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

Luis O. Lucifora, Alberto L. Cione, Roberto C. Menni and Alicia H. Escalante

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 *Aphanius*, 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.

L. O. Lucifora (lolucif@mdp.edu.ar), Inst. Nacional de Investigación y Desarrollo Pesquero, Casilla de Correo 82, Correo Central, Mar del Plata 7600, Argentina. – A. L. Cione, Museo de La Plata, Dept Científico Paleontología Vertebrados, Paseo del Bosque s/n, La Plata 1900, Argentina. – R. C. Menni, Dept Científico Zoología Vertebrados, Paseo del Bosque s/n, La Plata 1900, Argentina. – A. H. Escalante, Univ. Nacional de Mar del Plata, Dept de Biología, Funes 3250 3er. Piso, Mar del Plata 7600, Argentina.

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 characoid fishes splitted when Gondwana broke up (Helfman 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

role in the evolutionary history of *Notorynchus cepedianus* (Péron), *Cetorhinus maximus* (Gunnerus) and *Squalus acanthias* Linnaeus. The geographic distribution of *Sphyrna 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 symphysials 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
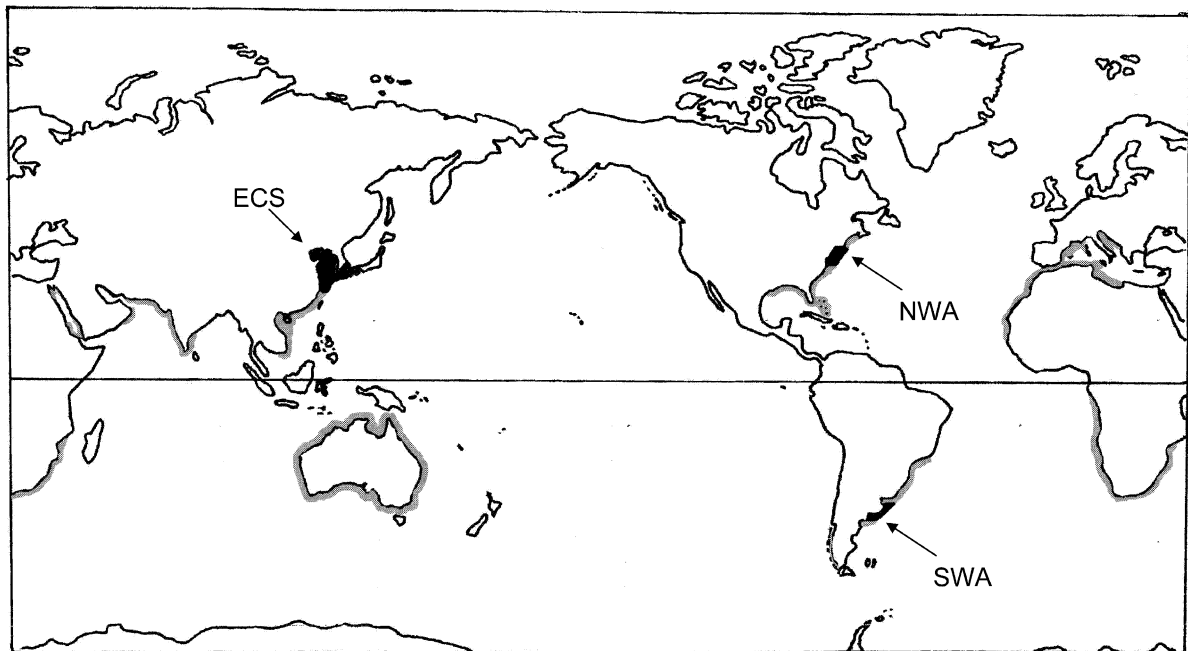

Fig. 1. Geographic distribution (grey areas) of the sand tiger shark *Carcharias taurus*. Black areas and arrows indicate the three regions from which dental samples were analysed. ECS: East China Sea, NWA: Northwest Atlantic, SWA: Southwest Atlantic.
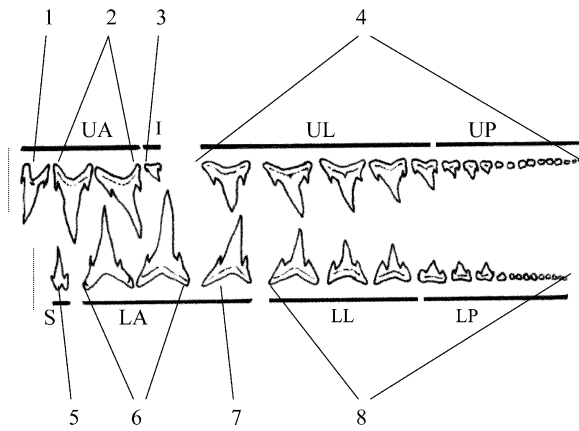
Fig. 2. Labial view of the left side of the dentition of a sand tiger shark *Carcharias taurus*. Bold lines and letters show the traditional tooth types recognized for this species. Numbers denote the tooth types as used in this study based on homology. UA: upper anterior tooth rows, I: intermediate tooth rows, UL: upper lateral tooth rows, UP: upper posterior tooth rows, S: symphysial tooth rows, LA: lower anterior tooth rows, LL: lower lateral tooth rows, LP: lower posterior tooth rows, 1: upper symphysial tooth rows, 2: upper anterior tooth rows, 3: upper intermediate tooth rows, 4: upper lateral tooth rows, 5: lower symphysial tooth rows, 6: lower anterior tooth rows, 7: lower intermediate tooth rows, 8: lower lateral tooth rows. The dotted vertical lines show the position of the upper and lower symphysis.

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 NW 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 χ^2 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 ($\chi^2 =$
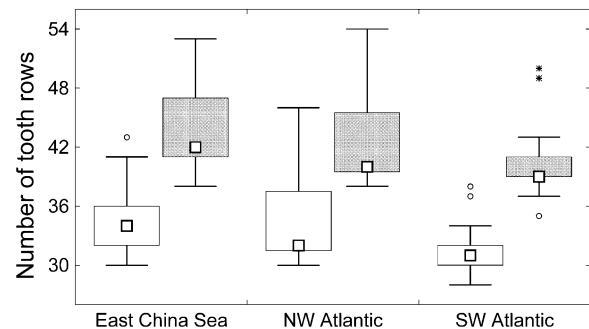

Fig. 3. Distributions of the total number of upper tooth rows (shaded boxes), and number of upper lateral tooth rows (empty boxes) of sand tiger sharks *Carcharias taurus*, from three different regions. Squares within boxes are median values, boxes enclose cases falling within the 25th and 75th percentile, whiskers limit the range of non-outlier minimum and maximum values, circles depict outliers, and asterisks are extreme values.
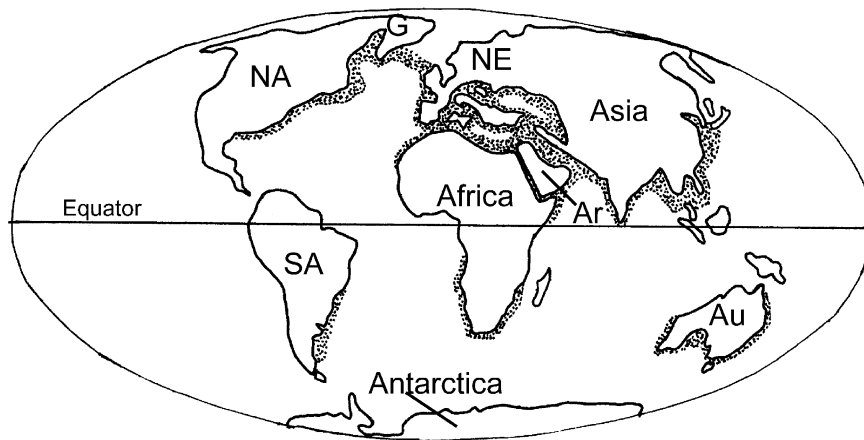
Fig. 4. World map of Middle Miocene. Dotted areas indicate the possible geographic distribution of sand tiger sharks *Carcharias taurus*. Ar: Arabian Peninsula, Au: Australia, G: Greenland, NA: North America, NE: North Europe, SA: South America.

1.13, DF = 2, p = 0.57) and number of lateral cusplets on each tooth (corrected $\chi^2 = 0.17$, DF = 1, n = 43, p > 0.05).

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 os 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 Gatún Formation from Panama (Gillette 1984). During the cold periods of glacial cycles in the late Pleistocene, tropical areas shrinked (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 as 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 population. 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 (Hrbek 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 (Hrbek 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*.

References

Antunes, M. T. and Jonet, S. 1970. Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. – Rev. Fac. Ciênc. Lisboa 16: 119–280.

Applegate, S. P. 1965. Tooth terminology and variation in sharks with special reference to the sand shark, *Carcharias taurus* Rafinesque. – L. An. Cty. Mus. Contr. Sci. 86: 3–18.

Bass, A. J., D'Aubrey, J. D. and Kistnasamy, N. 1975. Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. – Investl. Rep. Oceanogr. Res. Inst. Durban 39: 1–102.

Biddle, J. P. 1993. Liste des élasmobranches du Crétacé inférieur du bassin de Paris. – Cossmanniana 2: 49–51.

Bigelow, H. B. and Schroeder, W. C. 1948. Sharks. – In: Tee Van, J. et al. (eds), Fishes of the Western North Atlantic. Mem. Sears Found. Mar. Res. 1. Yale Univ, pp. 59–546.

Branstetter, S., Musick, J. A. and Colvocoresses, J. A. 1987. A comparison of the age and growth of the tiger shark, *Galeocerdo cuvieri*, from off Virginia and from the northwestern Gulf of Mexico. – Fish. Bull. 85: 269–279.

Brown, J. H., Stevens, G. C. and Kaufman, D. M. 1996. The geographic range: size, shape, boundaries, and internal structure. – Annu. Rev. Ecol. Syst. 27: 597–623.

Cappetta, H. 1987. Handbook of Paleoichthyology. Vol. 3B. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. – Gustav Fischer.

Cigala-Fulgosi, F. and Mori, D. 1979. Osservazioni tassonomiche sul genere *Galeocerdo* (Selachii, Carcharhinidae) con particolare riferimento a *Galeocerdo cuvieri* (Péron & Lesueur) nel Pliocene del Mediterraneo. – Boll. Soc. Paleont. Ital. 18: 117–152.

Cigala-Fulgosi, F. et al. 2000. Evidence of interspecific low mitochondrial divergence between *Mustelus asterias* and *M. manazo* (Chondrichthyes, Triakidae). – Biol. Mar. Medit. 7: 440–443.

Cione, A. L. 1988. Los peces de las formaciones marinas del Cenozoico de Argentina. – Ph.D. thesis, Univ. Nac. La Plata.

Cione, A. L. and Tonni, E. P. 1995. Chronostratigraphy and "land-mammal ages" in the Cenozoic of southern South America: principles, practices, and the "Uquian" problem. – J. Paleontol. 69: 135–159.

Compagno, L. J. V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Vol. 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). – FAO Sp. Cat. Fish. Purposes 1: 1–269.

Conover, W. J. 1980. Practical Nonparametric Statistics, 2nd ed. – Wiley.

Cornée, J. J. et al. 2002. Messinian events: new constraints from sedimentological investigations and new $^{40}Ar/^{39}Ar$ ages in the Melilla-Nador Basin (Morocco). – Sedim. Geol. 151: 127–147.

Crowley, T. and North, G. 1991. Paleoclimatology. – Oxford Univ. Press.

Cvancara, A. L. and Hoganson, J. W. 1993. Vertebrates of the Cannonball Formation (Paleocene) in North and South Dakota. – J. Vert. Paleont. 13: 1–23.

Dingerkus, G. 1992. La distribución de los tiburones. – In: Stevens, J. D. (ed.), Tiburones. Plaza y Janes-Tusquets-Museu de la Ciència., pp. 36–47, Spanish translation.

Ebert, D. A. 1985. Color variation in the sevengill shark, *Notorynchus maculatus* Ayres, along the California coast. – Calif. Fish and Game 71: 58–59.

Feldheim, K. A., Gruber, S. H. and Ashley, M. V. 2001. Population genetic structure of the lemon shark (*Negaprion brevirostris*) in the western Atlantic: DNA microsatellite variation. – Mol. Ecol. 10: 295–303.

Gillette, D. 1984. A marine ichthyofauna from the Miocene of Panama, and the Tertiary Caribbean faunal province. – J. Vert. Paleont. 4: 172–196.

Gilmore, R. G. 1993. Reproductive biology of lamnoid sharks. – Environ. Biol. Fish. 38: 95–114.

Gomes, U. L. and Fernandes dos Reis, M. A. 1990. Observações sobre a heterodontia onteogenética em *Eugomphodus taurus* (Rafinesque, 1809) – (Lamniformes, Odontaspididae). – An. Soc. Nordest. Zool. 3: 315–330.

Helfman, G. S., Collette, B. B. and Facey, D. E. 1997. The diversity of fishes. – Blackwell.

Hrbek, T. and Meyer, A. 2003. Closing of the Tethys Sea and the phylogeny of Eurasian killifishes (Cyprinodontiformes: Cyprinodontidae). – J. Evol. Biol. 16: 17–36.

Kemp, N. R. 1991. Chondrichthyans in the Cretaceous and Tertiary of Australia. – In: Vickers-Rich, P. et al. (eds), Vertebrate paleontology of Australasia. Monash Univ. Publ., pp. 497–568.

Kerr, R. 1993. The greatest extinction gets greater. – Science 262: 1370–1371.

Kohler, N. E., Casey, J. G. and Turner, P. A. 1998. NMFS cooperative shark tagging program, 1962–93: an atlas of shark tag and recapture data. – Mar. Fish. Rev. 60: 1–87.

Kotlyar, A. N. 1998. Species composition and distribution of holocentrids in the oceans of the world (Holocentridae, Beryciformes). – J. Ichthyol. 38: 170–189.

Landini, W. and Menesini, E. 1978. L'ittiofauna plio-pleistocenica della sezione della Vrica (Crotone-Calabria). – Boll. Soc. Paleont. Ital. 17: 143–175.

Last, P. R. and Stevens, J. D. 1994. Sharks and rays of Australia. – CSIRO.

Long, D. J. 1994. Quaternary colonization or Paleogene persistence?: historical biogeography of skates (Chondrichthyes: Rajidae) in the Antarctic ichthyofauna. – Paleobiology 20: 215–228.

Lucifora, L. O., Menni, R. C. and Escalante, A. H. 2001. Analysis of dental insertion angles in the sand tiger shark, *Carcharias taurus* (Chondrichthyes: Lamniformes). – Cybium 25: 23–31.

Lucifora, L. O., Menni, R. C. and Escalante, A. H. 2002. Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. – ICES J. Mar. Sci. 59: 553–561.

Marshall, L. G. 1988. Land mammals and the Great American Interchange. – Am. Sci. 76: 380–388.

Menni, R.C. 1985. Distribución y biología de *Squalus acanthias*, *Mustelus schmitti* y *Galeorhinus vitaminicus* en el Mar Argentino en agosto-setiembre de 1978 (Chondrichthyes). – Rev. Mus. La Plata (N. S.), Sec. Zool. 13: 151–182.

Norris, R. D. 2000. Pelagic species diversity, biogeography, and evolution. – In: Erwin, D. H. and Wing, S. L. (eds), Deep time, paleobiologys perspective. Paleobiology 26 (Suppl.): 236–258.

Purdy, R. et al. 2001. The Neogene sharks, rays and bony fishes from Lee Creek Mine, Aurora, North Carolina. – Smith. Contrib. Paleobiol. 90: 71–201.

Reif, W.-E. 1984. Pattern regulation in shark dentitions. – In: Malacinski, G. M. and Bryant, S. V. (eds), Pattern formation: a primer in developmental biology. Macmillan, pp. 603–621.

Reif, W.-E. and Saure, C. 1987. Shark biogeography: vicariance is not even half the story. – N. Jb. Geol. Paläont. Abh. 175: 1–17.

Ridley, M. 1993. Evolution. – Blackwell.

Sadowsky, V. 1970. On the dentition of the sand shark, *Odontaspis taurus*, from the vicinity of Cananéia, Brazil. – Bol. Inst. Oceanogr. São Paulo 18: 37–44.

Santos, R. S. and Travassos, H. 1960. Contribuição à paleontologia do Estado do Pará. Peixes fósseis da Formação Pirabas. – Monogr. Div. Geol. Mineral. 16: 1–35.

Scotese, C. et al. 1987. Atlas of Phanerozoic plate tectonic reconstructions. – Paleoceanographic Mapping Project, Inst. for Geophysics, Univ. Texas.

Servant, J. 2001. The 100 kyr cycle of deglaciation during the last 450 kyr: a new interpretation of oceanic and ice core data. – Global Planet. Change 29: 121–123.

Shimada, K. 1999. Dentition of lamniform sharks: homology, phylogeny, and paleontology. – Ph.D. thesis, Univ. Illinois at Chicago.

Shimada, K. 2002. Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). – J. Morphol. 251: 38–72.

Siverson, M. 1997. Sharks from the Mid-Cretaceous Gearle Siltstone, southern Carnarvon Basin, Western Australia. – J. Vert. Paleont. 17: 453–465.

Smith, A. G., Smith, D. G. and Funnell, B. M. 1994. Atlas of Mesozoic and Cenozoic coastlines. – Cambridge Univ. Press.

Springer, S. 1961. Dynamics of the feeding mechanism of large galeoid sharks. – Am. Zool. 1: 183–185.

Taniuchi, T. 1970. Variation in the teeth of the sand shark, *Odontaspis taurus* (Rafinesque) taken from the East China Sea. – Japan. J. Ichthyol. 17: 37–44.

Taniuchi, T. et al. 1993. Geographical variations in reproductive parameters of shortspine spurdog in the North Pacific. – Nippon Suisan Gakkaishi 59: 45–51.

Templeman, W. 1984. Variations in numbers of median dorsal thorns and rows of teeth in thorny skate (*Raja radiata*) of the Northwest Atlantic. – J. Northwest Atl. Fish. Sci. 5: 171–179.

Zar, J. H. 1984. Biostatistical analysis. – Prentice Hall.