First fossils of the extant blacktip shark *Carcharhinus limbatus* from Europe and the Mediterranean Basin

(Running title: ***Carcharhinus limbatus* from the Pliocene of Italy**)

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With 3 figures

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Abstract

Here we report on two fossil teeth attributed to the blacktip shark *Carcharhinus limbatus* (Elasmobranchii: Carcharhiniformes: Carcharhinidae) from lower Pliocene (ca. 5.1–4.5 Ma)

marine deposits of Tuscany (central Italy). A survey of the palaeoichthyological literature and online resources reveals that fossils of *C. limbatus* have been reported from Neogene and Quaternary deposits of the Americas and Indo-Pacific Asia. Therefore, the Tuscan specimens described herein represent the first occurrence of *C. limbatus* as a fossil from both Europe and the Mediterranean Basin. Our finds suggest that the blacktip shark reached a circumglobal distribution in warm waters (including the then warmer-than-today Mediterranean Sea) not later than the Pliocene; at the same time, they demonstrate that the continued study of the relatively well-investigated Neogene elasmobranch faunas of Italy can still result in significant novelties. Futher investigations on other shark tooth assemblages from shoreface, warm-water, marginal-marine deposits are likely to reveal new occurrences of *C. limbatus* in the Pliocene of the Mediterranean Sea and elsewhere (e.g., along the palaeontologically underexplored Atlantic and Pacific coasts of Africa).

Key words: Blacktip shark, Carcharhinidae, Italy, Mediterranean Sea, palaeobiogeography, palaeoichthyology, Pliocene, requiem sharks, Tuscany, Zanclean.

1. Introduction

The blacktip shark (*Carcharhinus limbatus* (MÜLLER & HENLE, 1839)) is an extant species of requiem sharks (Galeomorphii: Carcharhiniformes: Carcharhinidae) that inhabits the continental and insular shelves at tropical and warm-temperate latitudes, where this robust carcharhine can form loose aggregations (COMPAGNO 1984; CASTRO 1996; VOIGT & WEBER 2011). Reaching a maximum total body length of 255 centimetres, this member of the genus *Carcharhinus* BLAINVILLE, 1816 is characterised by black tips on pelvics and, usually, on most other fins (GARRICK 1982; SERENA 2005), hence its vernacular name. Blacktip sharks are fast-swimming predators that feed primarily on bony fishes (e.g., clupeids, sciaenids and mugilids) but also take other sharks and molluscs (CASTRO 1996; TAVARES 2008; MATICH et al. 2021). *Carcharhinus limbatus* is a circumglobal species, widespread in all tropical and warm-temperate shelf environments, including the Mediterranean Sea and the Atlantic coastal waters of southern Spain and mainland Portugal (GARRICK 1982; COMPAGNO 1984; SERENA 2005; BURGESS & BRANSTETTER 2009; VOIGT & WEBER 2011; EBERT & STEHMANN 2013).

In the present paper we report on fossil teeth attributed to *C. limbatus* from lower Pliocene (ca. 5.1–4.5 Ma) marine deposits of southern Tuscany and briefly discuss their palaeobiogeographic bearing.

2. Stratigraphic and palaeoecological framework

The shark teeth described herein were discovered and collected from a sand quarry at Arcille (Campagnatico, Grosseto Province; GPS geographic coordinates: 42°47′12″ N, 11°17′06″ E), which is located in the Baccinello-Cinigiano Basin of southwestern Tuscany (Fig. 1a). This basin is one of the tectonic depressions that developed along the western side (i.e., the hinterland) of the Northern Apennines in the framework of the late orogenic evolution of

these mountains (e.g., PASCUCCI et al. 2006). Like many other post-collisional basins of Tuscany, the Baccinello-Cinigiano Basin is filled with Miocene to Pleistocene continental and marine sediments that entomb conspicuous terrestrial and marine vertebrate fossils (e.g., BENVENUTI et al. 2001; TINELLI et al. 2012).

The deposits cropping out at the Arcille sand quarry are comprised of marine terrigenous sediments such as fossiliferous ocher sandstones and intervening conglomerates that are overlain by darkish shelf mudstones (TINELLI et al. 2012) (Fig. 1b). The sandstones from which the carcharhinid teeth described herein were collected testify to deltaic and shoreface, shallow-marine depositional settings (TINELLI 2013; DOMINICI & FORLI 2021). The associated shark and ray fauna consists of about 300 teeth and dermal denticles that have been assigned to several families of Squalomorphii (Hexanchidae), Squatinomorphii (Squatinidae), Galeomorphii (Carcharhinidae, Scyliorhinidae, Lamnidae and Carchariidae) and Batomorphii (Dasyatidae, Myliobatidae, Rajidae and Rhinobatidae) (BIANUCCI et al. 2019; MERELLA et al. 2020; COLLARETA et al. 2021c). The above assemblage also includes the holotype of the recently described, putative rajid skate *Nebriimimus wardi* COLLARETA et al., 2021c. Non-chondrichthyan vertebrate fossils from the same sediments consist of several skeletons of the extinct dugongid sirenian *Metaxytherium subapenninum* (BRUNO, 1839), two specimens of billfish (*Makaira* LACÉPÈDE, 1802), and the two known specimens of the extinct monodontid delphinoid *Casatia thermophila* BIANUCCI et al., 2019, along with teeth of bony fishes (mostly Labridae, Sparidae and Sphyraenidae) and rare remains of cheloniid turtles (SORBI et al. 2012; TINELLI et al. 2012; TINELLI 2013; BIANUCCI et al. 2019; MERELLA et al. 2020, in review; COLLARETA et al., 2021c).

The shelf mudstones exposed at Arcille entomb a microfossil assemblage that has been assigned by SORBI et al. (2012) to the lower part of the Zanclean, and in particular to the

Mediterranean Pliocene (=MPl) zone 2 of CITA (1975), whose bounding bioevents are calibrated at 5.08 and 4.52 Ma, respectively (VIOLANTI 2012).

3. Systematic palaeontology

Galeomorphii COMPAGNO, 1973

Carcharhiniformes COMPAGNO, 1973

Carcharhinidae JORDAN & EVERMANN, 1896

Carcharhinus BLAINVILLE, 1816

Carcharhinus limbatus (MÜLLER & HENLE, 1839)

(Figure 2)

Referred material: Two upper teeth, currently stored at Badia a Settimo (Scandicci, Florence Province, Italy), in the permanent exhibition of "Gruppo AVIS Mineralogia e Paleontologia Scandicci" (=GAMPS), under accession numbers GAMPS-00968 and GAMPS-00969.

Occurrence: Lower Pliocene (5.1–4.5 Ma) marine deposits cropping out at the Arcille sand quarry, Tuscany, central Italy (see Section 2 above).

Description: The complete upper right tooth GAMPS-00968 (Fig. 2a, b) is higher than wide and rather labiolingually compressed. The slender crown is comprised of a high, narrow, slightly oblique, acutely triangular cusp that grades basally into obliquely oriented mesial and distal heels. Consequently, the mesial and distal cutting edges (both of which are complete) are substraight close to the cusp apex and concavo-convex close to the crown base. Lateral cusplets are not present; in turn, both the mesial and distal cutting edges are finely and rather homogeneously serrated, slightly more prominently so on the heels than along the cusp. The

labial crown face is weakly convex, with no distinct costules; the lingual crown face is distinctly convex. The root is wider that the crown, bilobate, with rounded lobes; its base is slightly arched. The labial root face is flat; the lingual root face bears a low and transversely broad lingual bulge bisected by a narrow but evident nutrient groove.

Although mostly complete, the upper left tooth GAMPS-00969 (Fig. 2c, d) lacks the crown apex. It is similar in size and morphology to GAMPS-00968, from which it mainly differs on the basis of a somewhat more oblique main cusp, a gently more arched root, and slightly coarser serrations on the mesial and distal heels.

Based on comparisons with extant dentitions, GAMPS-00968 and GAMPS-00969 are here interpreted as deriving from anterior or proximal anterolateral tooth rows (following the nomenclatural scheme of VOIGT & WEBER 2011: fig. 3).

Remarks: The dental design of *Carcharhinus limbatus* is strikingly close to those of *Carcharhinus amblyrhynchoides* (WHITLEY, 1934) and *Carcharhinus tilstoni* (WHITLEY, 1950) (see e.g. VOIGT & WEBER 2011: pls. 4, 19, 30). More generally, these three extant carcharhines are almost indistinguishable from each other phenetically; furthermore, they are closely related and widely regarded as forming a monophyletic group, with *C. amblyrhynchoides* and *C. tilstoni* being recognised as sister species (OVENDEN et al. 2010; MORGAN et al. 2011; SORENSON et al. 2014). Strong similarities in tooth morphology in these closely related carcharhines strengthens the notion that the fossil teeth of carcharhinids can, in some instances, provide insights into the evolutionary origins of requiem shark species (cf. discussion in COLLARETA et al. 2021a).

Carcharhinus amblyrhynchoides and *C. tilstoni* are Indo-Pacific species thought to have emerged as regional offshoots of the more widespread *C. limbatus* (or a *C. limbatus*-like ancestral carcharhine, but note that KEENEY & HEIST 2006 found *C. limbatus* to be

paraphyletic with *C. tilstoni* on the basis of mtDNA control region sequencing) in Plio-Pleistocene or latest Miocene times (SORENSON et al. 2014), when the Indian Ocean Gateway that used to connect the Mediterranean Basin to the Indo-Pacific realm had already vanished (e.g., BIALIK et al. 2019, and references therein). Based on these considerations, our Tuscan Pliocene finds are assigned straightforward to *C. limbatus*.

4. General discussion and palaeobiogeographic inferences

A survey of the palaeoichthyological literature and online resources reveals that fossil teeth assigned to *Carcharhinus limbatus* have been reported from Neogene and Quaternary deposits of the Americas and Indo-Pacific Asia, namely: i) the Miocene of the U.S.A. (PURDY 1998; HEIM in BOURDON 1999), Mexico (GONZÁLEZ-RODRÍGUEZ et al. 2013), Colombia (CARRILLO-BRICEÑO et al. 2019), Venezuela (CARRILLO-BRICEÑO et al. 2015, 2016, as *Carcharhinus* cf. *C. limbatus*), India (BHALLA & DEV 1975, 1984) and Japan (NAKAGAWA 2021); ii) the Mio-Pliocene of the U.S.A. (BOYD 2016, as *Carcharhinus* cf. *C. limbatus*); iii) the Pliocene of Mexico (LIRA-BELTRÁN et al. 2020) and Japan (NAKAGAWA 2021); iv) the Plio-Pleistocene of Tobago (DONOVAN et al. 2001, as *Carcharhinus* sp. cf. *C. limbatus*); v) the Pleistocene of the U.S.A. (SCUDDER et al. 1995) and Jamaica (PURDY et al. 1996); and vi) the Holocene of Brasil (LOPES et al. 2016) (Fig. 3). All of these fossil occurrences but the Japanese ones (NAKAGAWA 2021) are from within the present-day range of *C. limbatus* (Fig. 3). Some of them were neither figured nor described (e.g., SCUDDER et al. 1995; GONZÁLEZ-RODRÍGUEZ et al. 2013), whereas some others are here deemed as unlikely to really represent *C. limbatus* judging from the available illustrations (e.g., HEIM in BOURDON 1999; DONOVAN et al. 2001).

The Mediterranean Pliocene *Carcharhinus* assemblage was recently summarised by

MARSILI (2007, 2008), who recognised teeth belonging to the following extant species: *Carcharhinus brachyurus* (GÜNTHER, 1870), *Carcharhinus falciformis* (BIBRON in MÜLLER & HENLE, 1839), *Carcharhinus leucas* (MÜLLER & HENLE, 1839), *Carcharhinus longimanus* (POEY, 1861), *Carcharhinus obscurus* (LESUEUR, 1818), *Carcharhinus perezi* (POEY, 1876) and *Carcharhinus plumbeus* (NARDO, 1827). Besides these living forms, some typically Miocene carcharhines such as *Carcharhinus priscus* (AGASSIZ, 1843) might also have been present in the Mediterranean Sea during the Pliocene (e.g., CAPPETTA & CAVALLO 2006); this extinct member of *Carcharhinus*, which some interpret as a species group rather than as a discrete species, could represent the stock from which the Recent carcharhines *C. brachyurus*, *C. limbatus* and *C. perezi* originated (ANDRIANAVALONA et al. 2015). Of all the Recent species that occur in the Mediterranean Pliocene, *C. brachyurus*, *C. falciformis*, *C. obscurus* and *C. plumbeus* do still inhabit the Mediterranean Sea (SERENA 2005, and references therein); conversely, the living species of *Carcharhinus* that occur in the present-day Mediterranean waters but are not represented among the Pliocene fossils studied by MARSILI (2007, 2008) include *Carcharhinus altimus* (SPRINGER, 1950), *Carcharhinus brevipinna* (MÜLLER & HENLE, 1839), *C. limbatus* and *Carcharhinus melanopterus* (QUOY & GAIMARD, 1824), the latter being known as a "lessepsian" migrant that has recently entered the Eastern Mediterranean from the Red Sea through the Suez Canal (COMPAGNO 1984; SERENA 2005).

In light of the above considerations, the fossil teeth described herein from the lower Pliocene of Arcille represent the first occurrence of *C. limbatus* as a fossil from both Europe and the whole Mediterranean Basin. Furthermore, they also comprise a significant addition to the Mediterranean Pliocene shark fauna – one that also strengthens the notion that the continued study of the relatively well-investigated Neogene elasmobranch faunas of Italy can

still result in significant novelties such as new distributional records (e.g., SPADINI & MANGANELLI 2015; COLLARETA et al. 2018), descriptions of new taxa (e.g., COLLARETA et al. 2021c) and other remarkable finds (e.g., CARNEVALE et al. 2006; COLLARETA et al. 2020a). Thus, along the Pliocene coasts of Tuscany, a largely modern carcharhine assemblage coexisted along with "Miocene survivors" among both the sharks (e.g., the extinct *Pachyscyllium distans* (PROBST, 1879) and *Megascyliorhinus miocaenicus* (ANTUNES & JONET, 1970); MANGANELLI & SPADINI 2019; COLLARETA et al. 2020b) and the rays (e.g., members of the extant genera *Aetobatus* BLAINVILLE, 1816 and *Anoxypristis* WHITE & MOY-THOMAS, 1941; COLLARETA et al. 2017, 2021b) – an observation that evokes a rather gradual transition from the pre-evaporitic Mediterranean assemblages of the Tortonian and Messinian (e.g., MENESINI 1967, 1969; ARAMBOURG 1927; WARD & BONAVIA 2001) through the Messinian Salinity Crisis (cf. discussion in CARNEVALE et al. 2019) and the subsequent Pliocene. Considering also the geographic scattering of other Neogene occurrences of *C. limbatus* (Fig. 3), it seems reasonable to hypothesise that this extant carcharhinid species reached a circumglobal distribution in warm waters – including the then warmer-than-today Mediterranean Sea (COLETTI et al. 2021, and references therein) – not later than the Pliocene. Discoveries of Miocene or Pliocene teeth of *C. limbatus* from the palaeontologically underexplored Atlantic and Pacific coasts of Africa could thus be anticipated.

Is the apparent rarity of teeth of *C. limbatus* in the Pliocene deposits of the Mediterranean Basin surprising? Nowadays, members of this species are rather rarely encountered in the Mediterranean Sea (CAPAPÉ et al. 2004; MOREY et al. 2008), and the Pliocene Mediterranean scenario might have been similar to the present-day one in this respect. Interestingly, *C. limbatus* is a seasonally migratory fish (CASTRO 1996; KAJIURA & TELLMAN 2016), and its migrations can be a reason for absence or presence of this species during few months of the

year in specific habitats (VOIGT & WEBER 2011). Such migrations might also contribute to explain a scanty fossil record in palaeo-areas that were inhabited by *C. limbatus* on a seasonal basis only. Palaeoenvironmental factors should also be taken into consideration. Extant blacktip sharks typically occur in nearshore, tropical or warm-temperate waters off beaches, in bays, in estuaries, off river mouths, in the more saline parts of mangrove swamps, in island lagoons, along dropoffs on coral reefs, and subordinately offshore; crucially, *C. limbatus* is only rarely found in waters deeper than 30 m (COMPAGNO 1984; SERENA 2005; BURGESS & BRANSTETTER 2009). The very nearshore, shallow-marine, river-influenced, (sub)tropical palaeo-area witnessed by the fossiliferous strata exposed at Arcille thus represents the best palaeoenvironmental scenario for *C. limbatus* to thrive. Futher investigations on other shark tooth assemblages from shoreface, warm-water, marginal-marine deposits are, in our opinion, likely to reveal new occurrences of *C. limbatus* in the Mediterranean Pliocene.

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Figure captions

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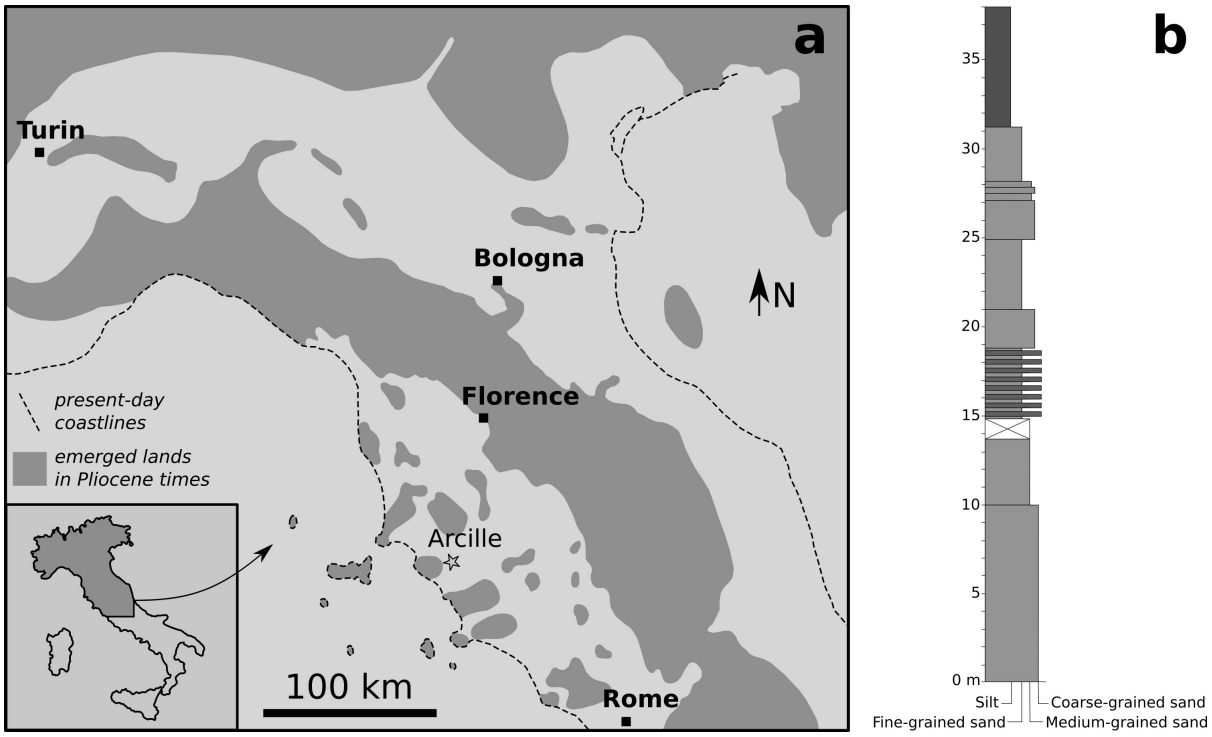
Fig. 1. Geographic and geological setting. **a** – Schematic palaeogeographic map of central and northern Italy in Pliocene times, showing the location of Arcille, the site where the carcharhinid teeth described herein were found. Paleogeographic reconstruction redrawn and modified after VAI (1989). **b** – Schematic stratigraphic section of the lower Pliocene sedimentary succession exposed at Arcille, modified after TINELLI (2013). The fossil specimens described herein come from the coarse-grained lower portion of the succession (extending up to ca. 31 m above the base of the section).

Fig. 2. Teeth of *Carcharhinus limbatus* from the lower Pliocene sandstones exposed at the Arcille sand quarry (central Italy). **a, b** – GAMPS-00968, upper right anterior or proximal anterolateral tooth in a) lingual and b) labial views. **c, d** – GAMPS-00969, upper left anterior or proximal anterolateral tooth in c) lingual and d) labial views.

Fig. 3. Present-day range and Neogene–Quaternary records of *Carcharhinus limbatus*. The base map is after the International Union for the Conservation of Nature's Red List of Threatened Species website (www.iucnredlist.org). Records from non-peer-reviewed online resources are in italics. Note that some of the fossil records are based on remains that were neither figured nor described, and some others are unlikely to represent *C. limbatus* (see the main text for further details).

Figures

Figure 1



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Figure 2

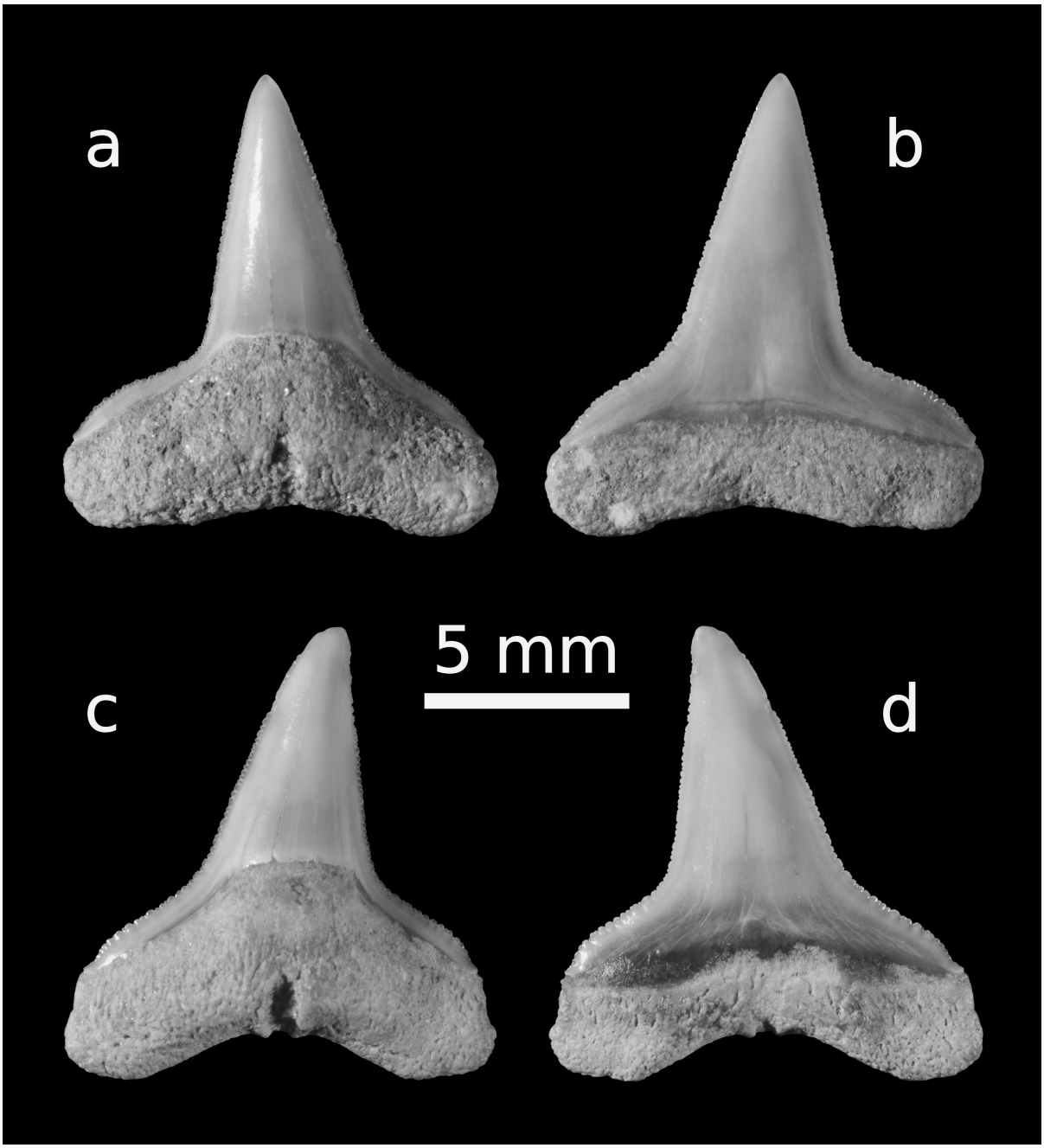
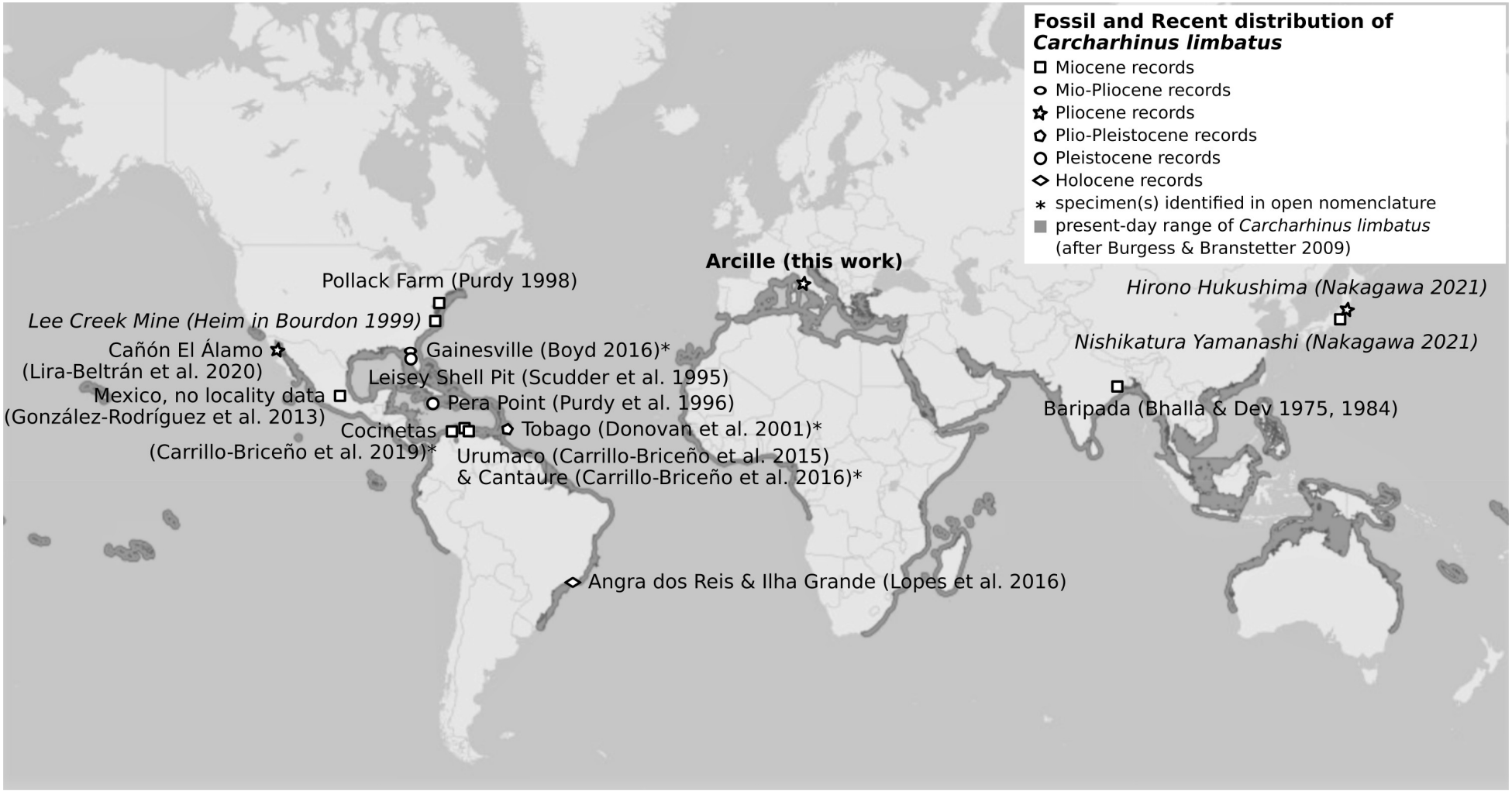


Figure 3


Fossil and Recent distribution of
Carcharhinus limbatus
Miocene records
Mio-Pliocene records
Pliocene records
Plio-Pleistocene records
Pleistocene records
Holocene records
specimen(s) identified in open nomenclature
present-day range of Carcharhinus limbatus
(after Burgess & Branstetter 2009)
Arcille (this work)
Pollack Farm (Purdy 1998)
Lee Creek Mine (Heim in Bourdon 1999)
Cañón El Álamo
(Lira-Beltrán et al. 2020)
Mexico, no locality data
(González-Rodríguez et al. 2013)
Gainesville (Boyd 2016)*
Leisey Shell Pit (Scudder et al. 1995)
Pera Point (Purdy et al. 1996)
Cocinetas
(Carrillo-Briceño et al. 2019)*
Tobago (Donovan et al. 2001)*
Urumaco (Carrillo-Briceño et al. 2015)
& Cantaure (Carrillo-Briceño et al. 2016)*
Angra dos Reis & Ilha Grande (Lopes et al. 2016)
Hirono Hukushima (Nakagawa 2021)
Nishikatura Yamanashi (Nakagawa 2021)
Baripada (Bhalla & Dev 1975, 1984)