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

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4

5 Simon Sweydan¹, Gilles Merzeraud², El Mabrouk Essid³, Wissem Marzougui³, Rim Temani³, Hayet
6 Khayati Ammar³, Laurent Marivaux¹, Monique Vianey-Liaud¹, Rodolphe Tabuce¹, Sylvain Adnet^{1*}

7

8 ¹ Laboratoire de Paléontologie, Institut des Sciences de l'Évolution de Montpellier (ISE-M, UMR 5554,
9 CNRS/UM/IRD/EPHE), c.c. 064, Université de Montpellier, place Eugène Bataillon, F-34095
10 Montpellier Cedex 05, France

11 ² Géosciences Montpellier (UMR-CNRS 5243), c.c. 060, Université de Montpellier, Place Eugène
12 Bataillon, F-34095 Montpellier Cedex 05, France

13 ³ Office National des Mines (ONM), 24 rue 8601, 2035 La Charguia, Tunis BP : 215, 1080 Tunis,
14 Tunisia

15 *Corresponding author: sylvain.adnet@umontpellier.fr

16

17

18 **Abstract**

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

28

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

31

32 **1. Introduction**

33 If the early Cenozoic is marked by a particularly warm climate; however, a global cooling linked to a
34 decrease in atmospheric carbon dioxide concentration (DeConto and Pollard, 2003) and a modification
35 in oceanic currents are recorded at the Eocene/Oligocene transition. Marked by large-scale extinction
36 and floral and faunal turnovers, there is a common consensus about these climatic changes, although
37 the debate remains open about the modalities of the cooling, especially in Egypt (e.g. see Peters et al.,
38 2010; Underwood et al., 2012, Gingerich et al., 2012). In the marine realm, these climatic changes are
39 responsible from the formation of the Antarctic ice sheet and a significant decrease in the sea level (e.g.
40 see Miller et al., 2005; Liu et al., 2009) occulting the main Oligocene marine deposits. In this transitional
41 context, between a relatively warm, ice-free world and a cooler world, the event known as the “Grande
42 Coupure” (~33.9 My) is marked by a faunal turn-over among marine (e.g. Haasl and Hansen, 1996) as
43 well as Holarctic terrestrial faunas (e.g. Zhang et al., 2012). In Africa, the effects of the “Grande Coupure”
44 on terrestrial faunas are conversely poorly documented, as only few localities have yielded vertebrates
45 from the Eocene/Oligocene transition (e.g., Seiffert, 2007, Benammi et al., 2017, Marivaux et al., 2017a-
46 b). Interestingly, these terrestrial faunas are generally associated with marine vertebrates, often
47 dominated by elasmobranchs. Among those, several Upper Eocene localities from the southwestern
48 Neotethys - Eastern Atlantic area have yielded elasmobranch assemblages (e.g. Case and Cappetta,
49 1990; Strougo et al., 2007; Adnet et al., 2007, 2010, 2011, Underwood et al., 2011, Murray et al., 2014,
50 Zalmout et al., 2012), even though most of them are located in its more oriental part and especially in
51 Egypt, near the Fayum depression (see Fig. 1). On the other hand, early Oligocene elasmobranch
52 faunas from the same area are much less known, and only a few localities have been studied in detail
53 (e.g. Adnet et al., 2007, Murray et al., 2014, Van Vliet et al., 2017). Thus, the faunal dynamic of
54 elasmobranchs in the southwestern Neotethys region during this transitional period is poorly known. A
55 new vertebrate fossil-bearing locality from Djebel Chambi in Tunisia (Mabrouk locality, named MBK),
56 supposedly dated around the Eocene/Oligocene transition, was discovered by the French-Tunisian
57 team during several fieldtrips in 2010-2012. Having recorded many elasmobranch fossils, this last allows
58 to fill a geographical gap in the western Tethys fossil record, and to further our knowledge about the
59 shark and ray faunas from this critical period.

60

61 **2. Geological Setting**

62 As part of the Central Tunisian Atlassic domain, the Djebel Chambi — the highest summit of Tunisia
63 (1544m) — is essentially constituted by Barremian to upper Senonian marls and limestones. On the
64 both flanks of this structure oriented NE-SW, these marine Cretaceous series are unconformably
65 covered by continental Eocene deposits (e.g. Sassi et al., 1984). On the northern flank, the Eocene
66 outcrops begins with a sequence of alluvial-fan conglomerates interbedded with lacustrine limestones
67 and alluvial-plain facies, composed of silty-clays and thick reddish matured paleosoils. In a lacustrine
68 limestone positioned in the middle part of this sequence, the first vertebrate fossil-bearing level (sites of
69 Chambi-1 and Chambi-2, F1 in Fig.2) yielded a rich mammalian fauna dated from the late Ypresian or

70 early Lutetian (see Marivaux et al., 2013, 2015, Ravel et al., 2016, Solé et al., 2016, Tabuce, 2018 for a
71 recent overview). At Bir-Om Ali locality, three kilometers northeast of Chambi-1, the Eocene outcrops
72 continue with evaporitic lagoonal sediments, showing gypsum concentrations, root traces and
73 paleosoils, grading-upwards into lacustrine or restricted marine facies. These levels yielded numerous
74 oogones of late Eocene charophytes *Nodosochara* (“*Raskyaechara*”) *baixanensis* and *Pseudolatochara*
75 sp. (see Vialle et al., 2013) (C in Fig.2) a few fossil remains of a large-bodied mammal (arsinoitheriid
76 embrithopod) (F2 in Fig.2, Bir Om Ali locality; see Vialle et al., 2013). Above these beds, a thick
77 alternation of marls and lignite levels is covered by a thin bed of monospecific shells. This facies
78 association characterize a shallow-water restricted area (swamp or marsh). These deposits are overlain
79 by a vertical evolution of facies that begins with fine-grained sandstones, organized into a set of planar
80 and through cross-bedded (Fig. 2 C1) of fluvial origin (sand bar of braided-river). This facies are capped
81 above by several levels of yellow colored, matrix supported, sandy-conglomerates of debris-flows (Fig.
82 2 C2). These levels, well-exposed at the Mabrouk locality (MBK), yielded the new elasmobranch fauna
83 here studied (F3 in Fig. 2). Above, pluridecimeteric beds of coarse-grained sandstones with planar cross-
84 bedding, characterizes ephemeral braided-streams (Fig. 2 C3). On the top of the series, a second set
85 of thick sandstones beds, with trough and planar cross-bedding, is observed and interpreted as fluvial
86 deposits. At the end of the section, a coarse-grained polygenic conglomerate is attributed to an alluvial
87 fan system. No marine deposit was clearly identified in the surrounding area, nor under nor above the
88 fossiliferous level F3 (Fig. 2). No other evidence of marine life (apart from elasmobranchs and some
89 rare remains of marine bony fish) was detected among the fluvial sands that constitute the MBK outcrops
90 (Fig. 2C).

91

92 3. Systematic Palaeontology

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

107 dating interest and environmental inference. Figured specimens are housed in the paleontological
108 collections of the museum of the “Office National des Mines” of Tunis, Tunisia

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

110

111 Carcharhiniformes Compagno, 1973

112 Carcharhinidae Jordan and Evermann, 1896

113 *Galeocerdo* Müller and Henle, 1838

114 *Galeocerdo* cf. *eaglesomei* White, 1955

115

116 Fig. 3. A-E

117 Material: more than 120 teeth, including figured MBK-01 to 03

118

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

139

140 **Discussion** – These specimens show some diagnostic features attributed to *Galeocerdo eaglesomei*,
141 such as a high crown (especially in anterior files) and a well-developed serration. However, the state of
142 preservation of teeth does not allow us to provide a formal specific identification of these specimens to
143 this taxon, which justifies the attribution to *G. cf. eaglesomei*. This species is relatively different from
144 contemporaneous and widely distributed *G. latidens* Agassiz, 1843, known elsewhere in deposits of
145 North Africa dating from the late Eocene (Case and Cappetta, 1990; Underwood et al. 2011; Mustafa

146 and Zalmout, 2002). Compared to *G. latidens*, *G. eaglesomei* have higher teeth (Case and Cappetta
147 1990, Case and Borodin, 2000), greater serrations that almost reaches the apex of crown, a character
148 which is never observed in *G. latidens*. Underwood et al. (2011) reported another *Galeocerdo* with fully
149 serrated teeth, *G. ?aegyptiacus* Stromer, 1905 from the middle-late Eocene of Egypt. Unfortunately the
150 type material is presumed lost and the validity of this small species remains dubious in absence of clear
151 figuration. *Galeocerdo eaglesomei* is widely distributed during the middle Eocene of North America (e.g.
152 Case and Borodin, 2000, Maisch et al., 2014) and Africa (e.g. White, 1955, Cappetta and Traverse,
153 1988, Strougo et al., 2007, Underwood et al., 2011) to the early late Eocene of Morocco (Adnet et al.,
154 2010). However, the latter teeth, twice to three times larger are likely belongs to an unnamed new
155 species.

156

157 *Carcharhinus* Blainville, 1816 or *Negaprion* Whitley, 1940

158

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

164 - A first group that gathers the whole Eocene carcharhinids characterized by completely
165 unserrated crowns on upper and lower teeth, thereby making their identification and attribution
166 difficult in both genera (e.g. cf. "*Carcharhinus*" *frequens* (Dames, 1883); *Negaprion* cf.
167 *eurybatrodon* Case and West, 1991, Case and Borodin, 2000; *Negaprion* sp. and *Carcharhinus*
168 sp.1 Adnet et al., 2007; cf. "*Carcharhinus*" *marcaisi* (Arambourg, 1952); *Carcharhinus* sp.
169 (Kriwet, 2005).

170 - A second group that consists of undoubted middle-late Eocene *Carcharhinus* species, that have
171 upper teeth sharing a complete serrated crown as firstly reported since the 19th in Egypt (*C.*
172 "*egertoni*" in Dames, 1883 : Fig. 5) and is currently represented by the large-sized *C.*
173 *balochensis* (Adnet et al., 2007) and many unnamed specimens (e.g. *Carcharhinus* cf. *egertoni*
174 in Stromer 1905; *Carcharhinus* sp. 1 in Case and Cappetta, 1990; *Carcharhinus* sp. 2 in Adnet
175 et al., 2007; *Carcharhinus* sp. in Underwood and Gunter, 2012; *Carcharhinus* sp. in Underwood
176 et al., 2011)

177 - and a third group of Eocene carcharhinid that have teeth with smooth massive cusp and low
178 lightly serrated heels on upper teeth. It concerns particularly three fossil species, belonging to
179 *Carcharhinus* or *Negaprion* according authors and/or time: cf. "*Negaprion*" *amekiensis* (White,
180 1926); cf. "*N.* *gibbesi* (Woodward, 1889) and cf. "*N.* *gilmoeri* (Leriche, 1942). The attribution to
181 the genus *Carcharhinus* remains uncertain considering that such tooth morphotype may be, as
182 for the first group, related to the living representatives of *Negaprion* (e.g. *N. brevirostris*) or
183 *Carcharhinus* (e.g. the Arabian sharks *C. hemiodon* or *C. leiodon*).

184 Consequently, isolated teeth of *Carcharhinus* are really difficult to distinguish from *Negaprion* before
185 the late Oligocene because they lack the usual complete serrated cutting edges on upper teeth as

186 observed in all living *Carcharhinus* species. Considering this dilemma, we consider, when not
187 discussed, as confer to the formally attribution of authors to *Negaprion* (and relative old synonym
188 *Hypoprion*) or *Carcharhinus* (and relative old synonyms *Aprionodon* and *Prionodon*)

189

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

191

192 Dames, 1883: *Aprionodon frequens* - fig. 7 a-e,i-p

193 ?Stromer, 1905: *Carcharias* sp. – pl. 16, Figs. 21 and 28

194 ?Priem, 1908: *Carcharias (Aprionodon)* aff. *frequens* – pl.15,

195 Fig. 6–7

196 ?Casier, 1971: *Aprionodon frequens* – pl. 1, Fig. 6

197 Case and Cappetta, 1990: *Carcharhinus frequens* – pl. 5, Figs. 104–

198 107; pl.7, Figs. 143–144 and 151–159

199 Adnet et al., 2010 : *Carcharhinus frequens*. Text only

200 Adnet et al., 2011: *Carcharhinus* aff. *frequens* – Fig. 3G–H

201 Underwood et al., 2011: *Negaprion* sp. – Fig. 5T–U

202 Zalmout et al., 2012: *Negaprion frequens* – Fig. 5A–D

203 ?Zalmout et al., 2012: *Carcharhinus* sp.1 – Fig. 5E–F

204 ?Murray et al., 2014: *Carcharhinus* sp. - Fig. 4C and ?*Misricthys stromeri*. - Fig. 4B, unknown in text

205 Van Vliet et al., 2017. *Negaprion frequens* – Fig. 12G

206

207 Fig. 3. I–J

208 Material: eight teeth, including figured MBK–06 and 07

209

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

217

218 **Discussion** – Often misidentified, "*Carcharhinus*" *frequens* was originally named by Dames (1883) from
219 teeth recovered in the late Eocene of Egypt, considering it was the most frequent carcharhinid in the
220 fossil assemblages of Birket-el-Qurun. In the original diagnosis, and despite an unclear figuration
221 (Dames, 1883: fig. 7) that possibly mixed other coeval carcharhinids, Dames (1883: p.144) reported the
222 lack of real serrations on the entire cutting edges, although some infrequent "undulation" can appear on
223 cutting edges of heels. Stromer (1905) and Priem (1908) subsequently reported other material from
224 Egypt among taxa, including some *Misricthys* teeth for instance (Case and Cappetta, 1990). Case and
225 Cappetta (1990) figured new teeth series from Birket-el-Qurun and provided an updated description of

226 this Egyptian species noting its fine and gracile lower teeth. If some figured material (e.g. Case and
227 Cappetta, 1990: Plate 5 fig. 104-105; Plate 7 fig. 147-148) belong in fact to other carcharhiniforms (e.g.
228 *Abdounia* sp. in Underwood et al., 2011), the most abundant morphotype recovered at Birket-et-Qurun
229 is the gracile unserrated tooth. Latter, Underwood et al. (2011: Tab.1) reported two distinct taxa from
230 Birket-el-Qurunt oo: some “occasional” robust teeth attributed to *Negaprion frequens* (Underwood et al.
231 2011 fig. 5V–W) and some “abundant” gracile and unserrated teeth identified as *Negaprion* sp.
232 (Underwood et al., 2011 fig Fig. 5T–U). Underwood and Gunter (2012: p.26) changed their previous
233 opinion by studying the type series of “*N.* *frequens* of Dames and reattributed the unserrated teeth
234 identified as *Negaprion* sp. from Birket-el-Qurun to “*N.* *frequens* and so, the “occasional” robust teeth
235 attributed to “*Negaprion*” *frequens* to *N.* sp. (see below), possibly conspecific with coeval “*N.*
236 *amekiensis*. Cf. “*C.* *frequens*, as considered here, appeared as a frequent medium-sized carcharhinid,
237 which frequented the south Tethys (Egypt : Dames, 1883, Stromer, 1905, Casier, 1971, Case and
238 Cappetta, 1990, Murray et al., 2010, Underwood et al., 2011, Zalmout et al., 2012) and western Atlantic
239 coasts (Southwestern Morocco : Adnet et al., 2011) during the late. Observed in Rupelian deposits of
240 the Qattara Depression, Egypt (Van Vliet et al., 2017), its occurrence in coeval deposits of the Fayum
241 (Quarries R and E, as *Carcharhinus* sp. and ?*Misrichtys stromeri* in Murray et al., 2014: fig. 4) remains
242 currently uncertain.

243

244 *Carcharhinus* sp. or *Negaprion* sp.

245

246 Case and Cappetta, 1990: *Carcharhinus* sp. 2 - Plate 5, figs. 100-101

247 Case and Cappetta, 1990: *Carcharhinus frequens* - Plate 5, fig. 102-103; Plate 7 fig. 145-146

248 Murray et al., 2010: *Carcharhinus* sp. – Fig. 1.D

249 Adnet et al., 2011: *Carcharhinus* sp. or *Negaprion* sp. -Fig. 3I–M

250 Underwood et al., 2011: *Negaprion frequens* - Fig. 5V–W

251 ?Zalmout et al., 2012: *Carcharhinus* sp.2 – Fig. 5G-H

252

253 Fig. 4. A-C

254 Material: twelve teeth including figured MBK-10 to 12

255

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

263

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

279 However, teeth of cf. "*C.*" *amekiensis* are smaller (not exceeding 8 mm height) and possess larger roots,
280 smooth cutting edges with rarely fine serrations on lateral heels only according White (1926) but contrary
281 to cf. "*C.*" *gibbesi*. The case of the subspecies cf. "*C.*" *gibbesi gilmorei* (Leriche, 1942), sometimes
282 erected as a species, is more complex. This was originally considered as to be a subspecies of cf. "*C.*"
283 *gibbesi* from the Ypresian of Alabama, reattributed after to middle-late Eocene (White, 1956). White
284 (1956, p. 139-144) reassigned cf. "*C.*" *gibbesi* and cf. "*C.*" *gibbesi gilmoeri* to the genus *Negaprion*,
285 indicating that the teeth of the latter "attained a slightly larger size than the typical form, up to 1.2 cm in
286 height. The crowns, especially of upper teeth, are somewhat relatively larger. Basal extensions of crown
287 on upper teeth are only faintly visible but on lower teeth they are coarsely crimped, smooth". Many
288 authors reported this largest subspecies "*C.*" *gilmorei* in middle-late Eocene deposits of USA (Case, 1980,
289 Kruckow and Thies, 1990, Muller, 1999, Parmley and Cicimurri, 2003, Manning, 2006), considering that
290 typical "*C.*" *gibbesi* is more likely post Eocene. However such an attribution appears quite dubious
291 considering that both morphologies were intergradational (Manning, 2006, Cicimurri and Knight, 2009).
292 Only new analyses will allow elucidating these uncertainties. Regardless of these differing point of views,
293 all these forms seems to be really close, both in morphology and in time occurrence.

294
295 *Carcharhinus perseus* Adnet, in Adnet et al., 2007
296

297 Fig. 3. F-H
298 Material: twenty teeth, including figured MBK-4 and 5
299

300 **Description** – In this taxon, the lower and upper teeth (Fig. 3, G) are virtually similar (Fig. 3, F, H), and
301 differ primarily in the presence of a more slender cusp and a less marked serrations characterizing lower
302 teeth. This species thus shows mainly a monognathic heterodonty. The teeth have a triangular cusp,

303 strongly labio-lingually compressed, rather large, high, and more or less curved, depending on their
304 position on the jaw. There are well-marked serrations on both mesial and distal cutting edges from the
305 root to the apex, as well as on the distal heel. Roots are relatively low, never larger than the crowns on
306 both the anterior and superior teeth. In lingual view, a shallow groove incises the root in its central part
307 (Fig. 3, F1-H1). The antero-lateral teeth have a cusp slightly slanted distally and a rounded distal heel
308 (Fig. 3, F1). Unlike the latter, the lateral teeth display a cusp more slanted distally, and the inferior part
309 of the mesial edge forms a greater angle with its superior part (Fig. 3, G-H). Moreover, the distal heel is
310 rather straight (Fig. 3, G-H).

311
312 **Discussion** – Specimens from MBK display morphological features very similar to those observable in
313 the species *C. perseus* recovered in Pakistan (see Adnet et al., 2007: Fig. 4), with a very limited dignathic
314 heterodonty, a reduced nutritive groove (in lingual view) and a strong labio-lingual compression of teeth
315 (Adnet et al., 2007). *Carcharhinus perseus* was originally described from the early Oligocene of
316 Baluchistan, Pakistan (Adnet et al. 2007). It is also known from the early Oligocene of, Oman (Thaytiniti,
317 quoted in Adnet et al., 2007) and Egypt (Jebel Qatrani, Quarries A and E ; Murray et al., 2014; Qattara
318 Depression: Van Vliet et al., 2017). This taxon has not been recorded in late Eocene localities of North
319 Africa, except if we consider the upper teeth with similar pattern reported and figured by Dames (1883:
320 pl.3, fig. 5). Misidentified with the Neogene species *C. egertoni* (Agassiz, 1843), the age and provenance
321 of the fossils reported by Dames (1883) remain uncertain but could testify of the first report of this
322 species in the Paleogene of North Africa, unless it corresponds to another coeval *Carcharhinus* with
323 large serrated upper teeth as *Carcharhinus* sp. 1 according Case and Cappetta (1990: Pl. 7 fig. 164-
324 165); *Carcharhinus* sp. 1 according Underwood et al. (2011: fig. 4N), or *Carcharhinus* sp.1 according
325 Adnet et al. (2011: fig.3D-F) from the late Eocene of Egypt.

326
327 *Misrichthys* Case and Cappetta, 1990
328 *Misrichthys stromeri* Case and Cappetta, 1990

329
330 Fig. 3. K-L
331 Material: Two teeth, including figured MBK-8 and 9

332
333 **Description** – This taxon, only known by two teeth in the MBK assemblage (Fig. 3, K-L), displays a
334 medium dignathic heterodonty. The anterior lower tooth (Fig. 3 K) have a relatively high, slender and
335 straight cusp. The root, although incomplete, is massive, with short but well-developed lobes, and we
336 can notice the presence of a deep median nutritive groove. The labial face of the crown is flat (Fig 3 K1),
337 whereas the lingual face is strongly convex (Fig. 3 K2). In profile, the crown is slightly sigmoid. The
338 upper tooth (Fig. 3 L) has a triangular cusp, rather large at its base and slanted distally. There are also
339 well-developed lateral heels. The mesial heel is rather elongated and follows the mesial cutting edge,
340 whereas the distal heel is short, rounded, and well separated from the distal cutting edge by a deep
341 notch. The root is relatively well developed, and bears in lingual view a median protuberance incised by
342 a short groove (Fig. 3 L2).

343

344 **Discussion** – A massive root with short lobes and deep nutritive groove are very peculiar features
345 among large fossil carcharhinids. These unusual characters are only known in the anterior teeth of
346 *Misrichthys stromeri*. Likewise, this species is characterized by a strongly marked dignathic heterodonty
347 (Case and Cappetta, 1990, Adnet et al., 2011, Cappetta, 2012). Despite a limited material sample, these
348 unique characters are observed in the MBK specimens, justifying the assignment to this taxon. Until
349 now, *Misrichthys* was a monospecific genus, geographically and stratigraphically constrained. Indeed,
350 this species is only known along the late Eocene coast of Middle East - North Africa, from Jordania
351 (Mustafa and Zalmout, 2002), Egypt (Case and Cappetta, 1990, Adnet et al., 2011, Underwood et al.,
352 2011) up to southwestern Morocco (Adnet et al., 2010). Murray et al. (2014: fig. 4B) figured a Rupelian
353 tooth (Quarry R) they considered as evidence of *Misrichthys stromeri*, but did not report this occurrence
354 in the material listed from the Jebel Qatrani Formation, Egypt (Murray et al., 2014: Tab.1). This tooth
355 probably belongs to a *Carcharhinus* lower jaw (see before).

356

357 Hemigaleidae Hasse, 1789

358 *Hemipristis* Agassiz, 1843

359 *Hemipristis curvatus* Dames, 1883

360

361 Fig. 5. A

362 Material: One tooth, figured MBK-13

363

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

371

372 **Discussion** – This unique specimen shows morphological features similar to those of the upper teeth
373 of the genus *Hemipristis*, as listed by Cappetta (2012), with the exception to the presence of a well-
374 developed serration on the mesial heel. However, the latter feature is not always present within all the
375 species of this genus, and the denticles of the mesial cutting edge are sometimes poorly developed (see
376 Case and Cappetta, 1990). Basically, the overall morphology of the tooth is similar to that of an antero-
377 lateral tooth from the late Eocene of Fayum attributed to *H. curvatus* by Case and Cappetta (1990 Fig.
378 4, 80-81). The groove is less developed on the MBK specimen, but this may be related to the wear.
379 Although this taxon is only known by one poorly preserved tooth, we can attribute this specimen to *H.*
380 *curvatus*, perhaps preferentially to *H. serra*, the latter having larger teeth, and a more developed
381 serration on both cutting edges (Case and Cappetta, 1990). *Hemipristis curvatus* is mainly known in the
382 middle-late Eocene, especially from the late Eocene of the eastern Tethys (Case and Cappetta, 1990,

383 Underwood et al., 2011, Adnet et al., 2010) to the western Atlantic (Case and Borodin, 2000), and also
384 from the late Eocene of the western Pacific (see Cappetta, 2012). Very few occurrences are reported in
385 early Oligocene deposits (e.g. Thomas et al. 1989), unless the strong resemblance with *H. serra*
386 (Chandler et al., 2006) currently known since the early Oligocene of Egypt (Van Vliet et al., 2017), Oman
387 (Thomas et al., 1989) and Pakistan (Adnet et al., 2010) makes particularly difficult its recognition.

388

389 Orectolobiformes Applegate, 1972

390 Ginglymostomatidae Gill, 1862

391 *Nebrius* Rüppell, 1837

392 *Nebrius obliquus* Leidy, 1877

393

394 Fig. 5. B-C

395 Material: four teeth, including figured MBK-14 and 15

396

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

405

406 **Discussion** – There are only a few *Nebrius* species known in the fossil record, especially in the
407 Paleogene. *Nebrius bequaerti* (Leriche, 1920) from the early Paleocene, *N. obliquus*, *N. thielensis*
408 (Winkler, 1873) and *N. blankehorni* (Stromer, 1905) from the Eocene, and depending if we consider the
409 latter as a junior synonym of *N. obliquus* (Noubhani and Cappetta, 1997). *Nebrius bequaerti* has only a
410 few lateral denticles, which is not the case on the MBK specimens and the other species of *Nebrius* (*N.*
411 *obliquus* and *N. thielensis*). *Nebrius thielensis* has often a bifid apron, which is never the case in *Nebrius*
412 *obliquus* (Noubhani and Cappetta, 1997) and on the teeth from the MBK assemblage. Furthermore, the
413 antero-lateral and lateral teeth from MBK illustrated in figure 5 (Fig. 5C and 5B respectively) are quite
414 similar to those illustrated by Noubhani and Cappetta (1997: plate 14, Fig. 1-2) and attributed to *N.*
415 *obliquus*. If the genus is widespread in the Paleogene and Neogene coastal deposits and principally in
416 the late Eocene (Underwood et al., 2011, Adnet et al., 2010, Adnet et al., 2007), *N. obliquus* is currently
417 known only from the early Eocene (e.g. Noubhani and Cappetta, 1997) to the late Eocene (Adnet et al.,
418 2007, 2010) of the southwestern Neotethysian region.

419

420 Incertae ordinis

421 *Odontorhytis* Böhm, 1926

422 *Odontorhytis* aff. *pappenheimi* Böhm, 1926

423

424 Fig. 5. D-E

425 Material: two teeth, figured MBK-16 and 17

426

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

431

432 **Discussion** – With the unusual tooth morphology, there is no doubt about the generic attribution of
433 these specimens to this very peculiar and ambiguous elasmobranch, *Odontorhynchus*, only known in the
434 Paleogene. The two teeth have a median labial cutting edge and no lateral denticles. Both features are
435 only recovered in the youngest species *O. pappenheimi* contrary to the oldest representative (early
436 Eocene), which shows lateral cutting edges and a pair of small cusplets at the base of the cusp (Case
437 and Cappetta, 1990, Cappetta, 2012). However, *O. pappenheimi* is generally characterized by an apico-
438 lingual barb (Case and Cappetta, 1990, Adnet et al., 2011, Cappetta, 2012), which is absent on both
439 specimens from MBK, thereby orienting our determination to *Odontorhynchus pappenheimi*. The latter is
440 the unique species to be known of this enigmatic genus. However, according to Case and Cappetta
441 (1990) and Cappetta (2012), there are probably several species that remain so far undescribed. Until
442 now, *O. pappenheimi* is only recovered from the middle to late Eocene coastal deposits and particularly
443 well-represented in Egypt (Case and Cappetta, 1990, Murray et al., 2010; Underwood et al., 2010, Adnet
444 et al., 2011). The genus, found in Pakistan and all African coastal deposits (Böhm, 1926, Case and
445 Cappetta, 1990, Case and West, 1991), is known until the early Rupelian of Jebel Qatrani (Quarry E),
446 Egypt (Murray et al., 2014), after what, it has no more fossil record.

447

448 Other elasmobranch taxa (Fig. 6)

449

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

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

494 Batoids from MBK are mostly represented by the two families Myliobatidae and Dasyatidae, even if
495 some scarce fragmentary teeth of Pristidae and Rhinobatidae were also collected from the locality. The
496 Myliobatidae are represented by three unnamed species of *Myliobatis* Cuvier 1816 (Fig. 6G), *Aetobatus*
497 Blainville 1816 (Fig. 6N), and the fossil genus *Leidybatis* Cappetta, 1986 (Fig. 6O). The material is
498 scarce and fragmentary, and the isolated teeth are always worn. No precise determination can be
499 reached based on the fragmentary teeth, because diagnosis of fossil myliobatids are often based on
500 tooth variability and junction on complete or partial tooth plates (e.g. Hovestadt and Hovestadt-Euler,
501 2013). Although if *Myliobatis* and *Aetobatus* are frequently known throughout the entire Cenozoic marine
502 deposits, it is worth noting that *Leidybatis* sp. is currently restricted to the Paleogene, from the late

503 Paleocene (e.g. Noubhani and Cappetta, 1997) to the late Eocene (e.g. Adnet et al., 2010, Underwood
504 et al., 2011). Although incomplete, the partial teeth showing a flat occlusal face (Fig. 6O) covered by an
505 unusual thick and strongly granular enameloid (Cappetta, 1986), is rather indicative of fossil genus
506 *Leidybatis*. In the MBK assemblage, dasyatids are represented by at least three different species., with
507 at least two distinct species belonging to subfamily of Dasyatinae (fig. 6 H-J), showing different types of
508 ornamentation. Numerous fossil species are known from the literature and would deserve a deep
509 revision regarding the recent advance in dasyatid systematics (e.g. Last et al. 2017) before any new
510 fossil attributions). The living genus *Pastinachus* (Dasyatidae hypolophin) is also represented in the
511 MBK locality (Fig. 6K), but as the former dasyatins, the rare material does not permit a precise attribution.
512 *Pastinachus* is known from the Bartonian (Adnet et al. 2018) and is frequently recorded in late Eocene
513 (e.g. Adnet et al., 2010, Underwood et al., 2011) and early Oligocene deposits of North African coasts
514 (Murray et al., 2014). A few oral teeth (and rostral denticles without posterior carena) of Pristidae
515 (*Anoxypristis*) and Rhinobatidae (?*Rhinobatos*) have been recovered from the MBK locality (e.g. Fig.
516 6L)..

517

518 4. Discussion

519 The MBK fauna is composed of numerous unnamed species from several genera (e.g. *Abdounia*,
520 *Carcharias*, *Rhizoprionodon*) that have a particularly extensive stratigraphical range through the
521 Cenozoic (Fig. 7). These taxa are therefore of low interest for discussing the age of this peculiar marine
522 association recovered in a strict fluvial deposit. Considering that there is no evidence of differential
523 degree of reworking on the fossil material, it is likely that this elasmobranch fauna documents a unique
524 former assemblage in a deposit that was likely reworked but not transported from a long distance before
525 to be redeposited in the detrital deposits corresponding to the MBK locality (see introductory paragraph
526 of the “Systematic Paleontology” section). Interestingly, a few taxa have a relatively small stratigraphic
527 range, which allows constraining the age of this association. Among them, *Galeocerdo eaglesomei*,
528 *Nebrius obliquus*, *Leidybatis* sp. and *Misrichthys stromeri* are known in the fossil record only until the
529 late Eocene, and are not documented in the numerous localities dating from the early Oligocene (e.g.
530 Fig. 7). Conversely, *Carcharhinus perseus* was only reported from the early Oligocene of Pakistan and
531 Egypt (if we exclude the dubious oldest reports from Egypt as *C. egyptoni*). Finally, although cf.
532 *Carcharhinus frequens* and *Odontorhynchus* can be found in few early Oligocene deposits from Egypt
533 (Quarries R and E, in Murray et al., 2014), these two taxa are in contrast frequently recorded in
534 numerous late Eocene deposits (e.g. Adnet et al., 2010, 2011, Case and Cappetta, 1990, Murray et al.,
535 2010, Underwood et al., 2010). Although likely reworked from a close marine deposit (unobserved on
536 the field), the faunal assemblage from this new locality then suggests a latest Priabonian – earliest
537 Rupelian age for the reworked MBK elasmobranch assemblage. The precise age of the detrital deposit
538 embedding this marine association is still unknown but could be almost contemporaneous to slightly
539 younger than the Eocene/Oligocene transition if we consider the rare but well-preserved mammal
540 remains recovered in association with the elasmobranchs (work in progress) at the MBK locality.

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

549 This elasmobranch assemblage, if homogeneous, is quite similar to those of the Baharya Oasis (Adnet
550 et al., 2011), Qattara Depression (Zalmout et al., 2012) – Western Desert, Egypt and those from
551 Birket-el-Qurun – Fayum, Egypt (Murray et al., 2010). Surprisingly, it also shares great similarities with
552 geographically distant faunas such as those from the late Priabonian of Morocco (Dakhla; Adnet et al.,
553 2010) and the Rupelian of Pakistan (Paali Nala; Adnet et al., 2007) for instance. The MBK faunal
554 assemblage is strongly dominated by Carcharhiniformes (39% species) and Myliobatiformes (26%
555 species). Among Carcharhiniformes, the greatest diversity is recorded among Carcharhinidae (e.g.
556 "*Carcharhinus*"/"*Negaprion*", *Galeocerdo*), systematically close to extant species known to live in
557 tropical coastal waters (see Compagno, 1984, Chiaramonte, 1998). The pelagic species
558 (Lamniformes) are also represented (9% species), although poorly sampled and represented by
559 fragmentary remains. Finally, several orders such as Hexanchiformes, Pristiophoriformes and
560 Squaliformes, which are generally indicators of deep waters (Ebert et al., 2013) are lacking in the MBK
561 assemblage. Among identified fossils, some of them are primarily marine taxa, but known to tolerate
562 brackish to freshwater environments (e.g. *O. pappenheimi*, *M. stromeri*, *Pastinachus* sp., some
563 *Carcharhinus*, pristid; see Martin 2004, Murray et al., 2010, Adnet et al., 2011), whereas others are
564 known to frequent pelagic area (e.g. Lamniformes), as is highlighted by the presence of numerous
565 albeit worn teeth of *Carcharias* sp., a typical marine taxa, which is absent in many other sub-
566 contemporaneous localities such as Dash-I-goran, Paali Nala (Pakistan; Adnet et al., 2007) and
567 Fayum Quarries or Km55 (Egypt, e.g. Underwood et al., 2011, Murray et al., 2010, 2011). Considering
568 this singular mixture of species, the peculiar preservation state of all teeth (worn and rolled) and the
569 fact that these fossils were found in fluvial deposit, is indicative of a reworking by river systems from a
570 sub-contemporaneous submarine fan. In comparison with Eocene-Oligocene localities from the
571 Fayum, this kind of depositional environment of 'phantom' marine deposits would be intermediate
572 between those of deltaic BQ-2 (Fayum, central north Egypt; Seiffert et al., 2008, Murray et al., 2010)
573 and those of 'Km55' (western north Egypt), where marine influence are noticed (Adnet et al., 2011).
574 This indicates that some of the shared elasmobranchs (e.g. *Pastinachus*, *Negaprion*, *Misrichthys*) may
575 have also lived in a broad range of habitats. Shallow water environments are rather common within
576 localities close to the Eocene/Oligocene transition. This kind of deposits has already been described
577 from several Neotethysian localities (e.g. see Otero and Gayet, 2001, Adnet et al., 2007, Murray et al.,
578 2014) and the frequent occurrences of this kind of deposal environment are probably related to
579 possible fall of sea level recorded between the late Eocene and the early Oligocene (Miller et al.,
580 2005).

581

582 5. **Conclusions**

583

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

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861 **Figure captions**

862

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

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

882 Figure 3. Shark teeth from the MBK fossil-bearing locality. **A-E**: *Galeocерdo* cf. *G. eaglesomei*; **A**: lateral
883 tooth MBK-01, 1. labial view, 2. lingual view; **B**: juvenile tooth MBK-, 1. lingual view, 2. labial view; **C**:
884 anterior tooth, 1. labial view, 2. lingual view; **D**: antero-lateral tooth MBK-02, 1. labial view, 2. lingual
885 view; **E**: lateral tooth MBK-03, 1. labial view, 2. lingual view. **F-H**: *Carcharhinus perseus*; **F**: upper antero-
886 lateral tooth MBK-04, 1. labial view, 2. lingual view; **G**: lower antero-lateral tooth MBK-05; **H**: upper
887 antero-lateral tooth, 1. labial view, 2. lingual view. **I-J**: cf. *Carcharhinus frequens*, **I**: upper tooth MBK-
888 06, 1. labial view, 2. lingual view; **J**: lower tooth MBK-07, 1. labial view, 2. lingual view. **K-L**: *Misrichthys*
889 *stromeri*, **K**: lower anterior tooth MBK-08, 1. labial view, 2. lingual view; **L**: upper tooth MBK-09, 1. labial
890 view, 2. lingual view. Scale bar= 5 mm.

891 Figure 4. Shark teeth from Mabrouk. **A-C**: *Carcharhinus* sp. or *Negaprion* sp, **A**: lateral upper tooth MBK-
892 10, 1. labial view, 2. lingual view; **B**: posterior upper tooth MBK-11, 1. lingual view, 2. labial view; **C**:
893 anterior lower tooth MBK-12, 1. labial view, 2. lingual view; **D**: draw of lower and upper teeth of
894 “*Carcharhinus* sp. or *Negaprion* sp.”, in Adnet et al., 2011: fig. 3I-M;. **E**: lower and upper teeth of
895 “*Negaprion*” *amekiensis* in White (1926: fig. 5 E). Scale bar= 5 mm.

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

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

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

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

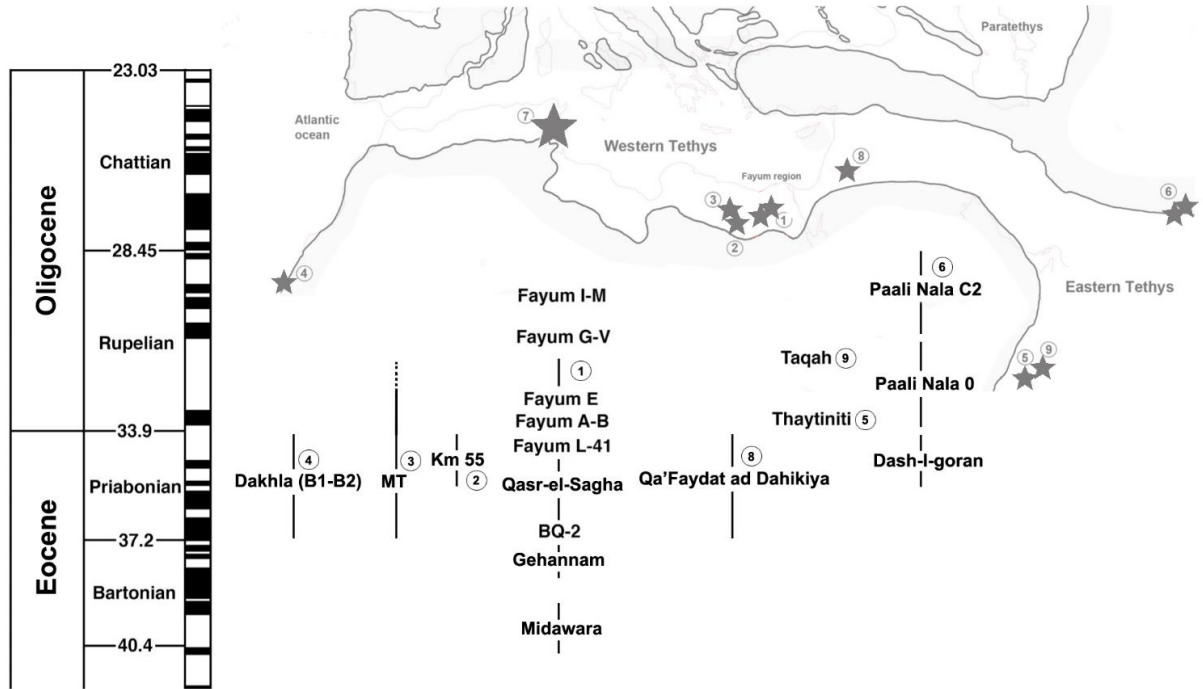
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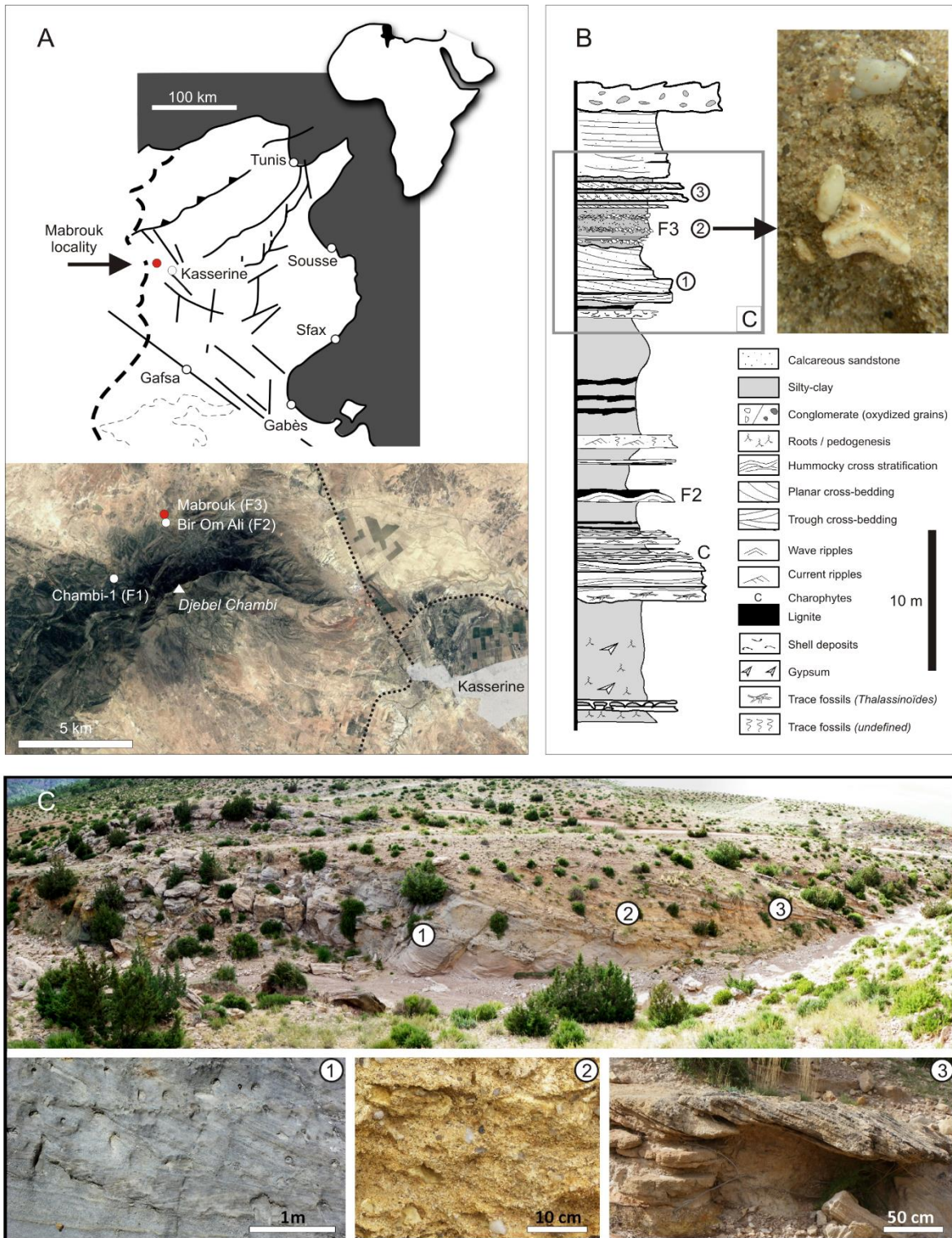
916 **Figures**

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

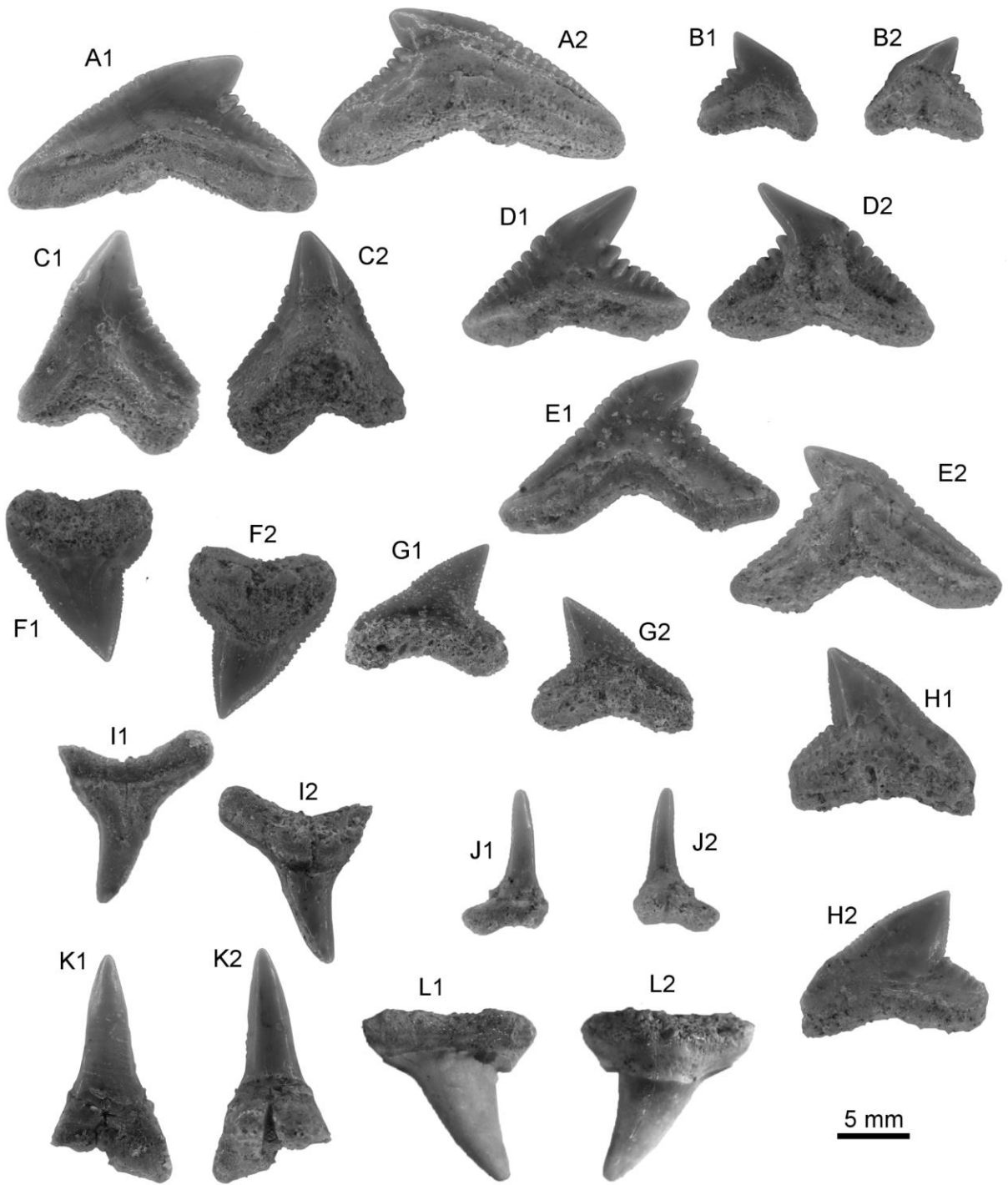


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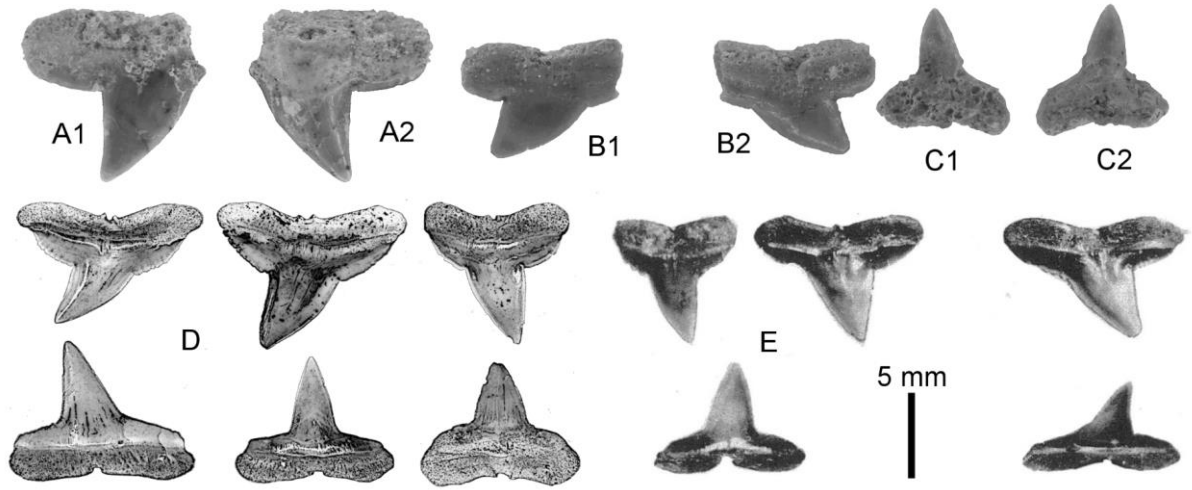
922 **Figure 2** (2-column fitting image)

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925 **Fig. 3** (2-column fitting image)

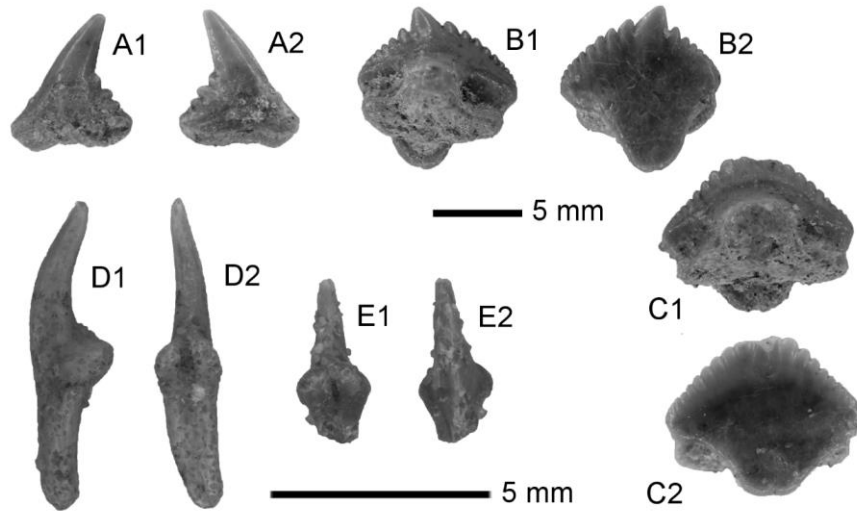


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927 **Fig. 4** (2-column fitting image)

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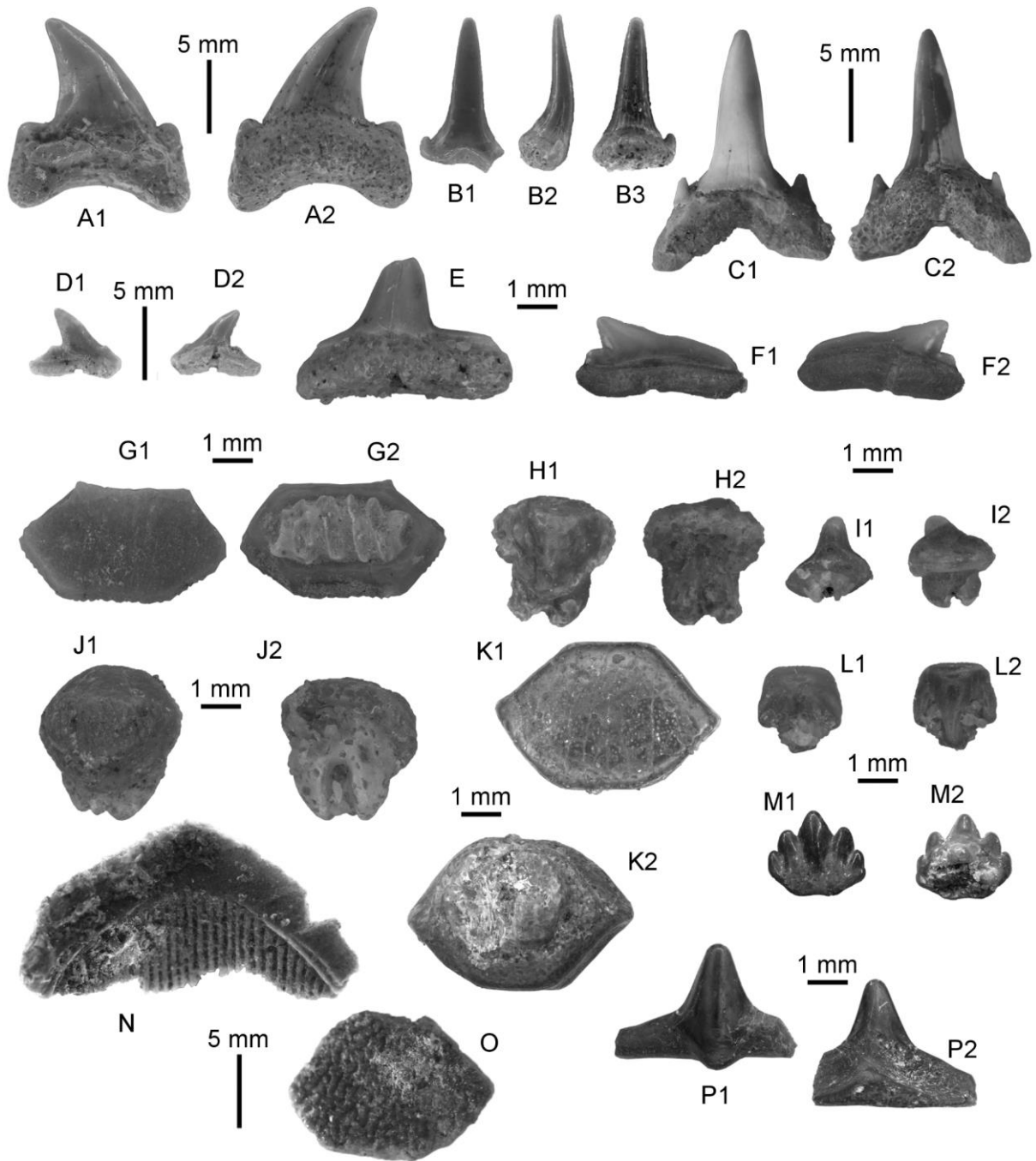
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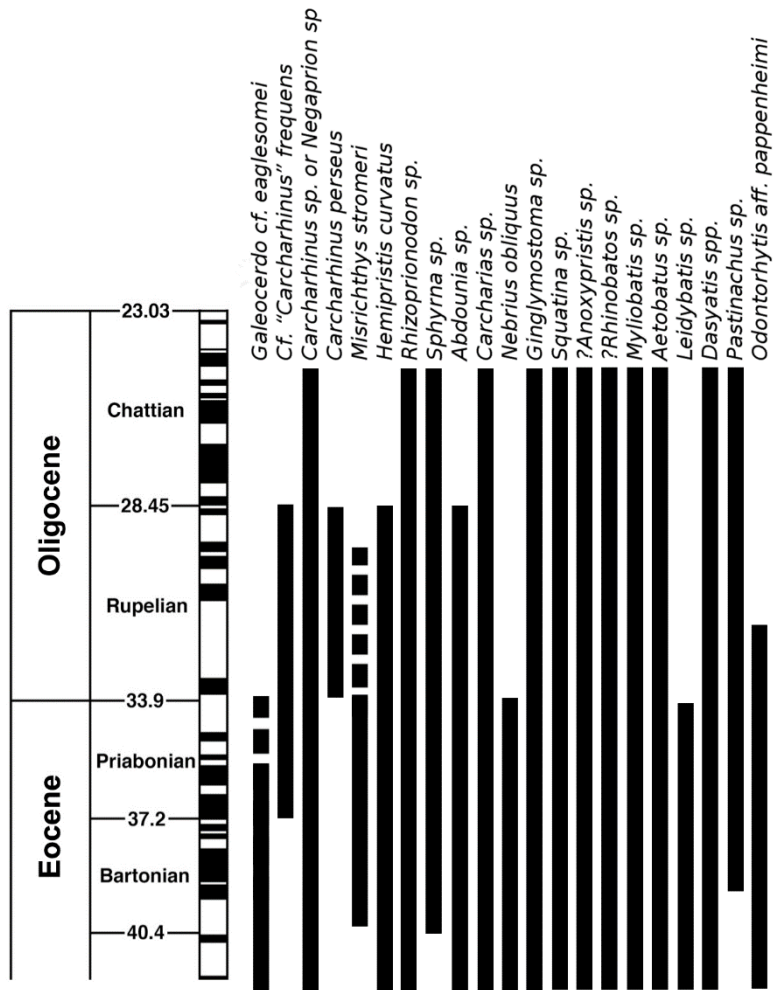
Fig. 5 (1.5 or 2-column fitting image)



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933 **Fig. 6** (2-column fitting image)

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936 Fig. 7 (1-column fitting image)