Tooth row counts, vicariance, and the distribution of the sand tiger shark *Carcharias taurus*

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Geographic variation in tooth row counts among sand tiger sharks *Carcharias taurus* (Chondrichthyes), from the SW Atlantic, NW Atlantic and the East China Sea is analyzed in this paper. We found significant differences between sand tigers from the SW Atlantic (Southern Hemisphere population) and each of the other two (Northern Hemisphere) regions in the number of upper lateral tooth rows, and between individuals from the SW Atlantic and the East China Sea in the total number of upper tooth rows. Sand tiger sharks from the two Northern Hemisphere populations did not differ in any of the studied variables. Our results agree with comparisons of vertebral counts between sand tiger sharks from Southern and Northern Hemispheres. Both lines of evidence suggest that Southern and Northern Hemisphere populations of *C. taurus* were isolated to a larger extent than populations of the Northern Hemisphere. The fossil record of the genus *Carcharias* begins in the Early Cretaceous and *C. taurus* is certainly known since the Late Miocene. During the Miocene, the Tethys Sea separating northern and southern land masses was still present and it provided a continuous temperate shallow sea that could allow dispersal of sand tiger sharks along Northern Hemisphere seas. Independent observations on the distribution and evolutionary history of the genera *Myripristis*, *Neoniphon*, *Sargocentron* and *Aphanus*, and genetic studies on the temperate shark genus *Mustelus* that indicate a close relationship between the Indo-Pacific *M. manazo* and the Mediterranean *M. asterias* suggest that this hypothesis is plausible and deserves to be tested.

The origin of disjunct geographic distributions is often difficult to explain. Usually they are the result of historical and ecological processes operating together to produce the observed pattern (Ridley 1993). Barriers (others than land) and continuities are more difficult to locate in the marine environment than on the land (Norris 2000). Hence, most examples of disjunct distributions due to vicariance come either from terrestrial or freshwater organisms. Examples include characid fishes splitted when Gondwana broke up (Hellman et al. 1997) as well as exchanges of fauna through the Bering land bridge and the Great American Biotic Interchange (Marshall 1988, Cione and Tonni 1995).

Disjunct distributions are common in the marine environment and there are several examples among sharks. Reif and Saure (1987) attempted to explain major patterns of shark distribution, offering a vicariance hypothesis to explain the disjunct distribution patterns of the genera *Lamna* Cuvier and *Somniosus* Le Sueur. They stated that vicariance could have played a

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role in the evolutionary history of Notorynchus cepedianus (Péron), Cetorhinus maximus (Gunnerus) and Squalus acanthias Linnaeus. The geographic distribution of Sphyra tiburo (Linnaeus) with populations to each side of the Isthmus of Panama, and of Ginglymostoma cirratum (Bonnaterre) with populations at both sides of the tropical Atlantic and Central America, have been interpreted as a result of vicariance events due to the elevation of Central America and the widening of the Atlantic Ocean (Dingerkus 1992). Among marine batoids, the origin of the extant Antarctic fauna has been suggested to be a result of the cooling and isolation of Antarctica (Long 1994). Thus, vicariance hypotheses have been proposed to explain the distribution patterns of several elasmobranch taxa.

The sand tiger shark Carcharias taurus Rafinesque (Chondrichthyes, Lamniformes), is a large (up to 318 cm total length) predator with a disjunct distribution in most of the warm temperate seas of the world, with an exception of the eastern Pacific (Fig. 1, Last and Stevens 1994, Compagno 2001). This species is restricted to coastal waters and it moves northwards and southwards depending on season (Compagno 2001, Lucifora et al. 2002) and reproductive stage (Gilmore 1993, Lucifora et al. 2002). Where the movements are known, they are highly predictable with few or no individual moving beyond the local range of the species (see tagging results by Kohler et al. 1998). In addition, different populations of sand tiger sharks are separated among them by wide and deep oceanic basins. These characteristics suggest that little or no gene flow exist between several of the known extant populations of C. taurus.

Carcharias taurus has, in general, long, narrow teeth well adapted for puncturing and grasping fish prey (Bigelow and Schroeder 1948, Springer 1961). The dentition of C. taurus is highly differentiated into several tooth types, namely upper and lower anterior, lower symphysial, upper intermediate, upper and lower lateral, and upper and lower posterior teeth (Fig. 2, Applegate 1965, Sadowsky 1970, Taniuchi 1970, Gomes and Fernandes dos Reis 1990, Compagno 2001, Lucifora et al. 2001). Based on tooth row homology, posterior tooth rows should be treated as lateral tooth rows, and intermediate, anterior, and symphysial are not truly homologous tooth rows (Shimada 2002). Tooth row counts vary in C. taurus, but this variation has been regarded as individual variability within one widespread species (Sadowsky 1970, Taniuchi 1970). In this paper, we analyze variations in tooth counts among three separate populations of sand tiger sharks, and we show that dental variation can be explained by vicariance events.

Methods

Meristic dental variables were compared among sand tiger sharks from three widely separated regions (Fig. 1): Southwest Atlantic (35°–40°S, Argentina), Northwest Atlantic (38°–40°N, U.S. Atlantic coast), and East China Sea (27°–29°N). We examined 19 jaws from

![Fig. 1. Geographic distribution (grey areas) of the sand tiger shark Carcharias taurus. Black areas and arrows indicate the three regions from which dental samples were analysed. ECS: East China Sea, NWA: Northwest Atlantic, SWA: Southwest Atlantic.](image)
sand tiger sharks caught by commercial fishermen off the Province of Buenos Aires, Argentina (SW Atlantic samples). Dental data from the NW Atlantic (n = 12) and the East China Sea (n = 23) were taken from Applegate (1965) and Taniuchi (1970), respectively. Jaws from SW Atlantic sharks were obtained when already excised from the sharks, and then size and sex could not be recorded. However, we estimated that the size of sampled sand tiger sharks were between 143 and 281 cm total length (TL), according to the regression equation between the largest lower anterior tooth (LAT) and TL presented by Shimada (1999) (i.e. TL(cm) = 10.189 × LAT(mm) – 14.28). Sharks from the SW Atlantic were between 112 and 273 cm TL (Applegate 1965) and those from the East China Sea were between 95 and 300 cm TL (Taniuchi 1970). Then specimens from all three regions were in about the same TL range. Sex could not be determined for sharks from the SW and NW Atlantic. Thus there is the implicit assumption in the analyses that there are not sex-related variations in tooth counts.

The tooth terminology used throughout the paper is that proposed by Shimada (2002), then lateral teeth refer to the lateral + posterior teeth of Applegate (1965). Tooth rows were identified as defined by Shimada (2002), i.e. each tooth row contains several individual teeth from the lingual to the labial part of the jaw. This is equivalent to the tooth families of Reif (1984). We evaluated differences in the following variables: 1) total upper tooth row count, 2) total lower tooth row count, 3) number of upper and 4) lower lateral tooth rows, and 5) number of lateral cusplets on each tooth. Thus, all comparisons were made between homologous tooth rows (sensu Shimada 2002). All counts include both right and left tooth rows. Meristic variables were preferred to morphometric ones because data from the three populations were taken by different authors in different years, and meristic counts appear to be less prone to sampling bias than morphometric measurements. In all cases, the statistical test performed was the non-parametric Kruskal-Wallis (Zar 1984), with an exception for the number of lateral cusplets (variable 5), which was assessed by means of the χ² test. When statistically significant differences were found, a non-parametric multiple comparisons test (Conover 1980) was performed in order to locate the differences.

**Results**

We detected significant differences in the total number of upper tooth rows and the number of upper lateral tooth rows ($\chi^2 = 10.69$, DF = 2, $p = 0.0048$ and $\chi^2 = 9.98$, DF = 2, $p = 0.0068$, respectively; Fig. 3). The total number of upper tooth rows was significantly different between sand tiger sharks from the SW Atlantic and the East China Sea (multiple comparisons test, $t = 15.98$, DF = 51, $p < 0.05$). Sand tiger sharks from the SW Atlantic differed from those from the East China Sea and the NW Atlantic in the number of upper lateral tooth rows ($t = 17.46$, DF = 51, $p < 0.001$; and $t = 11.54$, DF = 51, $p < 0.025$, respectively). No significant differences were found between sand tiger sharks from East China Sea and the NW Atlantic for any variable. No statistical differences were detected in the total number of lower tooth rows ($\chi^2 = 1.13$, DF = 2, $p = 0.57$), number of lower lateral tooth rows ($\chi^2 =$...
Fig. 4. World map of Middle Miocene. Dotted areas indicate the possible geographic distribution of sand tiger sharks _Carcharias taurus_. Ar: Arabian Peninsula, Au: Australia, G: Greenland, NA: North America, NE: North Europe, SA: South America.

Discussion

Two major factors, the ecological characteristics of the species and its history, interact to define the geographic distribution of a species and the degree of isolation of its populations (Brown et al. 1996). It is common that different populations of a given elasmobranch species differ in morphology (e.g. Templeman 1984), color pattern (e.g. Ebert 1985) and/or life history parameters such as size at maturity, fecundity (Menni 1985, Taniuchi et al. 1993), growth rate and age at maturity (Branstetter et al. 1987). This differentiation is very common in coastal species, including _Carcharias taurus_, which usually lives at depths <20 m (Compagno 2001). _Carcharias taurus_ is mainly a temperate shark, although it can occur sporadically in tropical areas (Last and Stevens 1994, Compagno 2001). In most areas where it occurs, equatorial waters are effective barriers separating populations from both hemispheres. For example in the western Atlantic, they are not recorded from Florida to Rio de Janeiro, and they are not recorded in the eastern coast of Africa (Compagno 2001). The ecological characteristics of _C. taurus_ prevent a steady gene flow between populations of both hemispheres, even when shallow (though equatorial) coastal habitats connecting them are present. This isolation hypothesis is supported by tagging experiments where all the individuals recaptured in the NW Atlantic had been tagged in the same region and did not travel across tropical areas (Kohler et al. 1998).

The genus _Carcharias_ has a long fossil record. It has been recorded since the Early Cretaceous (Cappetta 1987, Biddle 1993, Siverson 1997) and many fossil species of _Carcharias_ have been reported from younger strata. The recent species _C. taurus_ has been reported from the Middle Miocene of Portugal (Antunes and Jonet 1970), the Miocene of Australia (Kemp 1991), and the Paleocene (an isolated case; Cvancara and Hoganson 1993), Miocene and Pliocene of the eastern United States (Purdy et al. 2001). However, some of these (and additional) records should be revised (Cione 1988). One of us (ALC) is presently studying the Miocene records of _Carcharias_ from Argentina and we consider that the Paleocene record does not correspond to _C. taurus_. The present evidence indicates that _C. taurus_ appeared during the Late Miocene and perhaps the Middle Miocene.

During the Miocene, there still was a connection between the Mediterranean and the Indian Ocean (Cigala-Fulgosi and Mori 1979, Scotese et al. 1987, Smith et al. 1994). Apparently, it lasted until the Messinean crisis ca 6 Ma (Cornée et al. 2002). After the Messinean, there was apparently no seaway between the Mediterranean and the Indian Ocean (Cornée pers. comm.). For example, no Indian fish was reported from Pliocene and Pleistocene fauna at Vrica, southern Italy (Landini and Menesini 1978). This remnant of the Tethys Sea was included in a large warm temperate region that also included the northern Indian Ocean and the entire North Atlantic from Iceland to Florida and southern Morocco. This continuous shallow warm temperate habitat may have made possible a flux between populations of western and eastern extremes of the Northern Hemisphere (Fig. 4). At present, there is evidence indicating the occurrence of unstructured populations of large coastal sharks covering large geographic regions, provided that suitable habitats connecting the extremes are available (e.g. _Negaprion brevirostris_ [Poey] in the western Atlantic from Florida to Brazil: Feldheim et al. 2001).

Southern Hemisphere Miocene populations of _C. taurus_ could be isolated from Northern Hemisphere ones by a tropical belt along the equatorial region (Fig. 4). This is in accordance with the absence of _Carcharias_ from equatorial Miocene units such as the Pirabas...
Formation from Brazil (Santos and Travassos 1960) and Gatán Formation from Panama (Gillette 1984). During the cold periods of glacial cycles in the late Pleistocene, tropical areas shrunk (Crowley and North 1991) and one or more migration events could have taken place between North American and South American C. taurus populations. However, it seems that gene flow was not strong enough to elicit tooth differences. During the interglacial times (the last event ca 120 000 yr ago; Servant 2001), when temperature was higher than present in the Northern Atlantic (and other areas, Kerr 1993), some gene flow could have perhaps occurred between North American and European populations through the North Atlantic.

Thus, ecological and historical factors may account for the observed pattern of tooth row count variation, in which Northern Hemisphere populations do not differ in tooth row counts but they are significantly different from the studied Southern Hemisphere populations. Our hypothesis is in accordance with differences in vertebral counts between populations of C. taurus from Northern and Southern Hemispheres. The number of vertebrae differs between South African and Northeastern Atlantic sand tigers, but there are no differences between South African and South American individuals (Bass et al. 1975). Historical factors also suggest that Southern Hemisphere populations may have been isolated for a longer time period than Northern Hemisphere ones (Fig. 4).

Several lines of evidence, obtained independently for several warm temperate coastal fish taxa, support our hypothesis. The teleost genera Myripristis Cuvier, Neoniphon Castelnau, and Sargocentron Fowler (Teleostei, Holocentridae) have a geographical distribution in the Indo-West Pacific and in the Atlantic Ocean. This pattern has been interpreted by Kotlyar (1998) as the result of the splitting of a wider ancient (Miocene) distribution by the closure of the Tethys Sea. Species of the genus Aphanius Nardo (Teleostei, Cyprinodontidae) are distributed in brackish and freshwater along coastal areas of the entire Mediterranean, Arabian Peninsula, Iran, and the Persian Gulf (Hrbeck and Meyer 2003). Recent cladistic analyses showed that the phylogenetic pattern of Aphanius spp., which consists of two main clades (one for Mediterranean species and one for Arabian and Persian species) is consistent with the closure of the Tethys Sea (Hrbeck and Meyer 2003). A Tethys-Sea connection of the eastern and western extremes of Northern Hemisphere temperate shark populations has also been recently supported by mitochondrial DNA comparisons of Indo-Pacific and Mediterranean species of the shark genus Mustelus Linck (Cigala-Fulgosi et al. 2000). The evidence shows that the Mediterranean species M. asterias Cloquet was much more similar to the Indo-Pacific M. manazo Bleeker than to the sympatric M. punctulatus Risso and M. mustelus (L.) (Cigala-Fulgosi et al. 2000). When the number of nucleotide substitutions in the cytochrome b gene is used to estimate the time of divergence between M. asterias and M. manazo it is concluded that the divergence was at the time of the closure of the connection between the Mediterranean and Indian Ocean (Cigala-Fulgosi et al. 2000). The results presented here can be tested as a working hypothesis through genetic and morphological analyses of extant populations of C. taurus.

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