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SYSTEMATIC, PALEOECOLOGIC AND PALEOBIOGEOGRAPHIC ANALYSIS OF THE PLIO-PLEISTOCENE MEDITERRANEAN ELASMOBRANCH FAUNA

Abstract - A synthesis of the diversity of the Plio-Pleistocene elasmobranch fauna of the Mediterranean Sea is provided. The data deriving from the revision of Italian fossil elasmobranch teeth, and/or isolated elasmobranch teeth records of the Mediterranean area, are used to compile a database including all the Plio-Pleistocene elasmobranch taxa. 72 elasmobranch species included in 51 genera, 26 families, and 11 orders have been recognised. The revision of several fossil teeth from the Lower-Middle Pliocene deposits of Italy provides the first Pliocene record of the extinct *Isurus xiphodon* in the Mediterranean. Moreover, the Pliocene occurrence of *Carcharodon megalodon* into this basin is supported by six large teeth recorded in the Italian fossil teeth elasmobranch collections. The qualitative and quantitative analysis of the database confirms a decreasing trend in elasmobranch taxonomic diversity across the Plio-Pleistocene. The paleoecological and paleobiogeographical evolutionary patterns involved in the establishment of the present epi-mesopelagic, and deep-water Mediterranean elasmobranch fauna are also discussed.

Key words - Pliocene, Pleistocene, Elasmobranchii, shark, fish fauna, paleoecology, paleogeography, climate change, Mediterranean Sea.

Riassunto - *Analisi sistematica, paleoecologica e paleogeobiorafica della selacofauna plio-pleistocenica del Mediterraneo*. Viene presentata una sintesi della diversità della fauna a squali del Plio-Pleistocene del Mediterraneo. I dati raccolti attraverso la revisione di reperti italiani di denti fossili di squalo e/o segnalazioni isolate di reperti fossili dell'area mediterranea, sono stati utilizzati per costruire un database comprensivo di tutti i taxa di elasmobranchi presenti nel bacino del Mediterraneo durante il Plio-Pleistocene. 72 specie di squali e batoidi, inquadrate in 51 generi, 26 famiglie e 11 ordini sono state identificate. La revisione di un elevato numero di denti fossili provenienti dai depositi del Pliocene inferiore-medio dell'Italia, ha fornito il primo record fossile mediterraneo del taxon estinto *Isuru xiphodon*. Inoltre, la presenza di *Carcharodon megalodon* nel bacino è supportata da sei grandi denti conservati in alcune collezioni a denti fossili di elasmobranchi italiane. L'analisi qualitativa e quantitativa del database ha confermato un trend plio-pleisotcenico decrescente della diversità della fauna a squali e batoidi del Mediterraneo. Sono infine discussi i principali patterns paleoecologici e paleobiogeografici che hanno determinato l'attuale conformazione sia della fauna ad elasmobranchi epi-mesopelagica che di quella batipelagica del bacino del mediterraneo.

Parole chiave - Pliocene, Pleistocene, Elasmobranchii, squali, fauna a pesci, paleoecologia, paleogeografia, variazioni climatiche, Mediterraneo.

INTRODUCTION

The Mediterranean Sea, even thought represents a reduced water surface concerning the whole global marine system, provides an high elasmobranch diversity consisting of 81 species (47 sharks and 34 batoids) included into 43 genera, 23 families, and 7 orders (Serena, 2005). Serena (2005) estimated that the Mediterranean elasmobranch fauna represents about 8% of the total amount of elasmobranch species in the world. However, most of the Mediterranean elasmobranch diversity is restricted to the epipelagic and upper mesopelagic strata, where an high number of coastal and coastal-pelagic species, mainly including Carcharhinidae, Dasyatidae, Lamnidae, Myliobatidae, Odontaspididae, Rajidae, Sphyrnidae, and Torpedinidae, are widespread. The deepest strata of the Mediterranean are characterized by a rapid decrease in taxonomic diversity, as confirmed also by the studies performed on several invertebrate groups (see e.g. Bouchet & Taviani, 1992), as well as on teleostean fishes (Sardà *et al*., 2004). The negative hydrographic balance and peculiar environmental conditions, due to a combination of an anti-estuarine type model circulation, deep homothermic waters, nutrient depletion, and an high threshold in the Gibraltar area, operated as chemical and physical barriers to the entrance of the deep-water Atlantic species (see e.g. Bouchet & Taviani, 1992). This results in a severe impoverishment of the Mediterranean deep-water ecosystems. Most of the bathyal elasmobranch families, such as Hexanchidae, Dalatiidae, Centrophoridae and Squalidae, as well as several deep-water carcharhiniform sharks, are poorly represented in the Mediterranean marine biota (Sion *et al*., 2004).

In the last decades, scarce interest was devoted to sharks and batoids as paleoenvironmental markers. In fact, The present knowledge of the Plio-Pleistocene Mediterranean fish fauna is mostly due to the teleostean fossil record (see references in Landini & Sorbini, 2005a, b; Girone *et al*., 2006), while very few salient works were produced on the taxonomy, ecology and geographic distribution of elasmobranches (see references in Marsili, 2006).

The aim of this paper is to present an overview of the knowledge of the Plio-Pleistocene Mediterranean sharks and batoids diversity, in order to define the main ecological, geographical and evolutionary trends responsible of the establishment of the present elas-

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mobranch fauna. Finally, this work is part of a wider research project concerning the evolutionary history of the Neogene fish fauna of the Mediterranean (see also Landini & Sorbini, 2005b).

Material and method

27 species, included into 19 genera, 13 families and 8 orders, have been described after the revision of a large number of elasmobranch teeth housed in the «Museo di Storia Naturale e del Territorio» of the University of Pisa (MSNTC), «Museo di Storia Naturale, sezione di Geologia e Paleontologia» of the University of Firenze (MSNGP), «Museo di Geologia e Paleontologia G. Capellini» of the University of Bologna (MGPC), «Museo di Storia Naturale Accademia dei Fisiocritici» of the University of Siena (MUSNAF), «Museo Civico Giuseppe Scarabelli» of Imola (MCGS), «Museo Civico» of Reggio Emilia (MCRE) (Marsili, 2006; Marsili, 2007a; Marsili, 2007c; Marsili & Tabanelli, 2007), as well as from the study of new fossil shark teeth assemblages from the middle Pliocene of the Romagna region, and from the lower Pleistocene of southern Italy (Marsili, 2006; Marsili, 2007b; Marsili & Tabanelli, 2007). Moreover, data from as many publications as possible figuring and describing Plio-Pleistocene Mediterranean elasmobranch assemblages have been selected, in order to compile a database (Fig. 1), that includes all the Plio-Pleistocene fossil elasmobranch faunas (see also Marsili, 2006). Therefore, a total of 72 elasmobranch species-level taxa, 13 of which in open nomenclature, included into 51 genera, 26 families, and 11 orders, were recognized.

The taxonomy of the fossil and living taxa mostly follows De Carvalho (1996), McEachran *et al*. (1996), Purdy *et al*. (2001), and Cappetta & Cavallo (2006). Pliocene and Pleistocene stage follow Rio *et al*. (1998) and Rio *et al*. (1990), respectively.

In agreement with Purdy *et al*. (2001), the large number of teeth from the Lower-Middle Pliocene Italian deposits, formerly assigned to *Isurus hastalis*, have been recently assigned to the wide-toothed mako shark *I. xiphodon* (Marsili, 2007a; Marsili, 2007c), providing the first Pliocene record of this fossil taxon in the Mediterranean Basin. In addition, the presence of *Carcharodon megaldon* was confirmed on the base of six large teeth collected in the Pliocene deposits cropping out in several Tuscan localities. Such teeth extend the stratigraphic fossil record of *C. megalodon* in the Mediterranean region, to the lower Pliocene at least, confirming the presence of a permanent population of this shark in this basin (see also Marsili, 2006).

The review of a large number of teeth from the Lower-Middle Pliocene deposits of Italy, formerly assigned to *Carcharhinus egertoni*, provided the presence of seven species of the genus *Carcharhinus*, *C. brachyurus*, *C. falciformis*, *C. leucas*, *C. longimanus*, *C. obscurus*, *C. perezi*, *C. plumbeus* (Marsili, 2007a), confirming *C. egertoni* as a «wasted basket» species (Carnevale *et al*., 2006c; Marsili, 2007a).

Results

Sharks were the most diversified Plio-Pleistocene elasmobranch group, representing the 79.2% of the total fauna. Batoids were restricted to 20.8% of the total fauna, represented by very few taxa included in the orders Rajiformes, Torpediniformes and Myliobatiformes, today widely diversified in the Mediterranean Sea (Fig. 2). At the order level, the Plio-Pleistocene elasmobranch fauna is consistent with the present Mediterranean fauna, except for the lower-middle Pliocene presence of the extra-Mediterranean orders Orectolobiformes and Pristiophoriformes, as well as for the lack of fossil record of the batoid orders Rhinobatifomes and Pristiformes (Fig. 2). In particular, the Carcharhiniformes, represented by the 30.6% of the total fauna, was the most diversified elasmobranch order. Moreover, Lamniformes (16.6%), Squaliformes (16.6%) and Myliobatiformes (15.3) provided a relevant part of the faunal diversity, while Hexanchiformes (5.5%), Echinorhiniformes (1.4%), Squatiniformes (4.2%), Pristiophoriformes (2.8%), Orectolobiformes (1.4%), Rajiformes (4.2%), and Torpediniformes (1.4%), are poorly represented (Fig. 2).

The qualitative and quantitative analysis of the database compiled (Fig. 1; Marsili, 2006) provided a general Plio-Pleistocene decreasing trend in taxonomic diversity for the Mediterranean elasmobranch fauna (Fig. 3). Because of the scarse stratigraphic knowledge about many elasmobranch families (Scyliorhinidae, Dalatiidae, Rajidae, Dasyatidae), most of the record is considered to be characterized by the presence of «*Lazarus* taxa», mostly during the Upper Pliocene and Lower Pleistocene (Fig. 3). The highest elasmobranch taxonomic diversity occurred during the Lower Pliocene. In particular, sharks were strongly diversified during this period with an higher number of taxa in the respect to the present days, that persisted until the middle Pliocene (Fig. 4a). The scarce data about the fossil record of most batoid taxa do not allow a robust comparison with the present-day Mediterranean biota (Fig. 4b). More than 80% of the whole lower Pliocene assemblage was composed by pelagic and coastal-pelagic elasmobranch taxa, most of which represented by Miocene relict taxa (22.2%). However, also the Atlantic bathypelagic and bathydemersal shark species, such as *Mitsukurina* cf. *owstoni*, *Centroscymnus crepidater*, *Scymnodon* cf. *ringens*, *Scymnodalatias* aff. *garricki*, *Centrophorus* cf. *squamosus*, *Deania* cf. *calcea* or *Pristiophorus* sp., represented a relevant part of the Lower Pliocene elasmobranch fauna. Following to the «Messinian Salinity Crisis» hypothesis (Hsü *et al*., 1977), most of the Miocene biota survived in refugees areas or disappeared from the Mediterranean across the Upper Miocene-Lower Pliocene boundary, as a consequence of this catastrophic event. Recently, the occurrence of a number of marine teleostean fish remains from Italian «Lago-mare» deposits (Carnevale *et al*., 2006a, b), represent a crucial evidence for the persistence of a well developed marine fish fauna in the Mediterranean during the Upper Miocene. Most of the elasmobranch Miocene relict taxa, such

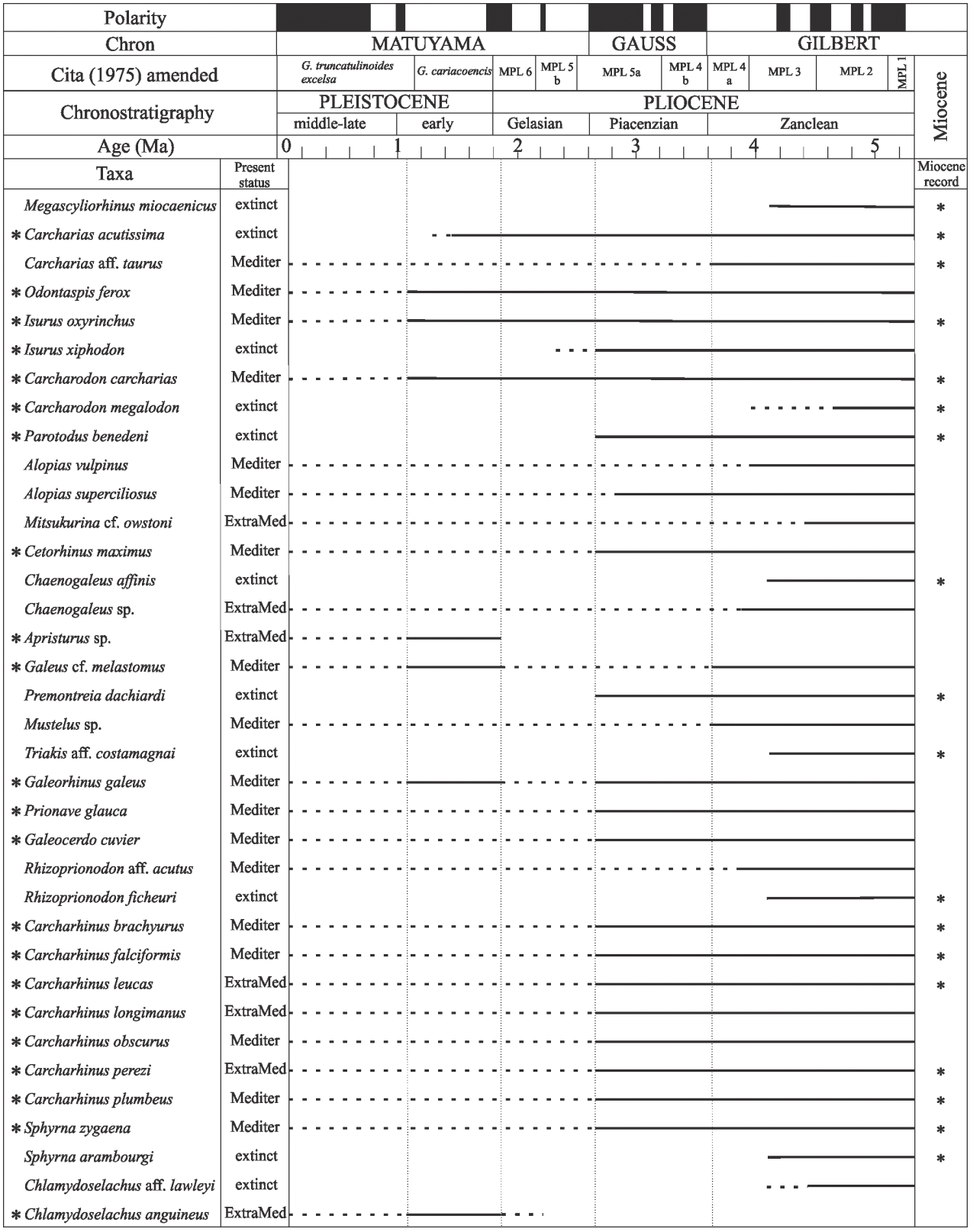

Fig. 1a - Statigraphic distribution of the Plio-Pleistocene elasmobranch taxa of the Mediterranean Sea.

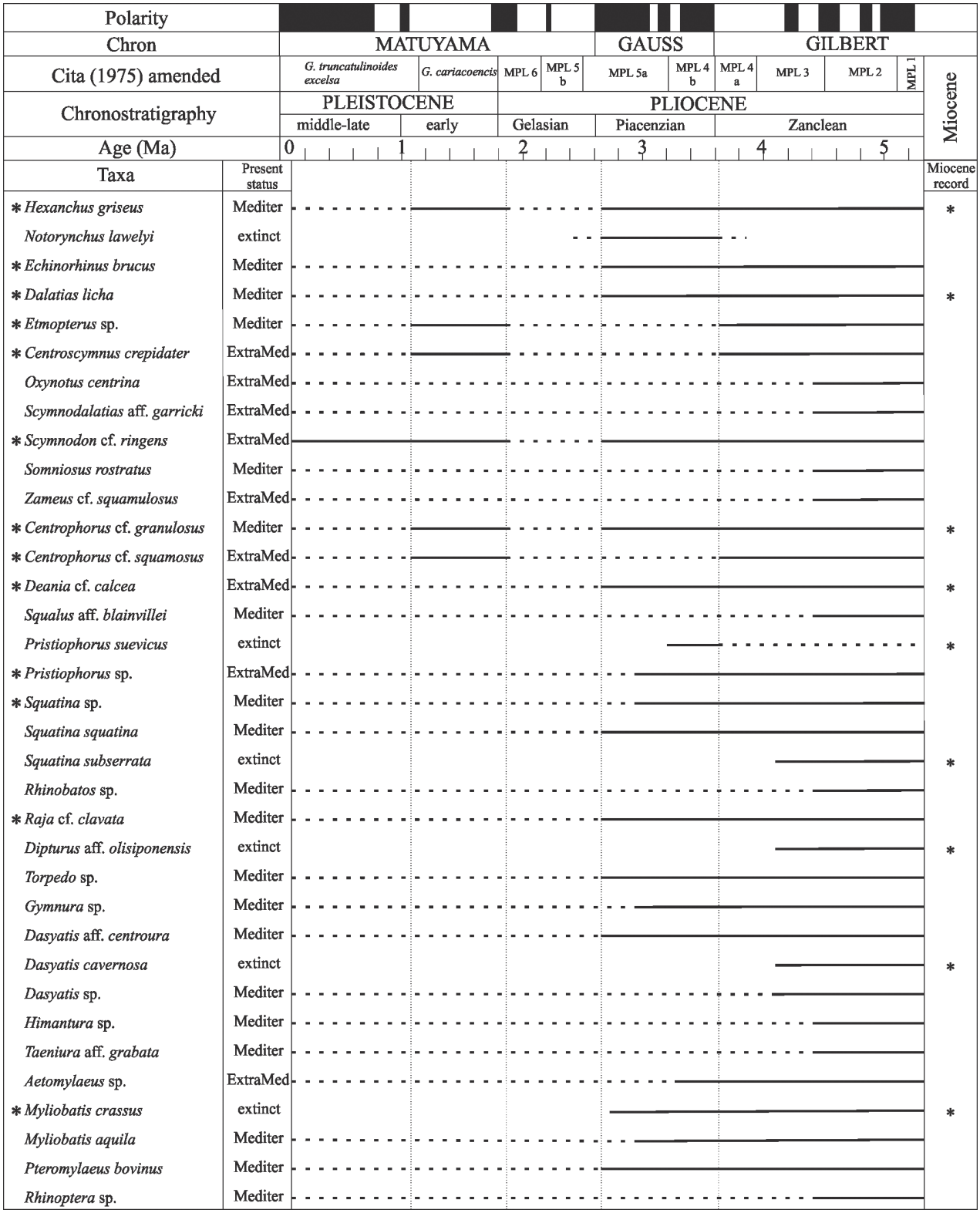

Fig. 1b - Statigraphic distribution of the Plio-Pleistocene elasmobranch taxa of the Mediterranean Sea.

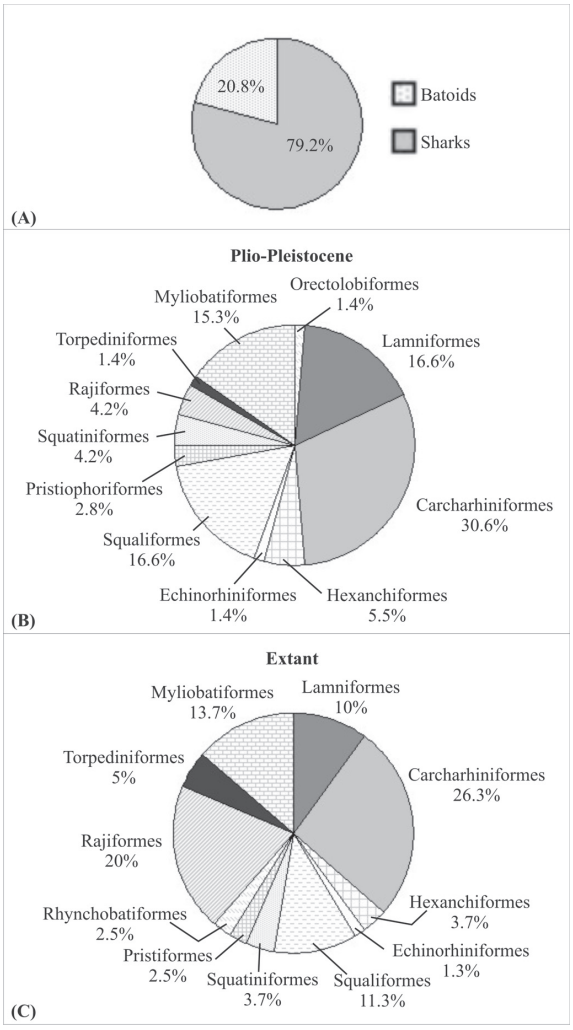

Fig. 2 - A) Shark *vs.* batoid in the Plio-Pleistocene Mediterranean area (in %). B) Plio-Pleistocene diversity of the Mediterranean elasmobranch fauna (at Order level). C) Extant diversity of the Mediterranean elasmobranch fauna (at Order level).

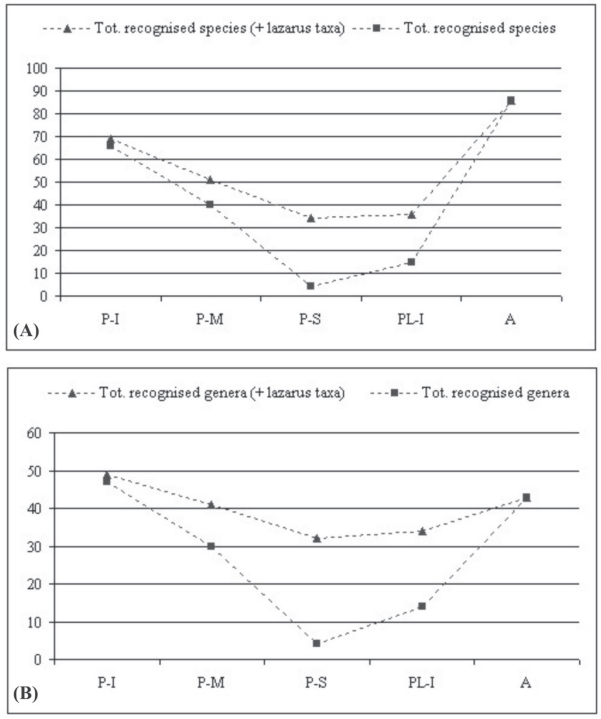

Fig. 3 - Trend in elasmobranch taxonomic diversity across the Plio-Pleistocene (A - Species; B - Genera).

as *Megascyliorhinus miocaenicus*, *Trakis* aff. *costamagnai*, *Rhizoprionodon fischeuri*, *Squatina subserrata*, *Dasyatis cavernosa*, or *Dipturus* aff. *olisiponensis*, *Myliobatis crassus* disappeared just at the end of the lower Pliocene from the Mediterranean. A few species, such as *Premontreia dachiardii*, *Isurus xiphodon*, *Parotodus benedeni*, and *Myliobatis* cf. *crassus*, persisted into this basin until the middle Pliocene, while *Carcharias acutissima* was recorded also during the Upper Pliocene-Lower Pleistocene. The 20.6% of the total taxa was represented by living species, such as *Carcharhinus brachyurus*, *C. falciformis*, *C. perezi*, *Sphyrna zygaena*, *Isurus oxyrinchus* and *Carcharodon carcharias*, which first occurred during the Miocene, and are now widely distributed in most of the marine ecosystems, including the Mediterranean. Finally, more than 50% of the total fauna was represented by species (e.g. *Galeocerdo cuvier*, *Prionace glauca*, *Rhizoprionodon* aff. *acutus*, *Odontaspis ferox*, *Cetorhinus maximus*, *Raja clavata*, *Pteromylaeus bovinus*) that first occurred during the lower Pliocene, among which *Chlamydoselachus lawleyi* is now extinct.

Across the Lower-Middle Pliocene boundary the decrease in taxonomic diversity was not balanced by new occurrences or originations. *Notorynchus lawleyi* representing the only Middle Pliocene new occurrence for the Mediterranean elasmobranch fauna (Fig. 1), quickly disappeared just at the end of this period. At generic and specific level the elasmobranch fauna of the Middle Pliocene was very similar to that existing today (Figg. 3, 4), except for the persistence of several Miocene relict taxa (e.g. *P. dachiardi*; *I. xiphodon*; *P. benedeni*; *M. crassus*), as well as of many extra-Mediterranean taxa (e.g. *Pristiophorus* sp., *D. calcea*, *C. perezi*, *G. cuvier*). Most of the pelagic and coastal-pelagic taxa widely recorded during the lower Pliocene, strongly persisted also during this period into the basin, confirming a faunal stability in the epipelagic and upper mesopelagic strata of the Mediterranean basin starting from lower-middle Pliocene. Concerning the middle Pliocene bathyal elasmobranch fauna, the lack of fossil record of many Zanclean deep-water Atlantic species, suggest a strong lower mesopelagic and bathypelagic faunal impoverishment during this period. Finally, the

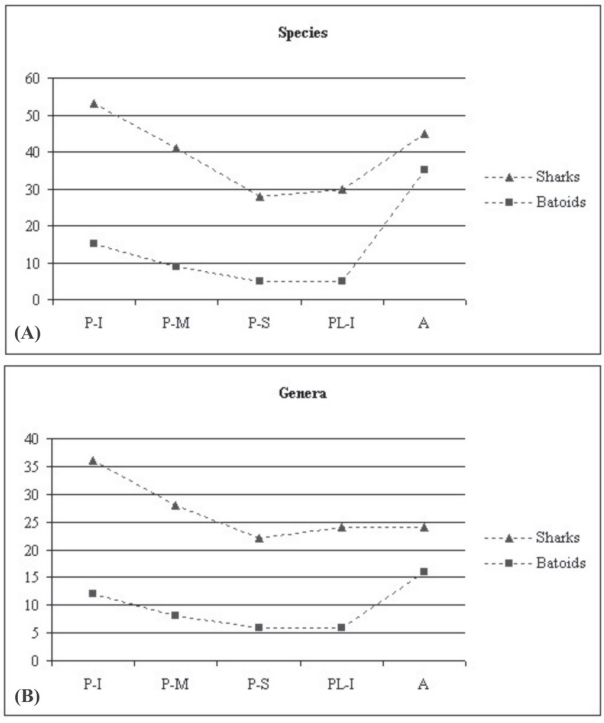

Fig. 4 - Trend in shark and batoid taxonomic diversity across the Plio-Pleistocene (A - Species; B - Genera).

scarse knowledge about batoids does not allow the understanding of the real diversity of this elasmobranch group among which the most common Mediterranean batoid genera, such as *Raja*, *Dasyatis*, *Gymnura* and *Myliobatis*, were recorded in the Mediterranean.

The lowest taxonomic diversity of the elasmobranch fauna concerns the upper Pliocene and lower Pleistocene (Figg. 3, 4), mainly because of the merger paleontological data. However, although these scarce fossil data, most of the coastal and coastal-pelagic shark and batoid species belonging to *Isurus*, *Carcharodon*, *Cetorhinus*, *Carcharhinus*, *Sphyrna*, *Raja* and *Myliobatis*, which represent a relevant component of the Upper Pliocene and Lower Pleistocene elasmobranch fauna of the Mediterranean Sea. Although the bathydemersal and bathypelagic fossil record, mostly based on the presence of upper Pliocene «*Lazarus* taxa», confirms a decreasing trend of this part of elasmobranch fauna starting from the Lower Pliocene, the recently occurrence of a new fossil deep-water shark assemblage from Fiumefreddo (Marsili, 2007b) represents a novelty in the understanding of the evolutionary pattern of the lower Pleistocene unknown deep-water elasmobranch fauna.

Discussion

The evolutionary history of the Mediterranean elasmobranch fauna was characterized by complex paleoecological and paleobiogeographical evolutionary patterns, providing major changes in shark and batoid taxonomic diversity across the Plio-Pleistocene. In particular, the epipelagic and upper mesopelagic families, such as Lamnidae, Odontaspididae, Carcharhinidae, Rajidae and Myliobatidae, were characterized by minor faunal changes starting from the lower-middle Pliocene. Such epi-mesopelagic faunal stability was mostly related to a progressive disappearance of Miocene relict taxa, as well as of several tropical to subtropical extra-Mediterranean thermophilous sharks. By contrast, the Plio-Pleistocene mesopelagic and bathypelagic strata of the Mediterranean were characterized by the most relevant faunal changes through several periods of diversification and crisis. These changes mainly involved Centrophoridae or Dalatiidae, as well as several scyliorhinid species, such as *Apristurus* sp. or *Galeus melastomus*. The basal Pliocene rapid refilling of the Mediterranean Basin, due to the re-establishment of a wider connection with the near Atlantic Ocean, and a rapid glacial eustatic sea-level rise (McKenzie *et al*., 1999), allowed the establishment of a rich marine biota, with a prominent Atlantic affinity. The early Zanclean occurrence of many extra-Mediterranean deep-water sharks, such as *Mitsukurina* cf. *owstoni*, *Centroscymnus crepidater*, *Scymnodon* cf. *ringens*, *Scymnodalatias* aff. *garricki*, *Centrophorus* cf. *squamosus*, *Deania* cf. *calcea* and *Pristiophorus* sp., as well as of many tropical to subtropical extra-Mediterranean sharks, such as *G. cuvier*, *C. leucas*, *C. perezi* or *R.* aff. *acutus*, confirms the strong Atlantic affinity of the Mediterranean fauna (see references in Marsili, 2006). Moreover, the Indo-Pacific taxa are poorly know in the Mediterranean, represented only by the fossil taxa *Chaeonogaleus affinis*, *Chaenogaleus* sp., and *Aetomylaeus* sp., which disappeared from the basin just at the end of the Lower Pliocene (see references in Marsili, 2006). The genus *Chaenogaleus*, widely recorded during the Miocene (Cappetta, 1987), includes the living species *C. macrostoma*, distributed in Pakistan, India, Singapore to China (Compagno, 1984). *Aetomylaeus* includes four living species, *A. maculatus*, *A. milvus*, *A. nichofii*, and *A. vespertilio*, widespread in the tropical and sutropical Indian and Pacific geographic areas (see e.g. Compagno & Last, 1999).

The Atlantic elasmobranch fauna established during the Plio-Pleistocene in the Mediterranean was characterized mainly by species with a worldwide geographic distribution. By contrast, those elasmobranch orders, such as Orectolobiformes and Heterodontiformes, mainly characteristic of the Indo-Pacific marine ecosystems (see e.g. Compagno, 1984), are scarcely represented. Moreover, *Megascyliorhinus miocaenicus*, recently assigned to the Orectolobiformes (Purdy *et al*., 2001), was a widespread taxon, of both Miocene and lower Pliocene deposits, recorded in the Mediterranean area, Portugal, North America, and Japan (see references in Marsili, 2006). The two orectolobid genera *Ginglymostoma* and *Rhincodon*, widely recorded during the Miocene (Cappetta, 1987), are presently distributed in the Indo-Pacific, and Atlantic marine ecosystems (Compagno, 1984). The scarcity of Indo-Pacific

elasmobranch taxa disagree with the Plio-Pleistocene teleostean fossil record. In fact, many Indo-Pacific teleostean taxa were recorded in the Mediterranean Basin at least until the upper Pliocene-lower Pleistocene (see e.g. Landini & Sorbini, 2005b).

The presence of the warm-water Indo-Pacific genera *Chaenogaleus* and *Aetomylaeus* during the Mediterranean lower-middle Pliocene, along with the occurrence of several tropical to subtropical thermophilous taxa, such as *G. cuvier*, *C. leucas*, *C. perezi* and *R. acutus*, confirms a warmer, more humid and less seasonal climate than the present in the Mediterranean area (Haywood *et al*., 2001). The Mediterranena fossil record of these warm-water supports the data from the study of the fossil record of many other marine vertebrate and invertebrate groups (Sprovieri, 1985; Ragaini, 1992; Monegatti & Raffi, 2001; Landini & Sorbini, 2005b). *Galeocerdo cuvier*, *Carcharhinus leucas*, *C. longimanus* and *C. perezi* among the thermophilous sharks are not included in the present Mediterranean fish fauna being mostly distributed in the Atlantic and/or Indo-Pacific Oceans warm-waters, with a latitudinal range of about 40°N-43°S and temperature of about 23-24°C (Compagno, 1984). In particular, *C. perezi* is characterized by a geographic distribution restricted to the Gulf of Mexico and the Caribbean Sea (Compagno, 1984). *G. cuvier* was recently recorded in the Mediterranean Sea, but however its presence must be confirmed (Serena, 2005). *C. falciformis* occasionally occurs in the western Mediterranean, mainly along the Spanish, Italian and north African coasts (Serena, 2005), even if it is mostly abundant in the tropical sectors of the Atlantic and Indo-Pacific Oceans. Finally, there is only an isolated record of the tropical *R.* aff. *acutus* in the present Mediterranean marine biota (Serena, 2005). In general terms, the progressive climatic deterioration and the consequent lowering of the sea surface water temperatures culminated during the middle-late Pliocene with the onset of the Antartic Ice Sheet and of the cyclical glacial/interglacial periods, caused a general impoverishment in warm-water taxa of the Mediterranean marine biota (Monegatti & Raffi, 2001; Landini & Sorbini, 2005b). Therefore, the strong reduction in the Mediterranean distribution of *C. falcifomis*, as well as the disappearance at the end of the middle Pliocene of the extra-Mediterranean *C. leucas*, *C. longimanus*, *C. perezi* and *G. cuvier*, supports this paleoenvironmental deterioration and the consequent impoverishment in tropical and subtropical thermophilous taxa.

The present Mediterranean Sea is characterized by a very impoverished bathyal biota; this is due to the peculiar hydrographical conditions of the basin and a very high threshold in the Gibraltar region, that operated as chemical and physical barriers to the entrance of many Atlantic bathyal species (Bouchet &Taviani, 1992). The present deep-water elasmobranch fauna is represented by very few species, such as *Hexanchus griseus*, *Galeus melastomus*, *Etmopterus spinax*, *Centroscymnus coelolepis* and *Centrophorus granulosus* (Sion *et al*., 2004; Serena, 2005). During the early Zanclean, the Mediterranean biota was enriched by the presence of several bathypelagic and bathydemersal elasmobranch species, migrated into the basin from the Atlantic. Lower Pliocene taxa include *Mitsukurina* cf. *owstoni*, *Centroscymnus crepidater*, *Scymnodon* cf. *ringens*, *Scymnodalatias* aff. *garricki*, *Centrophorus* cf. *squamosus*, *Deania* cf. *calcea* and *Pristiophorus* sp. (Marsili, 2006), today abundant along the Atlantic slope, from Portugal, Madeira to Senegal, and not included in the present Mediterranean biota (Compagno, 1984). Most of these deep-water Atlantic sharks have been recently recorded also in the Middle Pliocene and Lower Pleistocene Italian deposits. *Scymnodon* cf. *ringens* is the only Atlantic bathyal sharks with a continuous fossil record, from the Lower Pliocene to the Middle Pleistocene (Fig. 1). *Deania* cf. *calcea* and *Pristiophorus* sp. persisted in the basin until the middle Pliocene. *C. crepidater* and *C.* aff. *squamosus* occurred both in the Lower Pliocene and Lower Pleistocene elasmobranch fauna. Finally, *Chlamydoselachus anguineus* and *Apristurus* sp. represent new elements of the Lower Pleistocene elasmobranch fauna (Marsili, 2007b; Marsili & Tabanelli, 2007). Most of these new vertebrate and invertebrate Atlantic species were represented by Boreal and/or Artic cold stenotermic taxa, whose entrance into the basin was favoured by the progressive Plio-Pleistocene climatic deterioration and the consequent lowering of the sea-surface water temperature (Marsili, 2007b). None of the Atlantic bathydemersal and bathypelagic shark species recognised in the Plio-Pleistocene elasmobranch fauna is characterized by an exclusive Boreal or Artic geographic distribution, or a stenothermic character. Therefore, according with an oceanographic model proposed by several authors (see e.g. Di Geronimo and La Perna, 1996; 1997; Girone *et al*., 2006), their entrance may be due to both an estuarine Mediterranean model circulation during the Plio-Pleistocene, and a deeper threshold in the Gibraltar region, that provided major faunal interchanges with the near Atlantic Ocean. Moreover such an organized deep water shark fauna supports the establishment of a basin system characterized by a decreasing temperature (lower than 10 °C), a good deep nutrient supply and a better deep water circulation, that favoured the development of a more diversified and complex deep ecosystem in the Mediterranean Basin, supported by a well structured trophic system (Marsili, 2007b).

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