

## REVISION OF THE TEETH OF THE GENUS *CARCHARHINUS* (ELASMOBRANCHII; CARCHARHINIDAE) FROM THE PLIOCENE OF TUSCANY, ITALY

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**Abstract.** The great similar tooth morphologies that characterized the sharks of the genus *Carcharhinus* have suggested that the Neogene Mediterranean Sea were inhabited by only one or two widespread carcharhinid taxa, *Carcharhinus egertoni* and *C. priscus*. Five new shark species included into *Carcharhinus*, *C. aff. brachyurus*, *C. falciformis*, *C. leucas*, *C. perezi*, and *C. plumbeus*, have been identified by the review of some shark teeth from Tuscany (Italy) and housed in the Italian Museums of the Universities of Firenze, Bologna, and Pisa. Moreover, the Mediterranean records of the two Recent *C. longimanus* and *C. obscurus* has been confirmed too. Paleobiogeographic and palaeoecologic analysis have been produced on the presence of some species absent or doubtful for the extant Mediterranean shark community.

**Riassunto.** La grande uniformità morfologica osservabile nei denti che armano le mascelle superiore ed inferiore delle numerose specie che compongono il genere *Carcharhinus*, ha portato in passato a considerare il Mediterraneo abitato, durante il Neogene, da due specie fossili di carcarinidi, entrambe caratterizzate da un'ampia distribuzione stratigrafica e paleobiogeografica, *Carcharhinus egertoni* e *C. priscus*. La revisione di denti provenienti dai depositi della Toscana (Italia) e conservati nei Musei Italiani delle Università di Firenze, Bologna e Pisa, ha permesso di identificare e segnalare per la prima volta nel Pliocene del Mediterraneo cinque specie viventi inquadrabili in *Carcharhinus*, *C. aff. brachyurus*, *C. falciformis*, *C. leucas*, *C. perezi* e *C. plumbeus*, e di confermare inoltre il record di altre due specie, *C. longimanus* e *C. obscurus*, già note in questo bacino. La presenza di specie attualmente assenti o considerate dubbie nel Mediterraneo, ha suggerito inoltre alcune importanti considerazioni a carattere sia paleoecologico che paleobiogeografico.

### Introduction

The genus *Carcharhinus*, with thirty inshore and offshore dwelling species, ranging to tropical from temperate waters (Compagno 1984), is the most speciose

genus of the shark family Carcharhinidae. These sharks usually inhabit the coastal waters, except for *C. longimanus* and *C. falciformis*, which are considered primarily pelagic sharks (Garrick 1982; Compagno 1984). The bull shark *C. leucas* is the only carcharhinid species that can live and move freely in marine, brackish and freshwater environments. It has been observed to enter also for long distance into the African or the Central Southern American fluvial systems (see also Bigelow & Schroeder 1948; Myers 1952; Thorson 1972; Thomerson & Thorson 1977; Bass et al. 1973; Garrick 1982; Compagno 1984).

The carcharhinid sharks are top-predators and primary fish-eaters. They feed on bonefishes such as tunas, mullets, parrotfishes, herrings or other Chondrichthyens, such as sawfishes, dogfishes, torpedo rays, and other carcharhinid sharks (Compagno 1984). Molluscs and crustaceans may be also an important part of their diet (Compagno 1984). A few voracious species, such as *C. leucas*, *C. longimanus*, or *C. obscurus*, can also feed on marine vertebrates (cetaceans and turtles), and seabirds (Compagno 1984; Heithaus 2001).

At present, eight species belonging to the genus *Carcharhinus* are included in the Mediterranean fish fauna (Compagno 1984; Notarbartolo di Sciarra & Bianchi 1998). *C. brevipinna*, *C. limbatus* and *C. plumbeus* are widespread and commonly recorded in all the Mediterranean Sea (Tortonese 1950; Compagno 1984; Notarbartolo di Sciarra & Bianchi 1998), while *C. altimus*, *C. obscurus*, *C. brachyurus*, and *C. falciformis* are principally recorded in the western part of the basin (Moreno & Hoyos 1983; Compagno 1984; Notarbartolo di Sciarra & Bianchi 1998). However, both *C. obscurus* and *C. brachyurus* have been often con-

fused with other carcharhinid sharks during the field-identifications, and so their geographical distribution in the Mediterranean Sea should be considered much more widespread (Capapé et al. 1979; Cigala Fulgosi 1983; Compagno 1984; Notarbartolo di Sciara & Bianchi 1998). The black-tip reef shark *C. melanopterus*, commonly recorded in the Pacific and Indian Ocean and in the Red Sea (Compagno 1984), is recorded only along the Tunis, Israel and Cyprus coasts (Quignard & Capapé 1971; Capapé et al. 1975; Compagno 1984; Notarbartolo di Sciara & Bianchi 1998). This shark probably entered in the Mediterranean basin through the Suez Channel as a lessepsian migrant from the Red Sea (Compagno 1984; Notarbartolo di Sciara & Bianchi 1998). *C. longimanus* and in particular *C. leucas*, sporadically recorded in the Mediterranean, are considered doubtful in this basin, and they are excluded from its fish community (Tortonese 1950, 1963; Garrick 1982; Compagno 1984; Notarbartolo di Sciara & Bianchi 1998).

The sharks of the genus *Carcharhinus* are characterized by a great similar body and tooth morphologies. Several morphological, genetic, dental and morphometrical data have been produced in the last decades to better understand the relationships within this genus (see Bigelow & Schroeder 1948; Tortonese 1950, 1951; Springer 1950, 1951; Bass et al. 1973; Garrick 1982, 1985; Branstetter 1982; Cigala Fulgosi 1983; Compagno 1984, 1988; Naylor 1992; Naylor & Marcus 1994; Purdy et al. 2001; Antunes & Balbino 2004). Recently Naylor (1992), based on molecular data, supposed that all large and ridge-backed species of the genus *Carcharhinus* may be member of a monophyletic group (*C. altimus*, *C. falciformis*, *C. galapagensis*, *C. longimanus*, *C. obscurus*, *C. perezi* and *C. plumbeus*), that also included *Prionace glauca* (see also Musick et al. 2004). Garrick (1982) and Compagno (1988), based on morphological data, also argued relationships between members of this monophyletic group, and other species of *Carcharhinus*. However, molecular and morphological data often disagree each other (Naylor 1992; Musick et al. 2004), and the relationships within *Carcharhinus* are still far away to be solved.

Teeth, that often represent the only diagnostic shark features for a paleontologist, may become a powerful tool for systematic, phylogenetic, and faunistic shark analysis. In fact, teeth can be considered as a species-specific elements (Garrick 1982).

The aim of this paper is the review of the fossil teeth belonging to the genus *Carcharhinus* collected during the second half of the nineteenth century from several Pliocene deposits of Tuscany. Most of the teeth were collected and investigated by Roberto Lawley, the most important Italian shark palaeontologists. He gave credit for produce many important papers and

monographs on the Pliocene shark communities (Lawley 1875, 1876, 1877, 1878, 1879, 1881), and at present, his collection represents one of the most famous and important historical Neogene shark teeth collection in Italy.



Fig. 1 - Sketch map of Tuscany.

## Material

Two hundred and twenty nine teeth collected from different Tuscany Pliocene outcrops have been examined (Fig. 1). The specimen are housed in the "Museo di Storia Naturale, Sezione di Geologia e Paleontologia" of the University of Firenze, "Museo di Geologia e Paleontologia G. Capellini" of the University of Bologna and in the "Museo di Storia Naturale e del Territorio" of the University of Pisa. Most of the material belongs to the "Collezione Lawley", while only few teeth are from other ancient collections or donations. A new catalogue number has been assigned, when possible, to every *Carcharhinus* specimen (see Appendix 1). The carcharhinid teeth were often mixed and confused with other shark genera such as *Sphyrna*, *Prionace*, and *Isurus* (see Appendix 1). It has been also identified one teleost teeth, that based on its morphological features can be tentatively referred to the anglerfish genus *Lophius* (see Appendix 1).

Comparisons with extant dried jaws have been possible thanks to the material housed in the "Museo di Storia Naturale, Sezione di Zoologia «La Specola»" of the University of Firenze, "Museo Civico di Storia Naturale G. Doria" of the University of Genova, "Museo di Anatomia Comparata" of the University of Bologna, and "Museo di Storia Naturale e del Territorio" of the University of Pisa.

The morphological and dental characters used follow Bigelow & Schroeder (1948), Tortonese (1950, 1951), Springer (1950, 1951, 1964), Gilbert (1967), Bass et al. (1973, 1975), Branstetter (1982), Garrick (1982, 1985), Cigala Fulgosi (1983), Compagno (1984, 1988), Cappetta (1987), Cappetta & Nolf (1991), Herman et al. (1991), Antunes & Balbino (2004), Purdy et al. (2001) and Purdy (2003).

## Fossils Record

The earliest record of *Carcharhinus* dates back to the Middle Eocene of Egypt (Stromer 1905; Cappetta 1987), Morocco (Arambourg 1952), and North America (Woodward 1889; Case 1981; Cappetta 1987). This genus is also well represented in the Oligocene of Belgium (Leriche 1910), but it is only in the Miocene and Pliocene sediments (see Agassiz 1833-43; Probst 1878; Lawley 1876, 1881; De Stefano 1910, 1912; Arambourg 1927; Bauzá Rullán 1949a, b; D'Erasmus 1951; Schultz 1971, 1977; Cappetta 1970; Menesini 1968, 1974; Landini 1977; Longbottom 1979; Case 1980; Antunes et al. 1999; Antunes & Balbino 2004; Long 1993a; Bellocchio et al. 1991; Mora Morote 1996; Purdy 1998; Purdy et al. 2001) that it becomes one of the most prominent elements of the neritic fauna (Cappetta 1987). Concerning the Mediterranean basin, fossils clearly belonging to this genus have been recorded in the Miocene sediments of Italy (De Alessandri 1895; Pasquale 1903; Bassani 1915; Gemmellaro 1912; D'Erasmus 1924; Menesini 1968), Malta (Menesini 1974; Ward & Bonavia, 2001), France (Cappetta 1970; 1973), Libya (D'Erasmus 1951) and Algeria (Arambourg 1927), and in the Pliocene sediments of Italy (Lawley 1876, 1881; De Stefano 1910, 1912; Landini 1977; Cigala Fulgosi 1986; Bellocchio et al. 1991; Manganelli & Spadini 2003), France (Cappetta & Nolf 1991) and Spain (Bauzá Rullán 1949a, b; Mora Morote 1996).

Cappetta (1970: 53) suggested that the fossil teeth belonging to *Carcharhinus* should be divided into two groups, the *Carcharhinus egertoni* group and the *Carcharhinus priscus* group. *C. priscus* can be separated from *C. egertoni* because of a narrower and distally inclined cusp, sometime with a truncate appearance. Most of the teeth reviewed in this paper were included by Landini (1977) in *C. egertoni*. The Author considered these teeth as belonging to a single species with morphology near to the extant species *C. longimanus*, *C. leucas* or *C. falciformis* (see also De Stefano 1910; Arambourg 1927; Leriche 1957; Menesini 1974). *C. egertoni* was described by Agassiz (1833-43: 228) as *Corax egertoni*, from the Miocene of North America. It is characterized by a large and triangular shape cusps, distally inclined, with regularly serrated lateral cutting edges. The distal cutting edges is concave, sometime with an evident basal heel, while the mesial cutting edge may be straight, convex or slightly wavy, sometime characterized by an apical convexity.

## Paleontological Systematics

Order *Carcharhiniformes* Compagno, 1973

Family *Carcharhinidae* Jordan & Evermann, 1896

Genus *Carcharhinus* Blainville, 1816

The upper teeth of *Carcharhinus* are characterized by triangular, broad to rather narrow crown. The lateral cutting edges are always serrated, even if some species lack these serrations (e.g. *C. macloiti*) or have them poorly developed (e.g. *C. brevipinna*, *C. isodon*). The cusp may be clearly separated from a distal and mesial heels (e.g. *C. macloiti*), or from only a distal heel (e.g. *C. perezi*, *C. brachyurus*, *C. sorrah*, *C. albimarginatus*, *C. falciformis*), that may be smoothed to serrated, sometime with cusplets (e.g. *C. sealei*, *C. borneensis*, *C. porosus*, *C. cautus*, *C. macloiti*). The root is generally flat with a high basal face, characterized by a clear shallow axial groove (Garrick 1982; Compagno 1984, 1988; Cappetta 1987; Purdy et al. 2001). The lower teeth are characterized by a narrow and nail-like cusp, with smooth to serrated lateral cutting edges, clearly separated from a distal and mesial heel (Garrick 1982; Compagno 1984, 1988; Cappetta 1987; Purdy et al. 2001).

The monotypic genus *Galeocerdo* is characterized by a very peculiar cockscomb shape upper and lower dentition (Cigala Fulgosi & Mori 1979), and so it is very easy to separated it from all the other sharks of the family *Carcharhinidae*. *Triaenodon* may be separated from *Carcharhinus* because of a pair of very high lateral cusplets both on upper and lower teeth (Compagno 1984; Herman et al. 1991). *Negaprion* is characterized by narrow and erected cusps, with a completely smoothed lateral cutting edges. The larger specimens of this shark are sometime characterized by a stronger mesial cutting edge (Compagno 1988; Herman et al. 1991; see also plates in Bass et al. 1975). Laterally, there are evident smooth mesial and distal heels, that may be separated from the cusp by a more or less developed notch, and sometime characterized by a very coarse serrations, formed by 3 to 5, 6 very low and large denticles (Cappetta 1970). *Loxodon*, *Scoliodon*, and *Rhizoprionodon* are characterized by a very similar tooth morphologies (Springer 1964). The upper and lower teeth have a narrow and distally inclined cusps, with a completely smoothed lateral cutting edges. However, serrated lateral cutting edges have been observed in some large specimens of *Rhizoprionodon* (Springer 1964). An evident lateral distal heel is separated from the cusp by very deep notch. The root presents a deep lingual axial groove, that may notch also the basal face of the root (Bass et al. 1975, pl. 8-9; Herman et al. 1991, pl. 21-28.). The genus *Prionace* is characterized by upper triangular teeth, with cusps much more elongate than large. The root both in the upper and lower teeth have a thick protuberance in the middle of the lingual face, with a well developed deep axial groove, that broadly notches also the basal face of the root, so that the root-lobes are completely separated (Bass et al. 1975, pl. 6; Cappetta 1987).

Some *Carcharhinus* species have been often confused or included in the genus *Sphyrna* (e.g. Leriche 1942, 1957; Bauzá Rullán 1949b; D'Erasmus 1951; D'Alessandro et al. 1979). *Sphyrna* may be separated from *Carcharhinus* because of upper and lower teeth with a smooth, sometime weakly serrated, and distally inclined cusps, separated by a deep notch from an evident, convex and smooth edged or weakly serrated distal heel (Gilbert 1967; Bass et al 1975; Cappetta 1970, 1987). *Sphyrna mokarran* is the only species characterized by coarse serrated upper and lower teeth (Gilbert 1967; Bass et al. 1975; Compagno 1984; Cappetta 1987). The mesial cutting edge in the upper teeth is generally convex, while it is rectilinear or concave in the lower ones (Cappetta 1987). The root is characterized by a bulky and very high lingual face, with an evident deep axial groove, that broadly notched also the basal face of the root. The root-lobes are well separated (also Gilbert 1967; Bass et al. 1975; Cappetta 1987).

#### **Carcharhinus brachyurus** (Günther, 1870)

Pl. 1, figs 1-6

- 1843 *Corax egertoni* Agassiz, p. 228, pl. 36, fig. 6.  
 1942 *Prionodon egertoni* - Leriche, p. 80, pl. 7, fig. 4.  
 1942 *Sphyrna americana* Leriche, p. 86, pl. 6, fig. 7-8.  
 1942 *Sphyrna prisca eastmani* Leriche, p. 85, fig. 7, pl. 7, fig. 28-32a.  
 1969-70 *Carchabrinus egertoni* - Antunes & Jonet, p. 189, pl. 15, fig. 110-111.  
 1968 *Cestracion priscus* - Menesini, p.35, pl. 6, fig. 16.  
 1970 *Carchabrinus priscus* - Cappetta, p. 54, pl. 13, fig. 8-19.  
 1976 *Carcharhinus priscus* - De Ceuster, p. 142, pl. 6, fig. 13.  
 1978 *Carcharhinus brachyurus* - Applegate, p. 57, tab. 1.  
 1980 *Carcharhinus priscus* - Case, p. 89, pl. 6, fig. 7.  
 1991 *Carcharhinus egertoni* - Bellocchio et al., p. 57, pl.1, fig. 4.  
 1993b *Carcharhinus brachyurus* - Long, p. 12.  
 1996 *Carcharhinus priscus* - Mora Morote, p. 104, pl. 4, fig. 9.  
 1998 *Carcharhinus brachyurus* - Purdy, p. 133, pl. 2, fig. 4-5.  
 2001 *Carcharhinus brachyurus* - Purdy et al., p. 151, fig. 53a.

**Material.** 9 teeth examined: IGF8750V (1 tooth); IGF8752V (1 tooth); IGF8761 (1 tooth); IGF8787V (1 tooth); IGF8790V (1 tooth); IGF8799V (1 tooth); IGF13991 (1 tooth); I12967 (1 tooth); Tav. n. 15bis (1 tooth).

**Description.** The upper teeth are characterized by narrow, and distally inclined cusps. The lateral cutting edges are regularly serrated. According to Purdy et al. (2001), the mesial cutting edge is wavy, with a clear convexity or angle near the crown-apex, so that the cusps appear truncated. The mesial cutting edge have a basal coarse serrations that become finer near the crown apex. The distal cutting edge is almost vertical and fine serrated. Lateral to the cusp, there is a strongly serrated distal heel. The labial face of the crown is flat or slightly convex, while the lingual one is convex, with a clear neck-area between crown-base and the root. The root

is low, and characterized by an evident lingual axial groove.

**Remarks.** Garrick (1982: 174) considered *C. brachyurus* as “one of the few species (of carcharhinid sharks) which can, with virtual certainty, be identified by upper tooth shape alone” (Cigala Fulgosi 1983). The upper teeth of *C. perezii* can be separated from *C. brachyurus* because of the absence of apical convexity or angle along the mesial cutting edge and the cusps have not a truncate appearance.

According to Compagno (1984), the copper shark *C. brachyurus* is an inshore to offshore, warm-temperate habitant, occurring from the surf-line to at least 100 m. depth. It feeds on bony fishes and other elasmobranchs (Compagno 1984). The presence of this shark in the Mediterranean was confirmed by Cigala Fulgosi (1983), based on a specimen caught in the Sicilian Channel. At present, it is commonly recorded in the western part of this basin. However, the biology of *C. brachyurus* is poorly known, because of the misidentifications with other carcharhinid sharks, and probably its geographical distribution in the Mediterranean Sea should be much more widespread (Cigala Fulgosi 1983; Notarbartolo di Sciarra & Bianchi 1998).

*C. brachyurus* has been recorded in the North American Miocene deposits of Maryland (Agassiz 1833-43; Leriche 1942), North Carolina (Case 1980; Purdy et al. 2001) and Delaware (Purdy 1998), in the European Miocene deposits of Portugal (Antunes & Jonet 1969-70), France (Cappetta 1970), Belgium (De Ceuster 1976) and Italy (Menesini 1968), and in the Pliocene deposits of Italy (Bellocchio et al. 1991) and Spain (Mora Morote 1996). *C. brachyurus* has been recorded also in the Pliocene “Gloria Formation” in California (Applegate 1978) and in the Pleistocene deposits of the California Palos Verdes Sand Formation (Long 1993b). This may be considered the first confirmation for the Pliocene Mediterranean deposits.

#### **Carcharhinus falciformis** (Bibron 1841, in Müller & Henle 1839-1841)

Pl. 1, figs 7-10

- 1942 *Prionodon egertoni* - Leriche, p. 80, pl. 7, fig. 3.  
 1968 *Cestracion priscus* - Menesini, p. 35, pl. 6, fig. 15.  
 1968 *Prionodon egertoni* - Menesini, p. 31, pl. 7, fig. 5.  
 1978 *Carcharhinus falciformis* - Applegate, p. 57, tab. 1.  
 2001 *Carcharhinus falciformis* - Ward & Bonavia, p. 138.  
 2001 *Carcharhinus falciformis* - Purdy et al., p. 151, fig. 53b-f.

**Material.** 4 teeth examined: IGF8756V (2 teeth); IGF8776V (1 tooth); IGF8791V (1 tooth).

**Description.** The upper teeth are characterized by triangular shape, serrated and distally inclined cusp,

erected in the identified upper anterior tooth. The mesial cutting edge is straight, and characterized at the midpoint, by a notch or gap in the serrations (Purdy et al. 2001). The distal cutting edge is straight, and perpendicular to a line tangent to the basal margin of the root (Purdy et al. 2001). In the lateral teeth there is a distal heel separated from the cusp by a shallow notch. By contrast, in the anterior tooth there are a mesial and distal heels separated from the cusp by a deep notch. The serrations are coarser on the mesial and distal heels than along the lateral margins of the cusp. The lingual face of the crown is convex, and characterized by a very slightly neck-area. The labial face of the crown is flat. The root is high, and characterized by a deep lingual axial groove. The basal margin of the root is arched.

**Remarks.** The gap in the serrations along the mesial cutting edge and a straightness of this margin can be considered specific characters for *C. falciformis* (Purdy et al. 2001). *C. albimarginatus* may be separated from *C. falciformis* because of upper teeth with much more elongated, and apical hooked cusps, because of a clear shallow notch along the mesial and distal cutting edges of the first upper seven teeth (Purdy et al. 2001), and because of the absence of gap in the serrations along the mesial margins.

According to Compagno (1984), the silky shark *C. falciformis* is an oceanic, epipelagic and littoral, tropical habitant, with an open see range, from the surface line down to at least 500 m depth. This shark is a primary fish eater, and it feeds on pelagic and inshore bone fishes (Compagno 1984). *C. falciformis* is recorded only in the western part of the Mediterranean Sea, in particular in the Alboràn sea (Compagno 1984; Notarbartolo di Sciara & Bianchi 1998).

*C. falciformis* has been recorded in the American Miocene deposits of North Carolina (Purdy et al. 2001) and Maryland (Leriche 1942) and in the European Miocene deposits of Italy (Menesini 1968). In the Pliocene it has been recorded only in the "Gloria" Formation in California (Applegate, 1978). This may be considered as the first record of *C. falciformis* for the Mediterranean Pliocene deposits.

***Carcharhinus leucas*** (Valenciennes 1839,  
in Müller & Henle 1839-1841)

Pl. 1, figs 11-15

1843 *Corax egertoni* Agassiz, p. 228, pl. 36, fig. 7.

1942 *Prionodon egertoni* - Leriche, p. 80, pl. 7, fig. 11-12.

1963 *Carcharhinus* cf. *leucas* - Antunes, p. 54, pl. 4, fig. 16-21.

1974 *Carcharhinus* sp. - Uyeno & Matsushima, p. 61, pl. 23, fig. 4-5.

1974 *Carcharhinus egertoni* - Menesini, p. 144, pl. 7, fig. 12.

1978 *Carcharhinus leucas* - Applegate, p. 57, tab. 1.

1979 *Carcharhinus egertoni* - Longbottom, p. 61, fig. 8-12.

1991 *Carcharhinus egertoni* - Bellocchio et al., p. 57, pl. 2, fig. 7-8.

1995 *Carcharhinus leucas* - Scudder et al., p. 254.

1999 *Carcharhinus* cf. *leucas* - Antunes et al, p. 116.

1999 *Carcharhinus* cf. *obscurus* - Antunes et al., p. 116.

2001 *Carcharhinus leucas* - Purdy et al., p. 151, fig. 54a.

2004 *Carcharhinus* cf. *leucas* - Antunes & Balbino, p. 86, fig. 6h,i - 7a,b.

**Material.** 15 teeth examined: IGF8749V (2 teeth); IGF8755V (1 tooth); IGF8772V (1 tooth); IGF8784V (2 teeth); IGF8794V (1 tooth); IGF13976 (3 teeth); Tav. n. 8 (3 teeth); Tav. n. 8terzo (2 teeth).

**Description.** The upper teeth are characterized by a broad and triangular shape cusps, with serrated lateral cutting edges. The serrations are coarser near the base than near the crown-apex. The mesial cutting edge is straight, or slightly wavy, sometime weakly convex near the tip of the cusp (see also Purdy et al. 2001). The distal cutting edge is concave. Lateral to the cusp there is a coarse serrated distal heel, sometime separated from the cusp by a very shallow notch. The lingual face of the crown is convex, and characterized by a well developed neck-area between the crown-base and the root. The labial face of the crown is flat. The root is high, and characterized by a weakly lingual axial groove. The basal margin of the root is arched or angular.

The lower tooth identify is characterized by a broad and serrated crown, with a lateral margin parallel in the basal region and convex in the apical one, so that the cusp appears arrow-like. Lateral to the cusps there are a serrated mesial and distal heel. The basal margin of the roots is arched, or angular.

**Remarks.** *C. longimanus* is characterized by a much larger and elongated upper teeth than that of *C. leucas*, and a straight basal margin of the root (see also Purdy et al. 2001). *C. obscurus* can be separated from *C. leucas* because of upper teeth with an evident apical convex mesial cutting edges, with the tip of the cusps that appear to be distally deflected (Purdy et al. 2001). *C. leucas*, *C. longimanus* are characterized by a similar lower tooth morphologies. Purdy et al. (2001) suggested that the cusps of the anterior and anterior-laterals lower teeth seem to be more symmetrical in *C. leucas* than in the oceanic whitetip shark *C. longimanus*. However, more detailed studies on lower dentition in large population of these three shark species should be helpful to understand better the usefulness of these characters (Purdy et al. 2001).

The upper anterior lateral tooth identified by Menesini (1974, pl. 7, fig. 12) as *Carcharhinus egertoni* is morphologically very similar to the upper teeth of *C. leucas*, and it may belong to this species.

According to Compagno (1984), the bull shark *C. leucas* usually inhabits the coasts of all the tropical and subtropical seas, where it ranges from 30 m down to 150 m depth. *C. leucas* is the only carcharhinid sharks that can live freely in marine, brackish and fresh waters (Bigelow & Schroeder 1948; Myers 1952; Thorson 1972;

Thomerson & Thorson 1977; Bass et al. 1973; Garrick 1982; Compagno 1984). It is a versatile, opportunistic and voracious feeder, with a very large food spectrum that comprises bony fishes, other elasmobranchs, marine vertebrates, and sea birds (Compagno 1984; Heithaus 2001). At present, this shark is considered doubtful in the Mediterranean waters (Notarbartolo di Sciarra & Bianchi 1998).

*C. leucas* has been recorded in the American Miocene deposits of Maryland (Agassiz 1833-43; Leriche 1942), North Carolina (Purdy et al. 2001) and Ecuador (Longbottom 1979), in the European Miocene deposits of the Alvalade basin, Portugal (Antunes et al. 1999; Antunes & Balbino 2004), and Malta (Menesini 1974), and in the Pliocene deposits of the Lee Creek Mine, North Carolina (Purdy et al. 2001), in the "Gloria" Formation in California (Applegate 1978), in Luanda, Angola (Antunes 1963), and in Italy (Bellocchio et al. 1991). *C. leucas* has been recorded also in the Pleistocene deposits of the Leisey Shell Local Fauna in Florida (Scudder et al. 1995), and in Yokohama city, Japan (Uyeno & Matsushima 1974). This may be considered the first confirmation of *C. leucas* for the Italian Pliocene deposits.

### **Carcharhinus longimanus** (Poey, 1861)

Pl. 2, figs 8-19

1977 *Carcharhinus egertoni* - Landini, p. 113, pl. 4, fig. 8-25.

1987 *Pterolamiops longimanus* - Cappetta, p. 125, fig. D-E.

1991 *Carcharhinus* aff. *longimanus* - Cappetta & Nolf, p. 56, pl. 3, fig. 4-5.

1996 *Carcharhinus egertoni* - Mora Morote, p. 105, pl. 5, fig. 1-5.

1996 *Pterolamiops longimanus* - Mora Morote, p. 105, pl. 5, fig. 7-8.

2003 *Carcharhinus egertoni* - Manganeli & Spadini, p. 69, fig. 53.

**Material.** 61 teeth examined: IGF13975 (5 teeth); IGF13976 (2 teeth); IGF14009 (2 teeth); IGF14053 (1 tooth); IGF14058 (1 tooth); IGF14059 (1 tooth); IGF14060 (2 teeth); IGF14066 (1 tooth); IGF14068 (2 teeth); IGF14104 (4 teeth); IGF14107 (1 tooth); IGF14129 (2 teeth); IGF14132 (1 tooth); IGF8746V (3 teeth); IGF8758V (2 teeth); IGF8762V (4 teeth); IGF8767V (2 teeth); IGF8777V (1 tooth); IGF8782V (3 teeth); IGF8792V (3 teeth); Tav. n. 8 (2 teeth); Tav. n. 8bis (3 teeth); Tav. n. 8terzo (4 teeth); Tav. n. 13bis (3 teeth); Tav. n. 15bis (2 teeth); Tav. n. 17 (1 tooth); Tav. n. 17bis (1 tooth); Tav. n. 18 (2 teeth).

**Description.** The upper teeth are characterized by a very broad and triangular shape cusps, with serrated lateral cutting edges. The mesial cutting edge is straight, while the distal one is slightly concave. Lateral to the cusp, a distal coarse heel may be present. The anterior teeth are characterized by straight and regularly serrated lateral cutting edge. The labial face is flat, while the lingual one is convex, and characterized by a well developed neck-area between the crown-base and the root. The root is high and characterized by a weakly lingual

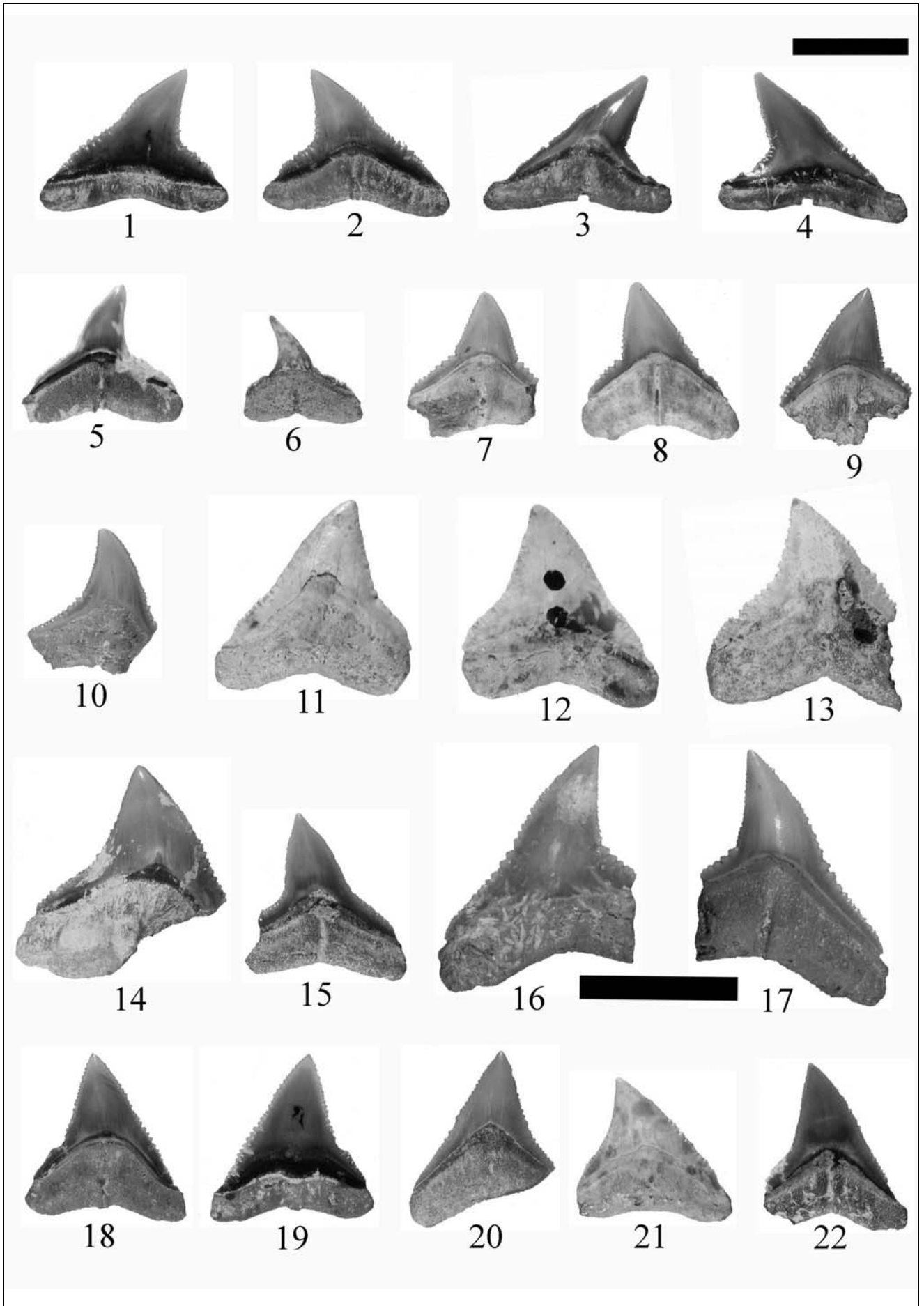
axial groove. The basal margin of the root is straight to slightly concave.

The lower teeth are characterized by a broad, erected and nail-like cusps. The lateral cutting edges are regularly serrated, but the serrations stop at the mid-way along the lateral margins. Lateral to the cusps, there are a smoothed mesial and distal heels. The basal margin of the root is straight to slightly concave.

**Remarks.** *C. obscurus* can be separated from *C. longimanus* because of upper teeth with an evident apically convex mesial cutting edges, with the tip of the cusps that appear to be distally deflected (Purdy et al. 2001). *C. altimus* and *C. galapagensis* are usually characterized by more elongate and narrow upper teeth than

### PLATE 1

- Fig. 1-6 - *Carcharhinus brachyurus* (Günther, 1870). Fig. 1. IGF8752V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 2. IGF8752V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 3. IGF8750V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 4. IGF8750V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 5. IGF8790V; Bagnai (Pisa); lower anterior-lateral tooth (lingual view). Fig. 6. IGF8799V; Unknown locality; lower anterior-lateral tooth (lingual view).
- Fig. 7-10 - *Carcharhinus falciformis* (Bibron, 1841, in Müller & Henle 1839-1841). Fig. 7. IGF8756V; Orciano (Pisa); upper anterior tooth (lingual view). Fig. 8. IGF8756V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 9. IGF8776V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 10. IGF8791V; Bagnai (Pisa); upper anterior-lateral tooth (lingual view).
- Fig. 11-15 - *Carcharhinus leucas* (Valenciennes, 1839, in Müller & Henle 1839-1841). Fig. 11. IGF8772V; Orciano (Pisa) upper anterior-lateral tooth (lingual view). Fig. 12. IGF8772V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 13. IGF8784V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 14. IGF8794V; Bagnai (Pisa); upper anterior-lateral tooth (lingual view). Fig. 15. IGF8784V; Orciano (Pisa); lower anterior-lateral tooth (lingual view).
- Fig. 16-17 - *Carcharhinus perezi* (Poey, 1876). Fig. 16. IGF8757V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 17. IGF8757V; Orciano (Pisa); upper anterior-lateral tooth (lingual view).
- Fig. 18-22 - *Carcharhinus plumbeus* (Nardo, 1827). Fig. 18. IGF8753V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 19. IGF8753V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 20. IGF8753V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 21. IGF8753V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 22. IGF8786V; Orciano (Pisa); upper anterior-lateral tooth (lingual view).
- Scale bars = 1 cm.



*C. longimanus*, while *C. plumbeus* is characterized by more labio-lingually compressed upper teeth.

*C. longimanus* was recorded for the first time in the Pliocene Mediterranean sediments by Cappetta & Nolf (1991). Moreover, the authors argued that the teeth identified by Landini (1977, pl. 4, fig. 8-25) as *Carcharhinus egertoni* are upper and lower teeth of *C. longimanus* (Cappetta & Nolf 1991). The teeth published and figured by Cappetta (1987, fig. D-E) as *Pterolamiops longimanus*, are an upper and lower teeth of *C. longimanus*: *Pterolamiops* is a junior synonym of *Carcharhinus* (Compagno 1988; Purdy et al. 2001).

According to Compagno (1984), the oceanic whitetip shark *C. longimanus* is an oceanic, epipelagic, tropical and warm-temperate shark (see also Garrick 1982), sometime recorded also near the coasts. *C. longimanus* feeds primarily on bony fishes and other elasmobranchs. However, its diet may also include invertebrates, and marine vertebrate (Compagno 1984; Heithaus 2001). At present, this shark is considered doubtful in the Mediterranean waters (Tortonese 1950, 1963; Garrick 1982; Compagno 1984; Notarbartolo di Sciara & Bianchi 1998).

*C. longimanus* has been recorded in the American Pliocene deposits of North Carolina (Cappetta 1987), and in the European Pliocene deposits of France (Cappetta & Nolf 1991), Spain (Mora Morote 1996) and Italy (Landini 1977; Manganelli & Spadini 2003).

### **Carcharhinus obscurus** (Lesueur, 1818)

Pl. 2, figs 1-7

1978 *Carcharhinus obscurus* - Applegate, p. 57, tab. 1.

1986 *Carcharhinus* cf. *obscurus* - Applegate, p. 160.

1986 *Carcharhinus* cf. *obscurus* - Cigala Fulgosi, p. 135.

1995 *Carcharhinus obscurus* - Scudder et al., p. 254.

2000 *Carcharhinus* cf. *obscurus* - Sánchez-Villagra et al., p. 959, fig. 5-6.

2001 *Carcharhinus obscurus* - Purdy et al., p. 153, fig. 55a.

**Material.** 11 teeth examined: IGF8748V (1 tooth); IGF8754V (2 teeth); IGF8773V (3 teeth); IGF8783V (3 teeth); IGF8793V (1 tooth); Tav. n. 9 (1 tooth).

**Description.** The upper teeth are characterized by a triangular shape, large, and not elongated crown, with regularly serrated lateral cutting edges. The mesial cutting edge is apical convex, and the tips of the teeth appear to be distally deflected (Purdy et al. 2001). The distal cutting edge is concave, or slightly vertical, with a serrated basal heel. The labial face is flat, while the lingual one is convex, with an evident neck-area between the crown-base and the root. The root is high and characterized by a weakly lingual axial groove. The basal margin of the root is arched.

**Remarks.** *C. obscurus* was recorded for the first time in the Pliocene of Italy by Cigala Fulgosi (1986) in

the sediments of the North Apennine. This shark can be separated from the other broad triangular shape carcharhinid sharks such as *C. longimanus*, *C. leucas*, *C. plumbeus*, *C. galapagensis* because of teeth characterized by an evident apical convex mesial cutting edges, and the tip of the cusps that appear to be distally deflected (Purdy et al. 2001).

The tooth figured by De Alessandri (1895, pl. 1, fig. 13) has a morphology similar to *C. obscurus*, and it may belong to this last species. However, the diagnosis is made on a picture drawn by the author, and not on the original tooth. The teeth published by Arambourg (1927, pl. 44, fig. 2-9) as *Carcharhinus egertoni*, are similar to the upper teeth of *C. obscurus*, and they may be included into this carcharhinid species.

According to Compagno (1984), the dusky shark *C. obscurus* is a coastal-pelagic, warm-temperate and tropical shark. It inhabits the inshore and offshore waters of the continental and insular shelves or the oceanic waters near them (Compagno 1984). This shark is a primarily fish-eater, and it feeds on bony fishes and other elasmobranchs (Compagno 1984). The presence of *C. obscurus* in the Mediterranean Sea has been mentioned for the first time by Capapé et al. (1979) along the Tunis coasts (Cigala Fulgosi 1983). The Dusky shark is commonly recorded in the western part of the Mediterranean basin (Compagno 1984; Notarbartolo di Sciara & Bianchi 1998), but its geographical distribution in this basin should be widespread, because of the misidentified with other carcharhinid shark, such as *C. plumbeus* (Notarbartolo di Sciara & Bianchi 1998).

*C. obscurus* has been recorded in the American Miocene deposits of the northern Venezuela (Sánchez-Villagra et al. 2000) and of the North America (Applegate 1986), in the American Pliocene deposits of North Carolina (Purdy et al. 2001) and California (Applegate, 1978), and in the European Pliocene deposits of the Northern Apennine, Italy (Cigala Fulgosi 1986). *C. obscurus* has been recorded also in the Pleistocene sediments of the Leisey Shell Local Fauna, Florida (Scudder et al. 1995).

### **Carcharhinus perezii** (Poey, 1876)

Pl. 1, figs 16-17

1998 *Carcharhinus perezii* - Purdy, p. 133, pl. 2, fig. 1-2.

1999 *Carcharhinus perezii* - Antunes et al., p. 116, pl. 1, fig. 1-7.

2000 *Carcharhinus* cf. *perezii* - Sánchez-Villagra et al., pp. 959-961, fig. 7-8.

2001 *Carcharhinus perezii* - Purdy et al., p. 154, fig. 55b.

2004 *Carcharhinus* cf. *perezii* - Antunes & Balbino, p. 88, fig. 7d.

**Material.** 4 teeth examined: IGF14056 (1 tooth); IGF8757V (1 tooth); IGF8770V (1 tooth); IGF8785V (1 tooth).



**Description.** The upper teeth are characterized by a narrow and distally inclined cusps, with regularly serrated lateral cutting edges. The mesial cutting edge is convex to slightly straight. The distal cutting edge is vertical or slightly concave, and characterized by a shallow angular notch. Lateral to the cusp there are a mesial and distal coarse heel. The serrations on the heels is coarser than along the distal lateral margin. The labial side of the crown is flat, while the lingual one is convex. The root is high, and characterized by a shallow lingual axial groove. The basal margin of the root is concave.

**Remarks.** The upper teeth of *C. albimarginatus* may be separated from *C. perezii* because of the evident shallow notch along the mesial and distal cutting edges, the hooked tip of the cusps (Purdy et al. 2001), and because of the abrupt change in the size of the serrations along the lateral cutting edges (Long 1993a). The upper teeth of *C. brachyurus* can be separated from *C. perezii* because of the apical convexity or angle along the mesial cutting edge, and because of the cusps with a truncated aspect (Purdy et al. 2001). The teeth examined compare favourably with the Recent species (Purdy, pers. com. 2005), and with that published by Purdy (1998), Antunes et al. (1999), and Purdy et al. (2001). The teeth published by Schultz (1971, pl. 4, fig. 18) and by Cappetta (1973, pl. 12, fig. 41) as *Carcharhinus priscus*, and the teeth published by D'Erasmus (1951, pl. 2, fig. 5-8, 15-16) as *Sphyrna prisca*, are characterized by morphology similar to that of the Caribbean reef shark *C. perezii*, and so they may belong to this species.

According to Compagno (1984), *C. perezii* is the commonest shark associated with the Coral Reef of the Caribbean Sea. It is a tropical, inshore bottom dwelling inhabitant, and it feeds on bony fishes (Compagno 1984). This shark is not included in the Mediterranean fish fauna.

*C. perezii* has been recorded in the Miocene deposits of the Lee Creek Mine, North Carolina (Purdy et al. 2001), Pollack Farm Site, Delaware (Purdy 1998), northern Venezuela (Sánchez-Villagra et al. 2000) and Alvalade basin, Portugal (Antunes et al. 1999; Antunes & Balbino 2004). In the Pliocene deposits of the Lee Creek Mine, North Carolina (Purdy et al. 2001).

This can be considered the first record of *C. perezii* for the Mediterranean Pliocene deposits.

### ***Carcharhinus plumbeus* (Nardo, 1827)**

Pl. 1, figs 18-22; Pl. 2, figs 20-22

1951 *Carcharias (Prionodon) egertoni* - D'Erasmus, p. 59, pl. 2, fig. 58-63.

1995 *Carcharhinus plumbeus* - Scudder et al., p. 254.

1999 *Carcharhinus* cf. *plumbeus* - Antunes et al., p. 116.

2001 *Carcharhinus plumbeus* - Purdy et al., p.154, fig. 56.

2004 *Carcharhinus* cf. *plumbeus* - Antunes & Balbino, p. 88, fig. 7c.

**Material.** 17 teeth examined: IGF13975 (1 tooth); IGF8747V (1 tooth); IGF8753V (3 teeth); IGF8774V (6 teeth); IGF8786V (3 teeth); IGF8800V (1 tooth); Tav. n. 8bis (1 tooth); Tav. n. 8terzo (1 tooth).

**Description.** The upper teeth are characterized by a triangular shape and labial-lingual compressed crown, with regular serrated lateral cutting edges. One tooth is characterized by a coarser serrations with two cusplets at the base of the mesial cutting edge. The labial face is usually flat, while the lingual one is slightly convex, with sometime an evident neck-area between the crown-base and the root. The root is high, with a weakly lingual axial groove. The basal margin of the root is linear or slightly concave.

**Remarks.** The upper teeth of *C. plumbeus* are much thinner and labio-lingually compressed (Cappetta & Nolf 1991) than that of other carcharhinid sharks, such as *C. leucas*, *C. longimanus* or *C. obscurus*, and less elongated than that of *C. altimus* or *C. galapagensis*. Purdy et al. (2001: 154) described as useful characters to separate *C. plumbeus* from *C. albimarginatus*: (*C. albimarginatus*) "the tip of the teeth are hooked, and midway between the tip and the root on both cutting edges there is a noticeable shallow notch. After the seventh tooth from the symphysis, the mesial notch is lost".

According to Compagno (1984), *C. plumbeus* is a coastal-pelagic shark, that inhabits the inshore and offshore, temperate and tropical waters. It is primarily a predator on relatively small benthic fishes, molluscs and crustaceans (Compagno 1984). The sandbar shark is very common in the Mediterranean waters (Tortonese 1950; Garrick 1982; Compagno 1984; Notarbartolo di Sciara & Bianchi 1998), but rare in the Adriatic Sea (Notarbartolo di Sciara & Bianchi 1998).

*C. plumbeus* has been recorded in the American Miocene deposits of North Carolina (Purdy et al. 2001), in the European Miocene deposits of Portugal (Antunes et al. 1999; Antunes & Balbino 2004) and Libya (D'Erasmus 1951), and in the Pliocene deposits of the Lee Creek Mine, North Carolina (Purdy et al. 2001). *C. plumbeus* has been recorded also in the Pleistocene sediments of the Leisey Shell Local Fauna, Florida (Scudder et al. 1995).

This may be considered the first record of the sandbar shark *C. plumbeus* for the Mediterranean Pliocene deposits.

### ***Carcharhinus* sp.**

**Material.** Sixty three teeth: IGF14074 (5 teeth); IGF14087 (4 teeth); IGF14127 (3 teeth); IGF14128 (7 teeth); IGF8751V (3 teeth); IGF8759V (12 teeth); IGF8768V (7 teeth); IGF8775V (5 teeth); IGF8788V (7 teeth); IGF8798V (7 teeth); Tav. n. 8 (1 tooth); Tav. n. 13bis (1 tooth); Tav. n. 15 (1 tooth).

**Remarks.** Most of the teeth are incomplete. They lack the root or part of the crown. They are too much incomplete for a correct species attributions.

### Discussion

Most of the teeth examined (167 teeth) come from Orciano (Pisa Province) (Fig. 1), a locality included into the Tora-Fine Basin (Giannini 1962; Menesini 1977; Lazzarotto et al. 1990; Bossio et al. 1993, 1999). The Orciano hills are characterized by great thickness of Pliocene deposits belonging to the “Argille Azzurre” Formation (Giannini 1962; Menesini 1977; Bartoletti et al. 1986; Lazzarotto et al. 1990). Giannelli et al. (1982), based on a biostratigraphic analysis of the geological section along the Livorno-Collesalveti road (see also Lazzarotto et al. 1990), identified four biozones that characterized this Pliocene formation, the Early Pliocene *Sphaerodinellopsis seminulina* Zone, *Globorotaria margaritae* Zone, *G. puncticulata* Zone, and the Middle Pliocene *G. crassaformis* s.l. Zone (Giannelli et al. 1982; Lazzarotto et al. 1990). Five teeth come from San Frediano (Pisa Province) (Fig. 1). This locality is completely included into the Pliocene “Calcareniti e sabbie ad *Amphistegina*” Formation (Marroni et al. 1990). The record of *Globorotaria aemiliana* in these sediments, allowed to include it in the Middle Pliocene *Globorotaria crassaformis* s.l. Zone (see Bossio et al. 1981; Marroni et al. 1990). The other reviewed teeth come from Pliocene deposits near Volterra (Province of Pisa) (7 teeth), Siena (1 tooth) (Fig. 1), or other locality in the Pisa Province (43 teeth) without any more detailed information.

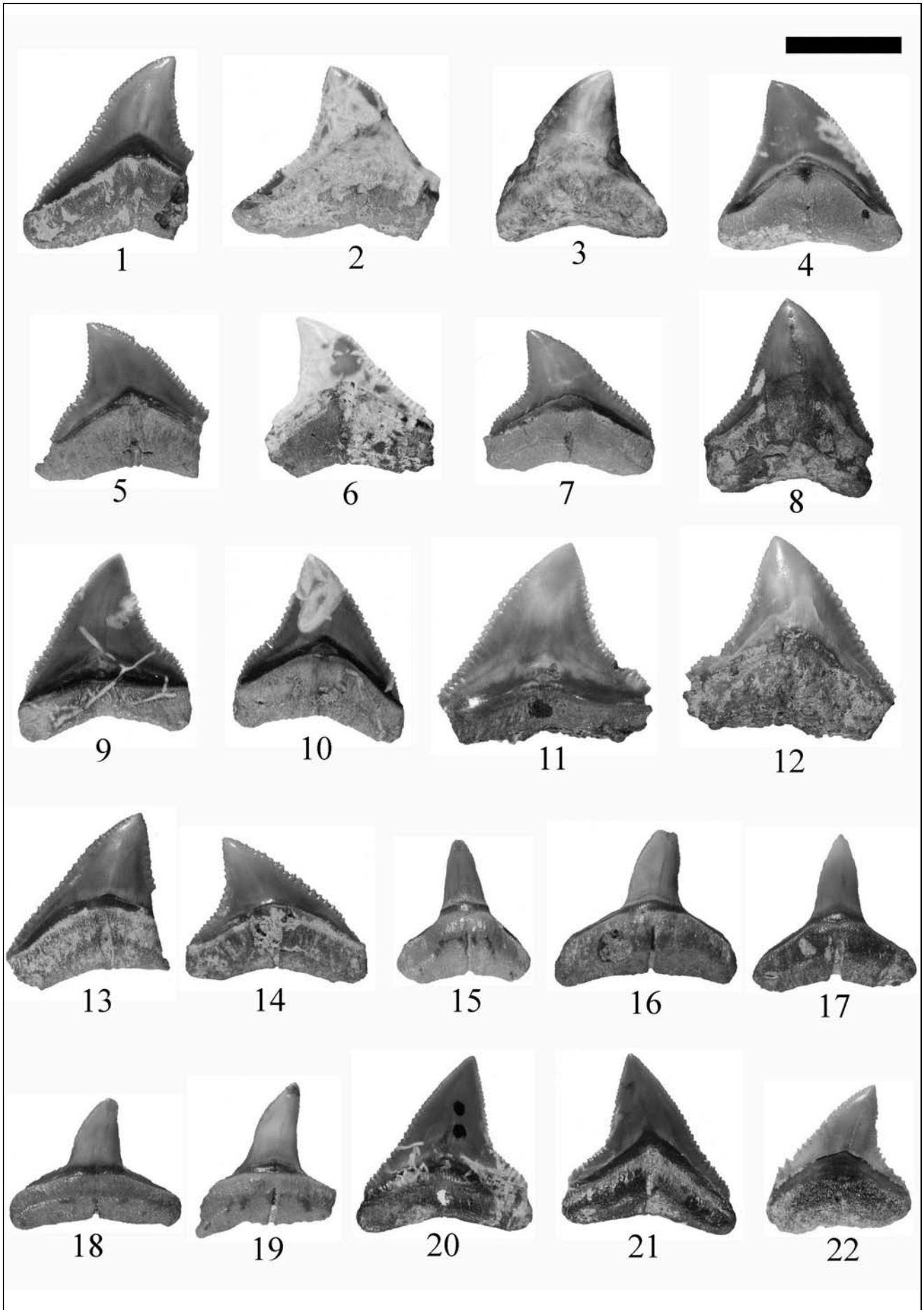
Seven species belonging to the genus *Carcharhinus* have been identified. *C. aff. brachyurus*, *C. falciformis*, *C. leucas*, *C. perezi* and *C. plumbeus* represent new species for the Mediterranean Pliocene sediments, while the presence of *C. obscurus* and *C. longimanus* corroborate the records of these sharks in the Mediterranean Pliocene sediments. In fact, *C. obscurus* was recorded for the first time by Cigala Fulgosi (1986) in the Pliocene sediments of the Northern Apennine, in Italy, while *C. longimanus* was recorded for the first time by Cappetta & Nolf (1991) in the Pliocene sediments of Le Puget-sur-Argens, in France. The most abundant species in the collections are *C. leucas* (15 teeth), *C. longimanus* (61 teeth), *C. obscurus* (11 teeth), and *C. plumbeus* (17 teeth), while the other taxa are represented by a few teeth, *C. brachyurus* (9 teeth), *C. falciformis* (4 teeth), and *C. perezi* (4 teeth).

Most of the teeth studied in this paper were included by Landini (1977, pl. 4, fig. 8-25) in *Carcharhinus egertoni*. This widespread carcharhinid fossil taxon, together with *C. priscus*, traditionally have character-

ized the Neogene Mediterranean shark fauna (Arambourg 1927; D’Erasmus 1951; Menesini 1968, 1974; Cappetta 1970, 1973; Landini 1977; Bellocchio et al. 1991; Mora Morote 1996), and also many European and American basins (Agassiz 1833-43, Leriche 1942; Schultz 1971, 1977; De Ceuster 1976; Longbottom 1979; Case 1980; Aguilera & De Aguilera 1984). The species identified from the Tuscany sediments give strength to the hypothesis that the *C. egertoni* may represent a “waste-basket species”, which included taxa characterized by strong tooth morphologies affinities (see also Cappetta & Nolf 1991). Long (1993a: 122), remarked that *C. egertoni* “...actually represents several species of Neogene carcharhinids with similar tooth morphologies, and I question its usefulness”. More recently, Purdy et al. (2001) have restudied the Agassiz’s syntypes of *Corax egertoni* (Agassiz, 1833-43, pl. 36,

### PLATE 2

- Fig. 1-7 - *Carcharbinus obscurus* (Lesueur, 1818). Fig. 1. IGF8748V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 2. IGF8754V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 3. IGF8773V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 4. IGF8783V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 5. IGF8754V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 6. IGF8783V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 7. IGF8773V; Orciano (Pisa); upper anterior-lateral tooth (lingual view).
- Fig. 8-19 - *Carcharbinus longimanus* (Poey, 1861). Fig. 8. IGF8792V; Bagnaia (Pisa); upper anterior-lateral tooth (lingual view). Fig. 9. IGF14068; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 10. IGF14068; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 11. IGF8746V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 12. IGF8746V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 13. IGF8792V; Bagnaia (Pisa); upper anterior-lateral tooth (lingual view). Fig. 14. IGF14058; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 15. IGF14059; Orciano (Pisa); lower anterior-lateral tooth (lingual view). Fig. 16. IGF8746V; Orciano (Pisa); lower anterior-lateral tooth (lingual view). Fig. 17. IGF14009; Orciano (Pisa); lower anterior-lateral tooth (lingual view). Fig. 18. IGF14129; Orciano (Pisa); lower anterior-lateral tooth (lingual view). Fig. 19. IGF14066; Orciano (Pisa); lower anterior-lateral tooth (lingual view).
- Fig. 20-22 - *Carcharbinus plumbeus* (Nardo, 1827). Fig. 20. IGF8774V; Orciano (Pisa); upper anterior-lateral tooth (labial view). Fig. 21. IGF8774V; Orciano (Pisa); upper anterior-lateral tooth (lingual view). Fig. 22. IGF8786V; Orciano (Pisa); upper anterior-lateral tooth (lingual view).
- Scale bars = 1 cm.



Species	Tropical	Subtropical	Warm-temperate	Temperate
<i>Carcharhinus brachyurus</i>		X	X	X
<i>Carcharhinus falciformis</i>	X	X	X	
<i>Carcharhinus leucas</i>	X	X		
<i>Carcharhinus longimanus</i>	X	X	X	
<i>Carcharhinus obscurus</i>	X	X	X	
<i>Carcharhinus perezi</i>	X			
<i>Carcharhinus plumbeus</i>	X	X	X	X

Tab. 1 - Recent climatic distribution of the identified *Carcharhinus* species.

fig. 6-7), and they have included them within the extant species *Carcharhinus brachyurus* (Agassiz, 1833-43, pl. 36, fig. 6) and *C. leucas* (Agassiz, 1833-43, pl. 36, fig. 7).

The carcharhinid sharks from the Tuscany are characterized by species of tropical to warm-temperate affinities (Tab. 1), with a latitudinal range between 43°N-43°S (Garrick 1982; Compagno 1984). *C. perezi* is the only shark with strong tropical affinities (see Tab. 1), while *C. brachyurus* is considered the only shark with a centre of abundance outside the tropics (Garrick 1982). *C. longimanus* commonly occurs in waters of 18°-28°C, but normally prefers temperature about 20°C (Bass et al. 1973; Garrick 1982; Compagno 1984). This carcharhinid shark is more abundant in the tropics from 20°N to 20°S (Compagno 1984). *C. leucas* has been recorded in waters with an average of 22,2°C in South Africa (Cliff & Dudley 1991), while *C. falciformis* commonly occurs in waters with 23°C-24°C range (Compagno 1984). The habitat and biology of these sharks, and in particular of *C. perezi*, infer an higher sea surface temperature for the Mediterranean during the Early-Middle Pliocene (see also Cigala Fulgosi & Mori 1979). This is in agreement with the benthic foraminifers, molluscs, pollen, geological and isotopic data (see also Thunell & Williams 1983; Sprovieri 1986; Fauquette et al. 1998, 1999; Haywood et al. 2000; Monegatti & Raffi 2001), that suggest a warmer (by 5°C), more humid (by 400-1000 mm/yr) and less seasonal climate than present for the Mediterranean basin during the Early Pliocene (Haywood et al. 2000).

Climatic changes, the establishment of an estuarine-type circulation in the Mediterranean (Benson 1975; van Harten 1984; Thunell et al. 1987; McKenzie et al. 1990; Cigala Fulgosi 1996), or changes in water circulation models, may have favoured different faunal interchanges between the Atlantic Ocean and the Mediterranean in the Early Pliocene. During this period the Mediterranean was characterized by a different fish community (Sorbini 1988; Landini & Sorbini 2005a,b), and it was inhabited by several shark species not included in its present fish fauna (Cigala Fulgosi & Mori 1979; Cigala Fulgosi 1986, 1996; Cappetta & Nolf 1991). Changes in paleobiogeographic distributions may be observed also for some species belonging to the genus *Carcharhinus* (Tab. 2). In particular, the Caribbean reef shark *C. perezi*, not included in the Mediterranean ba-

sin, commonly inhabits the Gulf of Mexico, the Caribbean Sea, and possibly the South-Western Atlantic coasts (Compagno 1984). The Miocene record of *C. perezi*, and the teeth described herein, emphasizes a much more widespread Neogene geographical distribution of this shark, including the North-Eastern Atlantic coasts and the Western Mediterranean Sea (Tab. 2). *C. longimanus* and *C. leucas*, widespread and recorded in all the tropical and subtropical seas (Bass et al. 1973; Garrick 1982, Compagno 1984), are considered doubtful in the Mediterranean Sea, where sporadically enter (Tortonese 1950; Garrick 1982; Compagno 1984; Notarbartolo di Sciara & Bianchi 1998). By contrast, their fossil record emphasized a wider distribution of these two sharks in the western part of the Mediterranean basin during the Neogene. In particular, *C. longimanus* has been recorded in the Pliocene sediments of Le Puyet-sur-Argens, in the South-East France (Cappetta & Nolf 1991), of Tuscany (Landini 1977; Manganelli & Spadini 2003), and of Alicante, in the South-East Spain (Mora Morote 1996). *C. leucas* has been recorded in the Miocene deposits of the Alvalade basin, Portugal (Antunes et al. 1999; Antunes & Balbino 2004), and of Malta (Menesini 1974), and in the Pliocene deposits of the Umbria region, Italy (Bellocchio et al. 1991).

The revision of the carcharhinid teeth from Tuscany introduce new top-predators in the Mediterranean basin, besides the well known sharks *Isurus oxrinchus*, *I. hastalis*, *I. xiphodon* (sensu Purdy et al. 2001), or *Carcharodon carcharias*. Sharks are at the top of every marine food-chains. They are primary fish-eaters, but they can also feed on different class of invertebrates or marine vertebrates. In particular, trophic interactions between sharks and cetaceans during the Pliocene have been reported by several authors (Deméré & Cerutti 1982; Cigala Fulgosi, 1990; Bianucci et al. 2000). Recently, Cigala Fulgosi (1990) described one of the best fossil documentation of a predation event or scavenging by a white shark *Carcharodon carcharias* on a complete skeleton of an odontocete, belonging to *Hemisyntrochelus cortesii* (Bianucci 1996). Some voracious species of the genus *Carcharhinus*, such as *C. obscurus*, *C. longimanus* or *C. leucas*, are considered as occasional or regular predators, or scavenging of cetaceans, in particular small Odontoceti (Heithaus 2001). However, predation events or scavenging by these sharks on marine mam-

Species	Mediterranean Sea		West Atlantic	East Atlantic	West Pacific	East Pacific	West Indian	East Indian
	Pliocene	Recent						
<i>Carcharhinus brachyurus</i>	X	X	X	X	X	X	X	
<i>Carcharhinus falciformis</i>	X	X	X	X	X	X	X	X
<i>Carcharhinus leucas</i>	X		X	X	X	X	X	X
<i>Carcharhinus longimanus</i>	X	?	X	X	X	X	X	X
<i>Carcharhinus obscurus</i>	X	X	X	X	X	X	X	X
<i>Carcharhinus perezi</i>	X		X					
<i>Carcharhinus plumbeus</i>	X	X	X	X	X	X	X	X

Tab. 2 - Recent geographic distribution of the identified *Carcharhinus* species.

mals can be only inferred by comparisons with the present data, because of no bite sign of *Carcharhinus* species have been still recorded in any cetacean skeleton.

### Conclusion

Six new shark belonging to the genus *Carcharhinus*, *C. brachyurus*, *C. falciformis*, *C. leucas*, *C. perezi* and *C. plumbeus*, have been described by the revision of the carcharhinid teeth from the early-middle Pliocene sediments of the Tuscany. Moreover, the presence of *C. longimanus* and *C. obscurus* in the collections, corroborate the record of these sharks in the Pliocene sediments of the Mediterranean Sea (Cigala Fulgosi 1986; Cappetta & Nolf 1991).

Paleoecologic and paleobiogeographic inferences have been based on the present geographical distribution, and strong tropical affinities of *C. perezi*, which represents the most interesting carcharhinid sharks identified.

Moreover, the species identified give strength to the hypothesis that one of the most common shark of the Pliocene sediments, *C. egertoni*, may represent a "wasted-basket species", that included several carchar-

hinid species characterized by a similar tooth morphologies (see Cappetta & Nolf 1991; Long 1993a).

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## APPENDIX (Catalogue numbers)

Teeth housed in the "Museo di Storia Naturale, Sezione di Geologia e Paleontologia" of the University of Firenze [published as *Carcharhinus egyptoni* by Landini (1977)]: *Carcharhinus brachyurus*: IGF8750V (1 tooth); IGF8752V (1 tooth); IGF8761 (1 tooth); IGF8787V (1 tooth); IGF8790V (1 tooth); IGF8799V (1 tooth); IGF13991 (1 tooth). *Carcharhinus falciformis*: IGF8756V (2 teeth); IGF8776V (1 tooth); IGF8791V (1 tooth). *Carcharhinus leucas*: IGF8749V (2 teeth); IGF8755V (1 tooth); IGF8772V (1 tooth); IGF8784V (2 teeth); IGF8794V (1 tooth); IGF13976 (3 teeth). *Carcharhinus longimanus*: IGF13975 (5 teeth); IGF13976 (2 teeth); ●IGF14009 (2 teeth); ●IGF14053 (1 tooth); IGF14058 (1 tooth); ●IGF14059 (1 tooth); ●IGF14060 (2 teeth); ●IGF14066 (1 tooth); ●IGF14068 (2 teeth); IGF14104 (4 teeth); IGF14107 (1 tooth); ●IGF14129 (2 teeth); IGF14132 (1 tooth); IGF8746V (3 teeth); IGF8758V (2 teeth); IGF8762V (4 teeth); IGF8767V (2 teeth); IGF8777V (1 tooth); IGF8782V (3 teeth); IGF8792V (3 teeth). *Carcharhinus obscurus*: IGF8748V (1 tooth); IGF8754V (2 teeth); IGF8773V (3 teeth); IGF8783V (3 teeth); IGF8793V (1 tooth). *Carcharhinus perezii*: IGF14056 (1 tooth); IGF8757V (1 tooth); ●IGF8770V (1 tooth); IGF8785V (1 tooth). *Carcharhinus plumbeus*: IGF13975 (1 tooth); IGF8747V (1 tooth); IGF8753V (3 teeth); IGF8774V (6 teeth); IGF8786V (3 teeth); IGF8800V (1 tooth). *Carcharhinus* sp.: IGF14074 (5 teeth); IGF14087 (4 teeth); IGF14127 (3 teeth); IGF14128 (7 teeth); IGF8751V (3 teeth); IGF8759V (12 teeth); IGF8768V (7 teeth); IGF8775V (5 teeth); IGF8788V (7 teeth); IGF8798V (7 teeth). *Isurus oxyrinchus*: IGF14009 (31 teeth); IGF8765V (1 tooth); IGF8778V (1 tooth). *Isurus* aff. *xiphodon*: IGF14009 (1 tooth). *Galeorhinus galeus*: IGF8766V (1 tooth). *Sphyrna zygaena*: IGF8779V (1 tooth); IGF8795V (1 tooth); IGF8897V (1 tooth). *Sphyrna* sp. IGF8763V (1 tooth); *Galeocerdo cuvieri*: IGF8780V (1 tooth); IGF8745V (1 tooth). *Prionace glauca*: IGF8744V (1 tooth); IGF8760V (1 tooth); IGF8765V (12 teeth); IGF8781V (1 tooth); IGF8789V (1 tooth); IGF8796V (1 tooth). cf. *Lophius*: IGF8771V (1 tooth). Not identify: IGF8764V (3 teeth).

Teeth housed in the "Museo di Storia Naturale e del Territorio" of the University of Pisa: *Carcharhinus brachyurus*: I12967 (1 tooth). *Sphyrna zygaena*: I13236.

Teeth housed in the "Museo di Geologia e Paleontologia G. Capellini" of the University of Bologna (no catalogue numbers): *Carcharhinus brachyurus*: Tav. n. 15bis (1 tooth). *Carcharhinus leucas*: Tav. n. 8 (3 teeth); Tav. n. 8terzo (2 teeth). *Carcharhinus longimanus*: Tav. n. 8 (2 teeth); Tav. n. 8bis (3 teeth); Tav. n. 8terzo (4 teeth); Tav. n. 13bis (3 teeth); Tav. n. 15bis (2 teeth); Tav. n. 17 (1 tooth); Tav. n. 17bis (1 tooth); Tav. n. 18 (2 teeth). *Carcharhinus obscurus*: Tav. n. 9 (1 tooth). *Carcharhinus plumbeus*: Tav. n. 8bis (1 tooth); Tav. n. 8terzo (1 tooth). *Carcharhinus* sp.: Tav. n. 8 (1 tooth); Tav. n. 13bis (1 tooth); Tav. n. 15 (1 tooth). *Sphyrna zygaena*: Tav. n. 13 bis (1 tooth). *Prionace glauca*: Tav. n. 15 (4 teeth); Tav. n. 15bis (3 teeth).

