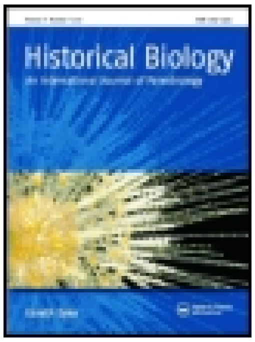

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A Serravallian (Middle Miocene) shark fauna from Southeastern Spain and its palaeoenvironment significance

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ABSTRACT

The study of a new Serravallian (Middle Miocene) locality from the Southeastern Spain has yielded a shark assemblage characterized by microremains of at least seven taxa (*Deania calcea*, †*Isistius triangulus*, †*Squaliolus* cf. *S. schaubi*, †*Paraetmopterus* sp., *Pristiophorus* sp., *Scyliorhinus* sp. and a cf. Squaliformes indet) of three different orders (Squaliformes, Pristiophoriformes and Carcharhiniformes). In addition, associated macroremains have also been found, including teeth of †*Cosmopolitodus hastalis*, *Isurus* sp., *Hemipristis serra*, *Odontaspis* sp., *Carcharhinus* spp. and †*Otodus* (*Megaselachus*) *megalodon*. The assemblage contains taxa with disparate environmental preferences including not only neritic and epipelagic sharks but also an important number of meso and bathypelagic representatives. The migration of deep water taxa to shallower waters through submarine canyons/coastal upwelling is proposed as the most plausible cause for explaining the origin of such assemblage. Interestingly, the composition of the deep-water taxa here reported contrast with the chondrichthyans assemblages from the Pliocene and extant Mediterranean communities. This entails a complex biogeographic history, where the Messinian salinity crisis strongly affected the posterior evolution of the Mediterranean ecosystems but some other factors, such us the existence of anoxic events during the Quaternary, could have also played an important role.

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Neogene; Iberian Peninsula; elasmobranchs; deep-water fauna

Introduction

The geological history of the Mediterranean Sea is characterized by a series of important events with remarkable consequences for the fauna that inhabited it. During the Late Miocene Messinian Stage (7.24–5.33 Ma), the Mediterranean Sea became gradually isolated from the Atlantic Ocean as the Betic and Rifian seaways were progressively closed, culminating in its desiccation during the Messinian salinity crisis at 5.59 Ma (Krijgsman et al. 1999; Gibert et al. 2013). Such closure caused drastic changes in climate, salinity and sea level fluctuations, with a drop in sea level over 1500 meters (García-Castellanos et al. 2009; García-Castellanos & Villasen 2011). These changes completely eliminated deep-sea environments, reducing available ecosystems and driving most species to extinction (Coll et al. 2010). At present, the Mediterranean Sea is recognized as one of the most diverse regions on the planet (Coll et al. 2010), which has its origin in the repopulation with fauna and flora from the Atlantic Ocean through the Strait of Gibraltar once it reopened about 5.33 Ma during the Zanclean flood (Coll et al. 2010; Gibert et al. 2013). It is important to notice that the deep-sea faunas of the Mediterranean seem to have a lower diversity than those of the Atlantic of similar depth, taking into account that the former come directly from the latter (Perés 1985). Elasmobranch faunas constitute one of the most evident examples in this sense. Although modern Mediterranean elasmobranchs show a high biodiversity represented by 45 species of sharks, 34 species of batoids and one species of chimaera (Compagno et al. 2005; Serena 2005; Ebert et al. 2013); most of these taxa are epipelagic or/and mesopelagic species inhabiting the neritic or oceanic realm, whereas the deepwater ones are characterized by a clear biodiversity impoverishment (Marsili 2008). In this regard, the comprehensive study of the pre- and post-Messinian elasmobranch faunas of both sides of the Strait of Gibraltar (in the Atlantic Ocean and the Mediterranean Sea) is needed for achieving a better understanding about the origin of the current diversity of this group of fishes in the Mediterranean.

Miocene elasmobranchs have been documented both in Portugal and Spain. The record from Portugal includes several publications with the descriptions of macro and micro dental remains (e.g. Antunes & Jonet 1970; Antunes et al. 1999a, 1999b, 2015; Antunes & Balbino 2003, 2004, 2007; Balbino 1995, 1996; among others). In contrast, the elasmobranch fossil from the Miocene of Spain is scarce, with few references of isolated shark teeth (e.g. *Otodus* (*Megaselachus*) *megalodon* in Medina-Gavilán et al. 2015, Reolid & Molina 2015). This lack of data represents an important bias on the knowledge of the Miocene elasmobranch diversity in this region of the Mediterranean Sea. Given this scenario, herein we described for the first time a shark fauna

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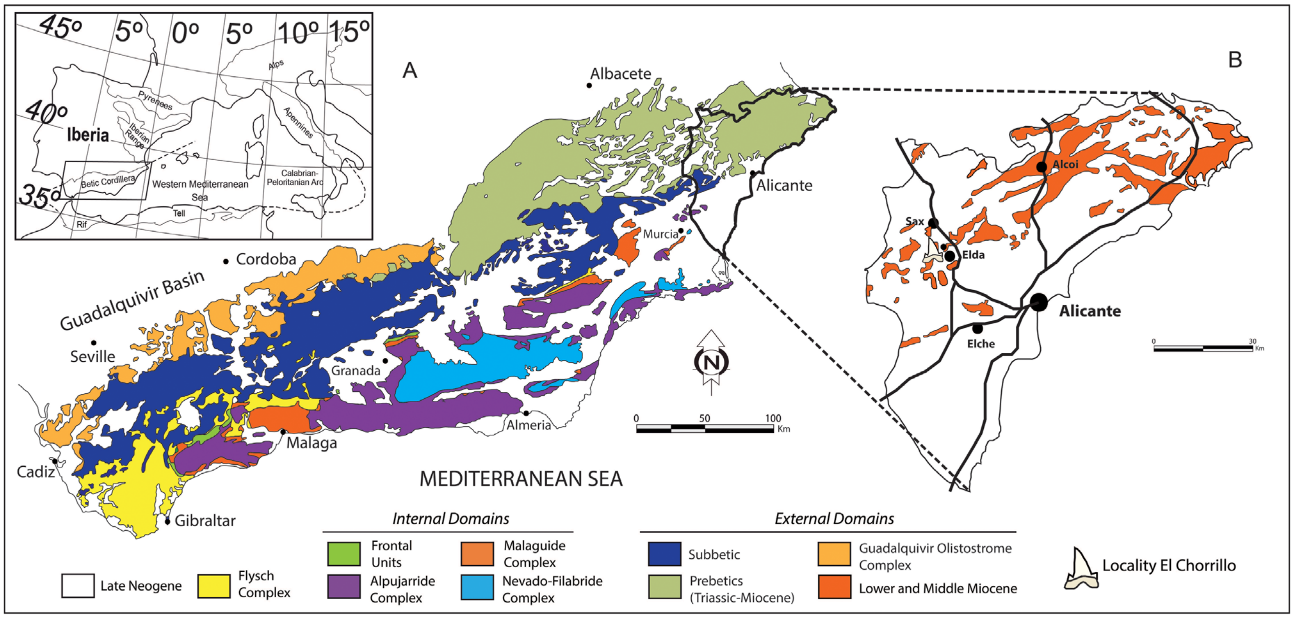

Figure 1. (A) Main divisions of the Betic Cordillera modified from Navas-Parejo 2012; based on Vera 2004; and Martín-Algarra 1987. (B) Location of the 'El Chorrillo' fossil-site in the Middle Miocene of the Alicante Province.

from the late-Middle Miocene (Serravallian) of the Southeastern Spain, resulting in an increased fossil record on the region and offering new light into the elasmobranch palaeobiodiversity before the Messinian salinity crisis event.

Geological setting

All the studied material comes from a Miocene outcrop of the center of the Alicante Province, Southeastern Spain. Geologically, the area of study belongs to the oriental part of the Betic Ranges. This cordillera can be subdivided into a number of distinct palaeogeographic zones, which differ in depositional history, tectonometamorphic evolution and timing of the Alpine Orogeny (Geel et al. 1992). These are from North to South: the Prebetic and the Subbetic (all together representing the External Zone), and the Internal Zone (Vera 2004) (Figure 1(A)). The External Zone is thought to represent the Mesozoic continental passive margin of the Iberian continental block, strongly tectonized during the Lower-Middle Miocene due to the collision between Iberia and Africa (e.g. García-Hernández et al. 1980; Hermes 1985; Geel et al. 1992). As a consequence, from the Lower Miocene up to the end of this epoch, the continuous plate movements develops a series of very narrow and elongated basins, that derived in the North Betic Strait or Betic Corridor, that communicated the Atlantic Ocean and Mediterranean Sea during that time (Soria et al. 1999; Reolid et al. 2012; Martín et al. 2014). In this context, during the Serravallian times, the Alicante Province (where our studied area is located) was part of the most eastern region of this North-Betic Strait, representing the connection of the Atlantic Ocean with the Mediterranean (Geel et al. 1992). During the Late Miocene, continuous plate movement between Iberia and Africa caused a progressive disconnection of the Mediterranean from the Atlantic that culminated with the total closure and the partial desiccation of the Mediterranean Sea during Messinian time (Late Miocene) (Gibert et al. 2013).

Material and methods

The El Chorrillo outcrop is located in the province of Alicante (Southeastern Spain) (Figure 1(B)), 3 km South from the Sax village, following the local road CV-833 that connect Sax with Elda, at the left bank of the Vinalopó River (geographic coordinates: 38°30′35.18″N, 0°48′25.70″O). The outcrop is characterized by a massive sandstone and calcarenites with abundant invertebrate fauna and glauconite, included in the so-called Tap 2 of Martínez del Olmo et al. (1978), and dated as Serravallian (13.5–11.5 Ma, Middle Miocene) according to the foraminiferal association (Martínez del Olmo et al. 1978). The fossil elasmobranchs described herein come from 25 kg of a calcarenitic-microconglomerate that were originally collected for micropalaeontological purposes (foraminifera). The sample was dissolved with acetic acid (c.a. 5–7%), and washed and screened with sieve meshes of 2, 0.125, and 0.063 mm, respectively. The picking process resulted in several hundreds of microfossils (e.g. sponges, corals, bryozoans, echinoderms foraminiferal and osteichthyans), but in contrast, a low abundance of elasmobranch teeth (~58 specimens) and a few dermal denticles were found. From the same locality, some large shark teeth have also been surface-collected (see discussion section and Table 1), however, those remains were not included in the present research, given that these are not housed in public collections and lack catalogue numbers.

All the elasmobranch microremains here studied are housed at the Museo de Geología de la University of Valencia (MGUV). The specimens were photographed using the scanning electron microscope Hitachi S4800, of the Central Service for Experimental Research of the University of Valencia, Spain. The taxonomy follows Cappetta (2012) and taxonomic identification was based on an extensive literature review and also comparative analyses with fossil and recent specimens from the following collections: Natural History Museum of Basel (NMB),

Table 1. Chondrichthyans found in the 'El Chorrillo' outcrop (Serravallian, Middle Miocene) including micro and macro remains. Ecological information obtained from Ebert et al. (2013) and Froese and Pauly (2017). Bathymetrical ranges: Neritic/Epipelagic (0–200 m); Bathyal/Meso-Bathypelagic (200–2000 m).

Fossil taxon	Extant species	Mode of life and habitat of extant representatives								
		Benthic	Benthopelagic	Pelagic	Neritic / Epipelagic	Bathyal / Meso-Bathypelagic	Bathymetriy depth (m)		Comments	Number of specimens
							Mn	Mx		
Deania calcea	*Deania calcea*		X		X	X	70	1470	usually 400-900 m	17
†*Isistius triangulus*	*Isistius* spp.			X	X	X	0	3700	usually 0-1000 m	4
†*Squaliolus* cf. *S. schaubi*	*Squaliolus* spp.			X	X	X	200	2000		13
†*Paraetmopterus* sp.	no extant species	-	-	-	-	-	-	-	Species within the genus associated to deepwater enviroments	10
cf. Squaliformes fam. et gen. indet.				X	?	?	?	?		9
Pristiophorus sp.	*Pristiophorus* spp.		X		X	X	0	1000	usually 100-300	1
Scyliorhinus sp.	*Scyliorhinus* spp.	X			X	X	1	780	Most of the spp. Inhabiting > 70 m	10
†*Cosmopolitodus hastalis**	no extant species	-	-	-	-	-	-	-	Regarded as an active pelagic shark	13
Isurus sp*	*Isurus* ssp.			X	X		0	750	usually 100-150	5
†*Hemipristis serra**	*Hemipristis elongata*	X			X		1	132		1
Odontaspis sp.*	*Odontaspis* spp.		X	X	X	X	10	2000	usually 13-880	2
Carcharhinus spp.*	*Carcharhinus* spp.		X	X	X		0	800	usually < 200 m	1
†*Otodus* (*Megaselachus*) *megalodon**	no extant species	-	-	-	-	-	-	-	Regarded as an active pelagic shark	2

Abbreviations: Mn (minimum); Mx (maximum).

*Those taxa are not housed in a public collection, and therefore were not figured or described in this contribution, but have been included after the personal observation of CMP and CH, in order to a better understanding of the assemblage origin.

Palaeontological Institute and Museum at the University of Zurich (PIMUZ), and René Kindlimann private collection, Uster, all of them in Switzerland.

Results

Systematic palaeontology

The shark microremains described herein, comprising teeth and dermal denticles, have allowed us to identify at least seven taxa attributed to seven genera, six families and three orders. Other teeth macroremains have been also found by private collectors (see Table 1), and although included in the discussion section, they have not been described or figured in the present work.

Clase Chondrichthyes Huxley, 1880
Superorder Squalomorphii Compagno, 1973
Order Squaliformes Goodrich, 1909
Family Centrophoridae Bleeker, 1859
Genus *Deania* Jordan and Snyder, 1902
Deania calcea Lowe, 1839
Figure 2(A)–(J)

Material – A total of 8 lower and 9 upper teeth (MGUV-35862-66; MGUV-35867).

Description – These specimens exhibit ranges in height of about 1.5–2.5 mm and, in width, between 1 and 1.5 mm. Upper teeth are labio-lingually compressed with a straight, symmetric and high cusp with smooth cutting edges. The apron is long and well-developed with a rounded end reaching the base of the root. The lingual surface is reduced and the basal section is flat, with a superior medio-lingual foramen and broad channel-shaped depression on the base. The root base is slightly flat. In reference to the lower teeth, they are labio-lingually compressed and wider than tall, with an unserrated crown and a distally inclined triangular cusp. The mesial cutting edge is convex towards the mesial end of the crown, and concave close to the top of the cusp; the distal heel is short, high and strongly convex. In labial view, the apron is wide and long, ending before reach the base of the root. In lingual view a short uvula, a well-develop infundibulum foramen and two small foramina in the mesial side can be observed. The base of the root is slightly convex.

Remarks – *Deania* ranges from the Lower Paleocene to the Recent (Cappetta 2012). The tooth morphology of the specimens herein referred is consistent with those teeth of *D. calcea* described by Ledoux (1970, 1972). In addition, the presence of *Deania calcea* in the Middle Miocene of Sax, represent the first fossil record of this taxon in the Neogene of Spain. *Deania* was referred also to the late Miocene of Portugal by Antunes and Jonet (1970).

Family Dalatiidae Gray, 1851
Genus *Isistius* Gill, 1864
†*Isistius triangulus* Probst, 1879
Figure 2(K), (L)

Material – one complete lower anterior tooth (MGUV-35868) and other three eroded fragments (MGUV-35869).

Description – The complete tooth displays a height of 3 mm and a width of 2 mm. It is compressed labio-lingually, with high equilateral triangular crown and cutting edges. The apron is flat with a poorly marked lower boundary that descends to the level of the elliptic opening. The root is very flat with a square shape. There is medial-lingual foramen and a medial-labial opening in the upper part of the button-hole. The other teeth remains are represented by fragmentary crowns.

Remarks – *Isistius* ranges from the Upper Paleocene to the Recent (Cappetta 2012), and its fossil record is represented by two extinct species: †*Isistius trituratus* Probst 1879, known from the Early Paleocene to the Eocene, and †*I. triangulus* Probst 1879 from the Miocene to the Pliocene (Cappetta 2012). According to Froese and Pauly (2017), only two extant species are recognized: *Isistius brasiliensis* Quoy and Gaimard 1824 and *Isistius plutodus* Garrick and Springer 1964.

The morphological features of our complete specimen (Figure 2(K), (L)) resemble those referred to the teeth of †*I. triangulus* described from the Neogene of Europe (e.g. Antunes & Jonet 1970; Ledoux 1972; Holec et al. 1995; Kocsis 2007; Brisswalter 2008; Vialle et al. 2011; Cappetta 2012). In addition, these specimens represent the first fossil record for this taxon in the Neogene of Spain

Genus *Squaliolus* Smith and Radcliffe, 1912
†*Squaliolus* cf. *S. schaubi* (Casier 1958)
Figure 2(M)–(P))

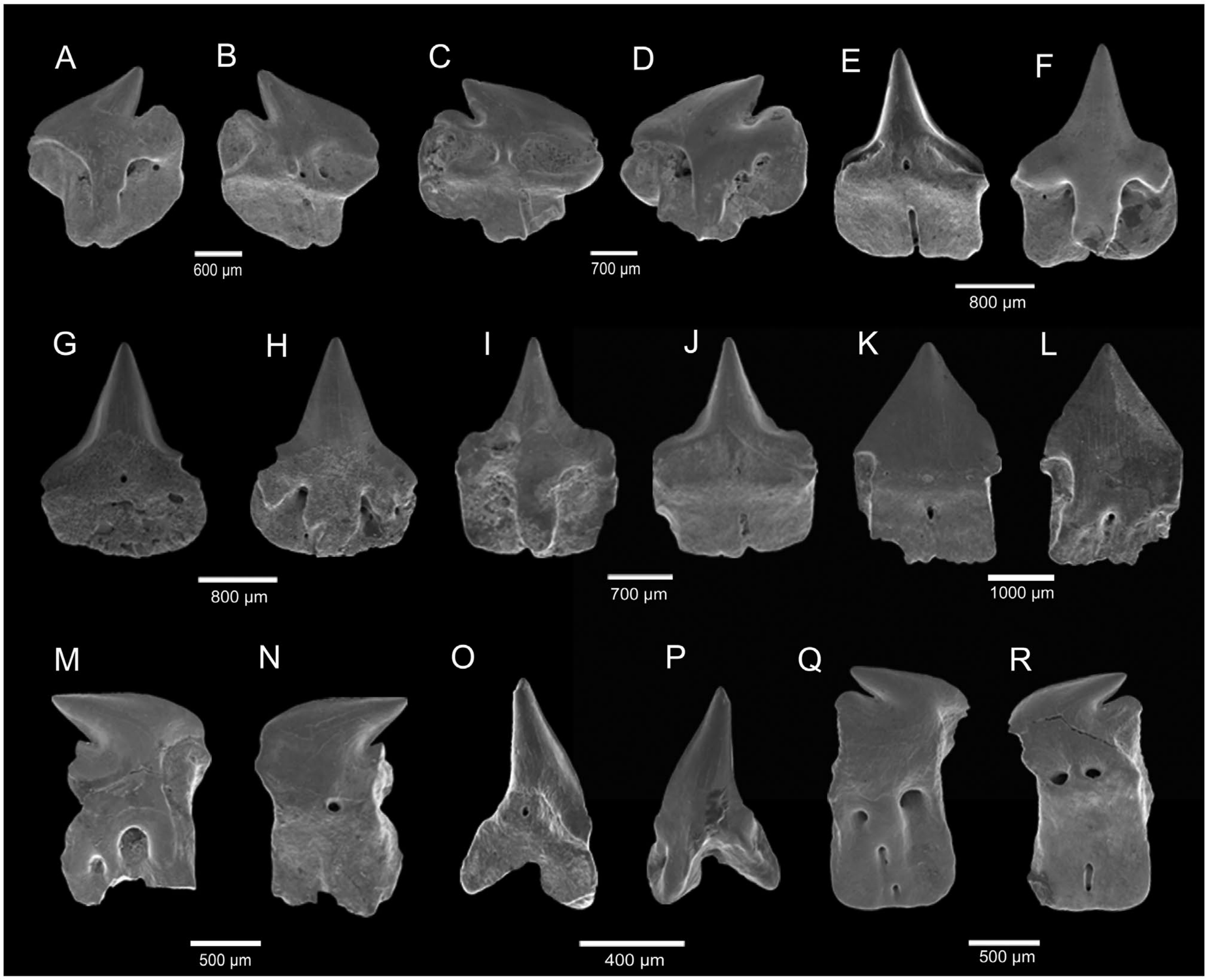

Figure 2. Squaliformes from the 'El Chorrillo' outcrop. (A)–(J) *Deania calcea* ((A)–(D): lower teeth, MGUV-35862 and MGUV- 35866; (E)–(J): upper teeth; MGUV-35863, MGUV-35865, MGUV-35864 respectively). (K)–(P) †*Isistius triangulus* (MGUV-35868). (M)–(P) †*Squaliolus* cf. *S. schaubi* (M-N: lower tooth, MGUV-35870; O-P; upper tooth, MGUV-35873). (Q)–(R) †*Paraetmopterus* sp. (lower tooth MGUV-35876).
Note: View: labial (A, D, F, H, I, P, L, M, Q), lingual (B, C, E, G, J, K, N, O, R).

Material – Two complete upper teeth (MGUV-35873 and MGUV-35874) and three incomplete lower teeth (MGUV-35870-72), together with other eight eroded fragments (MGUV-35875).

Description – The teeth exhibit ranges in height of about 0.5–1.4 mm and, in width, between 0.3 and 0.8 mm. The two upper teeth are slender, higher than wide and are characterized by a narrow triangular cusp with straight to slightly concave mesial and distal edges with unserrated cutting edges. In the labial view, the base of the cusp reaches part of the root lobes. In the complete specimen (Figure 2(O), (P)), the root has two well-differentiated lobes with a flat basal face. In the lingual projection, at the base of the crown, a small foramen can be observed. In the labial side, there is a large foramen at the base of the crown, between the lobes. In reference to lower teeth (Figure 2(M), (N)), these are labio-lingually flattened and higher than broad. The most complete specimens have an unserrated crown with a single and low cusp distally inclined and overhanging a small convex distal heel. The mesial cutting edge is convex towards the mesial end of the crown. The labial side is well covered by enameloid with a well-developed oval foramen present in the tooth midline. In the mesial side a large concavity is observed, reaching as far distally as level with the middle of the base of the cusp. The lingual side is flat and a well-developed foramen is present at the base of the enameloid.

Remarks – *Squaliolus* ranges from the Middle Eocene to the Recent, with a fossil record that includes Asia, Europe and America (Cappetta 1970, 2012; Ledoux 1972; Underwood & Schlögl 2013). The Neogene species †*Squaliolus schaubi* Casier 1958 was described from the early Miocene of the Caribbean (Casier 1958), and its fossil record includes Asia and Europe (Underwood & Schlögl 2013). The specimens herein described are morphologically similar to those teeth of †*Squaliolus* cf. *S. schaubi* described by Underwood and Schlögl (2013) from the early Miocene of Slovakia, which leads us to refer these tentatively to this taxon. These specimens from the Neogene of Spain represent the first fossil record for the taxon in the Iberian Peninsula.

Family Etmopteridae Fowler, 1934
Genus †*Paraetmopterus* Adnet 2006
†*Paraetmopterus* sp.
(Figure 2(Q), (R))

Material – One complete lower tooth (MGUV-35876) and 9 incomplete specimens (MGUV-35877).

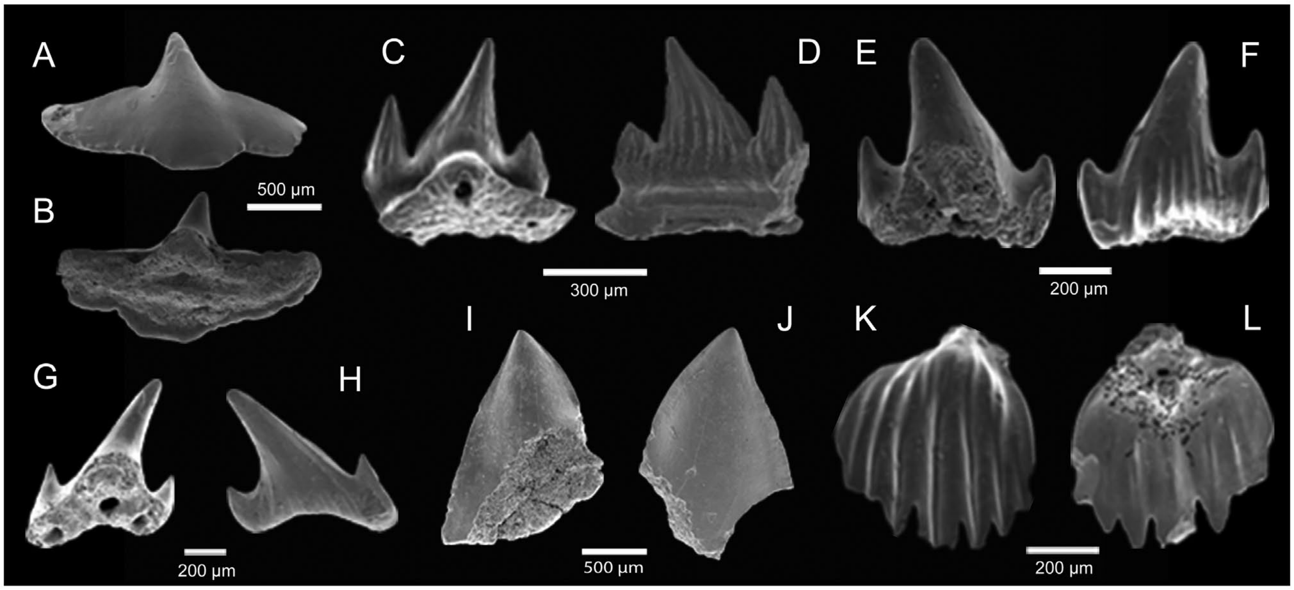

Figure 3. Pristiophoriformes, Carcharhiniformes and indet elasmobranchs from 'El Chorrillo' outcrop. (A)–(B). *Pristiophorus* sp. (MGUV-35879). C-H. *Scylorhinus* sp. ((C)–(D): MGUV-35882; (E)–(F): MGUV-35880; (G)–(H): MGUV-35881). (I)–(J) cf Squaliformes fam. et gen. indet. (MGUV-35878). (K)–(L) indet. dermal denticle (MGUV-35884).
Note: View: labial (A, D, F, H), lingual (C, E, G), basal (B, L), dorsal (K), indet. (I, J).

Description – The complete tooth displays a height of 1.5 mm and a width of 0.7 mm, it is labio-lingually flattened and higher than broad. The specimen has a general rectangular shape, but with a convex distal and concave mesial edges. The crown is characterized by unserrated cutting edges, and it has a single and low cusp distally inclined and overhanging a small convex distal heel. The mesial cutting edge is convex towards the mesial end of the crown. The root shows a rectangular-like shape with a straight basal edge. The labial face of the root bears two well-developed mesial/distal foramina close to the enameloid base of the crown, and two small foramina are present in the lower portion of the root and close to the tooth midline. The lingual face of the root has two well-developed foramina in the basal edge of the crown, and one elongated foramen in the lower-middle portion of the root.

Remarks – †*Paraetmopterus* ranges from Middle Eocene to Miocene, with a fossil record reported in Europe (Eocene of France and the Miocene of Germany and Slovakia) and Asia (Miocene of Japan) (Cappetta 2012; Underwood & Schlögl 2013 and references therein). Two species are recognized, †*Paraetmopterus nolfi* Adnet 2006; described from the Eocene of France and †*Paraetmopterus horvathi* Underwood & Schlögl 2013 from the early Miocene of Slovakia (Underwood & Schlögl 2013). Our complete specimen resembles more in shape to the teeth of †*P. horvathi* illustrated by Underwood and Schlögl (2013) than those of †*P. nolfi* (Adnet 2006). However, our specimen (Figure 2(Q), (R)) bears a third elongated foramen in the lower-middle portion of lingual face of the root, which is not present neither in †*P. nolfi* nor †*P. horvathi* (e.g. Adnet 2006 p. 36, Figure 10.1–10.7; Underwood & Schlögl 2013, Figure 8A–8F). Due to the scarcity of teeth from our assemblage, we prefer to keep the specimen to a generic level. The finding of these specimens form the Neogene of Spain represents the first fossil record of this taxon in the Iberian Peninsula.

cf. Squaliformes fam. et gen. indet.
(Figure 3(I), (J))

Material – Nine teeth (specimen figured MGUV-35878).

Description – The fragmentary, and best specimen, is markedly damaged, preserving only the cusp section. The fragmented crown resembles morphologically to some Squaliformes taxa (e.g. Squalidae and Centrophoridae); however, due to the fragmentary condition and bad preservation of the tooth, a more accurate taxonomic identification beyond cf. Squaliformes is not possible.

Order Pristiophoriformes Berg, 1958
Family Pristiophoridae Bleeker, 1859
Genus *Pristiophorus* Müller and Henle, 1837
Pristiophorus sp.
(Figure 3(A), (B))

Material – One complete oral teeth of indeterminate jaw position (MGUV-35879).

Description – The tooth is wider than high and displays a height of 0.8 mm and a width of 1.4 mm. The tooth has a central triangular cusp very well separated from the mesial and distal cutting edges, been the tooth considerably wider than higher. The labial side is rhombic in shape and slightly convex with a broad and rounded apron; in the lingual side a short uvula can be observed. Both lingual and labial sides of the crown are not ornamented, but small fold-like structures are present in the medial and distal basal borders of the labial side. The root is completely missing in our unique specimen.

Remarks – *Pristiophorus* ranges from the Lower Cretaceous to the Recent, with a worldwide fossil record (Cappetta 2012). A summary about the European Cenozoic record of *Pristiophorus* is discussed by Adnet (2006) and Underwood and Schlögl (2013). Most of the fossil record of *Pristiophorus* in the Neogene of Europe is represented by isolated rostral denticles (usually called rostral teeth; see Welten et al. 2015), which have been assigned to †*Pristiophorus suevicus* Jaekel 1890. According to Underwood and Schlögl (2013), the holotype of †*P. suevicus* could not be

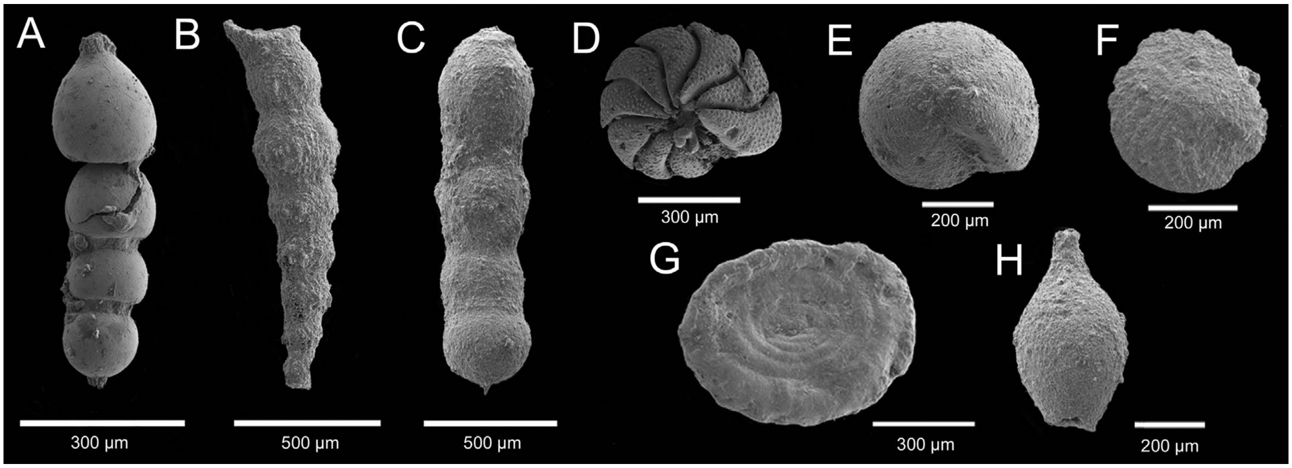

Figure 4. Foraminiferal assemblage recovered from 'El Chorrillo' outcrop. (A) *Siphonodosaria laevigate* MGUV-35886; (B) *S. lepidura,* MGUV-35888; (C) *S. vernuilli* MGUV-35889; (D) *Cibicides floridanus* MGUV-35887; (E) *Gyroidina neosoldanii* MGUV-35890; (F) *Elphidium crispum* MGUV-35891; (G) *Spirillina vivipara* MGUV-35893; (H) *Nodosaria* cf. *N. ridicula* MGUV-35892.

regarded as diagnostic as rostral denticles of *Pristiophorus* are not useful for accurate taxonomic identification. Our specimen, with a rhombic labial side, considerably wider than higher, and the central cusp well developed, representing less than half of height of crown but less than third of width of crown, are characteristics of *Pristiophorus.* However our specimen is quite different to those of †*Pristiophorus striatus* Underwood & Schlögl 2013; from the early Miocene of Slovakia, and due that the dental morphology in †*P. suevicus* is practically unknown, not allowing a complete comparison, we refrain its taxonomic identification at species level. The finding of this tooth represents the first fossil record of this taxon in the Neogene of Spain, existing closer records like the specimens referred from the Upper Miocene of Portugal (Antunes et al. 1999b).

Superorder Galeomorphii Compagno, 1973
Order Carcharhiniformes Compagno, 1973
Family Scyliorhinidae Gill, 1862
Genus *Scyliorhinus* Blainville, 1816
Scyliorhinus sp.
(Figure 3(C)–(H))

Material – Four teeth with complete crown and eroded root, and other six fragments (cusps), all of indeterminate jaw position (MGUV-35880-83).

Description – The teeth crown displays a height of 0.3 mm and a width of 0.2 mm. the crown is characterized by a mainly triangular and slender cusp with two smaller lateral cusplets on each side; all the cutting edges are unserrated. In the specimens with complete crown (Figure 3(C)–(H)), as well in the isolate cusps, both labial and lingual sides are ornamented by slightly strong folds. In the specimens with complete crown the root is eroded ant not well preserved, however, margin-lingual foramina can be observed.

Remarks – *Scyliorhinus* ranges from the Lower Cretaceous to the Recent with 17 extant species (Froese & Pauly 2017). This taxon has a wide fossil record that includes Africa, Asia, Europe and North America, (Cappetta 2012 and references therein). Dental pattern in extant *Scyliorhinus* is little known, a strong gynandric heterodonty is probably widespread, which should be taken with precaution, especially for taxonomical identification of fossil specimens (see Cappetta 2012). Due to the scarcity and bad preservations of our specimens, we could not find diagnostic character to be used in a more accurate taxonomic identification. The finding of these teeth represents the first fossil record of this taxon in the Neogene of Spain. Previous fossil record of this taxon in the Iberian Peninsula includes the Miocene of Portugal (Antunes et al. 1999b).

Chondrichthyes gen. et spp. indet.
(Figure 3(K), (L))

Material – 12 isolated scales (denticles) (specimen figured MGUV-35884, rest of material MGUV-35885) without any diagnostic features for a preliminary and accurate taxonomical determination, however, we do not rule out that these scales could belong to any of the shark taxa referred to the Sax locality.

Discussion

Shark palaeodiversity and the significance of the assemblage

The shark microremains described herein (Table 1) from the late Middle Miocene of Sax (Alicante) is attributed to seven taxa: *Deania calcea*, †*Isistius triangulus*, †*Squaliolus cf. S. schaubi*, †*Paraetmopterus* sp., *Pristiophorus* sp., *Scyliorhinus* sp., and a cf. Squaliformes indet., which are recorded for the first time in the Neogene of Spain. †*Squaliolus cf. S. schaubi* and †*Paraetmopterus* sp., represent the first fossil record of these taxa from the Iberian Peninsula. Other large shark teeth specimens have also been surface-collected by private collectors from this locality, including †*Cosmopolitodus hastalis* (Agassiz 1838), *Isurus* sp., *Hemipristis serra* (Agassiz 1835), *Odontaspis* sp., *Carcharhinus* spp. and †*Otodus* (*Megaselachus*) *megalodon* (CMP and CH pers. obs.). As it has been referred in the methods section, those remains were not included in this contribution, although they have been commented in this discussion section for a better understanding of the fossil assemblage.

The overall above referred taxa from the Sax locality have also been found in other Miocene localities of Europe (e.g. Antunes &

Jonet 1970; Brisswalter 2008; Cappetta 1970, 1973, 2012; Ledoux 1970, 1972; Holec et al. 1995; Balbino 1995, 1996; Antunes et al. 1999a, 1999b, Antunes & Balbino 2003, 2004; Kocsis 2007; Vialle et al. 2011; Reinecke et al. 2011; Bor et al. 2012; Underwood & Schlögl 2013; among others). Regarding the fossil elasmobranch microremains from Sax, only *Scyliorhinus* is nowadays a typical inhabitant of the Mediterranean Sea (Ebert et al. 2013), with two species: *Scyliorhinus canicula* (Linneaus 1758) and *Scyliorhinus stellaris* (Linneaus 1758). In contrast, *D. calcea*, *Isistius* [*Isistius brasiliensis* (Quoy and Gaimard 1824), *Isistius plutodus* Garrick and Springer 1964], *Pristiophorus* (*Pristiophorus schroederi* Springer and Bullis 1960) and *Squaliolus* (*Squaliolus laticaudus* Smith and Radcliffe 1912) are nowadays inhabitants of the Atlantic Ocean, but not of the Mediterranean Sea (Ebert et al. 2013).

The elasmobranch microremains from Sax contains taxa whose extant and extinct relatives are characterized by diverse environmental and bathymetric affinities. Taxa such as *Deania calcea*, †*Squaliolus* cf. *S. schaubi*, †*Paraetmopterus* sp., and *Pristiophorus* sp., likely could suggest affinities with deep-water preferences (Table 1). According the Ebert et al. (2013), the extant *Deania calcea* can be found in depths between 70 and 1470 m, although this species is typically found between 400 and 900 meters depth. The two extant species of *Squaliolus* also prefer depths between 200 and 2000 meters (e.g. Froese & Pauly 2017), and the extinct †*Paraetmopterus* has been exclusively associated with deep-water palaeoenviroments (e.g. Adnet 2006; Underwood & Schlögl 2013). Although extant species of *Pristiophorus* inhabit both shallow and deep waters (see Kiraly et al. 2003; Compagno et al. 2005; Froese & Pauly 2017), many species prefer depths greater than the inner shelf (>50 m), being frequent also on the outermost margin of the continental shelves (Kiraly et al. 2003; Compagno et al. 2005; Froese & Pauly 2017). The extant species of *Isistius* are typical inhabitants of the pelagic-bathypelagic zone, being found mostly between the surface and depths up to 3700 m (Compagno et al. 2005; Froese & Pauly 2017). *Isistius* also occur in shallower depths at night, as these sharks perform nocturnal vertical migrations from deep to shallow waters (see Carrillo-Briceño et al. 2015 and references therein). In America and Europe, *Isistius triangulus,* as well as other fossil species referred as *Isistius* sp., have been found in both shallow and deep water palaeoenviroments (see Antunes & Jonet 1970; Holec et al. 1995; Aguilera & Rodrigues de Aguilera 2001; Kocsis 2007; Cigala-Fulgosi et al. 2009; Vialle et al. 2011; Cappetta 2012; Carrillo-Briceño et al. 2014, 2015; Pollerspöck & Beaury 2014 and references therein). In reference to *Scyliorhinus*, the 17 extant species have wide environmental preferences, inhabiting both shallow and deep-water environments (Compagno et al. 2005; Froese & Pauly 2017). Nevertheless, most of these species show depth preferences greater than the inner shelf (see Froese & Pauly 2017). *Scyliorhinus canicula* and *S. stellaris*, which are the only representatives nowadays in the Mediterranean, show depth preferences between 10 and 780 m (usually 80–100 m) and 1–400 m (usually 20–63) respectively (Froese & Pauly 2017). The Paleogene and Neogene record of *Scyliorhinus* in Europe, suggest for the fossil species, a wide range of environments (see Cappetta 1970; Antunes et al. 1999b; Adnet 2006; Reinecke et al. 2008, 2011; Brisswalter 2009; Bor et al. 2012 and references therein).

Although the shark assemblage from the Sax locality likely suggest deep-water environment, there is a contrast, with the sedimentary and foraminiferal evidence, which suggest a coastal environment. The Sax locality, characterized by coarse grain sediments and the presence of glauconite, suggests an inner shelf depositional environment. In reference to the foraminiferal assemblage, it contains some species typical from coastal environments such as *Cibicides floridanus* (Cushman 1918), *Elphidium crispum* (Linné 1758), *Gyroidina neosoldanii* Brotzen 1936, *Siphonodosaria laevigate* (Silvestri 1872), *Siphonodosaria lepidura* (Schwager), *Siphonodosaria vernuilli* (d'Orbigny), *Spirillina vivipara* Ehrenberg or *Nodosaria* cf. *N. ridicula* (Linné) (Figure 4(A)–(H)). The composition of the whole foraminiferal assemblage, together with the total absence of pelagic foraminiferal, suggests a marine inner platform environment not deeper than 40 meters.

Chondrichthyan assemblages with a mixture of shallow and deep water taxa has been previously recorded in Neogene sediments of America (Carrillo-Briceño et al. 2015) and Europe (Vialle et al. 2011). In this sense, Vialle et al. (2011) and Carrillo-Briceño et al. (2015) proposed two alternative for explaining such ecological incongruence: (1) the migration of deep water taxa/elements to shallower waters through submarine canyons/coastal upwelling, or (2) the transport or washed of shallow water elements into deeper water environments by turbidity currents or slumping. The sedimentological and foraminiferal evidence, in accordance with the wide bathymetric ranges expected for the fossil shark taxa (see above), could support an origin more congruent with the former hypothesis. In fact, important vertical migrations have been recorded in deep waters sharks as *Isistius* (Laurito 1996; Carrillo-Briceño et al. 2015), *Deania calcea* (Parker & Francis 2012), and *Squaliolus* (Compagno 1984; Froese & Pauly 2017), typically associated with feeding habits in near-shore environments. Similarly, some other species also migrate to shallower and more restricted areas for breading, as juvenile forms benefit from greater food supply and are less vulnerable there than in the abyssal zones (Priede et al. 2006). However these ecological aspects are difficult to check with our data, in order to explain our chondrichthyan assemblage. Therefore, although the Sax locality would had been deposited in a upper-inner or lower-middle shelf environment; future fossil evidences, including accurate taxonomical studies in other taxa as bony fishes (which remains are abundant in our sample), could offer other lights about this interesting and potential fossiliferous locality. In addition, the presence of other neritic/oceanic taxa of the orders Lamniformes (†*C. hastalis*, *Isurus* sp., *Odontaspis* sp., and †O. *megalodon*) and Carcharhiniformes (*H. serra* and *Carcharhinus* sp.) in the Sax locality (represented by teeth macroremain, see above), does not offer a direct environmental inference, as these fossil taxa and their extant relatives have been found in a wide range of environments worldwide, suggesting that these large species were able to move along significant distances over oceanic basins (see Reinecke et al. 2011; Cappetta 2012; Carrillo-Briceño et al. 2015, 2016 and references therein).

Implications for the post-Messinian Mediterranean deep-sea ecosystems

One of the most important events that largely determined the current biodiversity of the Mediterranean Sea was its almost complete desiccation during the so-called Messinian salinity crisis 5.59 Ma ago (Krijgsman et al. 1999; Gibert et al. 2013). The drastic changes in climate, salinity, anoxia and sea level fluctuation (Flores et al. 2005; Cita 2006; García-Castellanos et al. 2009; García-Castellanos & Villasen 2011; Goldhammer et al. 2015) entirely eliminated deep-water environments, reducing available ecosystems and driving most species to extinction (Coll et al. 2010). As a consequence, the actual diversity of the Mediterranean Sea comes directly from the repopulation of the Atlantic Ocean faunas through the Gibraltar Strait since its opening at the Zanclean flood (Gibert et al. 2013). But interestingly, the deep-water ecosystems in the Mediterranean Sea show a severe diversity impoverishment compared to those of the Atlantic Ocean of similar depth (Perés 1985). The deep-water chondrichthyan community is not an exception in this sense (Perés 1985; Marsili 2008). Thus, the present Mediterranean Sea deep-water selachian fauna is represented by very few taxa: *Hexanchus griseus* (Bonnaterre 1788), *Galeus melastomus* Rafinesque 1810, *Etmopterus spinax*, *Centroscymnus coelolepis* Barbosa du Bocage and Brito Capello 1864 and *Centrophorus granulosus* (Bloch and Schneider 1801) (Sion et al. 2004; Serena 2005; Marsili 2008). This selachian community differs substantially from the pre-Messinian taxonomic composition, as suggested by several Middle Miocene fossil elasmobranch assemblages (e.g. Cappetta et al. 1967; Cigala-Fulgosi 1984, 1986, 1996; Cappetta & Nolf 1991; Adnet 2006; Vialle et al. 2011; Underwood & Schlögl 2013), including the one here described. These important differences have been linked with the peculiar deep-sea environmental conditions that have characterised the current Mediterranean Sea after the reopening, about 5.33 Ma, during the Zanclean flood (Coll et al. 2010). Different factors have been proposed as ecological and physical barriers that hindered the colonization of the Mediterranean by deep-water Atlantic species, including: (1) aspects of its model circulation, (2) deep homothermic waters (with temperatures about 10 °C higher than in the Atlantic Ocean at the same depth), (3) nutrient depletion, and (4) a high threshold in the Gibraltar area (being the Strait the only natural connection with the Atlantic Ocean and acting as a biogeographic barrier due to its 320 m deep and 14 km wide) (e.g. Bouchet & Taviani 1992; Krijgsman et al. 1999; Galil 2004; Sardà et al. 2004; Marsili 2008; Coll et al. 2010, among others).

On the other hand, abyssal assemblages with a significant number of deep-water chondrichthyan taxa have also been described in the Pliocene and Pleistocene of the Mediterranean region, including genera such as *Mitsukurina, Centroscymnus, Scymnodon, Scymnodalatias, Centrophorus, Deania* and *Pristiophorus* (see Marsili 2006), most of them currently inhabiting only the Atlantic side (Compagno 1984; Marsili 2008; Ebert et al. 2013). This diversity indicates that important colonization events from the Atlantic Ocean took place in post-Messinian times, establishing a relatively high-diversity deep-water selachian communities. However, these differences between the Mio-Pliocene and the extant chondrichthyan communities suggest that other more recent events, posterior to the Messinian salinity crisis, should have promoted the impoverishment of the current bathyal selachian faunas seen nowadays. In this sense, the water column of the present Mediterranean Sea is characterised by oxygenated conditions above the sea-floor (Stanley 1985). However, the alternating sequences of light and dark sediments in Pliocene-Quaternary cores indicate that sea-floor conditions have varied in the past (Sardà et al. 2004; Gallego-Torres et al. 2010), with the presence of successive oxic-anoxic events and the production of sapropels (see, e.g. Rossignol-Strick et al. 1982; Rohling 1994; Rohling et al. 2015). Therefore, we propose that the recurrent stagnant (dysoxic and anoxic) Quaternary episodes, including the most recent Holocene 'S1 sapropel deposition' (10.2–6.4 kyr ago, Mercone et al. 2000; Gallego-Torres et al. 2010; Jiménez-Espejo et al. 2015; Martínez-Ruiz et al. 2015), could have played a key role in the taxonomic impoverishment of the Mediterranean deep-water selachian communities, in a similar way than they affected other bathyal groups (Galil 2004; Hayward et al. 2009). Consequently, the biogeographic history of the deep-sea Mediterranean sharks seems to have a more complex history, with several colonization events after the Zanclean flood, but driven by different factors that could have acted promoting or hindering the establishment of such taxa in the Mediterranean abyssal environments (Lasram et al. 2008). Thus, the impoverishment of the current deep-sea selachian community cannot be interpreted as a direct consequence of the Messinian salinity crisis, and the role of other more recent events, such as the Pliocene-Quaternary anoxic events, should be studied in the future for achieving a better understand of the origin of the extant Mediterranean deep-sea chondrichthyan community.

Conclusion

The study of a new Serravallian (Middle Miocene) locality from the Southeastern Spain, have yielded a shark fauna with deep-water preferences. At least seven taxa are recorded for first time in the Neogene of Spain and two from the Iberian Peninsula, with strong faunal affinities with other elasmobranch assemblages from the Miocene of Europe. This suggests that the lack of data in Spain could be mainly due to a low sampling effort for this kind of micro-remains. This shark fauna from Sax differs considerably from the recent deep-water communities present in the Mediterranean Sea and those referred from the Pliocene and Pleistocene of the region, suggesting a more complex biogeographic history linked with the closure and desiccation of the Mediterranean Sea during the Messinian salinity crisis (Upper Miocene) and the posterior evolution of the basin. In this sense, although the Messinian salinity crisis strongly affected the palaeobiogeographic history of the Mediterranean, some other factors, as more recent anoxic event, should be also involved in the recovery and composition of the deep-water communities.

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