at the Earth Sciences Department of Pisa University (Pisa, Italy) is only partially consistent with the values indicated by Adnet *et al*. (2007). Indeed, in female jaws, the length/height ratio is < 1 in the anterior and anterolateral teeth, *ca*. 1 in the laterals, and > 1 in the posteriors. Even if the length/height ratio is not completely discriminating, we agree with Adnet *et al*. (2007) in regarding the morphology of the first syntype of *C. priscus* figured by Agassiz (1843) as more consistent with teeth belonging to the bull-group of Cappetta (1987).

Similarly problematic is the systematic assignment of the teeth that have been attributed to the fossil taxon *C. priscus*. The close morphological affinities between the teeth of *C. priscus* and those of some extant species (*e.g*., *C. brachyurus*, *Carcharhinus limbatus* (Valenciennes, 1839) and *Carcharhinus perezi* (Poey, 1876)) have been highlighted by various authors (*e.g*., Cappetta & Cavallo 2006, Laurito & Valero 2008, Reinecke *et al*. 2011, Kent 2018). Reinecke *et al*. (2011) also acknowledged the close resemblance between the teeth of *C. priscus* and those of the aforementioned extant species; at the same time, these authors recognized the existence of a morphological set of fossil teeth that compares favorably with Agassiz's type of *C. priscus* while being distinguishable from *C. brachyurus*, *C. limbatus*, and *C. perezi*.

To date, the taxonomic status of the nominal Neogene species *C. egertoni* and *C. priscus* is still problematic and needs a comprehensive revision effort, which is however well beyond the scope of the present study. Many of the numerous fossil teeth attributed to these two fossil taxa likely belong to various extant species (*e.g*., *C. brachyurus*, *C. leucas*, *C. limbatus*, and *C. perezi*) or to extinct species as well (Adnet *et al*. 2007). As a matter of fact, teeth belonging to *C. brachyurus* have often been reported under the name *C. priscus* (Marsili 2007). For the purposes of the present study, we checked the fossil records of *C. egertoni* and *C. priscus* only when bona fide copper shark teeth were not reported under the name *C. brachyurus* in an entire geographic district for one of the above defined geological time-slices. Only in these cases we searched the literature for figured teeth, attributed to *C. egertoni* or *C. priscus*, that could be reassigned to *C. brachyurus*. If so, *C. brachyurus* was included in our paleobiogeographic dataset for those particular geographic districts and geological time-slices.

Genetic phylogeographic background: Benavides *et al*. (2011) tested the genetic relationships among the extant copper shark populations from three major coastal regions of the Southern Hemisphere (Australia-New Zealand, South Africa-Namibia, and Peru), separated by oceanic expanses. Benavides *et al*. (2011) relied on the analysis of the mitochondrial genetic loci, which, by virtue of a maternal mode of inheritance, record a signal of genetic differentiation even if female-mediated gene flow is low and male-mediated gene flow is high. They also hypothesized that ocean basins form a barrier to gene flow in extant populations and predicted differences in mitochondrial haplotype frequencies among populations separated by this kind of biogeographic restrictors. Although the study by Benavides *et al*. (2011) was conducted on large samples from Namibia, South Africa, Australia, New Zealand and Peru, limited samples (consisting of one individual each) from Spain, Brazil, and the Pacific coast of Mexico were also included in order to provide preliminary insights into how the copper shark populations from these regions may relate to the others. Two highly divergent mtCR clades, perfectly segregated by geographical barriers, were identified: the first one includes South Africa, Namibia, Brazil, and Spain, whereas the second one is restricted to Australia, New Zealand, Peru, and the Pacific Mexico (Fig. 1). The analysis of divergence time between southern Africa and Australasia resulted in an estimate of 3.48 million years ago (hereinafter: Ma), while the comparison between southern Africa and Peru resulted in an estimate of 2.36 Ma. The amount of divergence between the Atlantic-western Indian and the eastern Indian-Pacific clades was estimated at 3.5-2.4 Ma, which was regarded by Benavides *et al*. (2011) as consistent with a vicariance event induced by the rise of the Isthmus of Panama rather

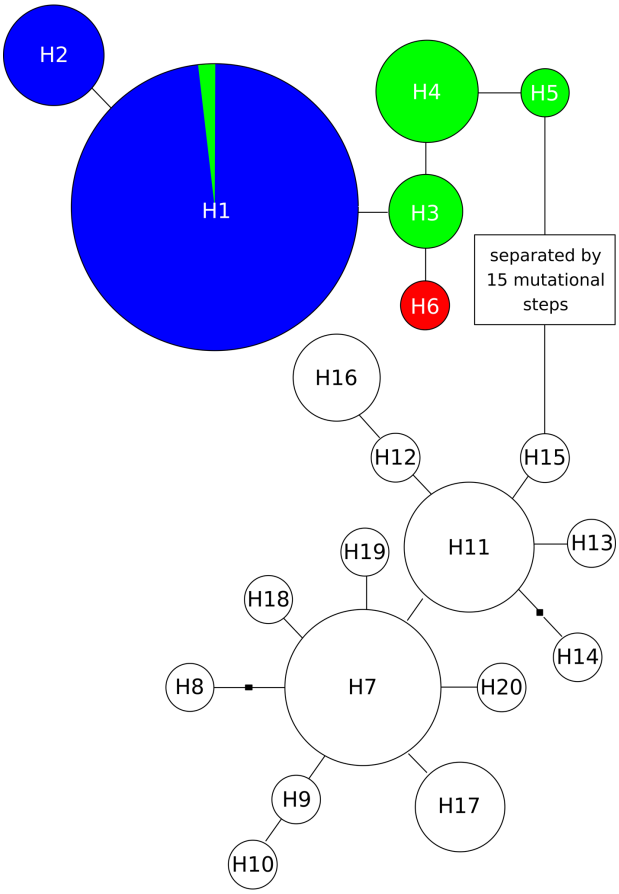

Fig. 1 – Haplotype network of the mitochondrial control region of *Carcharhinus brachyurus*, with haplotypes numbered in circles. Small squares represent inferred mutational steps. Blue circles represent haplotypes observed in Australia and New Zealand; green circles or slices are Peruvian haplotypes, the red circle is the Mexican haplotype; white circles are haplotypes from South Africa and Namibia. Redrawn after Benavides *et al*. (2011).

than by the closure of the Eastern Tethys Seaway (occurred around 20 Ma). Benavides *et al*. (2011) thus hypothesized that the center of origin of *C. brachyurus* was located in the present-day eastern Pacific or Atlantic oceans before the separation of these ocean basins; with the rise of the Isthmus of Panama (*ca*. 3 Ma), the Atlantic and western Indian clades started to diverge. In the eastern Pacific, the estimated divergence time between Australasia and Peru indicates that the founding of the Australasian populations was relatively recent (*ca*. 160 ka).

RESULTS

Our review of paleontological literature demonstrates that *Carcharhinus brachyurus* has a relatively long fossil record that stretches back to the early Miocene (*e.g.*, Purdy *et al*. 2001, Marsili 2007, Landini *et al*. 2019). This is not particularly surprising as similar distributional patterns are also shown by *Carcharias taurus* Rafinesque, 1810, *Rhyncodon typus* Smith, 1828, *Isurus oxyrinchus* Rafinesque, 1810, as well as other bona fide members of *Carcharhinus* such *Carcharhinus falciformis* (Müller & Henle, 1839), *Carcharhinus leucas* (Valenciennes *in* Müller & Henle, 1839), *Carcharhinus macloti* (Müller & Henle, 1838) and *Carcharhinus perezi* (Poey, 1876) (*e.g.*, Kent 2018). More in general, the fossil record of several extant elasmobranchs has recently been shown to extend deep into the geological time, and as such, it holds great potential to provide a deep-time perspective on how the living forms of sharks and rays have responded to environmental changes in the past (Paillard *et al*. in press).

The distribution of fossil teeth of *C. brachyurus* through sediments of early Miocene to Pleistocene age and different geographic districts is detailed in the following sections; furthermore, a summary of it is synoptically presented in Fig. 2 as well as in Table I.

Early Miocene (23.03-15.97 Ma) dataset
(Fig. 2A)

Southern East Pacific

Peru, Chilcatay Formation (Burdigalian), Landini *et al*. (2019).

Central West Atlantic

Colombia, Jamol Formation (Early Burdigalian), Carrillo-Briceño *et al*. (2019).

Venezuela, Cantaure Formation (Burdigalian-?Langhian), Carrillo-Briceño *et al*. (2016).

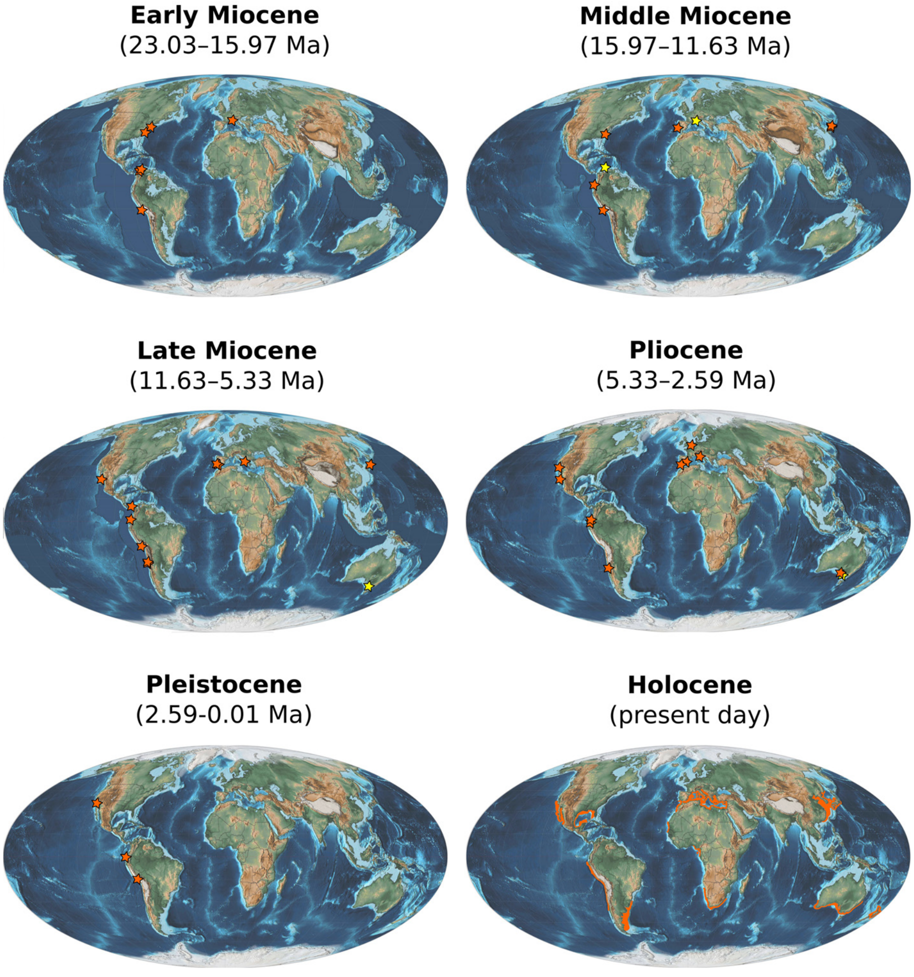

Fig. 2 – Occurrences of *Carcharhinus brachyurus* through six time-slices in the Neogene and Quaternary. **A**: Early Miocene; **B**: Middle Miocene; **C**: Late Miocene; **D**: Pliocene; **E**: Pleistocene; **F**: Holocene (Recent). The orange-colored stars indicate the unambiguous fossil occurrences of *C. brachyurus*; the yellow-colored stars indicate possible, yet to be confirmed fossil occurrences of *C. brachyurus*; the orange-colored areas indicate the present-day range of extant *C. brachyurus*. The palaeogeographic maps reproduced in the six panels are after Scotese (2014). The distribution of extant *C. brachyurus* shown in the bottom right panel is modified after Duffy & Gordon (2003); see the main text for data sources for all other panels. Ma = Million years ago.

Table I – Distribution of fossil remains of *Carcharhinus brachyurus* through five time-slices (early, middle, and late Miocene; Pliocene; and Pleistocene) and eight geographic districts (Northern and Southern West Pacific; Northern, Central, and Southern East Pacific; Central and Northern West Atlantic; and Central East Atlantic, including the Mediterranean Sea). Records of copper shark teeth that were previously reported as belonging to other species or tentatively attributed to *C. brachyurus* are indicated via their original taxonomic identification. See the main text for data sources. Ma = Million years ago.

	Early Miocene (23.03-15.97 Ma)	Middle Miocene (15.97-11.63 Ma)	Late Miocene (11.63-5.33 Ma)	Pliocene (5.33-2.59 Ma)	Pleistocene (2.59-0.01 Ma)
Northern West Pacific		present (as *C. priscus* and *C.* aff. *brachyurus*)	present (as *C. priscus*)		
Southern West Pacific			[possibly present (as *C.* cf. *brachyurus*)]	present (as *C.* cf. *brachyurus*)	
Northern East Pacific			present	present	present
Central East Pacific		present	present	present (including unpubl records from Ecuador)	present
Southern East Pacific	present	present	present	present	present (including unpubl records from Peru)
Central West Atlantic	present	present	present		
Northern West Atlantic	present				
Central East Atlantic	present (as *C. priscus*)	present (as *C. egertoni*)	present	present	

Northern West Atlantic

North Carolina (USA), Pungo River Formation (Burdigalian levels), Purdy *et al.* (2001).

Delaware (USA), Calvert Formation (Burdigalian), Purdy (1998).

Central East Atlantic

France, as *Carcharhinus priscus*, Montpellier region, Burdigalian-?Langhian, Cappetta (1970).

The most consistent fossil record of *Carcharhinus brachyurus* from the early Miocene is comprised in a somewhat limited area between 14°S and 38°N latitude, and 65°W and 76°W longitude. This area includes the central South American coast of the East Pacific (Peru), the northern coast of South America (Colombia and Venezuela), and the Atlantic U.S. coast of North Carolina and Delaware. Interchanges within this area were facilitated by extensive communication through the Panamanian Seaway and by the wider-than-today Florida Strait. During the earliest Miocene, several basins within this area were affected by sea transgressions that inundated much of the lower coastal plains in southern Peru (East Pisco Basin), the northern margin of South America (*e.g.*, the Cocinetas and Falcon basins), and the U.S. Atlantic coast from Florida to Georgia and the Carolinas (Popenoe 1990, Zachos *et al.* 2001, Di Celma *et al.* 2017, 2018a). Outside this area, the copper shark was recorded from the Burdigalian-?Langhian of Montpellier (France) with teeth attributed by Cappetta (1970) to *Carcharhinus priscus* (see also Purdy *et al.* (2001) and Marsili (2007) for a reattribution of these finds to *C. brachyurus*). This late early Miocene record seemingly testifies to the first dispersal event from the Center of Origin Area (hereinafter: COA), as identified by Benavides *et al.* (2011), to the central East Atlantic.

Middle Miocene (15.97-11.63 Ma) dataset
(Fig. 2B)

Northern West Pacific

Japan, as *Carcharhinus* aff. *brachyurus*, Bessho and Aoki formations of the Nagano Prefecture, Takakuwa *et al.* (2009).

Japan, as *Carcharhinus priscus*, from several formations of the Hokuriku District, Karasawa (1989).

Southern East Pacific

Peru, Pisco Formation (Langhian-Serravallian levels), Bosio *et al.* (2020), Collareta *et al.* (in press).

Central East Pacific

Ecuador, Angostura Formation, Carrillo-Briceño *et al.* (2014).

Central West Atlantic

?Venezuela, as *Carcharhinus* cf. *brachyurus*, Cantaure Formation (Burdigalian-?Langhian), Carrillo-Briceño *et al.* (2016).

North Carolina (USA), Pungo River Formation (Langhian levels), Purdy *et al.* (2001).

Central East Atlantic

Portugal, as *Carcharhinus egertoni*, Lisbon region, Langhian (Helvetian)-Tortonian, Antunes & Jonet (1969-70).

?France, as *Carcharhinus priscus*, Montpellier region, Burdigalian-?Langhian, Cappetta (1970).

The most significant biogeographic event that appears to be witnessed by the middle Miocene record of *C. brachyurus* is its westward, trans-Pacific dispersal from the eastern Gatunian (Pacific) district, leading to the first occurrence of this species along the Japanese coast. Within the COA, the biological connectivity was high, potentially ranging from North Carolina (Caloosahatchian province) to Peru (southeastern Gatunian province) through the Venezuelan coast, although the stratigraphic extension of the Cantaure Formation into the Langhian is dubious (Carrillo-Briceño *et al.* 2016). In the central East Atlantic district, the record from the Portuguese coasts confirms the persistence of *C. brachyurus* in this region.

Late Miocene (11.63-5.33 Ma) dataset
(Fig. 2C)

Northern West Pacific

Japan, as *Carcharhinus priscus*, from the Takakubo Formation of the Hokuriku District, Karasawa (1989).

Southern West Pacific

?Australia, as *Carcharhinus* cf. *brachyurus*, in the latest Miocene (Cheltenhamian)-early Pliocene (Kalimnan), Fitzgerald (2004).

Northern East Pacific

Mexico, Baja California, Gonzáles-Rodríguez *et al.* (2013).

Central East Pacific

Ecuador, Angostura Formation, Carrillo-Briceño *et al.* (2015).

South Eastern Pacific

Peru, Miramar Formation, Apolín *et al.* (2004), González Barba & Martínez (2010).

Peru, Pisco Formation, Alván de la Cruz (2008), Landini *et al.* (2017a, b).

Chile, La Portada Formation, Suárez *et al.* (2003).

Chile, Bahía Inglesa Formation, Suárez *et al.* (2002).

Central West Atlantic

Panama, Chagre Formation, Carrillo-Briceño *et al.* (2015).

Central East Atlantic

Portugal, as *Carcharhinus egertoni*, Lisbon region, Langhian (Helvetian)-Tortonian, Antunes & Jonet (1969-70).

Spain, Arcillas de Gibraleón Formation, Toscano Grande (2016).

Italy, as *Cestracion priscus*, Pietra Leccese Formation, Menesini (1968).

The most significant biogeographic events of the late Miocene occurred within the COA. In its Atlantic sector (Caloosahatchian and western Gatunian provinces), the copper shark populations were almost completely extirpated, with the significant exception of the coasts of Panama, which are closely associated with the Panamanian Seaway. On the contrary, in the eastern Pacific, *Carcharhinus brachyurus* increased both its southern and northern latitudinal ranges, thus reaching the Chilean and Californian coasts, respectively. No new geographical districts were colonized during the late Miocene.

Pliocene (5.33-2.59 Ma) dataset
(Fig. 2D)

Southern West Pacific

Australia, as *Carcharhinus* cf. *brachyurus*, Pledge (1985).

Northern East Pacific

California (USA), Gloria (= Tirabuzón) Formation, Applegate (1978).

Mexico, Baja California, Gonzáles-Rodríguez *et al.* (2013), Lira-Beltrán *et al.* (2020).

Central East Pacific

Ecuador, Onzole Formation (Pliocene levels of Camarones), Landini *et al.* (unpubl. data, work in progress).

Southern East Pacific

Peru, Miramar Formation (Pliocene levels), González Barba & Martínez (2010).

Chile, Horcón Formation, Carrillo-Briceño *et al.* (2013).

Central East Atlantic

Belgium, as *Carcharhinus priscus*, Antwerpen region, De Ceuster (1976).

Spain, Arenas de Huelva Formation, Toscano Grande (2016).

Spain, as *Carcharhinus priscus*, Alicante region, Mora Morote (1996).

Italy, Tuscany region, Marsili (2007), Collareta *et al.* (accepted).

During the Pliocene (or latest Miocene; see the paragraph on the late Miocene above) the copper shark reached Australia. In the central East Atlantic, *C. brachyurus* extended its latitudinal range to Belgium (approximate latitude 51°N), which represents the highest latitude reached in the Northern Hemisphere by this shark species. The Mediterranean occurrences from Spain and Italy complete the record of *C. brachyurus* in this geographical district.

Pleistocene (2.59-0.01 Ma) dataset
(Fig. 2E)

Northern East Pacific

California (USA), Palos Verdes Sand Formation, Long (1993).

Central East Pacific

Ecuador, Canoa Formation, Carrillo-Briceño *et al.* (2015).

Southern East Pacific

Peru, Pongo Formation (*sensu* DeVries 2020), Landini *et al.* (unpubl. data, work in progress).

All the Pleistocene fossil records of *C. brachyurus* come from the eastern Pacific coast, from California to Peru. As the global fossil record of extant elasmobranch species is relatively poor in the Pleistocene (Pimiento & Benton 2020), this is not particularly surprising.

DISCUSSION

Sharks and their relatives are broadly known as featuring an abundant fossil record compared to most groups of marine vertebrates (Hubbell 1996, Cappetta 2012, Pimiento & Benton 2020). Nevertheless, and generally speaking, the fossil record is inherently incomplete, and the same can be said about the rock record in which the former is hosted: such a fragmentary nature of the geological and paleontological heritage inevitably challenges the suitability of fossil occurrence data for reconstructing paleobiogeographic patterns and pathways. Furthermore, some broad geographic districts such as Antarctica feature a much-limited fossil record compared to *e.g.,* Europe or the Americas; similarly, the record of elasmobranch teeth is uniform throughout the Neogene and relatively poor in the Pleistocene (*e.g.*, Pimiento & Benton 2020). That said, concerning *Carcharhinus brachyurus* in particular, our literature review demonstrates that fossils of this living shark species account for some tens of distinct occurrence data worldwide. Consequently, the fossil record of *C. brachyurus* can be regarded as rather conspicuous, at least in the broader framework of the marine vertebrates. In light of these considerations, *C. brachyurus* stands out as a much promising research target for paleobiogeographic reconstructions informed by the fossil record.

Nowadays, *C. brachyurus* inhabits temperate and subtropical seas of the Northern and Southern hemispheres, although it also occurs in the warm waters of Equatorial Guinea (Fig. 2F). Such a disjunct, antitropical distribution is linked to the presence of tropical water masses at the low latitudes of the major ocean basins. These tropical water masses are believed to act as barriers that inhibit the transoceanic dispersal of copper sharks, thus reducing or even preventing the biological connectivity among different geographical districts, both by displaying seawater temperatures that are higher than those preferred by *C. brachyurus* and by lacking stepping-stone habitats suitable as nursery grounds (Benavides *et al.* 2011). During the Neogene, the intra- and trans-oceanic biogeographic relationships of the copper shark populations have been strongly influenced by major tectonic, eustatic, and climatic events that resulted in strong changes in the superficial and deep circulation and modified the level of biological connectivity among different oceanic basins.

By coupling the literature data on these abiotic events with both the relatively rich fossil record of *C. brachyurus* reviewed in this work and the haplotype network provided by Benavides *et al.* (2011) (Fig. 1), here we propose a reconstruction of the historical and ecological patterns that gave rise to the present-day segregated distribution of the copper shark. In doing so, a caveat must be mentioned: indeed, the herein proposed reconstruction should ultimately be regarded as provisional, as we anticipate that the hopeful discovery of new shark tooth-bearing deposits featuring fossil specimens of *C. brachyurus* as well as new molecular data on the living copper shark populations will likely contribute to reassess some of the more problematic aspects of the biogeography and paleobiogeography of this extant elasmobranch species. Nevertheless, by building upon our thorough review of the paleontological literature in light of the results of the relatively comprehensive molecular investigation by Benavides *et al.* (2011), the main events of the paleobiogeographical history of *C. brachyurus* can be highlighted and rather confidently linked to major paleogeographic and paleoceanographic episodes and transitions.

Center of origin

On the basis of genetic and paleontological data, Benavides *et al.* (2011) hypothesized that the center of origin of *C. brachyurus* was located in the East Pacific-West Atlantic area. Before the definitive closure of the Panamanian Seaway around 3 Ma, these sea regions (collectively comprising the COA) were indeed well connected with each other. Our fossil dataset, and especially the discovery of the oldest copper shark nursery grounds in the East Pisco Basin of Peru (both in the early Miocene of the Chilcatay Formation and in the late Miocene of the Pisco Formation; Landini *et al.* 2017a, b, 2019), are consistent with this hypothesis. Through most of the Neogene, the COA was divided into two distinct biogeographic districts, namely, the Caloosahatchian (from North Carolina to the Yucatán peninsula, through the then-broad Florida Strait and the Northern Gulf of Mexico) and Gatunian (including the remainder of the tropical Atlantic up to Brazil and the East Pacific, from California to Peru) provinces, directly communicating via the Panamanian Seaway (Petuch 1982, Coppard & Alvarado 2013, Coppard *et al.* 2013, Vermeij 2005). During the early Miocene, western boundary currents in the Caribbean region were weak or absent (Vermeij 2005) and limited exchanges between the Gatunian and Caloosahatchian provinces are supported by the distribution of some mollusks such as the gastropod genera *Lyria* and *Enaeta* (Landau & Vermeij 2011). Interchanges via the Panamanian Seaway was dominated by a strong Pacific throughflow into the western North Atlantic, and the mid-latitude Atlantic Meridional Overturning Current (AMOC), influenced by these low-salinity waters from the eastern Pacific, was overall weak (Kirillova *et al.* 2019). The first dispersal of the copper shark took place in this paleogeographic and paleoceanographic scenario, in a context of high resilience of the Gatunian/Caloosahatchian boundary and absence of geographical or oceanographic barriers. After the Langhian, a regional extinction can be observed in the West Atlantic sector of the Gatunian province and in the northern sector of the Caloosahatchian one. As the closure of the Panamanian Seaway approached, the Caribbean region gradually became cut-off from the eastward flow of the Pacific water masses, and consequently, the Caribbean waters became warmer and saltier (Robertson *et al.* 2009). Nowadays, the transfer of the warm, high-salinity Caribbean waters to the North Atlantic represents an essential component of the AMOC (Kirillova *et al.* 2019). The AMOC was already active during the Miocene but underwent a significant strengthening in late middle or early late Miocene times. In particular, after 9 Ma, following a further step in the process of y the Central American Isthmus and the consequent decrease in the flow of Pacific low-salinity water into the Caribbean region, the AMOC became stronger (Kirillova *et al.* 2019). Furthermore, around 10 Ma, the Gulf Stream system was almost as strong as today (Kirillova *et al.* 2019). Eustatic oscillations also affected the coasts of the Caloosahatchian province, from North Carolina to Florida, during the middle and late Miocene, as in Tortonian the sea level was generally low and most of the coastal plain and continental shelf was exposed to subaerial erosion (Popenoe 1990). During this Tortonian regressive phase, the Gulf Stream was forced offshore across the central Blake Plateau and around the Charleston Bump (Popenoe 1990). The regional extinction of the copper shark populations from the northern sector of the Caloosahatchian province is probably related to the combination of the Tortonian regressive phase and the strengthening of the warm Gulf Stream that flows from the Florida Strait along the coasts of Georgia, the Carolinas, and Delaware. The geologically youngest West Atlantic fossil occurrence of *C. brachyurus* is from the late Miocene Chagre Formation of Panama (Carrillo-Briceño *et al.* 2015). Given the geographical closeness of this area with the then-open Panamanian Seaway, it probably represents an offshoot of the central East Pacific populations. Temporary interchanges with the Pacific Ocean, mostly limited to the Panamanian area, have already been documented by Collins *et al.* (1996). While observing the occurrence of foraminiferans with Pacific affinities in the Chagre Formation, these authors inferred that the entrance of Pacific taxa into the Caribbean had no apparent effect on the subsequent composition of the Caribbean fauna. In the Pacific Gatunian sector, the fossil record of *C. brachyurus* is in turn substantially continuous from the early Miocene to the present day. In the East Pisco Basin of southern Peru, teeth of the copper shark are the most frequently collected shark remains, both from Burdigalian (Bianucci *et al.* 2018, Di Celma *et al.* 2018b, Landini *et al.* 2019) and Tortonian (Landini *et al.* 2017 a, b) sediments. According to these authors, based on the high abundance of teeth belonging to immature individuals, during the Miocene the East Pisco Basin played a pivotal role as a nursery area for some coastal and pelagic sharks, including *C. brachyurus* as well as *Isurus oxyrhinchus* and *Cosmopolitodus hastalis*. In the middle Miocene, *C. brachyurus* also occurred in Ecuador and, during the late Miocene, it increased its northern and southern latitudinal range, reaching the Californian and Chilean coasts, respectively. The present-day East Pacific distribution of the copper shark retains these extreme latitudinal limits. The Pleistocene record of the Canoa Formation of Ecuador (Carrillo-Briceño *et al.* 2015) is consistent with the presence of some subtropical and temperate taxa of teleosts and mollusks that, according to Landini *et al.* (2002), are currently limited to the Californian, Oregonian or Peruvian provinces. These records have been interpreted as markers of biological incursions correlated with periods of strengthened upwelling of the cold waters of the California and Humboldt currents at the low latitudes of the East Pacific (Landini *et al.* 2002, Jorgensen *et al.* 2009).

The westward Pacific dispersal

In the western part of the Pacific Ocean, living populations of *C. brachyurus* have been reported from Japan, Australia, New Zealand, and possibly the Gulf of Thailand (Garrick 1982, Compagno 1984, Duffy & Gordon 2003). Benavides *et al.* (2011) recognized a perfectly segregated mtCR clade that includes the Australian, New Zealand, Peruvian, and Pacific Mexican populations, and identified Peru as the dispersal center for the colonization of Australasia (Fig. 1). Coupling genetic and paleontological data, it is possible to identify some biogeographic events that might have led to the colonization of the western districts of the Pacific Ocean. The first dispersal event likely occurred during the middle Miocene, leading *C. brachyurus* to colonize Japan from the central East Pacific (Gatunian province). Probably, this trans-Pacific dispersal took place at the eve of the closure of the Indonesian Seaway. According to Kennett (1985), the distribution of the early Miocene faunas of the North Pacific indicates that the gyral circulation system was then only weakly developed, and became stronger only starting from the late Miocene, when temperate faunas were displaced northward as the Kuroshio Current intensified. A westward dispersal was hypothesized by Benavides *et al.* (2011), with the Pacific islands serving as stepping-stone habitats for *C. brachyurus*. Following the same biogeographic pathway, but moving in the opposite direction, other carcharhiniforms (*e.g.*, the scalloped hammerheads and black tip sharks) are believed to have colonized the East Pacific (Duncan *et al.* 2006, Keeney & Heist 2006). The second trans-Pacific dispersal event is related to the colonization of Australasia, which likely started from the southern East Pacific (Peru and Chile). The fossil record indicates that *C. brachyurus* certainly occurred in

Australia as early as in the early Pliocene (Pledge 1985), and Fitzgerald (2004) even lists this shark in the latest Miocene (Cheltenhamian)-early Pliocene (Kalimnan). According to Carter *et al.* (2004), the New Zealander fossil assemblages reveal the dominance of warm-water taxa until the middle Miocene, followed by signals of cooling through the remainder of the Neogene, leading to the eventual disappearance of most warm-water taxa. Based on these data, we hypothesize that the colonization of Australasia by the copper shark occurred during the late Miocene-early Pliocene time span. The high degree of biological connectivity of the extant populations spreading along New Zealand and Australia coasts is likely facilitated by the presence of several potential stepping-stone habitats across this narrow oceanic expanse (*e.g.*, the Challenger Plateau, Lord Howe Rise, Norfolk Ridge, and the seamounts to the west of the aforementioned highs) (Benavides *et al.* 2011).

The eastward Atlantic dispersal

The present-day East Atlantic populations of copper sharks range from France to Morocco, in Equatorial Guinea (where this taxon is rare), and from Namibia to the Atlantic and Indian coasts of South Africa (Garrick 1982, Compagno 1984, Last & Stevens 1994, Walter & Ebert 1991). In the Mediterranean Sea, *C. brachyurus* ranges through most of the basin, even if its stock structure is largely unknown (Duffy & Gordon 2003). Primary nursery areas are known from the Eastern Cape waters of South Africa (Smale 1991, Cliff & Dudley 1992) and northwestern Africa (Rio de Oro and Pulpito Bay) (Garrick 1982). In the Mediterranean Sea, neonates and small-sized juveniles have been reported from Rhodes, Nice, and the West Alboran Basin (Garrick 1982, Fergusson & Compagno 1995). Benavides *et al.* (2011) recognized a perfectly segregated mtCR clade that includes the South African, Namibian, Brazilian, and Spanish populations, and identified the central West Atlantic as the COA. According to the fossil record, the first occurrence of copper shark teeth in the East Atlantic geographic district took its place in the Mediterranean Basin (Montpellier region, France), most likely during the Burdigalian age: in fact, several of the specimens assigned by Cappetta (1970) to *C. priscus* have been recognized as belonging to *C. brachyurus* by Purdy *et al.* (2001) and Marsili (2007). These teeth seemingly testify to an eastward trans-Atlantic dispersal event that, in our opinion, could be related to the early Miocene spread of the copper shark in the Caloosahatchian province. Indeed, in early Miocene times, the Atlantic basin was somewhat narrower than it is today and both the AMOC and the Gulf Stream, although present, were weak and did not constitute true biogeographic restrictors for this shark species (Lunt *et al.* 2008, Kirillova *et al.* 2019). In turn, since the late Miocene, the North Atlantic circulation has worked in a relatively modern way, with salty warm waters flowing from the tropics northwards (Kirillova *et al.* 2019). Alternatively, a putative trans-Indo-Pacific dispersal, starting from the Pacific American coasts and passing throughout the Eastern Tethys, could be taken into consideration. Until the early Burdigalian, before the rise of the so-called "*Gomphotherium* landbridge", an open oceanic seaway connected both the Mediterranean and Paratethyan basins with the Indian Ocean. Subsequently, for a short time, a middle Miocene (early Langhian) transgression caused the Mediterranean and Paratethys to be temporarily flooded by waters coming from the Indian Ocean (Rögl 1999). Therefore, considering also the limitations imposed by our fossil dataset, the only time intervals that are consistent with marine interchanges through the Eastern Tethys Seaway are the early Burdigalian and the early Langhian. Notwithstanding the remarkable distance that separates the Mediterranean from the putative center of origin of *C. brachyurus*, various paleontological, ecological, and genetic constraints allow us to exclude a biogeographic pathway through the Eastern Tethys Seaway. Firstly, *C. brachyurus* was not recorded from the Miocene fossil fish assemblages of India. Even if the Indian Miocene carcharhinid record includes *Carcharhinus priscus* (Ralte *et al.* 2011, Sharma & Patniak 2014), in our opinion the specimens described by these authors are not consistent with the morphological traits of the extant species *C. brachyurus*. Secondly, there is a significant ecological constraint related to the thermal conditions of this hypothetical route. During the lower Miocene, the tropical waters of the then-broad Indonesian Seaway would have inhibited the dispersal potential of the copper shark, strongly limiting the presence of habitats suitable for its reproduction (Kennett 1985, Benavides *et al.* 2011). Finally, as reported above, by testing the genetic relationships among the copper shark populations from different areas of both the East and West Atlantic (*i.e.*, Spain, South Africa, Namibia, and Brazil), Benavides *et al.* (2011) identified the existence of an Atlantic mtCR clade that significantly differs from the Pacific ones. As the East Atlantic populations are seemingly more closely related to the West Atlantic communities than to the Pacific ones, the genetic data also suggest a trans-Atlantic (rather than trans-Pacific) dispersal route. Outside the Mediterranean realm, in the central East Atlantic, the fossil record of the copper shark is stratigraphically continuous from the middle Miocene to the Pliocene, teeth of this species having been collected from *e.g.* the Serravallian of Portugal, the late Miocene (Tortonian to Messinian) of the Gulf of Cadiz (Atlantic Spain), and the early Pliocene of the Belgian coast; the latter occurrence represents the northernmost location ever recorded for *C. brachyurus*. In the Mediterranean Sea, the youngest Miocene record of *C. brachyurus* comes from the Tortonian of the "Pietra leccese" (southern Italy, Menesini 1968, as *Cestracion priscus*), and it is followed by the early Pliocene finds from Tuscany (Marsili 2007, Collatera *et al*. accepted). Whereas it seems reasonable to hypothesize that the biological connectivity between the Mediterranean and non-Mediterranean populations of the central East Atlantic was significantly affected, during the late Miocene, by the paroxysmal events of the Messinian Salinity Crisis (Carnevale *et al*. 2006, 2018), the paucity of latest Miocene elasmobranch assemblages from the Mediterranean Sea prevents from drawing definitive conclusions on this issue.

The ghost paleobiogeographic districts

Coupling neontological and paleontological data, substantial differences emerge in the geographical distribution of the copper shark within the different oceanic basins. Whereas in the Pacific Ocean there is a good correspondence between the areas that are currently occupied by the copper shark and those that host fossil teeth of this species, fossil occurrence data from the coasts of the Indian Ocean are nonexistent, apart for a single record of *C. priscus*, possibly consistent with *C. brachyurus*, from the Miocene of Madagascar (Andrianavalona *et al*. 2015). A similar lack of fossil occurrence data frustrates any attempt to reconstruct the origin of the copper shark populations living along the coasts of South Africa, which are genetically closely connected with those of the Atlantic coasts, including Namibia (Benavides *et al*. 2011). In turn, the biogeographic history of the copper shark in the Atlantic Ocean is complex and open to several questions. Removed from the western Central Atlantic and the northern sector of the Caloosahatchian province since the middle Miocene, *C. brachyurus* still inhabits the Gulf of Mexico. In the South Atlantic, *C. brachyurus* occurs on both sides of Africa as well as along the South American coastline, and the close genetic similarities detected by Benavides *et al*. (2011) between the eastern and western South Atlantic populations suggest a high degree of transoceanic biological connectivity. The rather fragmentary nature of the South Atlantic elasmobranch fossil record makes the reconstruction of the paleobiogeographic paths that led to the present-day distribution particularly difficult and uncertain.

The Gulf of Mexico

The present-day copper shark community of the Gulf of Mexico constitutes a small biogeographic enclave. Unfortunately, given the absence of a paleontological and genetic background for this population, its historical relationships cannot be unambiguously reconstructed. That said, the origin of this present-day population can be alternatively connected to two different dispersal centers. During the Miocene, the Gulf of Mexico was part of the Caloosahatchian province, in the northern sector of which (corresponding to the coasts of Delaware and North Carolina) *C. brachyurus* was reported from Burdigalian and Langhian sediments. The most parsimonious hypothesis consists in considering the Gulf of Mexico copper shark population as a relict that survived the regional extinction of the northern Caloosahatchian communities which followed a significant increase in northward heat transport along the North Atlantic American coast (from Florida to North Carolina). Nowadays, the Caribbean Sea waters enter into the Gulf of Mexico through the Yucatán Channel and feed the Loop Current system, which is regarded as the starting point of the Gulf Stream (Gyory *et al*. 2011a, b, c, Aarø 2011). Furthermore, the Florida Strait acts as an important restrictor for the dispersal of marine organisms, as documented by the different fish faunas that are found at the opposite sides of this strait (Briggs 1974, Aarø 2011). Therefore, enclosed as it is between the Loop Current (to the South) and the Florida Strait (to the East), the Gulf of Mexico represents a biogeographically isolated district. The origin of the present-day copper shark community of the Gulf of Mexico could also be explained via another biogeographic pathway. During the late Miocene-early Pliocene interval, three main marine basins connected the East Pacific and Caribbean realms, namely: the San Carlos Basin of northern Costa Rica and southern Nicaragua, the Panama Canal Basin, and the Atrato Basin of northwestern Colombia (Collins *et al*. 1996, Robertson *et al*. 2009). Incursions from the closest central East Pacific waters to the Gulf Coast, probably through the northern corridor (*i.e*., the San Carlos Basin), might have occurred until the early Pliocene. Following the final closure of the Panamanian Seaway and the definitive set-up of the modern pattern of oceanic circulation, the Gulf of Mexico copper shark community would have been confined within the area it currently occupies. In our opinion, the latter hypothesis might find support in the occurrence of *C. brachyurus* in the late Miocene strata of the Chagre Formation (Carrillo-Briceño *et al*. 2015) – a datum that testifies to the pivotal role of this Panamic insular system for the dispersal of coastal sharks during the late Neogene.

The Southeastern Atlantic

Nowadays, along the central and southern Atlantic coasts of Africa, *C. brachyurus* ranges in Equatorial Guinea and from Namibia to South Africa. The latter coastal regions are characterized by the cold, nutrient-rich waters of the Benguela Upwelling System (BUS), which meet the warm, nutrient-poor waters of the tropical Angola Current (AC) just north of the Walvis Ridge. The AC/BUS front represents a thermal barrier for the copper shark. According to Hoetzel *et al*. (2015), during the late Miocene the Angola Current flowed southward over the Walvis Ridge; nevertheless, a latest Miocene or early Pliocene phase of strengthening of the meridional gradient of sea surface temperature, coupled with the uplift of southwestern Africa, might have led to the intensification of upwelling along the shoreline and over the Walvis Ridge as the BUS flowed northwards. Such a northern extension of the BUS, resulting in the compression of the AC flow and in the northward shift of the AC/BUS front, would have limited the effect of this thermal barrier in inhibiting the southward dispersal of the copper shark. The Equatorial Guinea district, in which *C. brachyurus* is currently present, could be interpreted as a residual area correlated with the oscillations of the AC/BUS front. Unfortunately, no molecular data exist regarding the Equatoguinean copper sharks, and no fossils of *C. brachyurus* come from the southeastern Atlantic. Neither the teeth from the Pliocene of Angola attributed by Antunes (1978) to *Carcharhinus* sp. 1 (= *Carcharhinus priscus*) nor those from the Neogene of Congo attributed by Dartevelle & Casier (1943, 1959) to *C. egertoni* and *Carcharhinus* (= *Sphyrna*) *priscus* are consistent with those of the extant copper shark. According to Benavides *et al.* (2011), the copper shark populations from South Africa, Namibia, and Spain belong a single mtCR clade. In the absence of paleontological data, these close genetic signatures are in our opinion suggestive of a southward dispersal from the central East Atlantic, probably during a phase when the AC/BUS front was significantly displaced northwards. The Indian Ocean stock of copper sharks, ranging mainly off southeastern South Africa, is genetically and biogeographically related to the Namibian and Atlantic South African communities.

The Southwestern Atlantic

In the western South Atlantic, the copper shark ranges from southern Brazil to northern Argentina (*e.g.*, Garrick 1982, Compagno 1984, Last & Stevens 1994, Benavides *et al.* 2011). Primary nursery areas have been identified in Bahía Blanca and northern Patagonia (Argentina) by Chiaramonte (1998) and Lucifora *et al.* (2005), and in Rio de Janeiro (Brazil) by Garrick (1982). With the significant exception of the aforementioned Venezuelan and Colombian localities, *Carcharhinus brachyurus* does not occur in the Neogene and Pleistocene fish tooth-bearing sites from the Atlantic coasts of the South America (*e.g.*, Arratia & Cione 1996, Cione *et al.* 2011, Dos Reis 2005, Costa *et al.* 2009, Távora *et al.* 2010, Aguilera & Tavares Páes 2012, Aguilera *et al.* 2017, 2020). Given the lack of any paleontological signal, in order to explain the current distribution of *C. brachyurus* in this geographic district, three different potential biogeographic pathways can be hypothesized. The first one relates to a dispersal event taking place along the Atlantic South American coast, starting from a Colombian or Venezuelan source area (*i.e.*, the Venezuelan sub-province) strictly connected to the Panamanian Seaway. The only time window in which such a route might have been passable by the copper shark was the Burdigalian-?Langhian interval, when *C. brachyurus* was still present in the Venezuelan sub-province. The regional fossil record does not bring support to this hypothesis. Only in the Pirabas Formation (Early Miocene, northern Brazil), the carcharhinid fossils include teeth referred to the ambiguous species *Carcharhinus priscus*, but the morphological traits of these dental remains are not consistent with those of *C. brachyurus*. The main constraint related to this putative southward dispersal is likely the barrier originated by the tropical condition of most of the northern coast of South America (Aguilera *et al.* 2017). Aguilera *et al.* (2011) suggested similar paleoenvironmental conditions and a close biogeographic link between the early-middle Miocene Cojimar Formation of Cuba and the early Miocene Pirabas Formation Brazil based on the shared occurrence of the swamp eel genus *Ophisternon* and similar remains of crocodiles, sirenians, turtles, and land mammals (*e.g.*, rodents) – an observations that supports the presence of a broad tropical district extending from the Caribbean realm to northern Brazil. Another potential biogeographic pathway could involve a southeastern Pacific route along the Peruvian and Chilean coastal waters (where the copper shark was largely diffused starting from early Miocene). Interchange between temperate populations inhabiting the Pacific and Atlantic coasts of South America through a circum-continental route was theoretically possible via the Drake Passage before the mid-Pliocene (*ca.* 3.5-3.2 Ma), when this southern route significantly cooled down (Hodell & Warnke 1991, Lessios 2008). However, according to Benavides *et al.* (2011), there is a significant discontinuity in mitochondrial haplotype frequencies between the southeastern Pacific and the southwestern Atlantic populations of *C. brachyurus*. On the other hand, the same genetic data allow to recognize the existence of a perfectly segregated Atlantic mtCR clade and suggest continuity of the gene flow within this oceanic basin. Following this genetic scenario, a trans-South Atlantic pathway connecting the Benguela province to Argentina can be hypothesized. The presence of several stepping-stone habitats (including the Walvis Ridge, Tristan da Cunha, and the Rio Grande rise) forming a sort of quasi-continuous elevation between 20°S and 30°S might have facilitated this dispersal event. A phase of strengthening of the cold flow of the Benguela Current (leading to an expansion of the influence of the BUS over the Walvis Ridge) and the emergence of the South Atlantic gyre might have allowed such a dispersal event from Southwestern Africa to Southeastern America, across the South Atlantic oceanic expanse.

CONCLUDING REMARKS

The present paper represents the first integrated reconstruction of the historical distributional patterns of the copper shark. The Neogene Gatunian and Caloosahatchian provinces stand out as the key areas of this paleobiogeographic history. On the basis of the genetic structure of the extant copper shark populations, Benavides *et al*. (2011) rejected the hypothesis that the antitropical, scattered distribution of the extant *Carcharhinus brachyurus* derives from a panmictic condition. In agreement with these authors, our research supports the notion that the present-day geographically segregated pattern is the product of historical biogeographic processes and events that might be traced back to an early Miocene East Pacific-central West Atlantic center of origin. The disjunct modern populations of *C. brachyurus* exhibit different degrees of segregation, at least in relation to the limited dispersal potential of the female copper sharks. With the significant exception of the Equatoguinean enclave, the copper shark populations inhabiting the East Pacific and East Atlantic coasts exhibit a symmetrical antitropical distribution, being indeed distributed over wide latitudinal ranges that interrupt in occurrence of the warm equatorial waters of the Panamanian and Tropical Eastern Atlantic provinces, respectively. Changes in the tropical ocean circulation regime may allow temporary biological incursions from neighboring provinces. The Pleistocene occurrence, in the tropical Panamic province, of *C. brachyurus* and other teleosts and mollusks with Californian and Peruvian affinities testifies to this mechanism, while oscillations of the AC/BUS front in the southern East Atlantic have also been reported. Within the Australasian district, a high connectivity is provided by the presence of stepping-stone habitats and well-distributed nursery areas along the southern coasts of Australia and New Zealand. In the northwestern Pacific, the Japanese district seems to have been settled by East Pacific immigrants since the middle Miocene. The rare modern reports of copper shark from the Gulf of Thailand could be linked to southward excursions from this area. A stricter isolation can be observed for the Gulf of Mexico population of copper sharks, which the surrounding warm waters of the Loop Current and Florida keep segregated in the more temperate Gulf waters. The almost null degree of biological connectivity between this and other populations of *C. brachyurus* suggests to identify the Gulf of Mexico copper sharks as comprising a critical relict population.

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REFERENCES

Aarø J 2011. Genetic diversification in the tropical western Atlantic Ocean: phylogeograhy of the gastropod *Bulla occidentalis*. MSc thesis, University of Bergen, Norway.

Adnet S, Antoine PO, Baqri SRH, Crochet JY, Marivaux L, Welcomme JL, Métais G 2007. New tropical carcharhinids (Chondrichthyes, Carcharhiniformes) from the late Eocene-early Oligocene of Balochistan, Pakistan: Paleoenvironmental and paleogeographic implications. *J As Earth Sci* 30: 303-323.

Agassiz L 1843. Recherches sur les Poissons fossiles. Petitpierre, Neuchâtel et Soleure.

Aguilera OA, Tavares Páes E 2012. The Pirabas Formation (Early Miocene from Brazil) and the Tropical Western Central Atlantic Subprovince. *Bol Mus Para Emílio Goeldi Cienc Nat Belém* 7: 29-45.

Aguilera OA, Ramos MJ, Tavares Páes E, Costa S, Sánchez-Villagra M 2011. The Neogene tropical American fish assemblage and the paleobiogeography of the Caribbean region. *Swiss J Palaeontol* 130: 217-240.

Aguilera OA, Luz Z, Carrillo-Briceño JD, Kocsis L,Vennemann TW, De Toledo PM, Nogueira A, Amorin KN, Moraes-Santos H, Polck MR, De Lourdes Ruivo M, Linhares AP, Monteiro-Neto C 2017. Neogene sharks and rays from the Brazilian 'Blue Amazon'. *PLoS ONE* 12: e0182740.

Aguilera O, Bencomo K, de Araújo OMO, Dias BB, Coletti G, Lima D, da Silva-Caminha SAF, Polck M, Alves Martins MV, Jaramillo C, Tavares Kütter V, Lopes RT 2020. Miocene heterozoan carbonate systems from the western Atlantic equatorial margin in South America: The Pirabas formation. *Sediment Geol* 407: 105739.

Alván de la Cruz A 2008. Geología de Ocucaje: aportes en la sedimentología y paleontología de Lomas de Ullujaya (Ica, Perú). *Rev Inst Investig Fac Ing Geo Min Metal Geogr* 11(21): 51-59.

Andrianavalona TH, Ramihangihajason TN, Rasoamiaramanana A, Ward DJ, Ali JR, Samonds KE 2015. Miocene shark and batoid fauna from Nosy Makamby (Mahajanga Basin, Northwestern Madagascar). *PLoS ONE* 10: e0129444.

Antunes MT 1978. Faunes ichtyologiques du Néogène supérieur d'Angola, leur âge, remarques sur le Pliocène marin en Afrique australe. *Ciênc Terra* (UNL) 4: 59-90

Antunes MT, Jonet S 1969-70. Requins de l'Helvetien superior et du Tortonien de Lisbonne. *Rev Fac Cienc Univ Lisboa* 16: 119-280.

Apolín J, Gonzales-Barba G, Martínez JN 2004. Selaceos del Mioceno Superior de Quebrada Pajaritos (Piura, Perú). *Publ Esp Soc Geol Perú* 6: 401-404.

Applegate SP 1978. Phyletic studies: Part I; tiger sharks. *Univ Nal Autòn Mexico Inst Geol Rev* 2: 55-64.

Arratia G, Cione AL 1996. The record of fossil fishes of southern South America. *Münchn Geowiss Abh A Geol Paläontol* 30: 9-72.

Bass AJ, D'Aubrey JD, Kistnasamy N 1973. Sharks of the east coast of Southern. Africa. I. The genus *Carcharinus* (Carcharhinidae). *Invest Rep Ocean Res Inst* 33: 1-168.

Bearez P 1996. Lista de los peces marinos del Ecuador continental. *Rev Biol Trop* 44(2): 731-741.

Benavides MT, Feldheim LA, Duffy CA,Wintner S, Braccini JM, Boomer J, Huveneers C, Roger P, Mengel JC, Alfaro-Shigueto J, Cartamil DJ, Chapman DD 2011. Phylogeography of the copper shark (*Carcharhinus brachyurus*) in the Southern Hemisphere: implications for the conservation of a coastal apex predator. *Mar Freshw Res* 62: 861-869.

Bianucci G, Collareta A, Bosio G, Landini W, Gariboldi K, Gioncada A, Lambert O, Malinverno E, Muizon C de, Varas-Malca RM, Villa IM, Coletti G, Urbina M, Di Celma C 2018. Taphonomy and palaeoecology of the lower Miocene marine vertebrate assemblage of Ullujaya (Chilcatay Formation, East Pisco Basin, southern Peru). *Paleogeogr Palaeoclim Palaeoecol* 511: 256-279.

Bosio G, Malinverno E, Collareta A, Di Celma C, Gioncada A, Parente M, Berra F, Marx FG, Vertino A, Urbina M, Bianucci G 2020. Strontium Isotope Stratigraphy and the thermophilic fossil fauna from the middle Miocene of the East Pisco Basin (Peru). *J S Am Earth Sci* 97:102399.

Briggs JC 1974. Marine Zoogeography. McGraw-Hill, New York.

Cappetta H 1970. Les sélachiens du Miocène de la région de Montpellier. *Paleovertebrata* Mém Extr 1-139.

Cappetta H 1987. Mesozoic and Cenozoic Elasmobranchii, Chondrichthyes II. *In* Schultze HP ed, Handbook of Paleoichthyology, vol. 3B. Verlag Dr. Friedrich Pfeil: 1-193.

Cappetta H 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. *In* Schultze HP ed, Handbook of Paleoichthyology, vol. 3E. Verlag Dr. Friedrich Pfeil: 1-512.

Cappetta H, Cavallo O 2006. Les sélaciens du Pliocène de la région d'Alba (Piémont, Italie Nord-Ouest). *Riv Piemont Stor Nat* 27: 261-304.

Carnevale G, Landini W, Sarti G 2006. Mare versus Lago-mare. Marine fishes and the Mediterranean environment at the end of the Messinian Salinity Crisis. *J Geol Soc Lond* 163: 75-80.

Carnevale G, Dela Pierre F, Natalicchio M, Landini W 2018. Fossil marine fishes and the 'Lago Mare' event: has the Mediterranean ever transformed into a brackish lake? *Newsl Stratigr* 51(1): 57-72.

Carrillo-Briceño JD, Gonzales-Barba G, Landaeta MF, Nielsen SN 2013. Condrictios fosiles del Plioceno Superior de la Formacion Horcon, Region de Valparaíso, Chile central. *Rev Chil Hist Nat* 86(2): 191-206.

Carrillo-Briceño JD, Aguilera OA, Rodriguez F 2014. Fossil Chondrichthyes from the central eastern Pacific Ocean and their paleoceanographic significance. *J S Am Earth Sci* 51: 76-90.

Carrillo-Briceño JD, De Gracia C, Pimiento C, Aguilera OA, Kindlimann R, Santamarina P, Jaramillo C 2015. A new late Miocene Chondrichthyan assemblage from the Chagres Formation, Panama. *J S Am Earth Sci* 60: 56-70.

Carrillo-Briceño JD, Aguilera OA, De Gracia C, Aguirre-Fernandez G, Kindlimann R, Sánchez-Villagra MR 2016. An early Neogene elasmobranch fauna from the southern Caribbean (western Venezuela). *Palaeontol Elect* 19(2): 1-32.

Carrillo-Briceño JD, Luz Z, Hendy A, Kocsis L, Aguilera OA, Vennemann T 2019. Neogene Caribbean elasmobranchs: diversity, paleoecology and paleoenvironmental significance of the Cocinetas Basin assemblage (Guajira peninsula, Colombia), *Biogeosci* 16: 33-56.

Carter RM, McCave IN, Carter L 2004. Leg 181 synthesis: fronts, flows, drifts, volcanoes, and the evolution of the southwestern gateway to the Pacific Ocean, eastern New Zealand. *Proc ODP Sci Results* 181: 1-111.

Chiaramonte GE 1998. The shark genus *Carcharhinus* Blainville, 1816 (Chondrichthyes: Carcharhinidae) in Argentine waters. Mar *Freshw Res* 49(7): 747-752.

Cione AL, Cozzoul MA, Dozo MT, Hospitaleche CA 2011. Marine vertebrate assemblages in the southwest Atlantic during the Miocene. *Biol J Linn Soc* 103: 423-440.

Cliff G, Dudley SFJ 1992. Sharks caught in the protective gill nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Günther). *S Afr J Mar Sci* 12(1): 663-674.

Collareta A, Di Celma C, Bosio G, Pierantoni PP, Malinverno E, Lambert O, Marx FG, Landini W, Urbina M, Bianucci G (in press). Distribution and paleoenvironmental framework of middle Miocene marine vertebrates along the western side of the lower Ica Valley (East Pisco Basin, Peru). *J Maps*.

Collareta A, Mollen FH, Merella M, Casati S, Di Cencio A accepted. Remarkable multicuspid teeth in a new elusive skate (Chondrichthyes, Rajiformes) from the Mediterranean Pliocene. *PalZ*.

Collins LS, Coates AG, Berggren WA, Aubry MP, Zhang J 1996. The Late Miocene Panama Isthmian Strait. *Geology* 24: 687-690.

Compagno LJV 1984. FAO species catalogue. Vol 4: Sharks of the World, Part 2 – Carcharhiniformes. *FAO Fish Synop* 4(2): 251-633.

Compagno LJV 1988. Sharks of the Order Carcharhiniformes. Princeton University Press, Princeton.

Compagno LJV, Dando M, Fowler S 2005. Sharks of the World. Princeton University Press, Princeton.

Coppard SE, Alvarado JJ, 2013. Echinoderm diversity in Panama: 144 years of research across the Isthmus. *In* Alvarado JJ, Solís-Marín FA eds, Echinoderm Research and Diversity in Latin America. Springer: 107-144.

Coppard SE, Zigler KS, Lessios HA 2013. Phylogeography of the sand dollar genus *Mellita*: cryptic speciation along the coasts of Americas. *Mol Phylogenet Evol* 69: 1033-1042.

Costa SAF, Richter M, Toledo PM, Moraes-Santos HM 2009. Shark teeth from Pirabas Formation (Lower Miocene), northeastern Amazonia, Brazil. *Bol Mus Para Emílio Goeldi Cienc Nat Belém* 4(3): 221-230.

De Ceuster J 1976. Stratigrafische interpretatie van jong-cenozoische afzettingen bij Rumst (België, provincie Antwerpen) en beschrijving van de in een post-Mioceen basisgrind aangetroffen vissenfauna, II. Systematische beschrijvingen en conclusies. *Meded Werkgr Tert Kwart Geol* 13: 119-172, Borgerhout.

Dartevelle E, Casier E 1943. Les poissons fossiles du Bas-Congo et des régions voisines. *Ann Mus Congo Belge Sér A (Min Géol Paléontol)* 3, 2(1): 1-200.

Dartevelle E, Casier E 1959. Les poissons fossiles du Bas-Congo et des régions voisines. *Ann Mus Congo Belge Sér A (Min Géol Paléontol)* 3, 2(3): 257-568.

DeVries TJ 2020. Lithostratigraphy and biostratigraphy of Pliocene and Pleistocene marine deposits and age of the highest marine terrace from the Sacaco Basin and its environs (southern Peru). *Bol Soc Geol Perù* 114: 20-48.

Di Celma C, Malinverno E, Bosio G, Collareta A, Gariboldi K, Gioncada A, Molli G, Basso D, Varas-Malca RM, Pierantoni PP, Villa IM, Lambert O, Landini W, Sarti G, Cantalamessa G, Urbina M, Bianucci G 2017. Sequence stratigraphy and paleontology of the upper Miocene Pisco Formation along the western side of the lower Ica valley (Ica Desert, Peru). *Riv Ital Paleontol S* 123(2): 255-274.

Di Celma C, Malinverno E, Bosio G, Gariboldi K, Collareta A, Gioncada A, Landini W, Pierantoni PP, Bianucci G 2018a. Intraformational unconformities as a record of late Miocene eustatic falls of sea level in the Pisco Formation (southern Peru). *J Maps* 14(2): 607-619.

Di Celma C, Malinverno E, Collareta A, Bosio G, Gariboldi K, Lambert O, Landini W, Pierantoni PP, Gioncada A, Villa IM, Coletti G, de Muizon C, Urbina M, Coletti G, Bianucci G 2018b. Facies analysis, stratigraphy and marine vertebrate assemblage of the lower Miocene Chilcatay Formation at Ullujaya (Pisco basin, Peru). *J Maps* 14(2): 257-268.

Di Celma C, Pierantoni PP, Malinverno E, Collareta A, Lambert O, Landini W, Bosio G, Gariboldi K, Gioncada A, Muizon C de, Molli G, Marx FG, Varas-Malca RM, Urbina M, Bianucci G 2019. Allostratigraphy and paleontology of the lower Miocene Chilcatay Formation in the Zamaca area, East Pisco basin, southern Peru. *J Maps* 15(2): 393-405.

Dos Reis MAF 2005. Chondrichthyan Fauna from the Pirabas Formation, Miocene of Northern Brazil, with comments on paleobiogeography. *An Inst Geocienc* 28(2): 31-58.

Duffy C, Gordon I 2003. *Carcharhinus brachyurus*. The IUCN Red List of Threatened Species 2003: e.T41741A10551730. http://dx.doi.org/10.2305/IUCN.UK.2003.RLTS.T41741A10551730.en

Duncan KM, Martin AP, Bowen BW, De Couet HG 2006. Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). *Mol Ecol* 15: 2239-2251.

Feldheim KA, Gruber SH, Ashley MV 2004. Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris*. *Evolution* 58(10): 2332-2342.

Fergusson IK, Compagno LJV 1995. Annotated elasmobranch species list and bibliography for the Mediterranean. Unpublished report, IUCN.

Fitzgerald EMG 2004. A review of the Tertiary fossil Cetacea (Mammalia) localities in Australia. *Mem Mus Victoria* 61(2): 183-208.

Froese R, Pauly D 2019. FishBase Website, 2019. http://www.fishbase.org

Garrick JAF 1982. Sharks of the Genus *Carcharhinus*. NOAA Tech Rep NMFS Circ 445: 1-194.

González-Barba G, Martínez JN 2010. Comparaciones faunísticas de los tiburones y rayas del Neógeno del norte y sur del Perú. *In* Resúmenes extendidos del XII Congreso Peruano de Geología: 1-4.

González-Rodríguez KA, Espinosa-Arrubarrena L, González-Barba G 2013. An overview of the Mexican fossil fish record. *In* Arratia G, Schultze HP, Wilson MVH eds, Mesozoic Fishes 5: Global Diversity and Evolution. Verlag Dr Friedrich Pfeil: 9-34.

Gyory J, Mariano AJ, Ryan EH 2011a. Ocean surface currents: The Caribbean Current. http://oceancurrents.rsmas.miami.edu/caribbean/caribbean.html

Gyory J, Mariano AJ, Ryan EH 2011b. Ocean surface currents: The Guiana Current. http://oceancurrents.rsmas.miami.edu/atlantic/guiana.html

Gyory J, Mariano AJ, Ryan EH 2011c. Ocean surface currents: The Yucatan Current. http://oceancurrents.rsmas.miami.edu/caribbean/yucatan.html

Hodell DA, Warnke DA, 1991. Climatic evolution of the Southern Ocean during the Pliocene epoch from 4.8 million to 2.6 million years ago. *Quat Sci Rev* 10: 205-14.

Hoetzel S, Dupont LM, Marret F, Jung G, Weler G 2015. Miocene-Pliocene stepwise intensification of the Benguela upwelling over the Walvis Ridge off Namibia. *Clim Past Discuss* 11: 1913-1943.

Hubbell G 1996. Using tooth structure to determine the evolutionary history of the white shark. *In* Klimley AP, Ainley DG, eds, Great White Sharks: The Biology of *Carcharodon carcharias*. Academic Press: 9-18.

Jacquet J, Alava JJ, Ganapathiraju P, Henderson S, Zeller D 2008. In hot soup: sharks captured in Ecuador's waters. *Environ Sci* 5(4): 269-283.

Jorgensen SJ, Reeb CA, Chapple TK, Anderson SD, Perle C, Van Sommeran SR, Fritz-Cope C, Brown AC, Klimley AP, Block BA 2009. Philopatry and migration of Pacific white sharks. *Proc R Soc Lond* Ser B 277: 1-10.

Karasawa H 1989. Late Cenozoic elasmobranchs from the Hokuriku district, Central Japan. *Sci Rep Kanazawa Univ* 34(1): 1-57.

Keeney DB, Heist EJ 2006. Worldwide phylogeography of the blacktip shark (*Carcharhinus limbatus*) inferred from mitochondrial DNA reveals isolation of western Atlantic populations coupled with recent Pacific dispersal. *Mol Ecol* 15: 3669-3679.

Kennett JP 1985. Miocene planktonic foraminiferal biogeography and paleoceanographic development of the Indo-Pacific region. *Geol Soc Am Mem* 163: 197-236.

Kent BW 2018. The Cartilaginous fishes (chimaeras, sharks, and rays) of Calvert Cliffs, Maryland, USA. *Smiths Contrib Paleobiol* 100: 45-160.

Kirillova V, Osborne AH, Störling T, Frank M 2019. Miocene restriction of the Pacific-North Atlantic throughflow strengthened Atlantic overturning circulation. *Nat Commun* 10(1): 1-7.

Landau B, Vermeij GJ 2011. New Lyriinae (Mollusca: Volutidae) from the Lower Miocene Cantaure Formation of Venezuela. *Novapex* 12(3-4): 119-123.

Landini W, Bianucci G, Carnevale G, Ragaini L, Sorbini C, Valeri G, Bisconti M, Cantalamessa G, Di Celma C 2002. Late Pliocene fossils of Ecuador and their role in the development of Panamic bioprovince after the rising of Central American Isthmus. *Can J Earth Sci* 39: 27-41.

Landini W, Altamirano-Sierra A, Collareta A, Di Celma C, Urbina M, Bianucci G 2017a. The late Miocene elasmobranch assemblage from Cerro Colorado (Pisco Formation, Peru). *J S Am Earth Sci* 73, 168-190.

Landini W, Collareta A, Pesci F, Di Celma C, Urbina M, Bianucci G 2017b. A secondary nursery area for the copper shark *Carcharhinus brachyurus* in the late Miocene of South Peru. *J S Am Earth Sci* 78, 164-174.

Landini W, Collareta A, Di Celma C, Malinverno E, Urbina M, Bianucci G 2019. The early Miocene elasmobranch assemblage from Zamaca (Chilcatay Formation, Peru). *J S Am Earth Sci* 91, 352-371.

Last PR, Stevens JD 1994. Sharks and Rays of Australia. CSIRO Publishing, Melbourne.

Laurito C, Valerio AL 2008. Ictiofauna de la localidad de San Gerardo de Limoncito, Formación Curré, Mioceno Superior, Cantón de Coto Brus, provincia de Puntarenas, Costa Rica. *Rev Geol Am Cent* 39: 65-85.

Lessios HA 2008. The Great American Schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annu Rev Ecol Evol Syst* 39: 63-91.

Lira-Beltrán RM, Gonzáles-Barba G, Macías JL, Solis-Añorve A, Garcia-Tenorio F, García-Sánchez L, Osorio-Ocampo S 2020. Fauna de tiburones y rayas de la Formación Tirabuzón (Plioceno) en el Cañón El Álamo, sierras de La Reforma-El Aguajito, Baja California Sur, México. *Rev Mex Cienc Geol* 37(1): 40-63.

Long DJ 1993. Preliminary list of the marine fishes and other vertebrate remains from the Late Pleostocene Palos Verdes Sand Formation at Costa Mesa, Orange County, California. *Paleobios* 15(1): 9-13.

Lucifora LO, Menni RC, Escalante AH 2005. Reproduction and seasonal occurrence of the copper shark, *Carcharhinus brachyurus*, from north Patagonia, Argentina. *ICES J Mar Sci* 62(1): 107-115.

Lunt DJ, Valdes PJ, Haywood A, Rutt IC 2008. Closure of the Panama Seaway during the Pliocene: implications for climate and Northern Hemisphere Glaciation. *Clim Dyn* 30: 1-18.

Martínez-Ortiz J, Galvan-Magaña F, Carrera-Fernandez M, Mendoza-Intrago D, Estupiñán-Montaño C, Cedeño-Figueroa L 2007. Abundancia estacional de tiburones desembarcados en Manta – Ecuador. *In* Martínez-Ortíz J, Galván-Magaña F eds, Tiburones en el Ecuador: Casos de Estudio. EPESPO-PMRC: 9-27.

Marsili S 2007. Revision of the teeth of the genus *Carcharhinus* (Elasmobranchii; Carcharhinidae) from the Pliocene of Tuscany, Italy. *Riv Ital Paleontol Stratigr* 113(1): 79-96.

Mejía-Falla PA, Navia AF, Salcedo-Reyes JC 2019. Checklist of marine elasmobranchs of Colombia. *Univ Scientiarum* 24(1): 164-199.

Menesini E 1968. Ittiodontoliti Miocenici di Terra d'Otranto. *Palaeontogr Ital* 65: 1-61.

Mora Morote P 1996. Peces galeomorfos y squatinomorfos en el Plioceno de Guadamar del Segua (Alicante). *Cidaris* 5: 98-124.

Müller J, Henle FGJ 1839-1841. Systematische Beschreibung der Plagiostomen. Veit, Berlin.

Paillard A, Shimada K, Pimiento C in press. The fossil record of extant elasmobranchs. *J Fish Biol*.

Petuch EJ 1982. Geographical heterochrony: contemporaneous coexistence of Neogene and Recent molluscan faunas in the Americas. *Palaeogeogr Palaeoclim* 37: 277-312.

Pimiento C, Benton MJ 2020. The impact of the Pull of the Recent on extant elasmobranchs. *Palaeontol* 63: 369-374.

Pledge NS 1985. An Early Pliocene shark tooth assemblage in South Australia. *S Aust Dep Min Energ Spec Publ* 5: 287-299.

Poey F 1876. Enumeratio Piscium Cubensium (Parte III). *An Soc Esp Hist Nat* 5: 373-404.

Popenoe P 1990. Paleoceanography and paleogeography of the Miocene of the southeatern United States. *In* Burnett WC, Riggs SR eds, Phosphate deposits of the world III. Neogene to modern phosphorites. Cambridge University Press: 352-380.

Portnoy D, McDowell J, Heist E, Musick J, Graves J 2010. World phylogeography and male-mediated gene flow in the sandbar shark, *Carcharhinus plumbeus*. *Mol Ecol* 19: 1994-2010.

Psomadakis PN, Vacchi M, Di Muccio S, Sara M 2009. First historical record of *Carcharhinus brachyurus* (Chondrichthyes, Carcharhiniformes) in the Mediterranean Sea. *Ital J Zool* 76(2): 201-207.

Purdy RW 1998. Early Miocene fish fauna from the Pollack Farm site, Delaware. *Delaware Geol Surv Spec Publ* 21: 153-174

Purdy RW, Schneider VP, Applegate SP, McLellan JH, Meyer RL, Slaughter RT 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. *Smiths Contrib Paleobiol* 90: 71-202.

Rafinesque CS 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia con varie osservazioni sopra i medesimi. Sanfilippo, Palermo.

Ralte VZ, Tiwari RP, Malsawma J 2011. Selachian fishes from Bhuban Formation, Surma Group, Aizawl, Mizoram. *J Geol Soc India* 77(4): 328-348.

Reinecke T, Louwye S, Havekost U, Moths H 2011.The elasmobranch fauna of the late Burdigalian, Miocene, at Werder-Uesen, Lower Saxony, Germany, and its relationships with Early Miocene faunas in the North Atlantic, Central Paratethys and Mediterranean. *Palaeontos* 20: 1-170.

Robertson DR, Christy JH, Collin R, Coole RG, D'Croz L, Kaufmann KW, Moreno SH, Maté JL, O'Dea A, Torchin ME 2009. The Smithsonian Tropical Research Institute: Marine Research, Education, and Conservation in Panama. *Smiths Contrib Mar Sci* 38: 73-93.

Rögl F 1999. Mediterranean and Parathethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geol Carpath* 50(4): 339-349.

Schultz JK, Feldheim KA, Gruber SH, Ashley MV, McGovern TM, Bowen BW 2008. Global phylogeography and seascape genetics of the lemon sharks (genus *Negaprion*). *Mol Ecol* 17: 5336-5348.

Scotese CR 2014. Atlas of Neogene paleogeographic maps (Mollweide projection), Maps 1-7, Vol. 1, The Cenozoic. *In* PALEOMAP Atlas for ArcGIS, PALEOMAP Project.

Sharma KM, Patniak R 2014. Miocene fishes from Baripada beds, Orissa and their palaeoenvinomntal, palaeogeograhic and palaeoclimatic significance. *Spec Publ Palaeontol Soc India* 5: 291-323.

Smith A 1828. Descriptions of new, or imperfectly known objects of the animal kingdom, found in the south of Africa. *S Afr Comm Advert* 3: 2.

Smith SE, Au DW, Show C 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Ma*r Freshw Res* 49: 663-678.

Smale MJ 1991. Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the eastern Cape Coast of South Africa. *S Afr J Mar Sci* 11(1): 31-42.

Suárez ME, Chávez M, Marquardt C 2002. Nuevos hallazgos de vertebrados marinos de la formación Bahía Inglesa (Mioceno-Plioceno) Caldera, Norte de Chile. Abstract. *In* 1° Congreso Latinoamericano de Paleontología de Vertebrados, Resúmenes: 50-51.

Suárez ME, Marquardt C, Lavenu A, Marinovic N, Wilke HG 2003. Vertebrados marinos Neógenos de la Formación La Portada, II Región, Chile. *In* 10°Congreso Geológico Chileno, Actas: ST3.

Takakuwa AY, Koike H, Narita K 2009. Outline of fossil elasmobranchs from the Middle Miocene Bessho and Aoki Formations, Nagano Prefecture, Japan. *Res Rep Shinshushinmachi Foss Mus* 13: 7-18.

Távora V, Dos Santos AAR, Araújo RN 2010. Localidades fossiliferas da Formação Pirabas (Mioceno Inferior). *Bol Mus Para Emílio Goeldi Cienc Nat Belém* 5(2): 207-224.

Toscano Grande A 2016. Vertebrados marinos del Neógeno del suroeste de la Península Ibérica. PhD thesis, University of Huelva.

Vermeij GJ 2005. One-way traffic in the western Atlantic: causes and consequences of Miocene to early Pliocene molluscan invasions in Florida and the Caribbean. *Paleobiol* 31: 624-642.

Walter JP, Ebert DA 1991. Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. *S Afr J Mar Sci* 10: 37-44.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686-693.

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