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A reworked elasmobranch fauna from Tunisia providing a snapshot of Eocene-Oligocene Tethyan faunas.

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Abstract

A post-Priabonian fluviatile debris-flows in Mabrouk (MBK), Djebel Chambi – Tunisia, have yielded a surprisingly rich assemblage of reworked marine elasmobranchs (23 taxa of sharks and rays). By comparison with their sub-coeval counterparts from northeastern Africa, this assemblage suggests an age ranging from the latest Priabonian up to the earliest Rupelian for the close marine deposit from where they were likely reworked. Moreover, it highlights the widespread east-west distribution of sharks and rays along North African coasts, a distribution that reflects the existence of roughly similar tropical environmental conditions in northern latitudes of Africa at that time. This discovery indicates that the Neotethysian elasmobranch communities remained particularly well diversified around the global cooling recorded at the Eocene/Oligocene transition.

Keywords: Tunisia, reworked elasmobranch, faunal dispersal, dating and paleoenvironmental inferences

1. **Introduction**

If the early Cenozoic is marked by a particularly warm climate; however, a global cooling linked to a decrease in atmospheric carbon dioxide concentration (DeConto and Pollard, 2003) and a modification in oceanic currents are recorded at the Eocene/Oligocene transition. Marked by large-scale extinction and floral and faunal turnovers, there is a common consensus about these climatic changes, although the debate remains open about the modalities of the cooling, especially in Egypt (e.g. see Peters et al., 2010; Underwood et al., 2012, Gingerich et al., 2012). In the marine realm, these climatic changes are responsible from the formation of the Antarctic ice sheet and a significant decrease in the sea level (e.g. see Miller et al., 2005; Liu et al., 2009) occulting the main Oligocene marine deposits. In this transitional context, between a relatively warm, ice-free world and a cooler world, the event known as the "Grande Coupure" (~33.9 My) is marked by a faunal turn-over among marine (e.g. Haasl and Hansen, 1996) as well as Holarctic terrestrial faunas (e.g. Zhang et al., 2012). In Africa, the effects of the "Grande Coupure" on terrestrial faunas are conversely poorly documented, as only few localities have yielded vertebrates from the Eocene/Oligocene transition (e.g., Seiffert, 2007, Benammi et al., 2017, Marivaux et al., 2017a-b). Interestingly, these terrestrial faunas are generally associated with marine vertebrates, often dominated by elasmobranchs. Among those, several Upper Eocene localities from the southwestern Neotethys - Eastern Atlantic area have yielded elasmobranch assemblages (e.g. Case and Cappetta, 1990; Strougo et al., 2007; Adnet et al., 2007, 2010, 2011, Underwood et al., 2011, Murray et al., 2014, Zalmout et al., 2012), even though most of them are located in its more oriental part and especially in Egypt, near the Fayum depression (see Fig. 1). On the other hand, early Oligocene elasmobranch faunas from the same area are much less known, and only a few localities have been studied in detail (e.g. Adnet et al., 2007, Murray et al., 2014, Van Vliet et al., 2017). Thus, the faunal dynamic of elasmobranchs in the southwestern Neotethys region during this transitional period is poorly known. A new vertebrate fossil-bearing locality from Djebel Chambi in Tunisia (Mabrouk locality, named MBK), supposedly dated around the Eocene/Oligocene transition, was discovered by the French-Tunisian team during several fieldtrips in 2010-2012. Having recorded many elasmobranch fossils, this last allows to fill a geographical gap in the western Tethys fossil record, and to further our knowledge about the shark and ray faunas from this critical period.

2. **Geological Setting**

As part of the Central Tunisian Atlassic domain, the Djebel Chambi — the highest summit of Tunisia (1544m) — is essentially constituted by Barremian to upper Senonian marls and limestones. On the both flanks of this structure oriented NE-SW, these marine Cretaceous series are unconformably covered by continental Eocene deposits (e.g. Sassi et al., 1984). On the northern flank, the Eocene outcrops begins with a sequence of alluvial-fan conglomerates interbedded with lacustrine limestones and alluvial-plain facies, composed of silty-clays and thick reddish matured paleosoils. In a lacustrine limestone positioned in the middle part of this sequence, the first vertebrate fossil-bearing level (sites of Chambi-1 and Chambi-2, F1 in Fig.2) yielded a rich mammalian fauna dated from the late Ypresian or early Lutetian (see Marivaux et al., 2013, 2015, Ravel et al., 2016, Solé et al., 2016, Tabuce, 2018 for a recent overview). At Bir-Om Ali locality, three kilometers northeast of Chambi-1, the Eocene outcrops continue with evaporitic lagoonal sediments, showing gypsum concentrations, root traces and paleosoils, grading-upwards into lacustrine or restricted marine facies. These levels yielded numerous oogones of late Eocene charophytes *Nodosochara* (''*Raskyaechara*'') *baixanensis* and *Pseudolatochara* sp. (see Vialle et al., 2013) (C in Fig.2) a few fossil remains of a large-bodied mammal (arsinoitheriid embrithopod) (F2 in Fig.2, Bir Om Ali locality; see Vialle et al., 2013). Above these beds, a thick alternation of marls and lignite levels is covered by a thin bed of monospecific shells. This facies association caracterize a shallow-water restricted area (swamp or marsh). These deposits are overlain by a vertical evolution of facies that begins with fine-grained sandstones, organized into a set of planar and through cross-bedded (Fig. 2 C1) of fluvial origin (sand bar of braided-river). This facies are capped above by several levels of yellow colored, matrix supported, sandy-conglomerates of debris-flows (Fig. 2 C2). These levels, well-exposed at the Mabrouk locality (MBK), yielded the new elasmobranch fauna here studied (F3 in Fig. 2). Above, pluridecimetric beds of coarse-grained sandstones with planar cross-bedding, characterizes ephemeral braided-streams (Fig. 2 C3). On the top of the series, a second set of thick sandstones beds, with trough and planar cross-bedding, is observed and interpreted as fluvial deposits. At the end of the section, a coarse-grained polygenic conglomerate is attributed to an alluvial fan system. No marine deposit was clearly identified in the surrounding area, nor under nor above the fossiliferous level F3 (Fig. 2). No other evidence of marine life (apart from elasmobranchs and some rare remains of marine bony fish) was detected among the fluvial sands that constitute the MBK outcrops (Fig. 2C).

3. **Systematic Palaeontology**

Fossil material was collected by surface collecting/picking and dry sieving (until 0.7 mm sieve) of 150 kg of crushed rock in the field. The elasmobranchs represent the largest part of fossil vertebrate remains recovered in situ, with about five hundred complete and broken specimens collected. The material consists of isolated teeth, often broken and worn, sometimes rolled and embedded in a hard rock matrix, leading fossil preparation challenging. Sand grains are usually embedded inside the numerous cracks of tooth crown and root (see Fig. 2), preventing a complete clearing of the specimens. The fossil elasmobranch association consists of 23 identified taxa. All specimens are in the same damaged state of preservation, and no taxa is preferentially worn or rolled, thereby indicating that none was more severely reworked. Microborings are visible on the whole teeth, especially on roots, indicating the presence of endolithic micro-organisms in the first steps of diagenesis or during the reworking. Without any significant difference of conservation state, all taxa are thus considered a priori as coeval and coming from a "phantom" marine deposit (unobserved on the field). Original marine deposit is/was probably located nearby to the outcrop, to southeastern considering the debris-flows way direction. The systematic paleontology voluntary focus on the eight significant taxa, notably regarding their related dating interest and environmental inference. Figured specimens are housed in the paleontological collections of the museum of the “Office National des Mines” of Tunis, Tunisia

Abbreviations: MBK: collection number for fossil material from the Mabrouk locality, Tunisia.

Carcharhiniformes Compagno, 1973
Carcharhinidae Jordan and Evermann, 1896
Galeocerdo Müller and Henle, 1838
Galeocerdo cf. *eaglesomei* White, 1955

Fig. 3. A-E
Material: more than 120 teeth, including figured MBK-01 to 03

Description - This taxon shows mainly a monognathic heterodonty. The teeth are rather large, mesio-distally elongated, labio-lingually compressed, and can reach 2 cm wide. Generally, these teeth have a rather high triangular crown, with a main cusp from slightly to strongly slanted distally, depending on the position on the jaw (in anterior and lateral files, respectively). The mesial cutting edge of the crown bears well-developed serrations from the mesial extremity approaching the top of the cusp, although it stops just before the apex. Although we can observe many specimens with smooth mesial and distal cutting edges on the superior part of the crown, we can nevertheless distinguish on the well-preserved specimens, well-developed serrations on both the lower and upper parts of the crown. Thus, the absence of these serrations on some specimens is probably due to the strong abrasion of the material during the taphonomic process, and as such it does not represent a morphological feature. The crowns have a distal heel, which bears strong serrations that decreases in size distally and forms an angle with the distal cutting edge of the cusp. The inferior part of the distal cutting edge is straight to concave, and mark an angle with the straight to concave distal heel. The labial face of the crown is flat, whereas the lingual face is convex. The root bears two lobes, and is always longer than the crown. In lingual view, all specimenspossess a well-marked median protuberance deeply incised by a short groove (Fig. 3, B2, C2-E2). Generally, the labial face of the crown strongly overhangs the labial face of the root (Fig. 3, A1, C1-E1). On the antero-lateral (Fig. 3, D) and lateral teeth (Fig. 3, A,B, and E), the crown is rather low, and the main cusp is strongly slanted distally. On the contrary, the anterior teeth (Fig. 3, C) have a high crown and a cusp slightly slanted distally. In addition to the size, there is no other significant morphological difference between juvenile teeth (Fig. 3, B) and adult teeth (Fig. 3, A, C-E).

Discussion – These specimens show some diagnostic features attributed to *Galeocerdo eaglesomei*, such as a high crown (especially in anterior files) and a well-developed serration. However, the state of preservation of teeth does not allow us to provide a formal specific identification of these specimens to this taxon, which justifies the attribution to *G.* cf. *eaglesomei*. This species is relatively different from contemporaneous and widely distributed *G. latidens* Agassiz, 1843, known elsewhere in deposits of North Africa dating from the late Eocene (Case and Cappetta, 1990; Underwood et al. 2011; Mustafa and Zalmout, 2002). Compared to *G. latidens*, *G. eaglesomei* have higher teeth (Case and Cappetta 1990, Case and Borodin, 2000), greater serrations that almost reaches the apex of crown, a character which is never observed in *G. latidens*. Underwood et al. (2011) reported another *Galeocerdo* with fully serrated teeth, *G. ?aegyptiacus* Stromer, 1905 from the middle-late Eocene of Egypt. Unfornunately the type material is presumed lost and the validity of this small species remains dubious in absence of clear figuration. *Galeocerdo eaglesomei* is widely distributed during the middle Eocene of North America (e.g. Case and Borodin, 2000, Maisch et al*.,* 2014) and Africa (e.g. White, 1955, Cappetta and Traverse, 1988, Strougo et al., 2007, Underwood et al., 2011) to the early late Eocene of Morocco (Adnet et al., 2010). However, the latterteeth, twice to three times larger are likely belongs to an unnamed new species.

Carcharhinus Blainville, 1816 or *Negaprion* Whitley, 1940

The Eocene-Oligocene fossil record of *Carcharhinus,* widely distributed but relatively scarce before the late Eocene, consists of rare materials often misidentified with *Negaprion,* leading some authors to undifferentiate the Eocene occurrences of *Carcharhinus* from those of *Negaprion* (e.g. Kriwet, 2005, Underwood and Gunter, 2012). We can however distinguish three morphological groups of large Eocene carcharhinids:

- A first group that gathers the whole Eocene carcharhinids characterized by completely unserrated crowns on upper and lower teeth, thereby making their identification and attribution difficult in both genera (e.g. cf. "*Carcharhinus" frequens* (Dames, 1883); *Negaprion* cf. *eurybatrodon* Case and West, 1991, Case and Borodin, 2000; *Negaprion* sp. and *Carcharhinus* sp.1 Adnet et al., 2007; cf. "*Carcharhinus" marcaisi* (Arambourg, 1952); *Carcharhinus* sp. (Kriwet, 2005).
- A second group that consists of undoubted middle-late Eocene *Carcharhinus* species, that have upper teeth sharing a complete serrated crown as firstly reported since the 19th in Egypt (*C. "egertoni"* in Dames, 1883 : Fig. 5) and is currently represented by the large-sized *C. balochensis* (Adnet et al., 2007) and many unnamed specimens (e.g. *Carcharhinus* cf. *egertoni* in Stromer 1905; *Carcharhinus* sp. 1 in Case and Cappetta, 1990; *Carcharhinus* sp. 2 in Adnet et al., 2007; *Carcharhinus* sp. in Underwood and Gunter, 2012; *Carcharhinus* sp. in Underwood et al., 2011)
- and a third group of Eocene carcharhinid that have teeth with smooth massive cusp and low lightly serrated heels on upper teeth. It concerns particularly three fossil species, belonging to *Carcharhinus* or *Negaprion* according authors and/or time: cf. "*Negaprion" amekiensis* (White, 1926); cf*. "N". gibbesi* (Woodward, 1889) and cf*. "N". gilmoeri* (Leriche, 1942). The attribution to the genus *Carcharhinus* remains uncertain considering that such tooth morphotype may be, as for the first group, related to the living representatives of *Negaprion* (e.g. *N. brevirostris)* or *Carcharhinus* (e.g. the Arabian sharks *C. hemiodon* or *C. leiodon).*

Consequently, isolated teeth of *Carcharhinus* are really difficult to distinguish from *Negaprion* before the late Oligocene because they lack the usual complete serrated cutting edges on upper teeth as observed in all living *Carcharhinus* species*.* Considering this dilemma, we consider, when not discussed, as confer to the formally attribution of authors to *Negaprion* (and relative old synonym *Hypoprion*) or *Carcharhinus* (and relative old synonyms *Aprionodon* and *Prionodon*)

cf*. "Carcharhinus" frequens* (Dames, 1883)

Dames, 1883: *Aprionodon frequens* - fig. 7 a-e,i-p
?Stromer, 1905: *Carcharias sp.* – pl. 16, Figs. 21 and 28
?Priem, 1908: *Carcharias (Aprionodon)* aff*. frequens* – pl.15,
Fig. 6–7
?Casier, 1971: *Aprionodon frequens* – pl. 1, Fig. 6
Case and Cappetta, 1990: *Carcharhinus frequens* – pl. 5, Figs. 104–
107; pl.7, Figs. 143–144 and 151–159
Adnet et al., 2010 : *Carcharhinus frequens.* Text only
Adnet et al., 2011: *Carcharhinus* aff*. frequens* – Fig. 3G–H
Underwood et al., 2011: *Negaprion* sp. – Fig. 5T–U
Zalmout et al., 2012: *Negaprion frequens* – Fig. 5A-D
?Zalmout et al., 2012: *Carcharhinus* sp*.*1 – Fig. 5E-F
?Murray et al., 2014: *Carcharhinus* sp. - Fig. 4C and ?*Misricthys stromeri*. - Fig. 4B, unknown in text
Van Vliet et al., 2017. *Negaprion frequens* – Fig. 12G

Fig. 3. I-J
Material: eight teeth, including figured MBK–06 and 07

Description – This taxon shows a rather moderate dignathic heterodonty. There is no serrations on either mesial and distal cutting edges as well as on the heels of these specimens. Upper teeth (Fig. 3I) have a relatively high cusp, rather long at its base, triangular, and more or less slanted distally depending on their position on the jaw. Lower teeth (Fig. 3, J) have a very high cusp, straight and slender. The root is well-developed, low and separated into two distinct lobes by a shallow nutritive groove. The two root lobes in lower teeth are shorter than those of the upper teeth and always separated by a nutritive groove. The labial face of the crown is flat (Fig. 3 I1, J1), whereas the lingual face is convex (Fig. 3 I2, J2).

Discussion – Often misidentified, "*Carcharhinus" frequens* was originally named by Dames (1883) from teeth recovered in the late Eocene of Egypt, considering it was the most frequent carcharhinid in the fossil assemblages of Birket-el-Qurun. In the original diagnosis, and despite an unclear figuration (Dames, 1883: fig. 7) that possibly mixed other coeval carcharhinids, Dames (1883: p.144) reported the lack of real serrations on the entire cutting edges, although some infrequent "undulation" can appear on cutting edges of heels. Stromer (1905) and Priem (1908) subsequently reported other material from Egypt among taxa , including some *Misrichtys* teeth for instance (Case and Cappetta, 1990). Case and Cappetta (1990) figured new teeth series from Birket-el-Qurun and provided an updated description of this Egyptian species noting its fine and gracile lower teeth. If some figured material (e.g. Case and Cappetta, 1990: Plate 5 fig. 104-105; Plate 7 fig. 147-148) belong in fact to other carcharhiniforms (e.g. *Abdounia* sp. in Underwood et al., 2011), the most abundant morphotype recovered at Birket-et-Qurun is the gracile unserrated tooth. Latter, Underwood et al. (2011: Tab.1) reported two distinct taxa from Birket-el-Qurunt oo: some "occasional" robust teeth attributed to *Negaprion frequens* (Underwood et al. 2011 fig. 5V–W) and some "abundant" gracile and unserrated teeth identified as *Negaprion* sp. (Underwood et al., 2011 fig Fig. 5T–U). Underwood and Gunter (2012: p.26) changed their previous opinion by studying the type series of "*N". frequens* of Dames and reattributed the unserrated teeth identified as *Negaprion* sp. from Birket-el-Qurun to "*N." frequens* and so, the "occasional" robust teeth attributed to "*Negaprion" frequens* to *N.* sp. (see below), possibly conspecific with coeval *"N". amekiensis.* Cf. *"C". frequens*, as considered here, appeared as a frequent medium-sized carcharhinid, which frequented the south Tethys (Egypt : Dames, 1883, Stromer, 1905, Casier, 1971, Case and Cappetta, 1990, Murray et al., 2010, Underwood et al., 2011, Zalmout et al., 2012) and western Atlantic coasts (Southwestern Morocco : Adnet et al., 2011) during the late. Observed in Rupelian deposits of the Qattara Depression, Egypt (Van Vliet et al., 2017), its occurrence in coeval deposits of the Fayum (Quarries R and E, as *Carcharhinus* sp. and *?Misrichtys stromeri* in Murray et al., 2014: fig. 4) remains currently uncertain.

Carcharhinus sp. or *Negaprion* sp.

Case and Cappetta, 1990: *Carcharhinus* sp. 2 - Plate 5, figs. 100-101
Case and Cappetta, 1990: *Carcharhinus frequens* - Plate 5, fig. 102-103; Plate 7 fig. 145-146
Murray et al., 2010: *Carcharhinus* sp. – Fig. 1.D
Adnet et al., 2011: *Carcharhinus* sp. or *Negaprion* sp. -Fig. 3I–M
Underwood et al., 2011: *Negaprion frequens* - Fig. 5V–W
?Zalmout et al., 2012: *Carcharhinus* sp.2 – Fig. 5G-H

Fig. 4. A-C
Material: twelve teeth including figured MBK-10 to 12

Description – This taxon is represented here by both inferior and superior teeth showing a marked dignathic heterodonty. Superior teeth (Fig. 4, A, B) have a high cusp that is labio-lingually compressed and distal inclined. The convex cutting edges are unserrated. The teeth have rounded, elongated, relatively high and slightly serrated lateral heels (Fig. 4, A), although the latter feature is rarely visible because of wear. The heels are separated from the mesial and distal cutting edges by a more or less marked notch. Lower teeth (Fig. 4, C) have a straight crown and a smaller cusp. The cutting edges of the cusp and the lateral heels do not bear any serration.

Discussion. Although the MBK specimens are often incomplete or worn, they have similar features to teeth recovered from the late Eocene of Egypt (Adnet et al., 2011 as *Negaprion* sp. or *Carcharhinus* sp.), or those rarely recovered from Birket-el-Qurun (Murray et al., 2010 as *Carcharhinus* sp.) and Gehannam (Case and Cappetta, 1990 as *Carcharhinus* sp. 2; Underwood et al., 2011 as *Negaprion frequens*). We considered all these coeval specimens as probably conspecific and belonging to the same unnamed species. As noticed by Underwood and Gunter (2012) regarding the Egyptian material, the formal attribution to *Carcharhinus* remains uncertain and debatable because this morph shares strong reminiscence with the smaller taxa cf. "*Negaprion" amekiensis* (White 1926) from the middle Eocene of Nigeria (late Lutetian-early Bartonian) but is likely late Eocene in age (Underwood and Gunter, 2012). First attributed to "*Carcharhinus*" (White, 1926), this species (see Fig. 5 E) was considered as belonging to *Negaprion* by its discoverer (White, 1955), but seems to correspond in fact to a variant of *cf. "Carcharhinus" gibbesii* (Woodward, 1889) according to Underwood and Gunter (2012). The latter is known from the Oligocene of Eastern (Case, 1980, Kruckow and Thies, 1990, Müller, 1999, Manning, 2006, Cicimurri and Knight, 2009) and Western Atlantic (Reinecke et al., 2014) until the early Miocene (Carrillo-Briceño et al., 2016).

However, teeth of *cf*. "*C." amekiensis* are smaller (not exceeding 8 mm height) and possess larger roots, smooth cutting edges with rarely fine serrations on lateral heels only according White (1926) but contrary to *cf*. "*C." gibbesi*. The case of the subspecies *cf*. "*C." gibbesi gilmorei* (Leriche, 1942), sometimes erected as a species, is more complex. This was originally considered as to be a subspecies of *cf*. "*C." gibbesi* from the Ypresian of Alabama, reattributed after to middle-late Eocene (White, 1956). White (1956, p. 139-144) reassigned *cf. "C." gibbesi* and *cf. "C." gibbesi gilmoeri* to the genus *Negaprion*, indicating that the teeth of the latter "attained a slightly larger size than the typical form, up to 1.2 cm in height. The crowns, especially of upper teeth, are somewhat relatively larger. Basal extensions of crown on upper teeth are only faintly visible but on lower teeth they are coarsely crimped, smooth". Many authors reported this largest subspecies *"C" gilmorei*in middle-late Eocene deposits of USA (Case, 1980, Kruckow and Thies, 1990, Muller, 1999, Parmley and Cicimurri, 2003, Manning, 2006), considering that typical *"C." gibbesi* is more likely post Eocene. However such an attribution appears quite dubious considering that both morphologies were intergradational (Manning, 2006, Cicimurri and Knight, 2009). Only new analyses will allow elucidating these uncertainties. Regardless of these differing point of views, all these forms seems to be really close, both in morphology and in time occurrence.

Carcharhinus perseus Adnet, in Adnet et al., 2007

Fig. 3. F-H

Material: twenty teeth, including figured MBK–4 and 5

Description – In this taxon, the lower and upper teeth (Fig. 3, G) are virtually similar (Fig. 3, F, H), and differ primarily in the presence of a more slender cusp and a less marked serrations characterizing lower teeth. This species thus shows mainly a monognathic heterodonty. The teeth have a triangular cusp, strongly labio-lingually compressed, rather large, high, and more or less curved, depending on their position on the jaw. There are well-marked serrations on both mesial and distal cutting edges from the root to the apex, as well as on the distal heel. Roots are relatively low, never larger than the crowns on both the anterior and superior teeth. In lingual view, a shallow groove incises the root in its central part (Fig. 3. F1-H1). The antero-lateral teeth have a cusp slightly slanted distally and a rounded distal heel (Fig. 3, F1). Unlike the latter, the lateral teeth display a cusp more slanted distally, and the inferior part of the mesial edge forms a greater angle with its superior part (Fig. 3, G-H). Moreover, the distal heel is rather straight (Fig. 3, G-H).

Discussion – Specimens from MBK display morphological features very similar to those observable in the species *C. perseus* recovered in Pakistan (see Adnet et al., 2007: Fig. 4), with a very limited dignathic heterodonty, a reduced nutritive groove (in lingual view) and a strong labio-lingual compression of teeth (Adnet et al., 2007). *Carcharhinus perseus* was originally described from the early Oligocene of Baluchistan, Pakistan (Adnet et al. 2007). It is also known from the early Oligocene of, Oman (Thaytiniti, quoted in Adnet et al., 2007) and Egypt (Jebel Qatrani, Quarries A and E ; Murray et al., 2014; Qattara Depression: Van Vliet et al., 2017). This taxon has not been recorded in late Eocene localities of North Africa, except if we consider the upper teeth with similar pattern reported and figured by Dames (1883: pl.3, fig. 5). Misidentified with the Neogene species *C. egertoni* (Agassiz, 1843), the age and provenance of the fossils reported by Dames (1883) remain uncertain but could testify of the first report of this species in the Paleogene of North Africa, unless it corresponds to another coeval *Carcharhinus* with large serrated upper teeth as *Carcharhinus* sp. 1 according Case and Cappetta (1990: Pl. 7 fig. 164-165); *Carcharhinus* sp. 1 according Underwood et al. (2011: fig. 4N), or *Carcharhinus* sp.1 according Adnet et al. (2011: fig.3D-F) from the late Eocene of Egypt.

Misrichthys Case and Cappetta, 1990
Misrichthys stromeri Case and Cappetta, 1990

Fig. 3. K-L
Material: Two teeth, including figured MBK-8 and 9

Description – This taxon, only known by two teeth in the MBK assemblage (Fig. 3, K-L), displays a medium dignathic heterodonty. The anterior lower tooth (Fig. 3 K) have a relatively high, slender and straight cusp. The root, although incomplete, is massive, with short but well-developed lobes, and we can notice the presence of a deep median nutritive groove. The labial face of the crown is flat (Fig 3 K1), whereas the lingual face is strongly convex (Fig. 3 K2). In profile, the crown is slightly sigmoid. The upper tooth (Fig. 3 L) has a triangular cusp, rather large at its base and slanted distally. There are also well-developed lateral heels. The mesial heel is rather elongated and follows the mesial cutting edge, whereas the distal heel is short, rounded, and well separated from the distal cutting edge by a deep notch. The root is relatively well developed, and bears in lingual view a median protuberance incised by a short groove (Fig. 3 L2).

Discussion – A massive root with short lobes and deep nutritive groove are very peculiar features among large fossil carcharhinids. These unusual characters are only known in the anterior teeth of *Misrichthys stromeri*. Likewise, this species is characterized by a strongly marked dignathic heterodonty (Case and Cappetta, 1990, Adnet et al., 2011, Cappetta, 2012). Despite a limited material sample, these unique characters are observed in the MBK specimens, justifying the assignation to this taxon. Until now, *Misrichthys* was a monospecific genus, geographically and stratigraphically constrained. Indeed, this species is only known along the late Eocene coast of Middle East - North Africa, from Jordania (Mustafa and Zalmout, 2002), Egypt (Case and Cappetta, 1990, Adnet et al., 2011, Underwood et al., 2011) up to southwestern Morocco (Adnet et al., 2010). Murray et al. (2014: fig. 4B) figured a Rupelian tooth (Quarry R) they considered as evidence of *Misrichthys stromeri*, but did not report this occurrence in the material listed from the Jebel Qatrani Formation, Egypt (Murray et al., 2014: Tab.1). This tooth probably belongs to a *Carcharhinus* lower jaw (see before).

Hemigaleidae Hasse, 1789
Hemipristis Agassiz, 1843
Hemipristis curvatus Dames, 1883

Fig. 5. A
Material: One tooth, figured MBK-13

Description – This taxon is only known by one tooth in the MBK assemblage (Fig. 5 A). Although it is poorly preserved, this tooth has a relatively high crown, which is compressed labio-lingually and slanted distally. Its mesial cutting edge is convex with small denticles at its base. In contrast, the distal cutting edge is straight, and forms an angle with an oblique distal heel. The latter is high and bears several well-developed denticles. The lingual face of the crown is convex (Fig. 5 A2), and the root bears a well-developed lingual protuberance, which is incised by a shallow groove. In labial view, the convex crown forms a bulge at its base, and strongly overhangs the low root (Fig. 5, A1).

Discussion – This unique specimen shows morphological features similar to those of the upper teeth of the genus *Hemipristis*, as listed by Cappetta (2012), with the exception to the presence of a well-developed serration on the mesial heel. However, the latter feature is not always present within all the species of this genus, and the denticles of the mesial cutting edge are sometimes poorly developed (see Case and Cappetta, 1990). Basically, the overall morphology of the tooth is similar to that of an antero-lateral tooth from the late Eocene of Fayum attributed to *H. curvatus* by Case and Cappetta (1990 Fig. 4, 80-81). The groove is less developed on the MBK specimen, but this may be related to the wear. Although this taxon is only known by one poorly preserved tooth, we can attribute this specimen to *H. curvatus*, perhaps preferentially to *H. serra*, the latter having larger teeth, and a more developed serration on both cutting edges (Case and Cappetta, 1990). *Hemipristis curvatus* is mainly known in the middle-late Eocene, especially from the late Eocene of the eastern Tethys (Case and Cappetta, 1990, Underwood et al., 2011, Adnet et al., 2010) to the western Atlantic (Case and Borodin, 2000), and also from the late Eocene of the western Pacific (see Cappetta, 2012). Very few occurrences are reported in early Oligocene deposits (e.g. Thomas et al. 1989), unless the strong resemblance with *H. serra* (Chandler et al., 2006) currently known since the early Oligocene of Egypt (Van Vliet et al., 2017), Oman (Thomas et al., 1989) and Pakistan (Adnet et al., 2010) makes particularly difficult its recognition.

Orectolobiformes Applegate, 1972
Ginglymostomatidae Gill, 1862
Nebrius Rüppell, 1837
Nebrius obliquus Leidy, 1877

Fig. 5. B-C
Material: four teeth, including figured MBK-14 and 15

Description – The oral teeth are relatively large without real dignathic heterodonty. The crown is asymmetric, high and thick labio-lingually. There are numerous denticles on the cutting edges, the central cusp is low, straight to slightly slanted distally, depending on the position on the jaw. The mesial cutting edge is convex, and longer than the distal one, which is concave or straight (on lateral teeth). The apron is well developed, elongated, thick in labial view, and strongly overhangs the root. This taxon is represented here by anterior teeth (Fig. 5, B), which are characterized by lateral cusplets disposed symmetrically around the main cusp, and by lateral teeth (Fig. 5, C), which have lateral cusplets arranged asymmetrically around the curved central cusp.

Discussion – There are only a few *Nebrius* species known in the fossil record, especially in the Paleogene. *Nebrius bequaerti* (Leriche, 1920) from the early Paleocene, *N. obliquus* ,*N. thielensis* (Winkler, 1873) and *N. blankehorni* (Stromer, 1905) from the Eocene, and depending if we consider the latter as a junior synonym of *N. obliquus* (Noubhani and Cappetta, 1997). *Nebrius bequaerti* has only a few lateral denticles, which is not the case on the MBK specimens and the other species of *Nebrius* (*N. obliquus* and *N. thielensis*). *Nebrius thielensis* has often a bifid apron, which is never the case in *Nebrius obliquus* (Noubhani and Cappetta, 1997) and on the teeth from the MBK assemblage. Furthermore, the antero-lateral and lateral teeth from MBK illustrated in figure 5 (Fig. 5C and 5B respectively) are quite similar to those illustrated by Noubhani and Cappetta (1997: plate 14, Fig. 1-2) and attributed to *N. obliquus*. If the genus is widespread in the Paleogene and Neogene coastal deposits and principally in the late Eocene (Underwood et al., 2011, Adnet et al., 2010, Adnet et al., 2007), *N. obliquus* is currently known only from the early Eocene (e.g. Noubhani and Cappetta, 1997) to the late Eocene (Adnet et al., 2007, 2010) of the southwestern Neotethysian region.

Incertae ordinis
Odontorhytis Böhm,1926
Odontorhytis aff. *pappenheimi* Böhm, 1926

Fig. 5. D-E
Material: two teeth, figured MBK-16 and 17

Description – This taxon is only known by two teeth (Fig. 5, D-E). These teeth are small, symmetrical, mesio-distally compressed, and have a high, sharp and strongly slanted lingually cusp, in lingual view (Fig. 5, D2, E2). The root is high, relatively thick and concave in profile view (Fig. 5, D1). It bears a well-marked protuberance incised by a median groove.

Discussion – With the unusual tooth morphology, there is no doubt about the generic attribution of these specimens to this very peculiar and ambiguous elasmobranch, *Odontorhytis*, only known in the Paleogene. The two teeth have a median labial cutting edge and no lateral denticles. Both features are only recovered in the youngest species *O. pappenheimi* contrary to the oldest representative (early Eocene), which shows lateral cutting edges and a pair of small cusplets at the base of the cusp (Case and Cappetta, 1990, Cappetta, 2012). However, *O. pappenheimi* is generally characterized by an apico-lingual barb (Case and Cappetta, 1990, Adnet et al., 2011, Cappetta, 2012), which is absent on both specimens from MBK, thereby orienting our determination to *Odontorhytis pappenheimi*. The latter is the unique species to be known of this enigmatic genus. However, according to Case and Cappetta (1990) and Cappetta (2012), there are probably several species that remain so far undescribed. Until now, *O. pappenheimi* is only recovered from the middle to late Eocene coastal deposits andparticularly well-represented in Egypt (Case and Cappetta, 1990, Murray et al., 2010; Underwood et al., 2010, Adnet et al*.,* 2011). The genus, found in Pakistan and all African coastal deposits (Böhm, 1926, Case and Cappetta, 1990, Case and West, 1991), is known until the early Rupelian of Jebel Qatrani (Quarry E), Egypt (Murray et al., 2014), after what, it has no more fossil record.

Other elasmobranch taxa (Fig. 6)

Numerous other elasmobranch fossil remains were recovered from the MBK deposits. Often restricted to rare broken and/or rolled isolated teeth, no specific determination was actually possible. Concerning sharks, several unnamed species of Carcharhiniformes have been noticed and belong to two carcharhinids genera (*Rhizoprionodon*, *Abdounia)* and a sphyrnid genus (*Sphyrna*). The genus *Rhizoprionodon* is widely known throughout the entire Cenozoic. Nevertheless, only a few species have been identified so far, mainly because of the conservative morphology of the genus (Adnet et al., 2011). It has been recovered from several Tethysian deposits, from the middle Eocene of Egypt (e.g. Strougo et al., 2007) to the late Eocene of Egypt (e.g. Case and Cappetta, 1990, Underwood et al., 2011, Adnet et al., 2011, Zalmout et al*.,* 2012), Pakistan (Adnet et al*.,* 2007), Jordan (Mustafa and Zalmout, 2002) and Morocco (Adnet et al., 2010). A single isolated tooth is attributed to *Abdounia* (Fig. 6D), but if its teeth have generally several cusplets, this is not the case on the specimen from MBK (Fig. 6D). This genus is exclusively restricted to the Paleogene and is widespread in numerous tropical seawaters from the early-middle Eocene (e.g. Noubhani and Cappetta, 1997, Gheerbrant et al., 2003, Case and

Borodin, 2000, Maisch et al., 2014, Cappetta and Case, 2016), to the early Oligocene of Europe (e.g. Mollen, 2007). Some rare teeth of a sphyrnid are present (Fig. 6 E-F). In *Sphyrna*, the tooth morphology differs greatly depending on the species. Indeed, living species sometimes have teeth similar to those of *Rhizoprionodon*, whereas some others have teeth with serrated cutting edges (*S. mokkaran*) or grinding morph (e.g. *S. tiburo*) for example (Cappetta, 2012). It is thus difficult to propose a specific attribution considering our scarce material. The first appearance of *Sphyrna* in the fossil record seems to be dated to the Eocene (Adnet et al., 2010). In the Neotethysian sea, it is known from the late Eocene of Egypt (Underwood et al., 2011) and Morocco (Adnet et al*.,* 2010) to the early Oligocene of Pakistan (Adnet et al., 2007).. Many lamniform teeth have been recovered in the MBK deposits. Teeth attributed to *Carcharias* sp. have a tall and slightly sigmoidal cusp and a small pair of lateral cups. (Fig. 6, B-C. These teeth are numerous, but very poorly preserved, thereby restricting any proper determination. The genus *Carcharias* is particularly widespread in the Neotethysian sea from the middle Eocene of Morocco (Tabuce et al., 2005) to the late Eocene of Egypt (Underwood et al., 2011, Zalmout et al., 2012) and Morocco (Adnet et al., 2010). Some rare teeth from the MBK deposit belong to an unknown large lamniform. Only one of these teeth is relatively well preserved (Fig. 6 A). The tooth is large, the cusp is slightly sigmoid in profile, and there are two lateral cusplets flanking the main cusp (Fig. 6A). The teeth display several features attributed to *Brachycarcharias* by Cappetta and Nolf (2005), although they are also similar to teeth attributed to *Tethylamna twiggsensis* by Case and Borodin (2000, plate 2, 13, 15). As the assignation remains unclear, we therefore attribute these specimens to an unnamed lamniform, pending for additional material. Added to *Nebrius obliquus*, another Orectolobiform specimen is represented in the MBK faunal assemblage (Fig. 6 M). This minute tooth is symmetrical, labio-lingually thick, and its crown bears a main cusp flanked by two pairs of lateral cusplets. Numerous species of *Ginglymostoma* are known from the Paleogene (e.g. *G. angolense* Dartevelle and Casier, 1943, *G. maroccanum* Nouhbani and Cappetta, 1997, *G. serra* Leidy, 1877) but our scarce material do not allow a clear identification. Finally, the order Squatiniformes is also represented here by a single tooth, mesio-distally wider than tall (Fig. 6P), with a sharp cusp and high heels. Although it certainly belongs to a species of *Squatina*, it remains difficult to identify a precise species, inasmuch as the dental morphology of the genus is conservative since its appearance in the fossil record (Cappetta, 2012). *Squatina prima* (Winkler, 1874) is the common Paleogene species widespread throughout all the marine realms. In the Neotethysian seas, fossils of *Squatina* are relatively scarce but were recovered in the late Eocene of Fayum, Egypt (e.g. Underwood et al., 2011).

Batoids from MBK are mostly represented by the two families Myliobatidae and Dasyatidae, even if some scarce fragmentary teeth of Pristidae and Rhinobatidae were also collected from the locality. The Myliobatidae are represented by three unnamed species of *Myliobatis* Cuvier 1816 (Fig. 6G), *Aetobatus* Blainville 1816 (Fig. 6N), and the fossil genus *Leidybatis* Cappetta, 1986 (Fig. 6O). The material is scarce and fragmentary, and the isolated teeth are always worn. No precise determination can be reached based on the fragmentary teeth, because diagnosis of fossil myliobatids are often based on tooth variability and junction on complete or partial tooth plates (e.g. Hovestadt and Hovestadt-Euler, 2013). Although if *Myliobatis* and *Aetobatus* are frequently known throughout the entire Cenozoic marine deposits, it is worth noting that *Leidybatis* sp. is currently restricted to the Paleogene, from the late

Paleocene (e.g. Noubhani and Cappetta, 1997) to the late Eocene (e.g. Adnet et al., 2010, Underwood et al., 2011). Although incomplete, the partial teeth showing a flat occlusal face (Fig. 6O) covered by an unusual thick and strongly granular enameloid (Cappetta, 1986), is rather indicative of fossil genus *Leidybatis* In the MBK assemblage, dasyatids are represented by at least three different species., with at least two distinct species belonging to subfamily of Dasyatinae (fig. 6 H-J), showing different types of ornamentation. Numerous fossil species are known from the literature and would deserve a deep revision regarding the recent advance in dasyatid systematics (e.g. Last et al. 2017) before any new fossil attributions). The living genus *Pastinachus* (Dasyatidae hypolophin) is also represented in the MBK locality (Fig. 6K), but as the former dasyatins, the rare material does not permit a precise attribution. *Pastinachus* is known from the Bartonian (Adnet et al. 2018) and is frequently recorded in late Eocene (e.g. Adnet et al., 2010, Underwood et al., 2011) and early Oligocene deposits of North African coasts (Murray et al., 2014). A few oral teeth (and rostral denticles without posterior carena) of Pristidae (*Anoxypristis)* and Rhinobatidae (*?Rhinobatos)* have been recovered from the MBK locality (e.g. Fig. 6L)..

4. **Discussion**

The MBK fauna is composed of numerous unnamed species from several genera (e.g. *Abdounia*, *Carcharias*, *Rhizoprionodon*) that have a particularly extensive stratigraphical range through the Cenozoic (Fig. 7). These taxa are therefore of low interest for discussing the age of this peculiar marine association recovered in a strict fluvial deposit. Considering that there is no evidence of differential degree of reworking on the fossil material, it is likely that this elasmobranch fauna documents a unique former assemblage in a deposit that was likely reworked but not transported from a long distance before to be redeposited in the detrital deposits corresponding to the MBK locality (see introductory paragraph of the “Systematic Paleontology” section). Interestingly, a few taxa have a relatively small stratigraphic range, which allows constraining the age of this association. Among them, *Galeocerdo eaglesomei*, *Nebrius obliquus*, *Leidybatis* sp. and *Misrichthys stromeri* are known in the fossil record only until the late Eocene, and are not documented in the numerous localities dating from the early Oligocene (e.g. Fig. 7). Conversely, *Carcharhinus perseus* was only reported from the early Oligocene of Pakistan and Egypt (if we exclude the dubious oldest reports from Egypt as *C. egertoni*). Finally, although cf. *Carcharhinus frequens* and *Odontorhytis* can be found in few early Oligocene deposits from Egypt (Quarries R and E, in Murray et al., 2014), these two taxa are in contrast frequently recorded in numerous late Eocene deposits (e.g. Adnet et al., 2010, 2011, Case and Cappetta,1990, Murray et al., 2010, Underwood et al., 2010). Although likely reworked from a close marine deposit (unobserved on the field), the faunal assemblage from this new locality then suggests a latest Priabonian – earliest Rupelian age for the reworked MBK elasmobranch assemblage. The precise age of the detrital deposit embedding this marine association is still unknown but could be almost contemporaneous to slightly younger than the Eocene/Oligocene transition if we consider the rare but well-preserved mammal remains recovered in association with the elasmobranchs (work in progress) at the MBK locality.

In this context, the stratigraphical and geographical ranges of *Galeocerdo eaglesomei* (already suspected in the late Eocene; see 'Systematic Paleontology' section) are now extended back to the latest Eocene (at least) of Tunisia. *Carcharhinus perseus* was previously only recorded in early Oligocene deposits of Egypt, Oman and Pakistan. The absence of *C. perseus* in the early to late Priabonian of Egypt (e.g. Gehanam Fm., Birket-el-Qurun, Qasr-el Saghr Fm., Daba'a Fm.) and Pakistan (e.g. Dash-i-Goran) suggests an earliest Oligocene age for the association, even though its presence in the latest late Eocene of Tunisia could be related to a dispersal event from West (Tunisia) to East (Egypt-Pakistan) part of the Neotethys at the Eocene/Oligocene transition.

This elasmobranch assemblage, if homogeneous, is quite similar to those of the Baharya Oasis (Adnet et al., 2011), Qattara Depression (Zalmout et al., 2012) – Western Desert, Egypt and those from Birket-el-Qurun – Fayum, Egypt (Murray et al., 2010). Surprisingly, it also shares great similarities with geographically distant faunas such as those from the late Priabonian of Morocco (Dakhla; Adnet et al., 2010) and the Rupelian of Pakistan (Paali Nala; Adnet et al., 2007) for instance. The MBK faunal assemblage is strongly dominated by Carcharhiniformes (39% species) and Myliobatiformes (26% species). Among Carcharhiniformes, the greatest diversity is recorded among Carcharhinidae (e.g. "*Carcharhinus"/"Negaprion"*, *Galeocerdo*), systematically close to extant species known to live in tropical coastal waters (see Compagno, 1984, Chiaramonte, 1998). The pelagic species (Lamniformes) are also represented (9% species), although poorly sampled and represented by fragmentary remains. Finally, several orders such as Hexanchiformes, Pristiophoriformes and Squaliformes, which are generally indicators of deep waters (Ebert et al., 2013) are lacking in the MBK assemblage. Among identified fossils, some of them are primarily marine taxa, but known to tolerate brackish to freshwater environments (e.g. *O. pappenheimi*, *M. stromeri*, *Pastinachus* sp., some *Carcharhinus*, pristid; see Martin 2004, Murray et al*.,* 2010, Adnet et al., 2011), whereas others are known to frequent pelagic area (e.g. Lamniformes), as is highlighted by the presence of numerous albeit worn teeth of *Carcharias* sp., a typical marine taxa, which is absent in many other sub-contemporaneous localities such as Dash-I-goran, Paali Nala (Pakistan; Adnet et al., 2007) and Fayum Quarries or Km55 (Egypt, e.g. Underwood et al., 2011, Murray et al., 2010, 2011). Considering this singular mixture of species, the peculiar preservation state of all teeth (worn and rolled) and the fact that these fossils were found in fluvial deposit, is indicative of a reworking by river systems from a sub-contemporaneous submarine fan. In comparison with Eocene-Oligocene localities from the Fayum, this kind of depositional environment of 'phantom' marine deposits would be intermediate between those of deltaic BQ-2 (Fayum, central north Egypt; Seiffert et al., 2008, Murray et al., 2010) and those of 'Km55' (western north Egypt), where marine influence are noticed (Adnet et al., 2011). This indicates that some of the shared elasmobranchs (e.g. *Pastinachus, Negaprion, Misrichthys*) may have also lived in a broad range of habitats. Shallow water environments are rather common within localities close to the Eocene/Oligocene transition. This kind of deposits has already been described from several Neotethysian localities (e.g. see Otero and Gayet, 2001, Adnet et al., 2007, Murray et al., 2014) and the frequent occurrences of this kind of deposal environment are probably related to possible fall of sea level recorded between the late Eocene and the early Oligocene (Miller et al., 2005).

5. Conclusions

Regarding North Africa, late Paleogene elasmobranchs were so far only documented from the late Eocene – early Oligocene of southwestern Morocco and Egypt. This new fossiliferous MBK locality, temporarily assigned to a coastal deposit dating from the latest Priabonian - earliest Rupelian, provides a remarkable snapshot regarding the paleodiversity of late Paleogene sharks and rays at that time.The carcharhinid ratio in the MBK area is currently unequalled compared to other coeval North Arican assemblages and include the possible oldest occurrence of *Carcharhinus perseus*. Despite the extensive East-West geographic distance, the majority of the MBK elasmobranchs are similar to those recovered from the Priabonian in Moroccan and Egyptian localities and from the Rupelian localities of Egypt and Pakistan. This clearly highlights the widespread East-West distribution of sharks and rays along North African coasts during the late Eocene – early Oligocene interval. This distribution reflects, to some extent, the existence of roughly similar tropical environmental conditions in southern Neotethys at that critical time marked by a global cooling event. Remarkably, the presence of numerous shark and ray taxa recovered both in late Eocene and early Oligocene epochs demonstrates that the elasmobranch faunas remained particularly diverse and stable near the global cooling recorded at the Eocene/Oligocene transition (Berggren and Prothero, 1992, Coxall et al., 2005, Lear et al., 2008, Zachos et al., 2008, Hren et al., 2013, Tramoy et al., 2016). Contrary to what it is generally recorded in the Holarctic Province for fish communities, similar assemblages of southwestern Neotethysian elasmobranchs rather indicate that these tropical regions were seemingly less affected by these climatic changes recorded at the Eocene/Oligocene transition (e.g., Marivaux et al., 2017b).

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7. **References**

Adnet, S., Antoine, P.-O., Hassan Baqri, S.R., Crochet, J.-Y., Marivaux, L.,Welcomme, J.-L., and Métais, G. 2007. New tropical carcharhinids (Chondrichthyes, Carcharhiniformes) from the late Eocene–early Oligocene of Balochistan, Pakistan: paleoenvironmental and paleogeographic implications. Journal of Asian Earth Sciences 30, 303–323.

Adnet, S., Cappetta, H., Tabuce, R. 2010. A middle–late Eocene vertebrate fauna (marine fish and mammals) from southwestern Morocco; preliminary report: age and palaeobiogeographical implications. Geological Magazine 147, 860–870.

Adnet, S., Cappetta, H., Elnahas, S., Strougo, A. 2011. A new Priabonian chondrichthyans assemblage from the Western Desert, Egypt: correlation with the Fayum Oasis. Journal of African Earth Sciences 61, 27–37.

Adnet, S., Mouana, M., Charruault, A.-L., Mabrouk, E., Khayati Ammar, H., Marzougui, W., Merzeraud, G., Tabuce, R., Vianey-Liaud, M., Marivaux, L. 2018. Teeth, fossil record and evolutionary history of the cowtail stingray Pastinachus Rüppell, 1829. Historical Biology DOI: 10.1080/08912963.2018.1431779

Agassiz, L. 1843. Recherches sur les Poissons fossiles. atlas Neuchâtel, Switzerland 3, viii + 390 + 32.

Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires du Service géologique du Maroc 92, 1–372.

Benammi, M., Adnet, S., Marivaux, L., Yans, J., Noiret, C., Tabuce, R., Surault, J., El Kati, I., Enault, S., Baidder, L., Saddiqi, O., Benammi, M. 2017. Geology, biostratigraphy and carbon isotope chemostratigraphy of the Palaeogene fossil-bearing Dakhla sections, southwestern Moroccan Sahara. Geological Magazine 1–16, doi10.1017/S0016756817000851.

Berggren, W. A., Prothero D. R. (eds.) 1992. Eocene-Oligocene Climatic and Biotic Evolution: An Overview. Princeton University Press, Princeton, New Jersey, 568 pp

Blainville, H.M. de 1816. Prodrome d’une nouvelle distribution systématique du règne animal. Bulletin de la Société philomatique de Paris 8, 105–124.

Böhm, J. 1926. Über tertiäre Versteinerungen von den Bogenfelser Diamantfeldern. Die Diamantenwüste Südwestafrikas, Bd. II, 55–87.

Cappetta, H. 1986. Myliobatidae nouveaux (Neoselachii, Batomorphii,) de l’Yprésien des Ouled Abdoun, Maroc. Geologica et Paleontologica 20, 185–207.

Cappetta, H., Traverse, M. 1988. Une riche faune de sélaciens dans le bassin à phosphate de Kpogamé-Hahotoé (Eocène moyen du Togo): Note préliminaire et précisions sur la structure et l’âge du gisement. Geobios 21, 359–365.

Cappetta, H., Nolf, D. 2005. Révision de quelques Odontaspidae (Neoselachii: Lamniformes) du Paléocène et de l'Eocène du Bassin de la mer du Nord. Bulletin de l'institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 75, 237–266.

Cappetta, H. 2012. Chondrichthyes: mesozoic and cenozoic elasmobranchii: teeth. In Handbook of palaeoichthyology. Vol. 3E. Edited by H.-P. Schultze. Verlag Dr. Friedrich Pfeil, München. 512 p.

Cappetta, H. and Case, G.R. 2016. A Selachian Fauna from the Middle Eocene (Lutetian, Lisbon Formation) of Andalusia, Covington County, Alabama, USA. Palaeontographica, Abt. A 307 (1–6), 43 – 103

Carrillo-Briceno, J.D., Ahuilera, O.A., De Gracia, C., Aguirre-Fernandez, G., Kindlimann, R., Sanchez-Villagra, M.R. 2016. An Early Neogene Elasmobranch fauna from the southern Caribbean (Western Venezuela). Palaeontologia Electronica 19.2.27A, 1–32

Case, G.R. 1980. A selachian fauna from the trent formation; Lower Miocene (Aquitanian) of eastern north Carolina. Palaeontographica 171, 75–103.

Case, G.R., West, R.M. 1991. Geology and Paleontology of the Eocene Drazinda Shale Member of the Khirthar Formation, central Western Pakistan, Part II Late Eocene fishes. Tertiary Research 12, 105–120.

Case, G.R., Borodin, P.D., 2000. A middle Eocene selachian fauna from the Castle Hayne Limestone Formation of Duplin County, North Carolina. Münchner Geowissenschashiche Abhandlungen 39, 17–34.

Case, G.R., Cappetta, H., 1990. The Eocene selachians fauna from the fayum depression in Egypt. Palaeontographica Abt. A 212, 1–30.

Casier, E. 1971. Sur un materiel ichthyologique des Midra (and Saila) shales du Qatar (Golfe Persique). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 47 (2), 1–9

Chandler, R.E., Chiswell, K.E., Faulkner, G.D. 2006. Quantifying a possible Miocene phyletic change in Hemipristis (Chondrichthyes) Teeth. Palaeontologia Electronica 9, 1–14.

Chiaramonte, G. E. 1998. Shark fisheries in Argentina. Marine and Freshwater Research 49(7), 601-609.

Cicimurri, D.J., Knight, J.L. 2009. Late Oligocene Sharks and Rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA. Acta Palaeontologica Polonica 54, 627–647.

Compagno, L. J. V. 1973. Interrelationships of living elasmobranchs, in: Greewod, P.H., Miles, R.S., Patterson, C. (Eds.), Interrelationships of Fishes, Zoological Journal of the Linnean Society Supp. 1, 15–61.

Compagno, L. J. V. 1984. FAO species catalogue. v. 4:(2) Sharks of the world. An annotated and illustrated catalogue of shark species known to date, pt. 2: Carcharhiniformes. FAO Fish. Synopsis. 125 (4) 2, 251-655

Cuvier, G., 1816. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides. Edition 1. Règne Animal (ed. 1) i-xviii + 1-532.Dames, V., W. 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel des Birket-el-Qurun im Fajum (Aegypten). Sitzungsberichte der deutschen Akademie der Wissenschaften zu Berlin VI, 129–153.

Dartevelle, E., Casier, E., 1943. Les poissons fossiles du Bas-Congo et des régions voisines. Annales du Musée du Congo Belge, Série A (Minéralogie, Géologie, Paléontologie) 3(1–2), 1–200.

DeConto, R. M., Pollard, D. 2003. Rapid Cenozoic glaciation of Antarctica induced by declining atmospheric CO2. Nature, 421(6920), 245-249.

Ebert, D.A., Fowler, S., Compagno, L. 2013. Sharks of the world: a fully illustrated guide, Wild Nature Press. ed. Plymouth, UK.

Gheerbrant, E., Sudre, J., Cappetta, H., Mourer-Chauvire, C., Bourdon, E., Iarochene, M., Amaghzaz, M., Bouya B. 2003. Les localités à mammifères des carrières de Grand Daoui, Bassin des Ouled Abdoun, Maroc, Yprésien : premier état des lieux. Bulletin de la Société Géologique de France 174(3), 279-293.

Gingerich, P. D., Zalmout, I. S., Antar, M. S. M., Williams, E. M., Carlson, A. E., Kelly, D. C., Peters, S. E. 2012. Large-scale glaciation and deglaciation of Antarctica during the late Eocene: Reply. Geology 40(3), e255.

Haasl, D. M., Hansen, T. A. 1996. Timing of latest Eocene molluscan extinction patterns in Mississippi. Palaios, 487-494.

Hren, M. T., Sheldon, N. D., Grimes, S. T. , Collinson, M. E., Hooker, J. J., Bugler, M., Lohmann, K. C. 2013. Terrestrial cooling in Northern Europe during the Eocene-Oligocene transition. Proceedings of the National Academy of Sciences of the United States of America 110, 7562–7567.

Hovestadt, D.C., Hovestadt-Euler, M. (2013) Generic Assessment and Reallocation of Cenozoic Myliobatinae based on new information of tooth, tooth plate and caudal spine morphology of extant taxa. Palaeontos, 24, 1-66.

Kriwet, J. 2005. Addition to the eocene selachian fauna of antarctica with comment on antarctic selachian diversity. Journal of Vertebrate Paleontology 25, 1–7.

Kruckow, T., Thies, D. 1990. Die Neoselachier der Paläokaraib (Pisces: Elasmobranchii). Courier Forschungsinstitut Senckenberg 119, 1–102.

Lear, C. H., Bailey, T. R., Pearson, P. N., Coxall, H. K., Rosenthal, Y. 2008. Cooling and ice growth across the Eocene-Oligocene transition. Geology 36, 251–254.

Leriche, M., 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la Plaine Côtière Atlantique et du centre des Etats-Unis. Les synchronismes des formations tertiaires des deux côtés de l'Atlantique. Mémoire de la Société Géologique de France 45, 1–110.

Leidy, J., 1877. Description of Vertebrates remains, chiefly from the phosphate beds of south Carolina. Journal of the Academy of Natural Sciences of Philadelphia 8, 209–261.

Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie, R.M., Pearson, A. 2009. Global cooling during the Eocene-Oligocene climate transition. Science, 323(5918), 1187-1190.

Maisch, H.M., Becker, M.A., Raines, B.W., Chamberlain, J.A. 2014. Chondrichthyans from the Lisbon–Tallahatta Formation Contact (Middle Eocene), Choctaw County, Silas, Alabama. Paludicola 9 (4), 183-209

Manning, E.M. 2006. The Eocene/Oligocene transition in marine vertebrates of the Gulf Coastal Plain. *In*: D.R. Prothero, L.C. Ivany, and E.A. Nesbitt (eds.), *From Greenhouse to Icehouse: The Marine Eocene–Oligocene Transition*, 366–385. Columbia University Press, New York.

Marivaux, L., Ramdarshan, A., Essid, E.M., Marzougui, W., Khayati Ammar, H., Lebrun, R., Marandat, B., Merzeraud, G., Tabuce, R., Vianey-Liaud, M. 2013. *Djebelemur*, a tiny pre-tooth-combed primate from the Eocene of Tunisia: a glimpse into the origin of crown strepsirhines. *PLoS ONE* 8, 1-21.

Marivaux, L., Essid, E.M., Marzougui, W., Khayati Ammar, H., Merzeraud, G., Tabuce, R., Vianey-Liaud, M., 2015. The early evolutionary history of anomaluroid rodents in Africa: new dental remains of a zegdoumyid (Zegdoumyidae, Anomaluroidea) from the Eocene of Tunisia. Zoologica Scripta 44, 117-134.

Marivaux, L., Adnet, S., Benammi, Mohamed, Tabuce, R., Benammi, Mouloud 2017a. Anomaluroid rodents from the earliest Oligocene of Dakhla, Morocco, reveal the long-lived and morphologically conservative pattern of the Anomaluridae and Nonanomaluridae during the Tertiary in Africa. Journal of Systematic Palaeontology 15, 539–569.

Marivaux, L., Adnet, S., Benammi, Mohamed, Tabuce, R., Yans, J., Benammi, Mouloud 2017b. Earliest Oligocene hystricognathous rodents from the Atlantic margin of northwestern Saharan Africa (Dakhla, Morocco): systematic, paleobiogeographical, and paleoenvironmental implications. Journal of Vertebrate Paleontology 7(5), e1357567.

Meulenkamp, J.E., Sissingh, W., 2003. Tertiary palaogeography and tectonostratigraphic evolution of the Northern and Southern Peri-Tethys platforms and the intermediate domains of the African-Eurasian convergent plate boundary zone. Palaeogeography, Palaeoclimatology, Palaeoecology 196, 209–228.

Martin, R.A. 2004. Evolution and zoogeography of freshwater elasmobranchs with notes on their conservation. Symposium Proceedings International Congress on the Biology of Fish, Manaus, Brazil, 1–14

Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Pekar, S.F. 2005. The Phanerozoic record of global sea-level change. Science 310(5752), 1293-1298.

Mollen, F. H. 2007. A new species of Abdounia (Elasmobranchii, Carcharhinidae) from the base of the Boom Clay Formation (Oligocene) in northwest Belgium. Geologica Belgica 10 (1-2), 69–77

Müller, J., Henle, J., 1838. Systematische Beschreibung der Plagiostomen. Berlin. Veit, pp. 1–200

Müller, A., 1999. Ichthyofaunen aus dem atlantischen Tertiär der USA. Systematik, Paläoökologie, Biostratigraphie und Paläobiogeographie. Leipziger Geowissenschaften 9/10, 1-360.

Murray, A. M., Cook, T. D., Attia, Y. S., Chatrath, P., Simons, E. L. 2010. A freshwater ichthyofauna from the late Eocene Birket Qarun Formation, Fayum, Egypt. Journal of Vertebrate Paleontology 30(3), 665-680.

Murray, A. M., Argyriou, T., Cook, T. D. 2014. Palaeobiogeographic relationships and palaeoenvironmental implications of an earliest Oligocene Tethyan ichthyofauna from Egypt. Canadian Journal of Earth Sciences, 51(10), 909-918.

Mustafa, H., Zalmout, I. 2002. Elasmobranchs from the late Eocene Wadi Esh-Shallala Formation of Qa'Faydat ad Dahikiya, east Jordan. Tertiary Research, 21(1/4), 77-94.

Noubhani, A., Cappetta, H., 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo Ichthyologica 8, 1–327.

Ozsvárt, P., Kocsis, L., Nyerges, A., Győri, O., Pálfy, J. (2016). The Eocene-Oligocene climate transition in the Central Paratethys. Palaeogeography, Palaeoclimatology, Palaeoecology 459, 471-487.

Otero, O., Gayet, M., 2001. Palaeoichtyofaunas from the Lower Oligocene and Miocene of the Arabian Plate: palaeoecological and palaeobiogeographical implication. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 141–169.

Parmley, D., Cicimurri, D.J., Campbell, B. 2003. Late Eocene Sharks of the Hardie Mine Local Fauna of Wilkinson. Georgia Journal of Science 61 (3), 153–179.

Peters, S. E., Carlson, A. E., Kelly, D. C., Gingerich, P. D. 2010. Large-scale glaciation and deglaciation of Antarctica during the Late Eocene. Geology 38(8), 723-726.

Priem, M.F. 1908. Etude des poissons fossiles du Bassin Parisien. Annales de Paléontologie : 1–144

Ravel, A., Adaci, M., Bensalah, M., Charruault, A.-L., Essid, E.M., Khayati Ammar, H., Mahboubi, M., Marzougui, W., Mebrouk, F., Merzeraud, G., Vianey-Liaud, M., Tabuce, R., Marivaux, L. 2016. Origine et radiation initiale des chauves-souris modernes : nouvelles découvertes dans l'Éocène d'Afrique du Nord. Geodiversitas 38(3), 355-434.

Reinecke, T., Balsberger, M., Beaury, B., Pollerspöck, J. 2014. The elasmobranch fauna of the Thalberg Beds, early Egerian (Chattian, Oligocene), in the Subalpine Molasse Basin near Siegsdorf, Bavaria, Germany. Palaeontos 26, 3-129.

Sassi, S., Triat, J.-M., Truc, G., Millot, G. 1984. Découverte de l'Eocène continental en Tunisie centrale : la Formation du Jebel Chambi et ses encroutements carbonatés. Compte rendu de l'Académie des Sciences, Paris 299, 357-364.

Seiffert, E.R., 2007. Evolution and extinction of Afro-Arabian primates near the Eocene-Oligocene boundary. Folia Primatologica 78, 314-327.

Seiffert E.R., 2010. Chronology of Paleogene mammal localities**.** In Werdelin L. and Sanders W.J. (eds.) *Cenozoic Mammals of Africa*. Berkeley: University of California Press, pp. 19-26.

Solé, F., Essid, E.M., Marzougui, W., Temani, R., Khayati Ammar, H., Mahboubi, A., Marivaux, L., Vianey-Liaud, M., Tabuce, R. 2016. New fossils of Hyaenodonta (Mammalia) from the Eocene localities of Chambi (Tunisia) and Bir el Ater (Algeria), and the evolution of the earliest African hyaenodonts. Palaeontologia Electronica 19, 1-23.

Stidham, T. A., and Smith, N. A. 2015. An ameghinornithid-like bird (Aves, Cariamae,? Ameghinornithidae) from the early Oligocene of Egypt. Palaeontologia Electronica 18(1), 1-8.

Stromer, E., 1905. Die Fischreste des mittleren und oberen Eocäns von Aegyten. Beiträge zur Palaeontologie und Geologie Oesterreich-Ungarns und des Orients Bd XVIII 1,3, 37–58, 163–192.

Strougo, A., Cappetta, H., Elnahas, S., (2007). A remarkable Eocene ichthyofauna from the Elgedida glauconitic sandstone, Bahariya oasis, Egypt, and its stratigraphic implications. Earth Science Series, vol. 21. Middle East Research Center, Ain Shams University, 81–98.

Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A. B., and Quillevéré, F. (2005). Aznag (bassin d'Ouarzazate, Maroc), nouvelle localité à sélaciens et mammifères de l'Eocène moyen (Lutétien) d'Afrique. Bulletin de la Société géologique de France, 176(4), 381-400.

Tabuce, R., 2018. New remains of *Chambius kasserinensis* from the Eocene of Tunisia and evaluation of proposed affinities for Macroscelidea (Mammalia, Afrotheria). Historical Biology 30, 251-266.

Thomas, H., Roger, J., Sen, S., Bourdillon-de-Grissac, C., Al-Sulaimani, Z., 1989. Découverte de vertébrés fossiles dans l'Oligocène inférieur du Dhofar (Sultana d'Oman). Comptes Rendus de l'Académie des sciences 22, 101–120.

Tramoy, R., M. Salpin, J. Schnyder, A. Person, M. Sebilo, J. Yans, V. Vaury, J. Fozzani, Bauer., H. 2016. Stepwise palaeoclimate change across the Eocene–Oligocene transition recorded in continental NW Europe by ineralogical assemblages and d15Norg (Rennes Basin, France). Terra Nova 28, 212–220.

Underwood, C.J., Ward, D.J., King, C., Antar, S.M., Zalmout, I.S., and Gingerich, P.D. (2011). Shark and ray faunas in the middle and late Eocene of the Fayum area, Egypt. Proceedings of the Geologists' Association 122, 47–66.

Underwood, C. J., King, C., and Steurbaut, E. (2012). Large-scale glaciation and deglaciation of Antarctica during the Late Eocene: Comment. Geology, doi:10.1130/G31820C.1.

Underwood, C.J., and Gunter, G. C. 2012. The shark *Carcharhinus* sp. from the Middle Eocene of Jamaica and the Eocene record of *Carcharhinus*. Caribbean Journal of Earth Science 44, 25–30

Van Vliet, H.J. and Schulp, A.S., Gebely, A.M.M. and Abu El-Kheir and Paijmans, T.M. and Bosselaers, M. and Underwood, C.J. (2017) A new Oligocene site with terrestrial mammals and a selachian fauna from Minqar Tibaghbagh, the Western Desert of Egypt. Acta Palaeontologica Polonica 62 (3), 509-525

Vialle, N, Merzeraud, G., Delmer, C., Feist, M., Jiquel, S. Marivaux, L., Ramdarshan, A. Vianey-Liaud, M., Essid EM. Marzougui, W. Khayati Ammar, H., Tabuce, R., 2013. Discovery of an embrithopod mammal (Arsinoitherium?) in the late Eocene of Tunisia. Journal of African Earth Sciences 87, 86-92

Winkler, T.C. 1874. Mémoire sur des dents de poissons du terrain bruxellien. Archives du Musée Teyler 3 (4), 295–304.

White, E.I., 1926. Eocene fishes from Nigeria. Bulletin of the Geological Survey of Nigeria 10, 1–82.

White, E.I., 1955. Notes on African Tertiary sharks. Colonial Geology and Mineral Resources 5, 319–325.

White, E.I., 1956. The Eocene fishes of Alabama. Bulletins of American paleontology 36, 123–150.

Whitley, G.P., 1940. The fishes of Australia. Part 1. The sharks, rays, devil fishes and other primitive fishes of Australia and New Zealand. Sydney: Royal Zoological Society of New South Wales : 230 pp.

Woodward, A.S., 1889. Catalogue of the fossil fishes in the British Museum. Part. I. British Museum (Nat. Hist.) 474 p.

Zachos, J. C., Dickens, G. R., Zeebe, R. E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451, 279–283.

Zalmout, I.S., Antar, M.S.M., Shafy, E.A., Metwally, M.H., Hatab, E.E., and Gingerich, P.D. (2012). Priabonian sharks and rays (late Eocene: Neoselachii) from Minqar Tabaghbagh in the Western Qattara Depression, Egypt. Contributions from the Museum of Paleontology, University of Michigan 32, 71–90.

Zhang, R., Kravchinsky, V. A., Yue, L. (2012). Link between global cooling and mammalian transformation across the Eocene–Oligocene boundary in the continental interior of Asia. International Journal of Earth Sciences 101(8), 2193-2200.

Figure captions

Figure 1. Stratigraphic position of the main localities with Elasmobranche fauna dated from the Priabonian and/or Rupelian (see text for details). Vertical bars indicate approximate range of temporal uncertainty. Absence of vertical bar indicates a very well constrained age; modified after Seiffert (2010). In background, late Eocene/early Oligocene map of the western Neotethys showing these localities: **1-3**: Egypt (**1**: Fayum and Wadi al Hitan; **2**: Bahariya Oasis; **3**: Qattara Depression); **4**: Morocco; **5, 9**: Oman; **6:** Pakistan; **7**: Mabrouk, Tunisia (this work); **8**: Jordania. The paleogeographical limits are drawn after the work of Meulenkamp and Sissingh (2003) and Ozsvárt et al. (2016). The studied site is located by the large star on the map.

Figure 2. Location map and stratigraphic position of the fossil-bearing Mabrouk locality (MBK) in central Tunisia. A) Simplified map of Tunisia locating the principal Paleogene vertebrate sites discovered on the northern flank of the Djebel Chambi Mountains east of Kasserine Township: Chambi-1 (F1, late Ypresian or early Lutetian), Bir Om Ali (F2, late Eocene), and Mabrouk (F3, latest Eocene or earliest Oligocene, indicated by the red circle). B) Lithostratigraphical log of the Paleogene sedimentological sequence including Bir Om Ali (F2) and Mabrouk (F3) localities; photograph of *Galeocerdo* cf. *G. eaglesomei* discovered in situ at Mabrouk. C) Photographs showing details of the lithostratigraphical sequence, which includes the MBK levels: 1) fine-grained sandstones, organized into a set of planar and through cross-bedded of fluvial origin (sand bar of braided-river); 2) yellow colored, matrix supported, sandy-conglomerates of debris-flows (MBK fossil-bearing levels); 3) pluridecimetric beds of coarse-grained sandstones with planar cross-bedding (ephemeral braided-streams).

Figure 3. Shark teeth from the MBK fossil-bearing locality. **A**-**E**: *Galeocerdo* cf. *G. eaglesomei*; **A**: lateral tooth MBK-01, 1. labial view, 2. lingual view; **B**: juvenile tooth MBK-, 1. lingual view, 2. labial view; **C**: anterior tooth, 1. labial view, 2. lingual view; **D**: antero-lateral tooth MBK-02, 1. labial view, 2. lingual view; **E**: lateral tooth MBK-03, 1. labial view, 2. lingual view. **F**-**H**: *Carcharhinus perseus*; **F**: upper antero-lateral tooth MBK-04, 1. labial view, 2. lingual view; **G**: lower antero-lateral tooth MBK-05; **H**: upper antero-lateral tooth, 1. labial view, 2. lingual view. **I**-**J**: cf. *Carcharhinus frequens*, **I**: upper tooth MBK-06, 1. labial view, 2. lingual view; **J**: lower tooth MBK-07, 1. labial view, 2. lingual view. **K**-**L**: *Misrichthys stromeri*, **K**: lower anterior tooth MBK-08, 1. labial view, 2. lingual view; **L**: upper tooth MBK-09, 1. labial view, 2. lingual view. Scale bar= 5 mm.

Figure 4. Shark teeth from Mabrouk. **A**-**C**: *Carcharhinus* sp. or *Negaprion* sp, **A**: lateral upper tooth MBK-10, 1. labial view, 2. lingual view; **B**: posterior upper tooth MBK-11, 1. lingual view, 2. labial view; **C**: anterior lower tooth MBK-12, 1. labial view, 2. lingual view; **D**: draw of lower and upper teeth of "*Carcharhinus* sp. or *Negaprion* sp.", in Adnet et al., 2011: fig. 3I-M;. **E**: lower and upper teeth of "*Negaprion" amekiensis* in White (1926: fig. 5 E). Scale bar= 5 mm.

Figure 5**.** Shark teeth from Mabrouk. **A**: *Hemipristis curvatus* MBK-13, 1. labial view, 2. lingual view. **B**-**C**: *Nebrius obliquus*, **B**: lateral tooth MBK-14, 1. lingual view, 2. labial view; **C**: anterior tooth MBK-15,

1. lingual view, 2. labial view. Scale bar = 5 mm; **D**-**E**: *Odontorhytis* aff. *pappenheimi*, **D**: MBK-16. profil view, 2. lingual view; **E**: MBK-17. labial view, 2. lingual view. Scale bar =5 mm

Figure 6. Other elasmobranches teeth from Mabrouk. **A**: Lamniforme indet. MBK-18, lateral tooth. 1. labial view, 2. lingual view. **B**-**C**: *Carcharias* sp., **B**: anterior tooth MBK-19, 1. labial view, 2. profil view, 3. lingual view; **C**: anterior tooth MBK-20, 1. labial view, 2. lingual view; **D**: *Abdounia* sp. MBK-21, 1. labial view, 2. lingual view, scale ba r= 5mm; **E**: *Sphyrna* sp., MBK-22, lower tooth, lingual view ; **F**: *Rhizoprionodon* sp. MBK-23, 1. labial view, 2. lingual view; **G**: *Myliobatis* sp. MBK-24, median tooth, 1. occlusal view, 2. basal view. **H**-**J**: *Dasyatis* sp., **H**: female tooth MBK-25, 1. occlusal view, 2. labial view. **I**: male tooth MBK-26, 1. lingual view, 2. labial view. **J**: female tooth MBK-27, 1. occlusal view, 2. labial view; **K**: *Pastinachus* sp. MBK-28, 1. occlusal view, 2. basal view; **L**: ?*Rhinobatos* sp. MBK-29, 1. labial view, 2. lingual view; **M**: *Ginglymostoma* sp. MBK-30, 1. labial view, 2. lingual view, scale bar = 1 mm; **N**: *Aetobatus* sp. MBK-31, occlusal view; **O**: *Leidybatis* sp. MBK-32, occlusal view, scale bar = 5 mm; **P**: *Squatina* sp. MBK-33, 1. labial view, 2. lingual view, scale bar = 1 mm.

Figure 7. Stratigraphical ranges of taxa recovered in fluviatile fossiliferous deposit F3 of Mabrouk (MBK), Djebel Chambi, Tunisia.

Figures

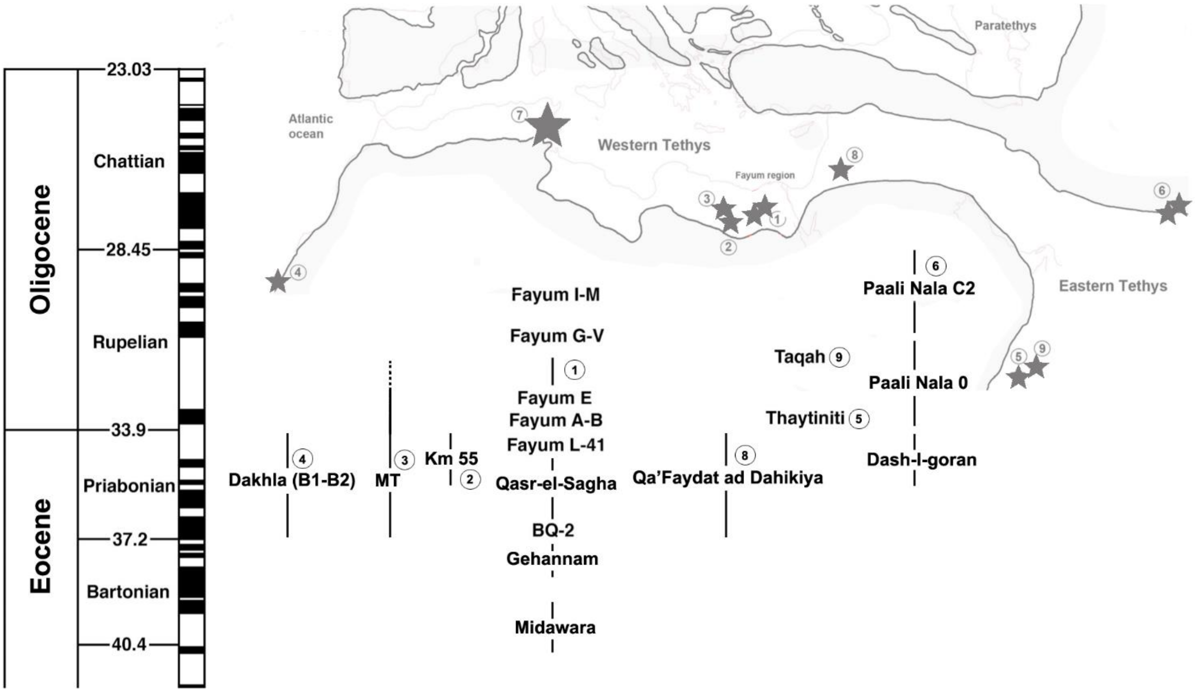
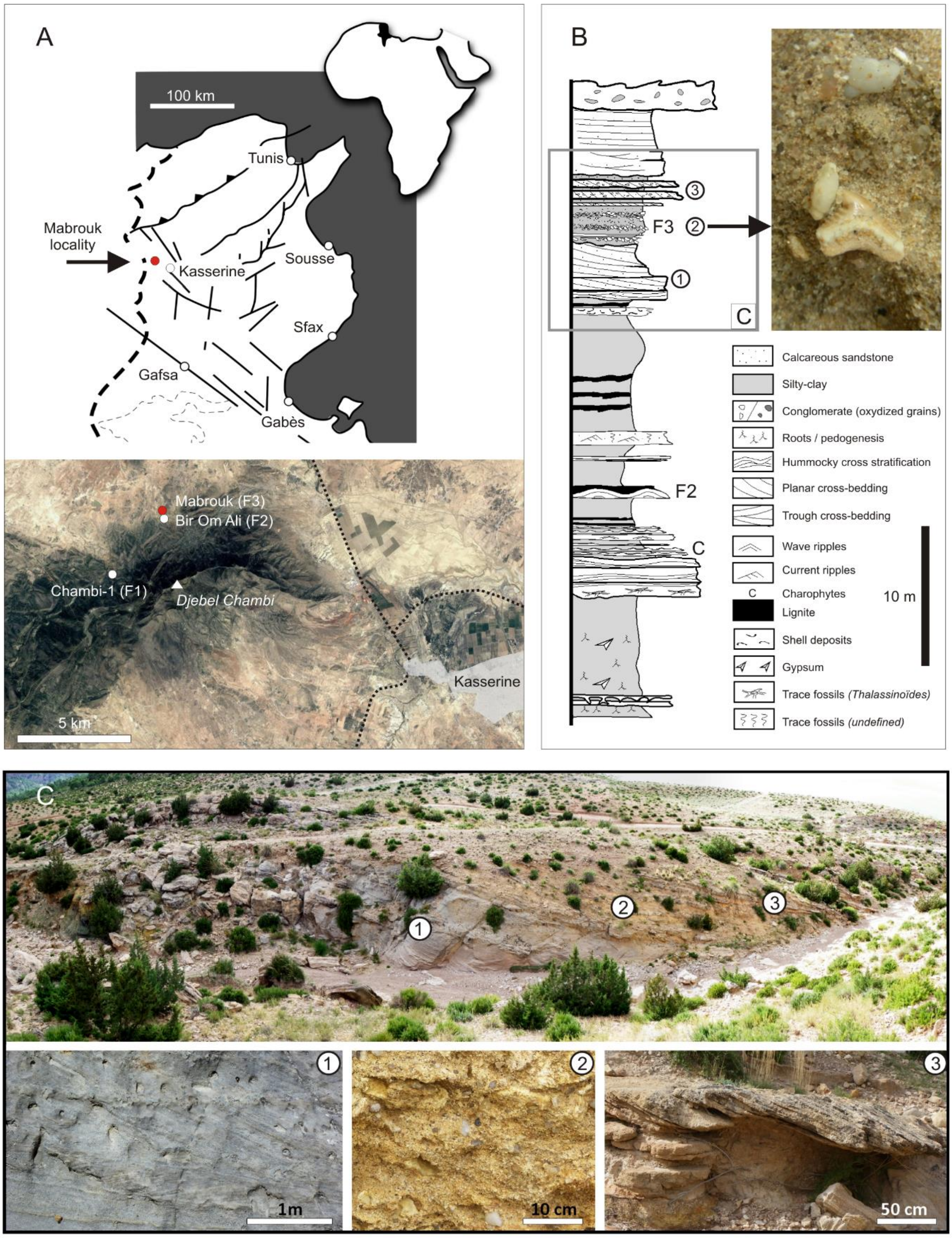


Fig. 1 (1.5 or 2-column fitting image)



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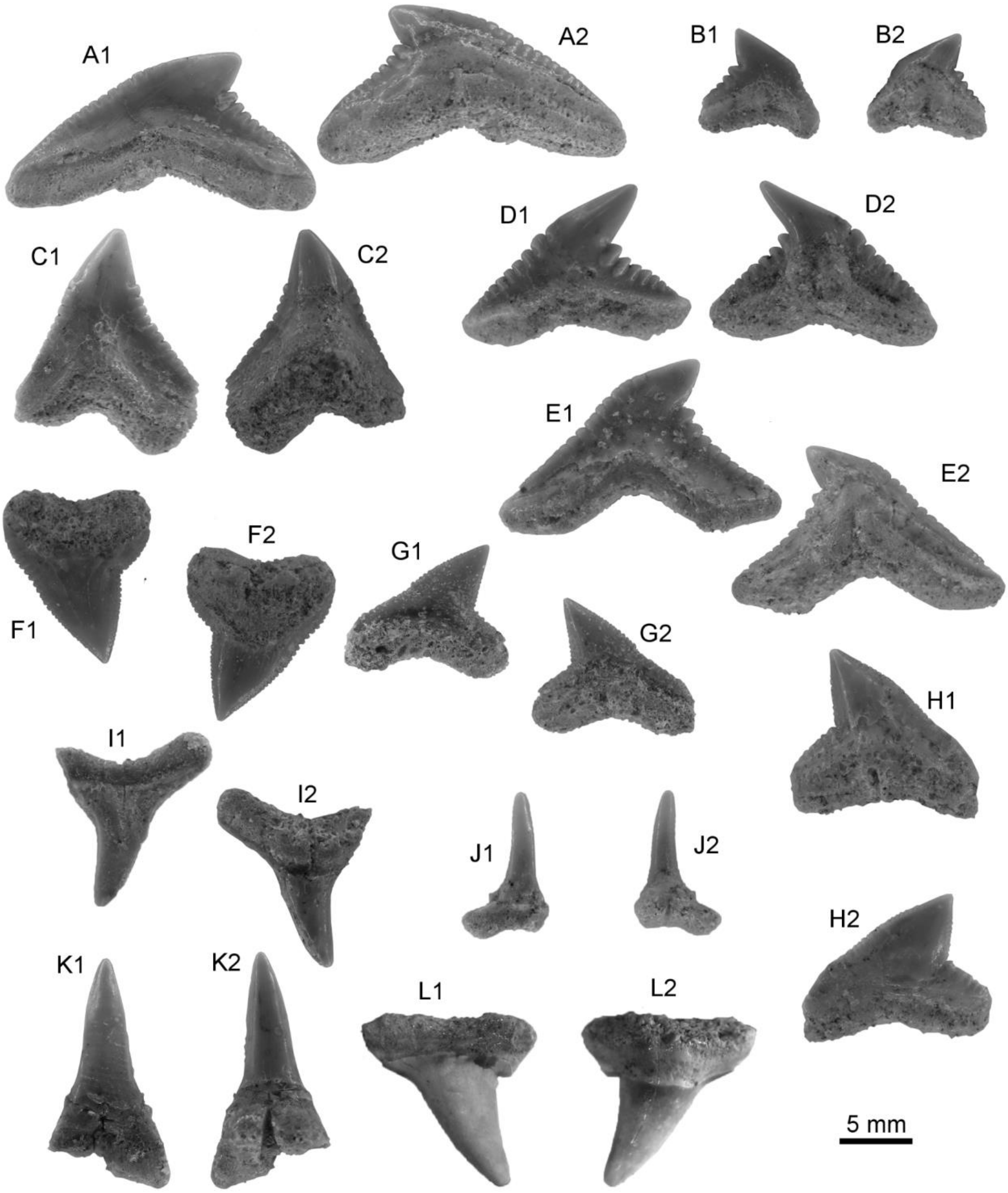

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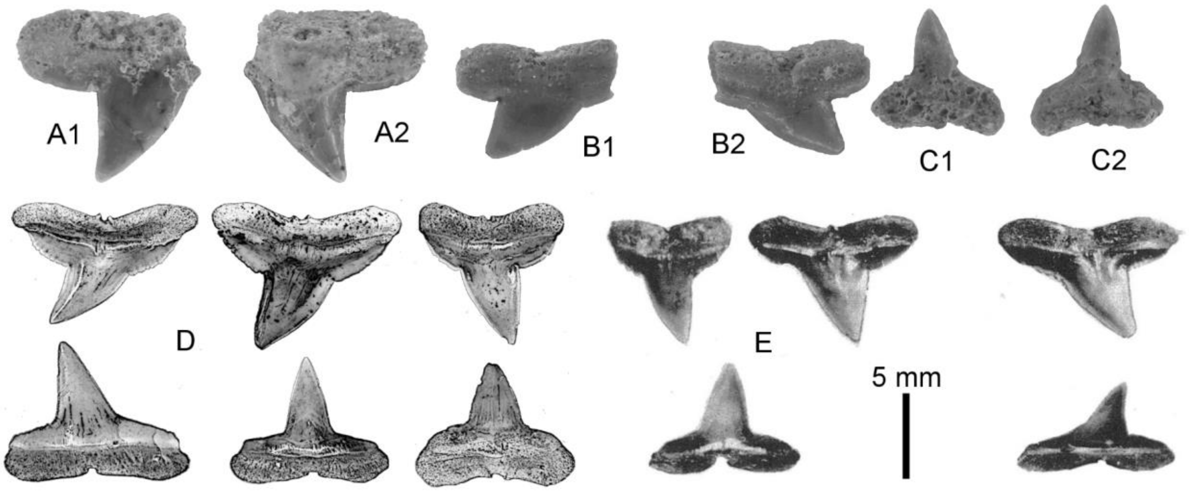

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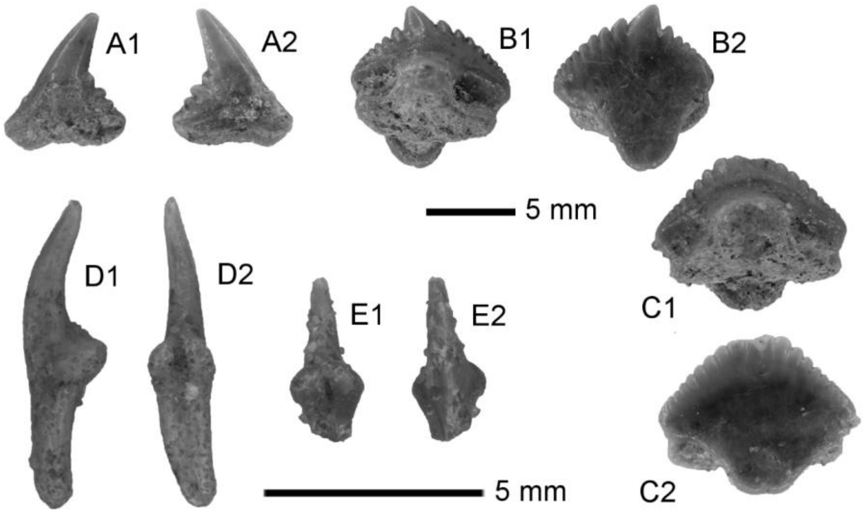

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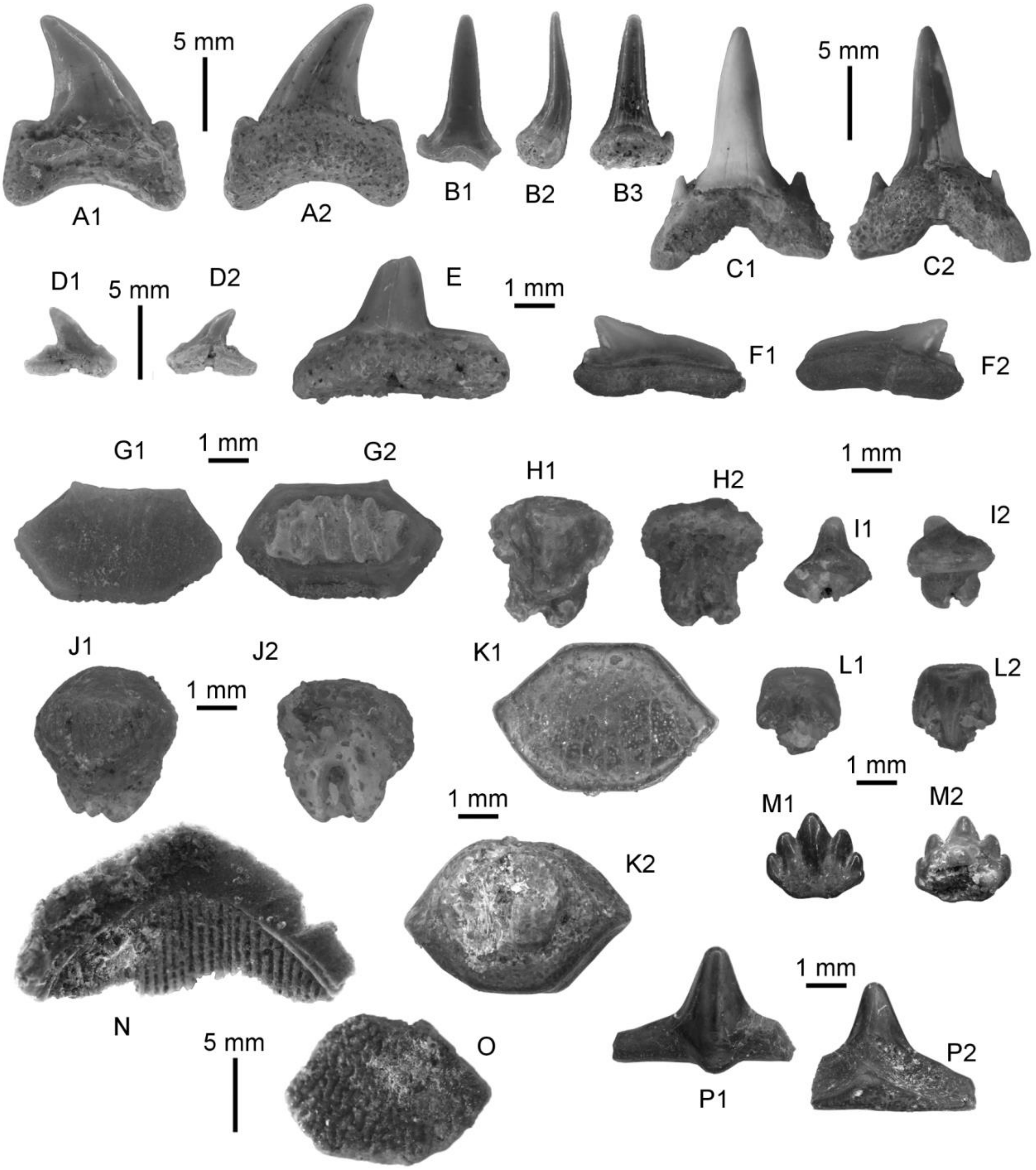

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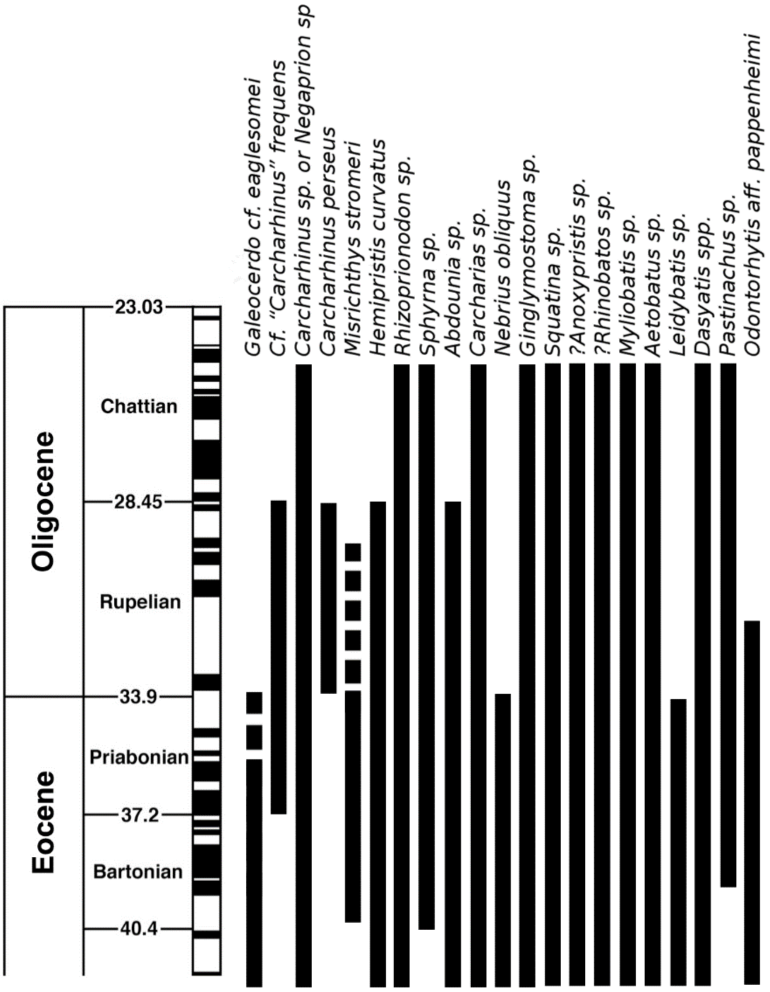

Fig. 7 (1-column fitting image)