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1 **Elasmobranchs from the upper Paleocene of Togo**

2

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16

17

18 **Abstract**

19 Bulk sampling and surface collecting of two glauconitic horizons located in Southern Togo  
20 yielded a diverse elasmobranch fauna described here. This fauna includes 30 species and is  
21 dominated by carcharhiniforms (11 species), myliobatiforms (nine species) and lamniforms  
22 (five species) and also comprises three orectolobiform, whereas the squatiniforms and  
23 rhinopristiforms are represented by species each. Although the poor preservation of the  
24 specimens hampered numerous species-level identifications, the vast majority of taxa  
25 identified were formerly reported from the Paleocene-Ypresian interval, six of which being  
26 exclusively known from the upper Paleocene. This, along with the six benthic foraminifera  
27 species, indicate a late Thanetian age for the sampled horizons and provide age constraints on  
28 a geographically widespread benchmark horizon in Western Africa. The composition of the  
29 elasmobranch assemblage shows strong resemblances with upper Paleocene faunas from  
30 Morocco and differs markedly from known assemblages from geographically closer localities  
31 in Niger and Nigeria, which suggests strong palaeoenvironmental control on the distribution  
32 of Thanetian elasmobranch diversity.

33

34 *Keywords:*

35 Chondrichthyans

36 Benthic foraminifera

37 Stratigraphy

38 Paleobiogeography

39

40

## 41 **1. Introduction**

42           The Paleocene epoch witnessed a major reorganization of both marine and terrestrial  
43 ecosystems. Among marine vertebrates, this epoch includes the diversification of numerous  
44 fish clades in the aftermath of the Cretaceous-Paleogene extinction and the settlement of the  
45 modern groups in the late Paleocene-Eocene interval (Guinot and Cavin, 2016). More  
46 specifically, the late Paleocene is marked by the diversification of several elasmobranch  
47 groups including lamniforms, carcharhiniforms, and myliobatiforms. Yet, the Paleocene  
48 elasmobranch fossil record is rather poorly known compared to the late Maastrichtian and  
49 post Paleocene Cainozoic (Guinot and Cavin, 2016). Furthermore, knowledge on late  
50 Paleocene elasmobranch assemblages is geographically heterogeneously documented and the  
51 dating of many of them is poor. Most reported faunas are restricted to North Africa (e.g.,  
52 Arambourg, 1952; Noubhani and Cappetta, 1997) and northern Europe (e.g., Baut and  
53 Genault, 1995; Casier, 1967, 1943; Herman, 1977; Moreau and Mathis, 2000), whereas other  
54 reports include Jordan (Cappetta et al., 2000), Angola and Democratic Republic of Congo  
55 (Dartevelle and Casier, 1959, 1943), Niger (Cappetta, 1972), Nigeria (White, 1934), and USA  
56 (Case, 1994; Ward and Wiest, 1990). Stromer (1910) described several elasmobranchs and  
57 other vertebrates from southern Togo that were attributed to the Eocene. Some elasmobranch  
58 specimens reported by Stromer (1910) originated from Dagbati (Djagbati in original  
59 publication), an area where only middle Eocene rocks outcrop (Johnson et al., 2000).  
60 However, other taxa were sampled from limestones in Adabion, a locality on the banks of the  
61 Mono River close to village of Tokpli, with additional material collected from exposures near  
62 the neighbouring city of Tabligbo. These limestones were subsequently attributed to the  
63 middle-late Paleocene (Da Costa et al., 2013b, 2013c). According to Stromer (1910), these  
64 horizons yielded *Myliobatis dixonii*, *Odontaspis elegans* var. *substriata*, *Xenodolamia* aff.  
65 *simplex*, *Ginglymostoma* aff. *thielense*, and *Hypolophites myliobatoides* along with

66 actinopterygian and tetrapod remains. Recent fieldwork in the Tabligbo area allowed the  
67 identification of a late Paleocene vertebrate-rich glauconitic horizon covering the limestone  
68 series. The fauna reported here adds to the knowledge on elasmobranch diversity as well as on  
69 their distribution along the Atlantic coast of Africa and provide age constraints on a  
70 geographically widespread benchmark horizon in Western Africa.

71

## 72 **2. Geographical and geological Settings**

73 The localities sampled are situated near the village of Tabligbo (Fig. 1(A)), southern  
74 Togo (Maritime Region). This region is part of the Togolese coastal sedimentary basin, which  
75 comprises a thick Upper Cretaceous to Neogene monoclinical sequence dipping South. The  
76 Campanian-Maastrichtian overlies the Dahomeyan basement and is characterized by various  
77 clastic facies that are mostly known from cores (Da Costa et al., 2009, 2013c, 2013b). This  
78 series is covered by a carbonate-dominated Paleogene sequence (Da Costa et al., 2013c;  
79 Johnson et al., 2000) that precedes Eocene shales, clays, and phosphorite series (Johnson et  
80 al., 2000). The sections studied in the present work (Fig. 1(B)) were accessed in the cement  
81 quarries WACEM (coordinates: 06°35'34.7''N, 1°33'25.8''E) and ScanTogo (coordinates:  
82 06°36'35.4''N, 001°34'05.4''E) respectively located 6 km and 8 km northeast of the city of  
83 Tabligbo. The lower part of the observable Paleocene succession is composed of a unit of  
84 yellow-weathering bioclastic limestone about four metres thick. This coquina limestone  
85 contains abundant bivalves, gastropods and echinoderms (including *Togocyamus seefriedi*  
86 Oppenheim, 1915) as well as rare foraminifera and numerous ostracods. The ostracod  
87 assemblage correlates with the Ewekoro Formation (Johnson et al., 2000) in the biozone P3  
88 (Adegoke, 1977). Stromer (1910) reported vertebrate remains that he received from Mr Koert,  
89 which originate from the banks of the Mono river at Adabion near the locality of Tokpli as  
90 well as additional material sampled from exposures near Tabligbo. Although the horizon from

91 which the specimens were sampled is not specified, Stromer (1910) indicated that the  
92 specimens he studied were preserved in an indurated yellow limestone containing abundant  
93 shells and gastropods, which most likely corresponds to the *T. seefriedi* limestones. In  
94 addition, prospections carried out in the area on the banks of the Mono river (close to the  
95 village of Sika-Kondji) resulted in the identification of the yellow limestones. While outcrops  
96 were overgrown and/or flooded, samples confirmed that these limestones are equivalent to the  
97 coquina *T. seefriedi* horizon described above. A diverse and abundant invertebrate fauna was  
98 subsequently described from the same area by Oppenheim (1915) and was later revised and  
99 completed by Furon and Kouriatchy (1948) who provided additional material from Adabion  
100 and Togblékopé. Although Furon & Kouriatchy (1948) indicated that their material was  
101 sampled from their layer 6 (glauconitic limestone, see below), it is clear from the faunal  
102 content that their specimens originate from the underlying *T. seefriedi* limestones (layer 7).  
103 These limestones are unconformably overlain by a compact limestone of two meters  
104 thickness, which comprises in its upper part a 30 cm thick oyster level and another  
105 unconformity. This is covered by a glauconitic series of less than one meter thick that  
106 includes a glauconitic biomicrite in its lower part and a 20 cm thick glauconitic sandstone in  
107 its upper part, which yielded the bulk of the elasmobranch described here. Numerous  
108 bioturbations containing crustacean remains mark the limit between the glauconitic biomicrite  
109 and the glauconitic sandstone. The glauconitic biomicrite level yielded planktonic  
110 foraminifera that suggest an upper Paleocene age (Biozone P4) (Da Costa et al., 2009, 2013d;  
111 Johnson et al., 2000), whereas previous biostratigraphic data provided contentious results for  
112 the glauconitic sandstone. Based on planktonic foraminifera, this level was assigned to the  
113 biozones P5-P6 (Da Costa et al., 2013a, 2009), whereas calcareous nannofossils indicate an  
114 age within the biozones NP9-10 (Da Costa et al., 2013c). Our samplings from this glauconitic  
115 sandstone layer yielded six species of benthic foramina (Fig. 2): *Frondicularia microdisca*

116 Reuss, 1860 known from the Upper Cretaceous of Germany and North America;  
117 *Fronicularia phosphatica* Russo, 1934 that ranges from the Thanetian of Senegal and North  
118 Africa; *Fronicularia vertebralis* Russo, 1934, known from the upper Paleocene of Senegal;  
119 *Lenticulina incisa* (Terquem, 1858) that ranges from the Paleocene and lower Eocene of  
120 Senegal and Ivory Coast; *Palmula sigmoicosta* Ten Dam & Sigal, 1950 known from the  
121 Paleocene of Algeria and Tunisia and *Nodosaria affinis* d'Orbigny, 1846, that ranges from the  
122 Upper Cretaceous of North America to the Paleocene of Senegal. This assemblage suggests a  
123 Thanetian age for this glauconitic sandstone horizon. The carbonate-dominated series is  
124 overlain by a thick (100 m) shaly series containing numerous benthic and planktonic foramina  
125 that are either attributed to various biozones (P3 to P6), which suggests condensation of the  
126 series (Johnson et al 2000) or to the basal Ypresian biozone P6 (Da Costa et al., 2013c, 2013a,  
127 2009).

128

### 129 **3. Material and methods**

130 About 40 kg of rock were bulk sampled from the glauconitic sandstone horizon and  
131 washed with water or diluted (7%) hydrogen peroxide. Small fossil remains were picked from  
132 residues that were formerly sieved down to 0.7mm mesh size, whereas most large specimens  
133 were surface picked in the field. One third of the rock samples were sieved with a 0.4mm  
134 mesh size, which did not yield additional identifiable elasmobranch specimens. About 300  
135 identifiable elasmobranch teeth were recovered. Specimen preservation is generally poor,  
136 most of fossils being broken due to sediment compaction and/or worn, while surface-collected  
137 samples show various degrees of surface alteration. The crowns of all elasmobranch teeth  
138 have a typical dark grey color and show a similar preservation with no signs of partial  
139 reworking. Elasmobranch teeth represent the largest fraction of the fossil material recovered,  
140 along with benthic foraminifera and fragmentary crustacean remains. Other associated fossils

141 include (listed by order of abundance): pycnodont and other incomplete actinopterygian teeth,  
142 gastropods (preserved as internal moulds), nautilid shells, rare coral polyps, chelonian and  
143 bivalve shell fragments.

144 Specimens from the underlying glauconitic limestone were sampled from 1 kg of rock  
145 that was processed using 7.5% buffered formic acid and sieved down to a 0.4mm mesh size.  
146 This sample yielded five elasmobranch teeth and numerous actinopterygian bone and tooth  
147 fragments, gastropods and crustacean fragments as well as cidaroid spines.

148 All figured and unfigured specimens are housed in the collections of the Geology Department  
149 of the University of Lomé. Official specimen numbers are preceded by 'ULDG TAB'  
150 (shorten here to 'TAB2' and 'TAB3' for specimens from the glauconitic sandstones and  
151 glauconitic limestones, respectively).

152

#### 153 **4. Systematic palaeontology**

154 Order Squatiniformes Buen, 1926

155 Family Squatinidae Bonaparte, 1838

156 Genus *Squatina* Dumeril, 1806

157 *Squatina* cf. *prima* (Winkler, 1876)

158 Fig. 3(A-B)

159 **Material:** Five incomplete teeth and several isolated crowns from the glauconitic sandstones.

160 **Description:** Teeth are small (less than 1.5mm high) and generally as broad as high. The  
161 crown comprises a triangular and erect main cusp flanked by a pair of lateral heels that are  
162 slightly inclined to the base and faintly oriented lingually. The cutting edges are moderately  
163 developed and run continuously from one heel to the other. An apron is present at the base of  
164 the labial root face, below the main cusp. This can vary in size and shape, being generally  
165 narrow and slightly displaced from the axis of the main cusp in anterior teeth or being wide



166 and short in laterals. The apron always extends below the basal root edge in labial view. The  
167 root has a concave basal face pierced by a large central foramen. The lingual root face  
168 displays a marked lingual protuberance, which is pierced by a central foramen.

169 **Remarks.** The morphology of these teeth is typical of the genus *Squatina*. Teeth of the  
170 species *S. prima* (Winkler, 1876a), described from the Selandian of Belgium (see also  
171 Herman, 1977), bears resemblances with the material reported here. However, the teeth  
172 described here are smaller than most of specimens referred to *S. prima*, but the poor  
173 preservation of the Togolese specimens preclude further identification of this taxon.

174

175 Order Orectolobiformes Appelgate, 1972

176 Family Hemiscylliidae Gill, 1862

177 Genus *Chiloscyllium* Müller & Henle, 1837

178 *Chiloscyllium* sp.

179 Fig. 3(C-D)

180 **Material:** Three incomplete teeth: two from the glauconitic sandstones and one from the  
181 glauconitic limestones.

182 **Description:** Teeth of this species are characterized by a rather short and wide main cusp that  
183 broadens in its lower region and connects to a pair of incipient but broad lateral cusplets. The  
184 cutting edges are faint but continuous from the apex of the main cusp to the lateral cusplets.

185 The labial crown face is slightly convex in profile view and tends to display an irregular  
186 surface in some teeth (Fig. 3(C)). The apron is short, wide and bifid in labial view with a  
187 markedly concave central region. The concave marginal area of the basal crown face  
188 separates the apron from the lateral cusplets. Anterior teeth are more mesio-distally  
189 compressed.

190 **Remarks:** Species of this genus have a conservative morphology and the poor preservation  
191 does not allow precise identification of the specimens reported here.

192

193 Family *Ginglymostomatidae* Gill, 1862

194 Genus *Hologinglymostoma* Noubhani & Cappetta, 1997

195 *Hologinglymostoma* sp.

196 Fig. 3(E-F)

197 **Material:** Two incomplete teeth from the glauconitic sandstones.

198 **Description:** The crown comprises an erect triangular main cusp flanked by low heels that  
199 bear three low and broad cusplets, well separated from each other and from the main cusp by  
200 notches. The apron is short, broad and concave in its median region, in labial view. The  
201 lingual face bears a broad and lingually developed uvula with a rounded lingual edge.

202 **Remarks:** This genus is so far represented by a single nominal species, *H. jaegeri* Noubhani  
203 and Cappetta, 1997 from the upper Paleocene of Morocco. Although incomplete, the  
204 specimens reported here concur with the diagnosis of the genus including a markedly concave  
205 labial crown face in profile view, a main cusp well separated from the heels, which bear  
206 several low and sharp (but broad) cusplets. Teeth of *H. jaegeri* have a holaulacorhize root,  
207 which was seemingly the case in one tooth with incomplete root from Tabligbo. These  
208 characters differentiate teeth of *Hologinglymostoma* sp. from those of *Ginglymostoma* sp.  
209 described below.

210

211 Genus *Ginglymostoma* Müller & Henle, 1837

212 '*Ginglymostoma*' sp.

213 Fig. 3(G-I)

214 **Material:** Four incomplete teeth from the glauconitic sandstones.

215 **Description:** Anterolateral teeth are as broad as wide. The main cusp is labio-lingually  
216 compressed, broad and triangular. At least three mesial cusplets of decreasing size towards the  
217 mesial crown edge are present, separated from each other by narrow notches. Both the main  
218 cusp and cusplets are inclined to the commissure. The apron is moderately broad with a flat  
219 basal edge. In labial view, the apron is well separated from the basal edge of the labial crown  
220 face by two concavities. Lateral teeth are broader than high with three cusplets on the distal  
221 heel and a fourth, incipient cusplet on the distal edge. The distal crown edge bears a vertical  
222 ridge oriented lingually that connects to the incipient cusplet. Four cusplets are present on the  
223 mesial heel. All cusplets and main cusp are strongly bent to the commissure. The apron is  
224 broad, moderately developed and protrudes labially, which confers a concave outline to the  
225 labial crown face in profile view. The apron is mesially positioned relative to the main cusp  
226 and is separated from the rest of the crown by concavities of the basal crown edge. A labial  
227 ridge is present on the distal half of the basal crown face in labial view. The ridge runs from  
228 the distal edge of the apron to the apex of the most distal cusplets and follows the basal edge  
229 outline of the labial crown face.

230 **Remarks:** Although lacking roots, the specimens described here resemble those of a number  
231 of Paleocene ginglymostomatids from Morocco including *G. botmaense* Noubhani and  
232 Cappetta, 1997, *G. erramii* Noubhani and Cappetta, 1997, and *G. pectinatum* Noubhani and  
233 Cappetta, 1997, which were included within the Recent genus *Ginglymostoma*. Yet, these  
234 species have strongly asymmetrical crowns with frequent labial ornament and more than two  
235 pairs of lateral cusplets in lateral teeth. In addition, the specimens described here and other  
236 Moroccan species (*G. botmaense*, *G. erramii*) bear a broad and relatively developed apron,  
237 placed mesially relative to the main cusp. These characters differ from the Recent  
238 *Ginglymostoma* and recall those found in the Recent *Nebrius* species (*N. ferrugineus*). The  
239 labial ridge on the distal half of the basal crown face present in the Togolese species is also

240 present in commissural teeth of the Recent *N. ferrugineus* (Herman et al., 1992). However,  
241 teeth of *N. ferrugineus* have a much more developed (both basally and labially) apron, which  
242 calls to a needed revision of Paleogene ginglymostomatids to elucidate the systematic position  
243 of these taxa. The character combination presents on the crown of the Togolese specimens  
244 (especially the mesio-lingual ridge and the labial ridge on the distal half of the basal crown  
245 face in lateral teeth) distinguish them from all other ginglymostomatids, but the scarcity and  
246 incompleteness of the specimens precludes the formal description of this species.

247

248 Order Lamniformes Berg, 1937

249 Family Serratolamnidae Landemaine, 1991

250 Genus *Serratlamna* Landemaine, 1991

251 *Serratlamna aschersoni* (Stromer, 1905)

252 Fig. 4(A-B)

253 **Material:** One tooth from the glauconitic sandstones.

254 **Description:** This tooth is 24 mm high and is characterized by its broad triangular main cusp  
255 strongly bent to the commissure. A pair of high and broad triangular cusplets is present,  
256 separated from the main cusp by a narrow but deep notch. The cusplets are strongly diverging  
257 and the distal one is curved to the posterior and shows a slight anticlockwise torsion in apical  
258 view. Two additional small external cusplets are present (the mesial one is broken) but  
259 reduced and erect. The main cusp and cusplets have a convex lingual face. The labial face of  
260 the cusplets is less markedly convex. The labial face of the main cusp shows a bulge that  
261 excludes the region near the cutting edges, which are well developed and sharp. The base of  
262 the labial crown face is bulged but does not overhang the root, except below the main cusp.  
263 One large median vertical notch corresponding to a vertical enameloid folding is present on  
264 the base of the main cusp, and some less marked additional ones are present on the margins of

265 the main cusp and below the distal cusplet. The root is moderately high and fairly labio-  
266 lingually compressed. The basal and labial faces are flat, the latter being slightly inclined  
267 labially. The lateral extremities of the root lobes are rounded, whereas the basal edge of the  
268 labial lobe faces are straight and joint medially in a broad triangular concavity in labial view.  
269 A large medio-lingual foramina opens on the angle between the lingual and basal root face,  
270 where there is no lingual bulge.

271 **Remarks:** This species, which has a complex taxonomic history (Case and Cappetta, 1990),  
272 was limited to the Ypresian and Lutetian of Africa and USA but Case (1994) reported this  
273 species from the uppermost Thanetian or lowermost Ypresian of Mississippi (Tuscahoma  
274 Fm.). However, it is unclear whether the specimens from Mississippi come from the Ypresian  
275 Bashi Formation and/or Tuscahoma Formation. In addition, specimens illustrated in Case  
276 (1994) differ from the sub-complete tooth series illustrated by Arambourg (1952) from the  
277 Ypresian of Morocco in having a root with an incipient medio-lingual notch as well as lower  
278 and broader cusplets with the distal one not being curved distally; which may indicate closer  
279 affinities with *Lamna gafsana* White, 1926. Both species were included in the genus  
280 *Serratolamna* by Landemaine (1991), along with the species *O. serrata* Agassiz, 1843, *L.*  
281 *caribaea* Leriche, 1938, *O. amonensis* Cappetta and Case, 1975 and *O. koerti* Stromer 1910,  
282 although the latter two species belong to distinct genera and families (Cappetta 2006, Vullo et  
283 al. 2016). Arambourg (1952, p. 110) also indicated that *S. aschersoni* is present in the  
284 Thanetian of Morocco, which has not been confirmed in Noubhani and Cappetta (1997). In  
285 the absence of illustrations, these Thanetian records were difficult to assess. The probable  
286 upper lateral tooth described here shows typical characters of *S. aschersoni* (morphology and  
287 number of cusplets, labial crown face, medio-central foramina) and represents the first  
288 definite Thanetian record of this species.

289

290 Family Otodontidae Glickman, 1964

291 Genus *Otodus* Agassiz, 1838

292 Subgenus *Otodus* Agassiz, 1838

293 *Otodus (Otodus) obliquus* Agassiz, 1838

294 Fig. 4(C-U)

295 **Material:** 36 mostly complete teeth and several tooth fragments from the glauconitic  
296 sandstones.

297 **Description:** Two morphs were recovered from our samplings. The first morph (Fig. 4(C-I))  
298 comprises incomplete teeth that are large and robust. Incomplete teeth from anterior files can  
299 reach 70 mm high and have an erect triangular main cusp with a strongly convex lingual face  
300 and a moderately convex labial face. The main cusp is relatively wide in its basal region but  
301 narrows toward a sharp apex. Some anteriors show a constriction of the crown base, near the  
302 cusplets. The lower edge of the labial crown face has a characteristic deep triangular notch.  
303 The cutting edges are well developed and smooth. The lingual root face bears a strong lingual  
304 protuberance pierced by a central foramen. Lower lateral teeth are of the same morphology  
305 but smaller with a flat labial crown face and less marked lingual protuberance. In upper  
306 laterals the main cusp is strongly inclined distally; its apex is slightly bent labially. The labial  
307 crown face is somewhat flat with a vertical concavity and a slight basal bulge. The pair of  
308 cusplets is well separated from the main cusp by a notch that is wider in the distal region.  
309 Cusplets are triangular and large, the distal one being more elongate and more diverging. The  
310 lingual collar is wide and the lingual root protuberance is marked, although less developed  
311 than in anteriors. Root lobes are well developed and separated by a broad and deep concavity  
312 of the basal edge of the root in labial view. The distal root lobe has a squared outline, whereas  
313 the mesial one is more rounded. Posterior teeth have the same morphology as laterals, but  
314 more mesio-distally elongate with a lower and more distally bend main cusp. Teeth of the

315 second, smaller morph (Fig. 4(J-U)) do not exceed 25 mm high. Anterior teeth have a narrow  
316 triangular and biconvex main cusp with a more bulged lingual face. A pair of strongly  
317 diverging cusplets is present, separated from the main cusp by a deep but narrow notch. The  
318 cusplets are biconvex with parallel mesial and distal margins in their lower region. The  
319 lingual root protuberance is wide and moderately developed. Root lobes are oriented labially  
320 and separated by a wide concavity. Both mesial and distal lobes are rather thin, the mesial one  
321 being narrower with a sharp extremity. The root lobes are wider and shorter in more lateral  
322 files where cusplets tend to have a concave outer edge. Upper lateral teeth are strongly mesio-  
323 distally developed with distally inclined main cusp showing a flat labial face. Root lobes have  
324 a squared outline and the lingual protuberance is wide. Posterior teeth have the same general  
325 morphology as laterals but with lower and proportionally wider cusplets and markedly square-  
326 shaped root lobes.

327 **Remarks:** This species is rather common in Paleocene-Ypresian samplings from Atlantic and  
328 Tethys oceans. The type specimens were described by Agassiz (1838) and originate from the  
329 Ypresian of Sheppey Island (see also Casier, 1966). Agassiz noted the marked size and  
330 morphological differences among the specimens he figured, which he attributed to  
331 heterodonty (monognathic, dignathic and ontogenic) indicating that large teeth with inclined  
332 main cusp were laterals (pl. 31 Figs. 1-2, 6-7) and that large teeth were from upper files (pl.  
333 31, Fig. 13), whereas more slender ones were from lower files (pl. 31, Figs. 8-9). He noticed  
334 the same variation in smaller teeth, which he concluded belonged to younger individuals (pl.  
335 36 Figs. 26-27), although he suggested that some of them might be upper intermediates of  
336 adult individuals. Subsequent records from numerous localities in the Selandian and Ypresian  
337 of the Cabinda enclave and in the Selandian of Democratic Republic of Congo (Darteville  
338 and Casier, 1959, 1943), from the Ypresian of Belgium (Casier, 1966) as well as from the  
339 upper Paleocene and Ypresian of Morocco (Arambourg, 1952), all include both the small and

340 large morphs and the same distribution is present in the samplings from Togo. Considering  
341 that teeth recovered from both morphs represent virtually all tooth files each, it is indeed  
342 reasonable to consider that the small morph represents teeth of young individuals. However, a  
343 number of records of this species were based exclusively on teeth of the small morph, which  
344 can be sometimes very difficult to differentiate from teeth of Paleocene *Cretolamna* species  
345 (Casier, 1966; Darteville and Casier, 1943). These reports include the Thanetian of France  
346 (Baut and Genault, 1995; Moreau and Mathis, 2000) and the Selandian and Danian of  
347 Alabama (Ehret and Ebersole, 2014), the latter being possibly the oldest record of the species  
348 but the lack of associated larger typical *O. obliquus* teeth make this record tentative. Other  
349 additional records include the Thanetian and Ypresian of Kazakhstan (King et al., 2013),  
350 although Zhelezko and Kozlov (1999) reported several subspecies in the pre-Thanetian  
351 Paleogene and the Ypresian of Uzbekistan (Malyshkina and Ward, 2016 - tooth fragment) and  
352 Romania (Neugeboren, 1851). Agassiz also described *Otodus lanceolatus* (Agassiz, 1843, p.  
353 269, pl. 37, Figs. 19-23) from the base of the ferruginous sands of Kressenberg (probably  
354 Kressenberg Fm, Ypresian), which he acknowledged was possibly synonymous with *O.*  
355 *obliquus* but differed in having larger cusplets and less marked lingual bulge of the crown.  
356 However, it appears that these variations fit the intraspecific variability seen in *O. obliquus*  
357 and so that *O. lanceolatus* is a junior synonym of *O. obliquus*.

358

359 Family Odontaspididae *sensu lato*

360 Genus *Jaekelotodus* Menner, 1928

361 *Jaekelotodus africanus* (Arambourg, 1952)

362 Fig. 5(A-I)

363 1952. *Odontaspis robusta* var. *africana* - Arambourg, p. 64, pl. 6, pl. 7, Figs. 1-6.

364 **Material:** 21 incomplete teeth and several isolated crowns from the glauconitic sandstones.



365 **Description:** Anterior teeth are higher than broad and can reach 30 mm in height. The main  
366 cusp is elongate and strongly sigmoid in profile view with a slight torsion of the apex in some  
367 specimens. The lingual face is strongly convex, whereas the labial face is only weakly convex  
368 to flat with a vertical central concavity on the lower half of the main cusp. The cutting edges  
369 are thin and taper in the basal region, where the main cusp broadens. The basal edge of the  
370 labial crown face is markedly concave and shows no bulge but it overhangs the root at all  
371 points in profile view. Very short and faint vertical folds are present on the basal edge of the  
372 labial crown face. The lingual collar is well marked. Lateral heels are very low and inclined  
373 basally. The heels bear a pair of lateral cusplets, which are short and curved both lingually  
374 and toward the main cusp. The root is bilobate with thin, V-shaped and elongated root  
375 branches. A very developed and relatively narrow lingual root protuberance is crossed by a  
376 deep nutritive groove. Lateral teeth are lower, more massive and mesio-distally developed.  
377 The main cusp is wide, biconvex and curved to the posterior in teeth from the upper files,  
378 whereas it is only slightly bent in lower teeth. The cutting edges are continuous from the apex  
379 of the main cusp to the notch separating the cusplets. The heels are low and short and bear a  
380 pair of lateral cusplets of similar shape and orientation as in anteriors, although smaller and  
381 less inclined towards the main cusp. The root lobes are rounded, labio-lingually compressed  
382 and rather developed but become reduced in more posterior files. The lingual root  
383 protuberance is wide but weakly developed. Posterior teeth are mesio-distally expanded and  
384 broader than high. The main cusp is low, triangular and inclined to the commissure and  
385 lingually. A pair of erect mesial cusplets and one distal cusplet is present, separated from the  
386 main cusp and from each other by a narrow notch. Cusplets adjacent to the main cusp are  
387 broad and low

388 **Remarks:** Previously, *Jaekelotodus africanus* was restricted to the upper Paleocene and  
389 Ypresian of Morocco and Tunisia (Arambourg, 1952, Noubhani and Cappetta, 1997). Teeth

390 of this species differ from those of *J. robustus* (Leriche, 1921) in being less massive and  
391 smaller with more gracile, more elongate and falciform upper lateral teeth. *Jaekelotodus*  
392 *speyeri* (Dartevelle and Casier, 1943) differs in having teeth with two pairs of cusplets as well  
393 as low and triangular main cusp, whereas *J. borystenicus* Glikman, 1964 have smaller and less  
394 elongate teeth with two pairs of cusplets. Neugeboren (1851) described *Lamna cavidens* from  
395 the Ypresian of Romania based on incomplete specimens among which only one (Pl.5, Fig.  
396 58) might belong to an undetermined *Jaekelotodus* species.

397

398 Genus *Palaeohypotodus* Glikman, 1964 *non* Zhelezko, 1989

399 *Palaeohypotodus* sp.

400 Fig. 5(J-K)

401 **Material:** Two incomplete teeth from the glauconitic sandstones.

402 **Description:** The anterior tooth displays a 3 mm high erect main cusp with convex lingual  
403 face and weakly convex labial face with fine incomplete cutting edges. The heels are missing  
404 and the basal edge of the labial crown face bears a line of protruding and erect tubercles that  
405 are more developed below the heels than below the main cusp. The crown of the lateral tooth  
406 displays a main cusp strongly bent distally and two mesial cusplets, well separated from each  
407 other and from the main cusp. The mesial-most cusplet is reduced and weakly inclined,  
408 whereas the second cusplet is more elongate and strongly bent towards the commissure.

409 **Remarks:** By their slender and widely separated cusplets and labial ornament made of  
410 protruding tubercles, the teeth described here can be assigned to the genus *Palaeohypotodus*  
411 but the lack of complete specimens precludes more precise identification.

412

413 Family Lamnidae Müller & Henle, 1838

414 Genus *Isurolamna* Cappetta, 1976

415 *Isurolamna* sp.

416 Fig. 5(L-R)

417 **Material:** Eight incomplete teeth from the glauconitic sandstones

418 **Description:** Anterior teeth can reach 20 mm high and have an elongate and rather narrow  
419 main cusp with a slightly sigmoid profile. The main cusp is nearly straight in presumed lower  
420 anteriors, whereas it is slightly oriented toward the commissure in teeth from upper files. The  
421 crown is smooth with a convex lingual face and flat labial face. The cutting edges are thin and  
422 taper just before reaching the heels, which are extremely low, poorly differentiated and  
423 inclined basally and labially. The basal edge of the labial crown face slightly overhangs the  
424 root by a weak bulge. The root bears a wide and moderately developed lingual protuberance  
425 where a short nutritive groove opens. The root branches are well differentiated and oriented  
426 labially. Teeth from anterolateral files are more asymmetrical with distally oriented main cusp  
427 and more developed distal root branch. Lateral teeth are mesio-distally expanded and lower  
428 with shorter root branches. The presence of cusplets cannot be excluded but the heels of most  
429 of them are poorly preserved.

430 **Remarks:** Two nominal *Isurolamna* species are commonly reported from Paleocene to lower  
431 Eocene deposits. *Isurolamna affinis* (Casier, 1946) was described from the Ypresian of  
432 Belgium and has been reported from various Ypresian and Lutetian localities. *Isurolamna*  
433 *inflata* (Leriche, 1906) was erected as a variety of *Lamna vincenti* (Winkler, 1876a) based on  
434 material from the Lutetian of Belgium with no illustration nor designation of type specimen  
435 and it is possible that *I. affinis* represents a junior synonym of *I. inflata* (Cappetta and Case,  
436 2016; Malyshkina and Ward, 2016). In addition, several reports of *Isurolamna* from  
437 Paleocene localities were assigned to *I. inflata* (Baut and Genault, 1995; Moreau and Mathis,  
438 2000; Noubhani and Cappetta, 1997) but these reports are based on more gracile and smaller  
439 teeth that might represent different species (Cappetta, 2012). The material reported here falls

440 within this latter category, along with specimens reported by Darteville and Casier (1959) as  
441 undetermined Lamniformes (pl. 30, fig. 4) from the lower Selandian of the Cabinda enclave.

442

443 Order Carcharhiniformes Compagno, 1973

444 Family Scyliorhinidae Gill, 1862

445 Genus *Foumtizia* Noubhani & Cappetta, 1997

446 *Foumtizia* aff. *gadaensis* Noubhani & Cappetta, 1997

447 Fig. 6(A-D)

448 **Material:** Six incomplete teeth from the glauconitic sandstones.

449 **Description:** The main cusp is triangular with a sharp apex and broad lower region that is  
450 widely united to high heels. The heels are elongate and oblique and can display up to four  
451 cusplets. The cusplets are low and poorly individualized from each other. The basal edge of  
452 the labial crown face is bulged and strongly concave. The labial bulge is scalloped by very  
453 short vertical folds that are unevenly distributed but mainly restricted to the basal crown edge.

454 **Remarks:** This genus ranges from the Danian (Nilsson, 2003; Noubhani and Cappetta, 1997)  
455 to the Priabonian (Malyshkina, 2006) and comprises seven nominal species. With the  
456 exception of an unnamed species from the Danian of Sweden (Nilsson, 2003), Paleocene  
457 species are restricted to Morocco (Noubhani and Cappetta, 1997) and include *Foumtizia*  
458 *abdouni* (Danian-Thanetian), *F. arba* (Danian), and *F. gadaensis* (Danian). Teeth of these  
459 species differ from those of their Eocene relatives (*F. deschutteri*, *F. pattersoni*, *F.*  
460 *poudenxae*, and *F. zhelezkoi*) by their weaker labial crown ornament. Considering the  
461 preservation of the material recovered from Togo, these specimens cannot be confidently  
462 assigned to any nominal species of this genus. However, the weak ornament restricted to the  
463 basal edge of the labial crown face and the number of cusplets of some lateral teeth of

464 *Foumtizia* sp. indicate close relationships with Paleocene *Foumtizia* species, particularly *F.*  
465 *gadaensis* based on similarities in the numbers of denticles and crown ornament.

466

467 Genus *Premontreia* Cappetta, 1992

468 Subgenus *Oxyscyllium* Noubhani & Cappetta, 1997

469 *Premontreia (Oxyscyllium) subulidens* (Arambourg, 1952)

470 Fig. 6(E-K)

471 For synonymy, see Noubhani & Cappetta (1997) and add:

472 1997. *Premontreia (Oxyscyllium) subulidens* (Arambourg, 1952) - Noubhani & Cappetta, p.

473 55, pl. 21, Figs. 1-11.

474 **Material:** Seven incomplete and several fragmentary teeth from the glauconitic sandstones.

475 **Description:** The main cusp is high, triangular, and fairly slender in anterior teeth. The  
476 lingual face of the main cusp is convex, whereas the labial face is nearly flat. The main cusp  
477 is slightly inclined lingually and flanked by a pair of lateral cusplets. Cusplets are sharp with a  
478 rather narrow and slightly diverging apex. Cusplets are well separated from the main cusp by  
479 a notch that does not interrupt the developed and sharp cutting edges, running from the apex  
480 of the main cusp to the margins of the cusplets. Faint vertical folds can be present but are  
481 restricted to the base of the labial face, below the main cusp and cusplets. The root has a  
482 flared and flat basal face with a wide and developed lingual protuberance. The nutritive  
483 groove is rather wide and shallow except on the lingual protuberance where it is deeper. In  
484 labial view, the margino-lingual edges of the root are strongly concave. A pair of foramina is  
485 present on each margino-lingual face. Lateral teeth have a broader and more distally bent  
486 main cusp with more diverging cusplets and occasionally an incipient second mesial cusplets.  
487 Posterior teeth are lower, with main cusp and cusplets strongly bent to the commissure as well  
488 as more marked and more numerous vertical folds on the basal edge of the labial crown face.

489 **Remarks:** Although incomplete, the teeth reported here display a morphology, ornament and  
490 heterodonty that concur with that of *P. (O.) subulidens*, known from the Danian to lower  
491 Ypresian of Morocco (Arambourg, 1952; Noubhani and Cappetta, 1997) and Ypresian of  
492 Tunisia (Arambourg, 1952). Teeth of this species differ from those of *P. (O.) carinatus*  
493 (Reinecke and Engelhard, 1997) from the Paleocene of Germany and *P. (O.) peypouqueti*  
494 Noubhani and Cappetta, 1997 from the upper Paleocene of Morocco in lacking crown  
495 ornament in anteriors and in having more gracile and elongate cusplets.

496

497 *Premontreia (Oxyscyllium)* sp.

498 Fig. 6(L-O)

499 **Material:** Nine incomplete teeth and numerous isolated cusps from the glauconitic  
500 sandstones.

501 **Description:** Teeth of this species show an elongate and gracile main cusp with a fairly  
502 narrow basal region. The lingual face of the main cusp is convex, whereas the labial face is  
503 reduced and flat. A pair of cusplets, although not preserved, appears well separated from the  
504 main cusp. A second pair of cusplets can be present in lateral teeth (Fig. 6(O)). The heel  
505 region is oriented labially. The basal edge of the labial crown face overhangs the root. Labial  
506 ornament is made of numerous fine but salient subvertical folds at the base of the labial crown  
507 face. The longest folds alternate with shorter folds and reach the base of the main cusp as well  
508 as most of the height of the cusplets. Folds below the cusplets converge towards the cusplets'  
509 apex, whereas those below the main cusp are oriented towards the apex of the latter. None of  
510 the specimens have their root preserved but some teeth show well developed root lobes with  
511 flared marginal extremities that are oriented laterally.

512 **Remarks:** These teeth differ from those of *P. (O.) subulidens* by a more gracile general  
513 morphology, fine but more salient vertical folds on the labial crown face that taper higher on

514 the crown, and by their basal edge of the labial crown face that overhangs the root in profile  
515 view.

516

517 Genus *Porodermoides* Noubhani & Cappetta, 1997

518 *Porodermoides spanios* Noubhani & Cappetta, 1997

519 Fig. 6(P-R)

520 1997. *Porodermoides spanios* nov. sp. - Noubhani & Cappetta, p. 69, pl. 34, Figs. 1-7.

521 **Material:** One incomplete tooth and one tooth fragment from the glauconitic sandstones.

522 **Description:** The incomplete tooth has an elongate, biconvex, and sharp main cusp. The  
523 upper two thirds of main cusp are bent towards the commissure and very slightly inclined  
524 lingually. The distal cusplet is not preserved but the mesial cusplet is rather low, triangular,  
525 and situated slightly more labially than the main cusp in profile view. The cusplet is weakly  
526 diverging and the apex is inclined lingually. The cutting edges run continuously from the apex  
527 of the main cusp to the marginal base of the cusplets. On the main cusp, the cutting edges are  
528 sigmoid in profile view and markedly positioned lingually in the upper half. In profile view,  
529 the base of the labial and marginal crown regions is constricted and slightly overhangs the  
530 root. The crown is smooth with the exception of the slight vertical ridge on the lower half of  
531 the labial cusplet face. The root is broader than high with a slightly convex and heart-shaped  
532 basal face. The root lobes are rounded, moderately developed and oriented mesio-distally. The  
533 labial and marginal faces of the root are strongly flared. The lingual protuberance of the root  
534 is broad and marked. The root lobes are separated by a wide nutritive groove that is deeper in  
535 the area of the lingual protuberance. Rather large marginolingual foramina open in the  
536 depression between the lingual protuberance and the root lobe.

537 **Remarks:** Although scarce, the material recovered here agrees with the morphology of the  
538 type series of *P. spanios*, described from the upper Paleocene of the Ouled-Abdoun Basin in

539 Morocco (Noubhani and Cappetta, 1997). Noubhani and Cappetta (1997) also reported a  
540 single tooth attributed to *P. aff. spanios*, from the Danian of the Ganntour Basin (Morocco),  
541 which differs from *P. spanios* by its strong labial ornament. This morphology was not  
542 recovered in our samplings and the tooth from the Ganntour Basin might correspond to a  
543 second, older *Porodermoides* species.

544

545 Family Triakidae Gray, 1851

546 Genus *Palaeogaleus* Gurr, 1962

547 *Palaeogaleus* sp.

548 Fig. 6(S-V)

549 **Material:** Eleven incomplete teeth and several isolated cusps from the glauconitic sandstones.

550 **Description:** These teeth have a short and broad main cusp that is strongly inclined to the  
551 commissure and do not reach the distal crown edge. The mesial heel is high, broadly convex  
552 with a sharp cutting edge that is not separated from that of the main cusp, where it tapers at  
553 mid height. Distal cusplets (up to three) are broad, triangular and strongly bent to the  
554 commissure. The basal edge of the labial crown face is irregular, sometimes scalloped, and  
555 bears a marked bulge with rare light folds on its marginal faces. The lingual crown face is  
556 smooth.

557 **Remarks:** These teeth show typical features of members of the genus *Palaeogaleus* (short  
558 and strongly distally inclined main cusp, marked labial bulge of the crown, low distal  
559 cusplets). Several *Palaeogaleus* species occur in the Paleocene: *P. brivesi* (Arambourg, 1952),  
560 *P. larachei* Noubhani and Cappetta, 1997, *P. prior* (Arambourg, 1952), and *P. vincenti*  
561 (Daimeries, 1888), as well as unnamed species from the Danian of Denmark (Adolfssen and  
562 Ward, 2015, 2014) and Sweden (Nilsson, 2003). Teeth of *Palaeogaleus* sp. differ from those  
563 of *P. prior*, *P. brivesi*, *P. vincenti*, and the specimens of Denmark and Sweden in the absence



564 of mesial cusplets. The Togolese material resembles the less ornamented specimens of *P.*  
565 *larachei*, but the latter have less developed distal cusplet and the preservation of the material  
566 reported here precludes its precise specific attribution.

567

568 Genus *Galeorhinus* Blainville, 1816

569 *Galeorhinus mesetaensis* Noubhani & Cappetta, 1997

570 Fig. 6(W-X)

571 1997. *Galeorhinus mesetaensis* nov. sp. - Noubhani & Cappetta, p. 80, pl. 43, Figs. 1-8 & pl.  
572 44, Fig. 1.

573 **Material:** 24 incomplete teeth and several tooth fragments from the glauconitic sandstones  
574 and two incomplete teeth from the glauconitic limestones.

575 **Description:** Teeth are generally broader than high except in anterior files where they are  
576 slightly higher than wide. The main cusp is thin, elongate, and bent towards the commissure  
577 with a convex lingual face and a slightly convex to nearly flat labial face. The mesial cutting  
578 edge of the main cusp is sharp, rectilinear to sigmoid in labial/lingual view, and continuous  
579 with the mesial heel. The mesial heel is sharp, oblique and moderately high, except in  
580 posterior files where it is more developed. The mesial heel has an irregular cutting edge. The  
581 distal cutting edge of the main cusp is convex and separated from the distal heel by a notch.  
582 The distal heel is more oblique and bears generally three and occasionally four cusplets  
583 oriented distally and decreasing in size toward the base of the crown. The basal edge of the  
584 labial crown face is concave. The lower part of the labial crown face is developed labially,  
585 especially below the heels where a strong bulge overhangs the root. These marginal labial  
586 bulges are covered with short, discontinuous, and flexuous folds that do not reach the heels.  
587 Fine vertical folds are present on lingual face but restricted to the area below the mesial heel.  
588 The root is holaulacorhize and low with a flat basal face and a slightly flared labial edge. The

589 marginal faces of the lingual root edge are concave in basal view and separated by a narrow  
590 lingual protuberance.

591 **Remarks:** The general morphology, number of cusplets, labial bulge of the basal crown edge  
592 below the heels and crown ornament all agree with the morphology of the type series of *G.*  
593 *mesetaensis* described from the upper Paleocene of the Ouled Abdoun Basin in Morocco  
594 (Noubhani and Cappetta, 1997). This species was also reported from the Danian of the  
595 Ganntour Basin (Noubhani and Cappetta, 1997). This is the first record of this species outside  
596 Morocco.

597

598 *Galeorhinus* sp.

599 Fig. 6(Y-A')

600 ? 1994. *Galeorhinus affinis* Probst - Case, p. 117, pl. 9, Figs. 186-194.

601 **Material:** Three teeth from the glauconitic sandstones.

602 **Description:** The main cusp is broad, inclined to the commissure and biconvex with slightly  
603 convex mesial and distal cutting edges. The mesial heel is oblique, low, and bears two to three  
604 incipient cusplets on its mesial half. The distal heel bears two wide triangular cusplets close to  
605 the main cusp and two low and broad incipient cusplets near the distal crown edge. The basal  
606 edge of the labial crown face is concave and bulged with short and coarse vertical folds.  
607 Slight vertical folds are present on the lingual face, below the mesial heel. The root is  
608 moderately high with a wide but poorly developed lingual protuberance.

609 **Remarks:** Teeth of this species resemble those of *G. mesetaensis* but differ in being larger  
610 and more robust with a wider and less sigmoid main cusp. Teeth of *Galeorhinus* sp. also have  
611 a higher root, less flared basal edge of labial crown face with shorter and coarser labial  
612 ornament, as well as finer lingual folds. In addition, the mesial heel is lower with  
613 individualized cusplets in *Galeorhinus* sp. whereas the mesial heel is only irregular in *G.*

614 *mesetaensis*. Case (1994) reported teeth from the Tuschoama and Bashi Formations  
615 (respectively uppermost Thanetian/lowermost Ypresian and Ypresian) of Mississippi that he  
616 assigned to the species ‘*Galeorhinus*’ *affinis* (Probst, 1878). However, this species should be  
617 included in the genus *Chaenogaleus* and is restricted to the Miocene. The morphology of  
618 specimens from Mississippi specimens closely resembles that of the material reported here  
619 and might be conspecific or closely-related.

620

621 Genus *Triakis* Müller & Henle, 1838

622 *Triakis* sp.

623 Fig. 7(A-C)

624 **Material:** Three incomplete teeth from the glauconitic sandstones.

625 **Description:** Anterior teeth are slightly higher than broad with a relatively broad and  
626 triangular main cusp bent to the commisure. The main cusp has a flat or slightly convex  
627 labial face and is flanked by pair of broad and low cusplets. Cusplets are well separated from  
628 the main cusp by a notch, although the latter occurs high on the crown. The mesial cusplet is  
629 lower and more erect than the distal one. The basal edge of the labial crown face is concave  
630 and overhangs the root. The labial crown faces is ornamented by strong vertical ridges that are  
631 very pronounced and blade-like on the basal edge. These ridges cover the labial face of the  
632 cusplets but taper towards half-height of the main cusp. Slight lingual vertical folds are  
633 present on the cusplets and at the base of the main cusp. More lateral teeth are slightly broader  
634 than high with developed oblique heels marginal to the pair of cusplets. Labial ornamentation  
635 runs up to the apex of the crown.

636 **Remarks:** The morphology of teeth of this species, with broad and low cusplets that are  
637 united to the main cusp on a large portion of the crown and strong labial ridges associated  
638 with lingual ornament, indicates close affinities with the genus *Triakis*. Although a number of

639 triakid species are known from the Paleocene, *Triakis*-like taxa are seldom during this time  
640 interval. Teeth of *Triakis antunesi* Noubhani and Cappetta, 1997 (upper Paleocene of  
641 Morocco) resemble those of the species described here but differ in having two pairs of  
642 cusplets and a less regular labial ornament on the main cusp. An unnamed species was  
643 reported from the Danian of Sweden (Nilsson, 2003) based on fragmentary specimens; its  
644 teeth display a comparable morphology to the Togolese ones but with more developed cutting  
645 edges and scarcer labial ridges.

646

647 **Triakidae ? indet.**

648 Fig. 7(D-J)

649 1997. *Scyliorhinus* sp. - Noubhani & Cappetta, p. 62, pl. 28, Fig. 7.

650 **Material:** Five incomplete teeth from the glauconitic sandstones.

651 **Description:** The crown is low with a stubby and lingually oriented main cusp as well as a  
652 labially developed basal region of the labial face. The cutting edges are marked and  
653 continuous with oblique heels that bear a pair of incipient cusplets weakly individualized from  
654 the main cusp. The basal edge of the labial crown face is strongly concave in its median  
655 region, whereas its areas are markedly convex. The lingual crown face is bulbous below the  
656 main cusp and cusplets. The labial ornament consists of strong vertical ridges that taper near  
657 the heels and the base of the main cusp. The lingual ornament is composed of finer ridges  
658 vertically oriented below the heels and toward the apex of the crown on the main cusp, where  
659 they can be flexuous near the basal crown edge.

660 **Remarks:** These teeth share characters with those of Recent triakids with crushing dentitions  
661 (*Mustelus* and *Scylliogaleus*) including a low and wide main cusp, a developed basal region of  
662 the labial crown face, and the presence of labial and lingual ornamentation. They differ from  
663 Recent triakids, however, by the presence of a concave basal edge of the labial crown face,

664 which is devoid of apron, and by the absence of uvula. Although the genus *Mustelus* is  
665 present in the Thanetian (Baut and Genault, 1995; Moreau and Mathis, 2000; Reinecke and  
666 Engelhard, 1997), the material reported here probably belongs to another unnamed taxon.  
667 Noubhani and Cappetta (1997) reported a single incomplete tooth as *Scyliorhinus* sp. from the  
668 Danian of Morocco that compares well with the Togolese material and may be congeneric, if  
669 not conspecific.

670

671 Family Carcharhinidae Jordan & Evermann, 1896

672 Genus *Abdounia* Cappetta, 1980

673 *Abdounia africana* (Arambourg, 1952)

674 Fig. 7(K-T)

675 1952. *Scyliorhinus africanus* nov. sp. - Arambourg, p. 126, pl. 23, Figs. 60-83.

676 1997. *Abdounia africana* Arambourg - Noubhani & Cappetta, p. 89, pl. 48, Figs. 1-13.

677 **Material:** Four incomplete and 16 incomplete teeth from the glauconitic sandstones.

678 **Description:** Anterior teeth are higher than wide with an erect main cusp inclined lingually,  
679 strongly convex lingual face, and a nearly flat labial face. The heels are oblique and bear a  
680 pair of fairly broad triangular cusplets, not reaching the lingually oriented lateral extremities  
681 of the heels, where an incipient cusplet can be present on the mesial edge. The cusplets are  
682 diverging and slightly protrude labially relative to the main cusp. These are well separated  
683 from the main cusp by a wide concavity, although both are largely united at their base. The  
684 base of the labial crown face slightly overhangs the root and is rectilinear to slightly concave  
685 below the main cusp. The root is high and bilobate with flared basal edge of the labial face.  
686 The distal root lobe is narrower and more elongate than the mesial one. A broad but short  
687 medio-lingual protuberance is present and divided by a wide nutritive groove that runs over  
688 the entire basal root face. Two foramina are present on each concave margino-lingual face.

689 The antero-lateral teeth are of similar morphology but as high as wide and occasionally bear a  
690 second pair of cusplets. Lateral teeth are more mesio-distally elongate with strongly distally  
691 inclined main cusp and a pair of lower, broader and more diverging cusplets that are less  
692 protruding labially. Latero-posterior teeth resemble laterals but are lower and can bear labial  
693 and lingual ornament on the lower part of the crown, which consists of fine vertical folds.  
694 Symphysial teeth are small, symmetrical with a short heel, a pair of low triangular cusplets,  
695 and a root with short lobes flared labially.

696 **Remarks:** This species was so far restricted to the Paleocene of Morocco (Arambourg, 1952;  
697 Noubhani and Cappetta, 1997). *Abdounia beaugei* (Arambourg, 1935) is known from the  
698 uppermost Thanetian/lowermost Ypresian (Case, 1994) to the Upper Eocene (Leder, 2013). It  
699 is represented by teeth of comparable general morphology, which differ from those of *A.*  
700 *africana* by their larger size and more common presence of two and often three lateral  
701 cusplets. Other records of Paleocene *Abdounia* include a taxon reported as *A. minutissima*  
702 (Winkler, 1874) from the Thanetian of France (Baut and Genault, 1995). However, the  
703 morphology of teeth illustrated by Baut and Genault (1995) does not agree with the type  
704 material from Belgium and one tooth (pl. 9, Fig. 5) resembles teeth of *A. africana*. *Abdounia*  
705 *biauriculata* (Casier, 1946) was reported from the Thanetian of France (Moreau and Mathis,  
706 2000), but the material was not illustrated, and this species seems to be restricted to the  
707 Ypresian (Casier, 1946) and Lutetian (Cappetta and Case, 2016).

708

709 Genus *Physogaleus* Cappetta, 1980

710 *Physogaleus* sp.

711 Fig. 7(U-Y)

712 1995. *Physogaleus secundus* (Winkler) - Baut & Genault, p. 208, pl. 9, Figs. 3-4.

713 **Material:** Two complete and numerous incomplete teeth from the glauconitic sandstones.

714 **Description:** Teeth are wider than high, not exceeding 3.5 mm wide. The main cusp is  
715 biconvex, but more developed lingually. The main cusp is lingually inclined and strongly bent  
716 towards the commissure with a marked sigmoid profile. The mesial heel is high and oblique,  
717 weakly separated from the main cusp, and with a blunt mesial edge. The distal heel bears two  
718 poorly differentiated cusplets that are oriented distally and well separated from the main cusp  
719 by a narrow and deep notch. The mesial cusplet is low and broader than the second, which is  
720 incipient. The distal edge of the distal heel is lingually oriented. The base of the labial crown  
721 face slightly overhangs the root/crown edge in the marginal faces of lateral teeth. The root is  
722 fairly low with a slightly flared and flat basal face, except on the extremities of the root lobes  
723 where it is convex and apically oriented. The lingual protuberance is developed and broad. A  
724 large nutritive groove is present on the basal face. The groove is deeper and narrower on the  
725 lingual region of the labial face, where a central foramen opens. The root lobes are laterally  
726 oriented with lingually curved extremities. The margino-lingual edges of the basal root face  
727 are strongly concave. Each margino-lingual root face bears four foramina that are lined up  
728 below the crown/root edge, the distal ones being more compressed, whereas mesial margino-  
729 lingual foramina often confer a scalloped basal edge. Several foramina open on the protruding  
730 lower half the labial root face, the largest foramen being close to the concavity of the nutritive  
731 groove in labial view.

732 **Remarks:** The morphology of these teeth is close to that of *P. secundus* (Winkler, 1876b) but  
733 much smaller with less cusplets on the distal heel, wider nutritive groove, and more marked  
734 concavities on the margino-lingual root edges in basal view. Teeth attributed to *P. secundus*  
735 from the Thanetian of France (Baut and Genault, 1995) closely resemble those of  
736 *Physogaleus* sp. described here, whereas a subsequent report from another French Thanetian  
737 locality by Moreau and Mathis (2000) lacks illustrations and cannot be assessed. This  
738 unnamed taxon represents one of the oldest record of the genus *Physogaleus*, along with

739 *Physogaleus americanus* Case, 1994 (uppermost Thanetian/lowermost Ypresian and Ypresian  
740 of Mississippi), which differs from teeth of most Paleocene and early Eocene species by its  
741 larger size and the presence of cusplets on both mesial and distal edges.

742

743 Superorder Batomorphii Cappetta, 1980

744 Order Rhinopristiformes Naylor, Caira, Jensen, Rosana, Straube & Lakner, 2012

745 Family Rhinobatidae Müller & Henle, 1838

746 Genus *Pseudobatos* Last, Séret & Naylor, 2016

747 *Pseudobatos matzensis* (Baut & Genault, 1995) comb. nov.

748 Fig. 7(Z-B')

749 1995. '*Rhinobatos*' *matzensis* nov. sp. - Baut & Genault; p. 211, pl. 10, Figs. 3-5.

750 **Material:** Four teeth from the glauconitic sandstones and one tooth from the glauconitic  
751 limestone.

752 **Description:** Anterior teeth are as high as wide and do not reach more than 1 mm. Teeth are  
753 of crushing morphology with convex labial face separated from the lingual face by a labially  
754 convex transverse crest, which is weak and does not reach the marginal angles. The lingual  
755 face bears a large median uvula, which is as high as wide and of irregular outline. The median  
756 uvula is weakly protruding lingually and faintly separated from the lateral uvulae by short and  
757 narrow notches. Lateral uvulae are little developed, weakly individualized from the rest of the  
758 crown, and connected to the marginal angles by a straight to slightly concave edge. The labial  
759 face has a triangular outline in occlusal view with rectilinear marginal edges that reach a weak  
760 apron with a straight labial edge. The root is rather high, faintly lingually projected, and  
761 holaulacorhize with a large nutritive groove, which is pierced by a large central and several  
762 paracentral foramina. The basal face of each root lobe is flat and inclined towards the median  
763 groove. The root lobes are triangular in basal view and devoid of individualized lingual



764 expansions. A pair of margino-lingual foramen is present in depressions located below the  
765 notches separating the median and lateral uvulae. Posterior teeth are smaller, with a flatter  
766 labial face, and more reduced lateral uvulae.

767 **Remarks:** The morphology of the material reported here agrees with that of the type  
768 specimens from the Late Thanetian of Paris Basin (Bracheux sands), which was previously  
769 the only occurrence of this species. Similar heterodonty is found between the French and  
770 Togolese specimens despite the low number of specimens in our samplings. Baut and Genault  
771 (1995) attributed the small-sized teeth with less developed lateral uvulae to juvenile  
772 individuals but these are likely from posterior files. The species *P. matzensis* comb. nov. was  
773 tentatively included in the genus '*Rhinobatos*' in the original description. The genus  
774 *Rhinobatos* has commonly been used for a variety of fossil taxa of undetermined affinities  
775 within Rhinopristiformes (and the same situation prevailed for living species until the revision  
776 of this clade by Last et al. (2016)). This was mainly due to the lack of data on tooth  
777 morphology in living taxa, which was restricted to line drawings of some species in Cappetta  
778 (1980). Subsequent illustrations of teeth of some living members of this order (Cappetta et al.,  
779 2016; Herman et al., 1997) enabled to better evaluate the morphological diversity of their  
780 teeth, although that of some genera (*Rhynchorhina*, *Acroteriobatus*) remains to be  
781 investigated (Guinot et al., 2018). Based on current knowledge, teeth of *P. matzensis* comb.  
782 nov. differ from the only living *Rhinobatos* species whose tooth morphology has been  
783 adequately illustrated (*R. rhinobatos*) in having a higher root, less individualized lingual  
784 expansions of the root lobes, labially convex transverse crest, and lateral uvulae less  
785 individualized from the median uvula. *Glaucostegus* teeth (*G. cemiculus*) are bulbous and  
786 much larger than those of *P. matzensis* comb. nov. with more developed and generally  
787 diverging lateral uvulae as well as more developed and rounded apron and marked lingual  
788 expansions of the root lobes. Teeth of living *Trygonorrhina* have a higher root than *P.*

789 *matzensis* comb. nov. with wider median uvula and flatten to concave lingual crown face  
790 bearing ornament. Teeth of *P. matzensis* comb. nov. share numerous characters with those of  
791 *Pseudobatos* (species *P. productus*) (Cappetta, 1980, 2012), including a labially convex  
792 transverse crest, lateral uvulae weakly developed and separated from the median uvula by a  
793 notch, and a root with triangular lobes devoid of individualized lingual expansions of the  
794 lobes. Considering the greater similarities in tooth morphology between the Thanetian species  
795 and those of the living *P. productus* in comparison with other rhinopristiforms, this species  
796 should be included in the genus *Pseudobatos*. However, this attribution needs to be confirmed  
797 by improving knowledge on tooth morphology of living rhinopristiforms, especially for the  
798 genera *Rhynchorhina* and *Acroteriobatus*.

799

800 Order Myliobatiformes Compagno, 1973

801 Family Dasyatoidea indet.

802 Genus *Arechia* Cappetta, 1983

803 *Arechia* sp.

804 Fig. 8(A)

805 **Material:** A single incomplete tooth from the glauconitic sandstones.

806 **Description:** The crown is composed of a reduced, flat and weakly basally inclined labial face  
807 with a convex labial edge and concave margin-labial borders. The lingual face is high with  
808 slightly concave margino-lingual faces. A high and thick transverse crest separates the lingual  
809 and labial faces but does not reach the blunt and somewhat flared marginal angles. The root is  
810 incomplete; it is lingually placed and is overhung labially by the crown in occlusal view.

811 Numerous foramina open on the labial root face.

812 **Remarks:** This genus is known by the type species *A. arambourgi* Cappetta, 1983 from the  
813 Ypresian of Morocco (Cappetta, 1983; Noubhani and Cappetta, 1997) and from other

814 unpublished reports from the Ypresian of Senegal and Mississippi (Cappetta, 2012), as well as  
815 from unfigured material from the Lutetian of Togo (Cappetta and Traverse, 1988) and  
816 Morocco (Tabuce et al., 2005). The fragmentary crown recovered here bears a typical broad  
817 and well-developed transverse crest not reaching the marginal angles, a developed and  
818 concave lingual crown face, as well as a short and basally inclined labial face. This specimen  
819 represents the oldest record of the genus.

820

821 Genus *Coupatezia* Cappetta, 1982

822 *Coupatezia* sp.

823 Fig. 8(B-H)

824 **Material:** Three incomplete teeth and one tooth fragment from the glauconitic sandstones.

825 **Description:** Female teeth (Fig. 8(B-F)) have a mesio-distally elongate and high crown and  
826 do not exceed 2 mm wide. The occlusal face is kidney-shaped and lingually bordered by a  
827 broad and marked transverse crest. The transverse crest is sub-rectilinear in its median portion  
828 and convex on its margins where it reaches the labial edges. The marginal angles are broad  
829 and blunt. The labial edge of the occlusal face strongly overhangs the root and is bevelled in  
830 profile view. The median region of the labial edge of the occlusal face is strongly concave and  
831 flanked by a pair of margino-labial angles that protrude labially. The lingual half of the  
832 occlusal face is strongly depressed and ornamented by fine and dense enameloid irregularities.  
833 The labial half of the occlusal face bears a high and irregular transverse ridge, which connects  
834 to the lingually positioned transverse crest and does not follow the labial edge of the occlusal  
835 face. This labial transverse ridge can bifurcate labially into several randomly arranged folds  
836 where concavities are occupied by similar ornament to the depression of the lingual half of the  
837 occlusal face. The labial edge of the occlusal face is smooth. The lingual crown face is high,  
838 smooth, and slightly flared close to the occlusal face. The lingual crown face is convex

839 transversally but bears a pair of slight concavities on the margino-lingual faces. The basal  
840 edge of the lingual crown face is straight to slightly convex and bears a narrow and shallow  
841 median concavity. The male tooth (Fig. 8(G-H)) is as high as wide with a heart-shaped  
842 occlusal face. The centre of the occlusal face is only slightly depressed and devoid of  
843 ornament. The depression is border labially by a fine discontinuous ridge that follows the  
844 labial outline of the crown and lingually by a broad transverse crest (incomplete). The lingual  
845 crown face is flared in its lower region and bears a wide and shallow median concavity on its  
846 basal edge.

847 **Remarks:** Female teeth are very similar to those of the species *Coupatezia woutersi* Cappetta,  
848 1982 but have a higher and more developed lingual crown face and a smooth and regular  
849 labial crown edge, whereas it is scalloped in *C. woutersi*. The male tooth described here also  
850 differs from those of *C. woutersi* by its reduced ornament of the labial crown face. *Coupatezia*  
851 *woutersi* is restricted to the Lutetian; other reports from the Thanetian and Ypresian of  
852 Mississippi (Case, 1994) and Selandian of Maryland (Ward and Wiest, 1990) are based on  
853 teeth that do not match the original description of the species (and might be closer to *C.*  
854 *boujoi*) and unfigured material, respectively. Teeth of *Coupatezia* sp. resemble those of *C.*  
855 *boujoi* (middle Ypresian of Morocco) in both size and general shape. However, lateral female  
856 teeth of the species described here differ in their much coarser ornament that occupies the  
857 labial half of the occlusal face, whereas in the Moroccan species this consists of a fine –  
858 sometimes bifurcating – ridge that follows the labial edge of the occlusal face. The incomplete  
859 tooth attributed to a male individual strongly resembles, based on the available characters (i.e.  
860 only crown), those of the type material of *C. boujoi* and only differs by its smaller size.

861

862 Genus *Dasyatis* Rafinesque, 1810

863 '*Dasyatis*' *sudrei* Cappetta, 1972

864 Fig. 8(I-N)

865 **Material:** Four incomplete teeth from the glauconitic sandstones.

866 **Description:** These dasytoid teeth are cuspidate and do not exceed 1 mm in width. The  
867 crown is labio-lingually compressed and mesio-distally elongate and overhangs the crown in  
868 all points in labial view. The labial crown face bears a marked median concavity bounded  
869 lingually by a salient transverse crest that tappers just before reaching the marginal angles,  
870 where the crest is oriented labially. The median depression is bordered labially by a ridge that  
871 follows the slightly convex and irregular labial outline of the crown. Ornamentation is present  
872 on the labial crown face and varies from strongly reticulate mostly near the edges of the  
873 depression to very finely reticulate. The lingual crown face bears a strong bulge underlying  
874 the transverse crest and overhanging the lower part of the lingual face in occlusal view. The  
875 bulge is sharp in its lower edge and bears the same ornament as on the labial face with  
876 stronger ridges located near the base of the bulge. A developed median cusp originates from  
877 the lingual crown face, below the transverse crest. The cusp is lingually oriented with a  
878 triangular profile that comprises the basal edge of the lingual face and the transverse crest at its  
879 base. The main cusp is mesio-distally compressed with a fine longitudinal ridge, which  
880 originates from the transverse crest and almost reaches the apex. The root is low and  
881 comprises two triangular and mesio-distally elongate lobes separated by a wide and deep  
882 notch where a median foramen opens.

883 **Remarks:** The teeth described here show a combination of characters including the main cusp  
884 originating from the lingual face (below the transverse crest), lingual and labial reticulate  
885 ornamentation, transverse crest morphology and typical profile outline that conform to the  
886 description of '*D. sudrei*' from the Thanetian of Niger (Cappetta, 1972). Records of this  
887 species have previously been restricted to the type locality as well as undescribed specimens  
888 from the Thanetian of Senegal (pers. com. S. Adnet and pers. obs. G. Guinot) and the material

889 from Togo suggests that '*D. 'sudrei*' was probably widespread in the Thanetian of western  
890 Africa.

891

892 '*Dasyatis*' sp.

893 Fig. 8(O-Q)

894 **Material:** Four incomplete teeth from the glauconitic sandstones.

895 **Description:** Non-cuspidate tooth crowns (Fig. 8(O-P)) are globular with a triangular and  
896 narrow lower region of the lingual face that is overhung by the rest of the crown in occlusal  
897 view. The margino-lingual faces are concave and separated by a narrow and vertical median  
898 ridge. The upper portion of the lingual crown face and the labial face are bulbous and  
899 ornamented by short irregular folds randomly oriented on the labial face but tend to be  
900 vertical on the lingual face. The labial and lingual faces can be separated by a faint and low  
901 transverse crest, which is absent in some teeth. The marginal angles are acute; the labial  
902 crown edge is convex with a broad and short median expansion. One cuspidate tooth (Fig.  
903 8(Q)) shows the same general morphology but differs in having a more marked transverse  
904 crest that is V-shaped in occlusal view, no lingual ornament and very scarce labial folds.

905 **Remarks:** These teeth show a typical dasyatid crown morphology and comparable sexual  
906 heterodonty. However, considering the Paleocene diversity of this group and the poor  
907 preservation of the material, it is not possible to more precisely identify this taxon.

908

909 Family Mobulidae Gill, 1893

910 Genus *Burnhamia* Cappetta, 1976

911 *Burnhamia* sp.

912 Fig. 8(U-W)

913 **Material:** One fragmentary tooth from the glauconitic sandstones.

914 **Description:** This incomplete crown is mesiodistally elongate and labiolingually compressed.  
915 The crown is displaced lingually relative to the root. The occlusal face is V-shaped in cross  
916 section with a shorter and more abrupt lingual side. The occlusal face has an irregular surface  
917 that bears a granulose ornamentation. The lateral extremity of the occlusal face is triangular  
918 and oblique. The lingual crown face is convex in its upper region but strongly concave near  
919 the basal edge where short, strongly developed and irregular folds are present. The labial  
920 crown face is flat with irregular vertical folds.

921 **Remarks:** Underwood et al. (2017) erected the genus *Sulcidens* for the species *Myliobatis*  
922 *sulcidens* Darteville and Casier, 1943 known from the Paleocene and Ypresian of Morocco  
923 and Cabinda Enclave. Differences between *Sulcidens* and *Burnhamia*, both known from  
924 associated tooth sets, are tenuous but the dentition of the former is more *Myliobatis*-like with  
925 large median teeth and very mesio-distally compressed laterals, whereas *Burhamia* species  
926 show a *Rhinoptera*-like gradation of tooth width away from the symphysis (Underwood et al.,  
927 2017). Separating species of these two genera on the basis of scarce and fragmentary material  
928 is difficult but teeth of *Sulcidens* also differ from those of *Burnhamia* by the presence of an  
929 antero-posterior notch on the lateral extremities of the occlusal crown face and by a  
930 symmetrical depression on the occlusal face with lingual and labial sides of the depression  
931 being of equal size. The tooth fragment recovered here lacks these characters and is therefore  
932 attributed to an undetermined *Burnhamia* species.

933

934 Family ?Mobulidae Gill, 1893

935 Genus *Archaeomanta* Herman, 1979

936 *Archaeomanta* sp.

937 Figs 8(R-T)

938 **Material:** A single tooth from the glauconitic sandstones.

939 **Description:** This tooth is less than 2.5 mm high and comprises a high lingually inclined main  
940 cusp and short incomplete root. The main cusp shows an erect lower half that is labio-  
941 lingually developed and mesio-distally compressed (especially in its labial part), and  
942 separated from the root by a collar. The labial and lingual edges of the lower half of the main  
943 cusp are slightly convex in profile view. The upper half of the cusp is strongly bent lingually,  
944 which confers a sharp labial angle in profile view. A fine labial cutting edge runs from the  
945 labial angle to the apex of the cusp where a finer lingual cutting edge originates and tapers  
946 before the concavity on the lingual crown face in profile view. The crown is damaged but its  
947 preserved lingual portion indicates that it is short and slightly wider than the crown.

948 **Remarks:** The genus *Archaeomanta* comprises three nominal species: *A. melenhorsti*  
949 Herman, 1979 (the type species) was described from the Ypresian of Belgium and also  
950 reported from the Ypresian of Morocco (Noubhani and Cappetta, 1997) and Mississippi  
951 (Case, 1994), as well as from the Lutetian of Belgium (Herman, 1979), Uzbekistan (Case et  
952 al., 1996) and England (Kemp et al., 1990). *Archaeomanta priemi* Herman, 1979 was  
953 described from the upper Paleocene of Morocco (Herman, 1979; Noubhani and Cappetta,  
954 1997) and *A. hermani* Kozlov, 2001 from the Bartonian of Kazakhstan. In addition, numerous  
955 reports of this genus have been made including in the Danian-Selandian of Morocco  
956 (Noubhani and Cappetta, 1997), Lutetian of Jordan (Cappetta et al., 2000), France (Dutheil,  
957 1997), Togo (Cappetta and Traverse, 1988), Guinea-Bissau (Cappetta, 2012) as well as in the  
958 Priabonian of Western Sahara (Adnet et al., 2010), and Egypt (Underwood et al., 2011). The  
959 intra-specific dental variation seems rather strong in *Archaeomanta*, which makes it difficult  
960 to separate species, especially considering the number of published records without  
961 illustrations. Furthermore, the higher-level systematics of this genus is problematic because,  
962 although resembling teeth of some filter-feeding mobulids, *Archaeomanta* teeth show a well-  
963 developed pulp cavity extending to the apex of the cusp (Underwood et al., 2011), which



964 would rather indicate affinities with Rajiformes. By its rather marked mesio-distal  
965 compression, strong lingual inclination of the cusp and rather pronounced baso-labial angle of  
966 the crown, the tooth described here is close to those of *A. melenhorsti* but also bears  
967 characters present in teeth of *A. priemi* (collar at the base crown/root edge). However, it  
968 differs from the latter species by its smaller size and higher lower half of the crown.  
969 Considering the scarcity and preservation of the material from Togo and the lack of  
970 knowledge on systematics of the genus *Archaeomanta*, it is preferable to leave the presence  
971 species in open nomenclature.

972

973 Family Myliobatidae Bonaparte, 1838

974 Genus *Myliobatis* Cuvier, 1816

975 '*Myliobatis*' *dixoni* Agassiz, 1843

976 Fig. 8(X-Z)

977 **Material:** Several incomplete teeth from the glauconitic sandstones.

978 **Description:** Teeth are of crushing type with concave labial edge and convex lingual edge in  
979 occlusal view with triangular lateral extremities. Labial and lingual curvings are more marked  
980 in upper teeth than in those from lower files. The labial crown face is labially inclined and  
981 overhangs the lingually displaced root. Ornament on the labial crown face consists of rather  
982 large and irregular vertical folds. The lingual crown face is labially inclined with numerous  
983 fine vertical folds and a horizontal bulge is present at the basal edge of the lingual face. This  
984 bulge is thin and undulating, following the shape of underlying root branches. The root is  
985 typically polyaulacorhize with numerous parallel branches of similar size except for the two  
986 lateralmost, which are triangular in basal view.

987 **Remarks:** The material described here, although fragmentary, agrees with the morphology of  
988 the *Myliobatis dixoni* species complex (Baut and Genault, 1995), which is known from a

989 variety of localities worldwide and is in need of revision. *Myliobatis dixonii* was reported by  
990 Stromer (1910) from the limestones of Adabion.

991

992 Genus *Aetomylaeus* Garman, 1908

993 *Aetomylaeus* sp.

994 Fig. 8(D'-F')

995 **Material:** Several incomplete teeth from the glauconitic sandstones and one incomplete tooth  
996 from the glauconitic limestone.

997 **Description:** This large median myliobatid tooth fragment is labio-lingually compressed and  
998 mesio-distally elongate. Judging from the crown morphology, the preserved portion of the  
999 specimen represents less than half of the complete tooth size; it measures 45 mm mesio-  
1000 distally. The crown is thicker at its center than at the edges and has a convex occlusal face in  
1001 labial view. The lateral crown extremities are rounded and the lingual crown face is high,  
1002 oblique, and overhangs the root. The lingual crown face bears worn irregular vertical wrinkles  
1003 and is bordered by a fine basal bulge. The labial crown face bears fine vertical folds and is  
1004 lower than the lingual face and abrupt, only slightly overhanging the root in occlusal view.  
1005 The polyaulacorhize root is of similar height from one lateral margin to the other. Root  
1006 branches are incompletely preserved on both the basal and lingual faces. The labial root face  
1007 is high and bears narrow vertical notches.

1008 **Remarks:** The crown of teeth from the median file is thicker at its center than at the edges,  
1009 which is typical of *Aetomylaeus*. This tooth morphology does not match any published  
1010 Paleogene myliobatid taxon and may represent one of the earliest reports of the genus,  
1011 although some species included in *Myliobatis* might belong to *Aetomylaeus* (Cappetta, 2012).  
1012 The specimens reported here differ from unworn *M. dixonii* teeth by their much larger size: the  
1013 illustrated specimen although representing about half the length of the original tooth is much

1014 larger (4.8 cm) than the largest complete *M. dixonii* teeth. *Aetomylaeus* sp. further differs from  
1015 *M. dixonii* by its much higher root and basally inclined distal region of the crown and root.

1016

1017 Family Rhinopteridae Jordan & Evermann, 1896

1018 Genus *Rhinoptera* Cuvier, 1829

1019 *Rhinoptera* cf. *raeburni* White, 1934

1020 Fig. 8(A'-C')

1021 **Material:** One tooth from the glauconitic sandstones.

1022 **Description:** This median tooth is 18mm wide and shows strong labio-lingual compression  
1023 and mesio-distal expansion. The crown is high and of constant thickness from one lateral  
1024 extremity to the other in lingual view. Lateral extremities are triangular in occlusal view and  
1025 slightly labially oriented. The occlusal face is flat and worn with no ornament. The lingual  
1026 face is flat and oblique with a marked lingual root overhang in profile/occlusal views. The  
1027 lingual crown face bears strong vertical folds that widen and taper near the occlusal edge. A  
1028 protruding basal vertical bulge is present on the lingual crown face, the base of which is  
1029 concave in profile view except near the lateral extremities where a vertical fold reaches the  
1030 basal bulge. The basal bulge is undulated, each concavity corresponding to the underlying  
1031 root branches. The labial crown face is oblique labially and strongly overhangs the root. The  
1032 labial crown face bears strong irregular vertical folds. The root is polyaulacorhize with worn  
1033 branches and lingually placed relative to the root. A line of labial foramina is present below  
1034 the crown/root edge. A pair of median foramina is present at the basal edge of each root  
1035 branch.

1036 **Remarks:** Teeth of this genus can be separated from those of juvenile myliobatid specimens  
1037 or small myliobatid species by their constant height from one lateral extremity to the other in  
1038 lingual view, whereas this is higher in the median region of myliobatid teeth. The (probably)

1039 Danian species *Rhinoptera prisca* Woodward, 1907 from Brazil and the Thanetian *Rhinoptera*  
1040 *raeburni* from Nigeria (White, 1934) and Democratic Republic of Congo (Darteville and  
1041 Casier, 1943) are the oldest representatives of the Rhinopteridae. Differences between teeth of  
1042 these two species are tenuous and precise assessment of their potential synonymy is hampered  
1043 by the quality of the illustrations of the type material of both species. The tooth recovered  
1044 here shows strong labio-lingual compression and mesio-distal expansion. As this morphology  
1045 is present in the type series of *Rhinoptera raeburni* but absent in the associated teeth of the  
1046 *Rhinoptera prisca* type series, the material reported here is tentatively attributed to the former  
1047 species.

1048

## 1049 **5. Discussion**

1050         The elasmobranch assemblage from the glauconitic sandstone comprises 30 species  
1051 and is dominated in both number of species and specimens by small nectobenthic  
1052 carcharhiniforms (11 species) along with lamniforms (five species) and rare but diverse  
1053 myliobatiforms (nine species). All taxa recovered from the underlying glauconitic limestone  
1054 bed (*Chiloscyllium* sp., *Galeorhinus mesetaensis*, *Pseudobatos matzensis*, *Aetomylaeus* sp.)  
1055 were also sampled in the glauconitic sandstone. Although species-level identifications are  
1056 hampered by the poor preservation of the specimens, the vast majority of taxa identified here  
1057 were formerly reported from the Danian-Ypresian interval, four of which are exclusively  
1058 known from the upper Paleocene of Morocco (*Hologinglymostoma*, *Porodermoides spanios*)  
1059 or Thanetian of France and Niger (*Pseudobatos matzensis*, '*Dasyatis*' *sudreii*). *Arechia* sp. is  
1060 the only taxon that was not known prior to the Eocene. This is in line with the benthic  
1061 foraminifera assemblage reported here that indicates a Thanetian age for the sampled  
1062 glauconitic sandstone. Both assemblages clarify previous reports on planktonic foraminifera  
1063 that did not report biomarkers for the glauconitic horizons and indirectly suggested either a

1064 late Paleocene (Slansky, 1962, p. 137) or a late Paleocene-early Eocene (Da Costa et al.,  
1065 2013b, 2013c, 2013d, 2009) age for this horizon. This glauconitic sandstone layer seems to  
1066 have a large geographical extent as it has been reported at the base of the Akinbo Formation  
1067 above the Ewekoro Formation in Nigeria (Adegoke et al., 1972; Petters and Olsson, 1979),  
1068 covering the *Togocyamus seefriedi* limestones in Benin (Bio-Lokoto et al., 1998) and on the  
1069 top of Late Paleocene limestones in Ghana (Kjemperud et al., 1992). Yet, no fossils were  
1070 described nor reported from this horizon. In Benin, a glauconitic level has been dated by  
1071 radiochronology at  $53 \pm 2$  Ma (Akpiti et al., 1985). However, this horizon is situated within  
1072 the upper argillaceous series (Akpiti et al., 1985) and it is unclear whether it is equivalent to  
1073 the glauconitic layer resting directly on top of the limestone series in the same area (Bio-  
1074 Lokoto et al., 1998) and in Togo, especially considering that other glauconitic levels are also  
1075 present in the argillaceous series in Togo and Benin (Slansky, 1962) as well as Nigeria  
1076 (Adegoke, 1977). In Nigeria, radiochronologic analysis of the glauconitic layer that forms the  
1077 base of the Akinbo Formation and of another glauconitic horizon situated three meters higher  
1078 within the upper argillaceous series yielded an average age of  $54,5 \pm 2,7$  Ma (Adegoke et al  
1079 1972). Yet, glaucony populations typically comprise grains with a long (5 myrs or more)  
1080 period of genesis, which can result in artificially young absolute radiochronologic ages (Smith  
1081 et al., 1998) and other biostratigraphic evidence suggest that the Paleocene/Eocene boundary  
1082 should occur in the middle part of the Akinbo Formation in southwestern Nigeria (Adegoke et  
1083 al., 1972; Petters and Olsson, 1979). A similar placement (within the overlying shaly  
1084 argillaceous series) of the Palaeocene/Eocene boundary was made in Togo (Johnson et al.,  
1085 2000; Slansky, 1962). This is consistent with the Thanetian age suggested by the benthic  
1086 foraminifera assemblage and by some elements of the elasmobranch fauna reported here and  
1087 indicates a late Thanetian age for the glauconitic horizons.

1088           The composition of the elasmobranch assemblage described here shows strong  
1089 resemblances with late Paleocene faunas from Morocco ('Sillon A' in the Ganntour Basin,  
1090 'Couche 2a' in the Ouled Abdoun Basin – see Yans et al. 2014 for discussion on the  
1091 stratigraphy) including *Hologinglymostoma*, *Serratolamna aschersoni*, *Otodus obliquus*,  
1092 *Jaekelotodus africanus*, small *Isurolamna* morph, *Foumtizia* aff. *gadaensis*, *Premontreia* (*O.*)  
1093 *subulidens*, *Porodermoides spanios*, *Galeorhinus mesetaensis*, *Abdounia africana*, *Myliobatis*  
1094 *dixonii*. The absence of *S. aschersoni* and *Arechia* in the Moroccan late Paleocene fauna would  
1095 indicate that the Moroccan Sillon A and Couche 2a assemblages most likely pre-late  
1096 Thanetian since these taxa are present in the late Thanetian Togolese fauna and in the younger  
1097 (likely Ypresian, see Yans et al. 2014) C1/C2 and C1 faunas in Morocco (Noubhani and  
1098 Cappetta, 1997). This is consistent with the Selandian-early Thanetian age provided by  
1099 chemostratigraphic analyses for the Couche 2a (Yans et al. 2014). Other differences between  
1100 the C2/Sillon A faunas (which include squaliforms and hexanchiforms) and the Togolese  
1101 assemblages (which include *Palaeohypotodus* and small *Physogaleus*) are more likely  
1102 environment-related or due to endemism (see below). In contrast, very few taxa reported here  
1103 are represented in the Thanetian of Niger (Cappetta, 1972) and Nigeria (White, 1934),  
1104 whereas all taxa reported from Nigeria (*Eotorpedo hilgendorfi*, *E. jaekeli*, *Squatiscyllium*  
1105 *nigeriensis*, *Ginglymostoma sokotoense*, *Hypolophites myliobatoides*, *Myliobatis wurnoensis*)  
1106 were found in Niger. Only the 'species' *Myliobatis dixonii* occurs both in Togo and Nigeria,  
1107 but this taxon is in need of revision (see above) and has wide geographical and stratigraphic  
1108 ranges. Similarly, '*Dasyatis*' *sudrei* is the only species shared by the Togolese and Nigerien  
1109 faunas, but this species is also known from the Thanetian of Senegal (Sylvain Adnet, pers.  
1110 com.). Comparison with Thanetian faunas from southeastern Atlantic (Darteville and Casier,  
1111 1959, 1943) is made difficult by the lack of micro-fossils in corresponding assemblages and  
1112 because their precise stratigraphic origin is sometimes uncertain. Reappraisal of the

1113 stratigraphic position of Dartevelle and Casier's samplings (Solé et al., 2018) suggests that the  
1114 only clear Thanetian assemblage that yielded elasmobranch remains is restricted to layer 18 of  
1115 Landana (Cabinda enclave), which comprises *Sulcidens sulcidens*, '*Cretolamna*  
1116 *appendiculata*' (possibly *Otodus (O.) obliquus*), *M. dixonii*, and ? *Carcharias substriatus*. A  
1117 number of other elasmobranch assemblages from Landana (layers 13-16) are Selandian-  
1118 Thanetian (Zone P4) and include similar species plus *Delpitioscyllium africanum* and  
1119 *Jaekelotodus speyeri*. Other assemblages from different layers at Manzadi Point VI  
1120 (Democratic Republic of Congo) are possibly Selandian (Solé et al., 2018) and include  
1121 *Delpitioscyllium africanum*, *Otodus (O.) obliquus*, '*Cretolamna appendiculata*', *Myliobatis*  
1122 *dixonii*, *Myliobatis nzadinensis*, and *Rhinoptera raeburni*. Despite the lack of precision on  
1123 both the stratigraphic origin and the microfauna composition of the Paleogene assemblages  
1124 reported by Dartevelle and Casier (1959, 1943), some cosmopolitan pelagic taxa from  
1125 Landana and Democratic Republic of Congo (*Otodus (O.) obliquus*, *Rhinoptera cf. raeburni*,  
1126 *Isurolamna*) were recorded in Togo but not in the faunas from the epicontinental sea of Niger  
1127 and Nigeria.

1128         The much stronger affinities between the Togolese assemblage and North African  
1129 faunas compared with Niger and Nigeria is unexpected. This is especially surprising  
1130 considering the probable connection between the Gulf of Guinea and Niger (and to a greater  
1131 extent, North Africa) in the Thanetian through the trans-Saharan seaway (Belkhodja and  
1132 Bignot, 2004) and the closer geographical position of the Togolese locality with Nigeria and  
1133 Niger. Such variations in faunal composition might be related to different  
1134 palaeoenvironmental conditions and/or stratigraphic positions. However, dating of Moroccan  
1135 (Yans et al., 2014), Nigerien, and Nigerian faunas within the Thanetian age is still in need of  
1136 precision. It is hence difficult to assess the effect of potential stratigraphic differences on the  
1137 variations in faunal composition of these assemblages. However, although most of the taxa

1138 from Niger and Nigeria are restricted to the Thanetian, the nectobenthic torpediniform *E.*  
1139 *hilgendorfi* ranges from the Selandian (Darteville and Casier, 1959, 1943) to Ypresian  
1140 (Arambourg, 1952; Case et al., 2015) and is absent from the Togolese glauconitic horizons.  
1141 Conversely, some cosmopolitan taxa from Landana and Democratic Republic of Congo and  
1142 Morocco (*Otodus (O.) obliquus*, *Isurolamna*) with long stratigraphic ranges were recorded in  
1143 Togo but not in the faunas from Niger and Nigeria. This tends to indicate that differences in  
1144 stratigraphic origins, if proven, might not be the sole factor that explains the faunal  
1145 differences observed. The Thanetian fauna from Morocco ('Sillon A' and 'couche 2a')  
1146 comprises hexanchiforms, diverse squaliforms, and pristiophoriforms that indicate an open  
1147 marine environment. Conversely, the Thanetian assemblage from Niger suggests a restricted  
1148 coastal palaeoenvironment (Cappetta, 1972) with freshwater to coastal osteichthyans  
1149 (Bagridae, Osteoglossiformes, Dipnoi) and numerous benthic elasmobranchs. Its similarity  
1150 with the assemblage from Nigeria (White, 1934) suggests a similar environment for the latter.  
1151 Although devoid of hexanchiforms, squaliforms and pristiophoriforms, the elasmobranch  
1152 assemblage reported here is dominated by small nectobenthic carcharhiniforms (mostly  
1153 Triakidae and Scyliorhinidae) and numerous pelagic batomorphs and lamniforms. The benthic  
1154 foraminiferal assemblage includes members of the Nodosaridae (*Fronicularia*, *Lenticulina*,  
1155 and *Palmula*), which indicates a coastal and warm environment. This faunal evidence,  
1156 alongside the absence of continental organisms and presence of nautiloids and rare coral  
1157 polyps suggests a plainly marine environment on the continental shelf, which may explain the  
1158 numerous elasmobranch taxa shared with the Moroccan fauna. In addition, the absence in  
1159 Niger and Nigeria of some cosmopolitan elasmobranch taxa known from Togo, Morocco, and  
1160 Angola lends support for a palaeoenvironmental control on the distribution of late Paleocene  
1161 elasmobranch faunas that differentiates an open-sea southeastern Atlantic fauna from a more  
1162 neritic fauna in the epicontinental trans-Saharan seaway. However, some degree of endemism



1163 is present among the former fauna, as exemplified by the number of taxa in the Togolese  
1164 assemblage (*Premontreia (Oxyscyllium)* sp., *Palaeogaleus* sp., '*Ginglymostoma*' sp., *Arechia*  
1165 sp., *Aetomylaeus* sp., *Archaeomanta* sp., and possibly *Coupatezia* sp. and *Burnhamia* sp.) that  
1166 despite their poor preservation probably correspond to new unnamed species. In addition,  
1167 none of the species reported from the underlying limestones in the Tabligbo area by Stromer  
1168 (1910) were recovered in our samplings, excepted *M. dixonii*. Among the other species  
1169 described by Stromer (1910), *Odontaspis elegans* var. *substriata* Stromer, 1910 was based on  
1170 a single incomplete specimen that makes the validity of this species dubious. Yet, it was  
1171 subsequently reported from Angola (Dartevelle and Casier, 1959, 1943) and Niger (Cappetta,  
1172 1972) based on specimens that indicate affinities with the genus *Brachycarcharias*. While  
1173 Stromer's *Xenodolamia* aff. *simplex* is an indeterminate tooth of a probable lamniform and  
1174 *Ginglymostoma* aff. *thielense* an indeterminate ginglymostomatid, the genus *Hypolophites*  
1175 Stromer, 1910 is also known from the Thanetian of Niger (Cappetta, 1972), Nigeria (White,  
1176 1934) and Angola (Leriche, 1913). The underlying limestones where Stromer's specimens  
1177 were sampled very likely correspond to a different palaeoenvironment, which may explain  
1178 those differences, although additional work on the stratigraphy of these levels is needed to  
1179 confirm their Thanetian age.

1180

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1189

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1431

1432 **Figure captions**

1433

1434 **Figure 1.** **A**, General geological map of the Coastal Sedimentary Basin in Southern Togo  
1435 (Maritime Region) and sampled sites. **B**, synthetic sedimentary log of the WACEM and  
1436 ScanTogo sections.

1437

1438 **Figure 2.** Benthic foraminifera sampled from the glauconitic sandstone. **A**: *Frondicularia*  
1439 *microdisca* (TAB2-1), **B**: *Frondicularia phosphatica* (TAB2-2), **C**: *Frondicularia vertebralis*  
1440 (TAB2-3), **D**: *Palmula sigmoicosta* (TAB2-4), **E**: *Nodosaria affinis* (TAB2-5), **F**: *Nodosaria*  
1441 *affinis* (TAB2-6), **G**: *Lenticulina incisa* (TAB2-7). Scale bars equal 500  $\mu$ m, excepted A-B (1  
1442 mm).

1443

1444 **Figure 3.** Squatiniformes and Orectolobiformes. **A-B**: *Squatina* cf. *prima*. **A**: lateral tooth  
1445 (TAB2-8) in labial view, **B**: anterior tooth (TAB2-9) in labial view. **C-D**: *Chiloscyllium* sp.  
1446 **C**: anterior tooth (TAB3-1) in labial view and **D**: lateral tooth (TAB2-10) in labial view. **E-F**:  
1447 *Hologinglymostoma* sp. **E**: lateral tooth (TAB2-11) in occlusal view, **F**: lateral tooth (TAB2-  
1448 12) in lingual view, **G-I**: '*Ginglymostoma*' sp. **G**: anterior tooth (TAB2-13) in labial view, **H**:  
1449 anterolateral tooth (TAB2-15) in labial view, **I**: posterior tooth (TAB2-14) in labial view. All  
1450 scale bars equal 500  $\mu$ m.

1451

1452 **Figure 4.** Lamniformes. **A-B**: *Serratolamna aschersoni*, upper lateral tooth (TAB2-16) in **A**,  
1453 lingual and **B**, labial views. **C-U**: *Otodus (Otodus) obliquus*. **C**: lower anterior tooth (TAB2-  
1454 17) in lingual view, **D**: lower lateroposterior tooth (TAB2-18) in lingual view, **E-F**: upper  
1455 lateral tooth (TAB2-19) in **E**, labial and **F**, lingual views; **G**: upper lateral tooth (TAB2-20) in  
1456 lingual view, **H**: upper lateral tooth (TAB2-21) in lingual view, **I**: upper lateroposterior tooth

1457 (TAB2-22) in lingual view, **J-K**: anterior tooth (TAB2-23) in **J**, lingual and **K**, labial views,  
1458 **L-M**: upper lateral tooth (TAB2-24) in **L**, lingual and **M**, labial views, **N-O**: upper lateral  
1459 tooth (TAB2-25) in **N**, lingual and **O**, labial views, **P**: upper intermediate? tooth (TAB2-26) in  
1460 lingual view, **Q**: upper lateral tooth (TAB2-27) in lingual view, **R-S**: upper lateral tooth  
1461 (TAB2-28) in **R**, labial and **S**, lingual views, **T**: posterior tooth (TAB2-29) in lingual view, **U**:  
1462 posterior tooth (TAB2-30) in lingual view. All scale bars equal 1 cm.

1463  
1464 **Figure 5.** Lamniformes. **A-I**: *Jaekelotodus africanus*. **A-C**: anterior tooth (TAB2-31) in **A**,  
1465 lingual, **B**, labial and **C**, profile views, **D-E**: upper lateral tooth (TAB2-32) in **D**, lingual and  
1466 **E**, labial views, **F-G**: upper lateral tooth (TAB2-33) in **F**, labial and **G**, lingual views, **H-I**:  
1467 posterior tooth (TAB2-34) in **H**, lingual and **I**, labial views. **J-K**: *Palaeohypotodus* sp. **J**:  
1468 lateroposterior tooth (TAB2-35) in lingual view, **K**: anterior tooth (TAB2-36) in labial view.  
1469 **L-R**: *Isurolamna* sp. **L-N**: upper anterior tooth (TAB2-37) in **L**, lingual, **M**, labial and **N**,  
1470 profile views. **O-P**: upper lateral tooth (TAB2-38) in **O**, labial and **P**, lingual views, **Q-R**:  
1471 lower lateral tooth (TAB2-39) in **Q**, labial and **R**, lingual views. Scale bars: 1 cm (A-G), 5  
1472 mm (H-I, L-R), 1 mm (J-K).

1473  
1474 **Figure 6.** Carcharhiniformes. **A-D**: *Foumtizia* aff. *gadaensis*. **A**: lateral tooth (TAB2-40) in  
1475 labial view, **B**: anterior tooth (TAB2-41) in labial view, **C-D**: anterior tooth (TAB2-42) in **C**,  
1476 lingual and **D**, labial views. **E-K**: *Premontreia (Oxyscyllium) subulidens*. **E**: anterior tooth  
1477 (TAB2-43) in lingual view, **F-G**: lateral tooth (TAB2-44) in **F**, lingual and **G**, labial views,  
1478 **H-I**: anterior tooth (TAB2-45) in **H**, labial and **I**, lingual views, **J-K**: posterior tooth (TAB2-  
1479 46) in **J**, lingual and **K**, labial views. **L-O**: *Premontreia (Oxyscyllium)* sp. **L-M**: lateral tooth  
1480 (TAB2-47) in **L**, lingual and **M**, labial views, **N**: lateral tooth (TAB2-48) in labial view, **O**,  
1481 lateral tooth (TAB2-49) in labial view. **P-R**: *Porodermoides spanios*. **P**: anterior tooth

1482 (TAB2-50) in labial view, **Q-R**: anterior tooth (TAB2-51) in **Q**, lingual and **R**, labial views.  
1483 **S-V**: *Palaeogaleus* sp. **S**: lateral tooth (TAB2-52) in labial view, **T**: lateral tooth (TAB2-53)  
1484 in labial view, **U**: lateral tooth (TAB2-54) in labial view, **V**: lateral tooth (TAB2-55) in labial  
1485 view. **W-X**: *Galeorhinus mesetaensis*. **W**: lateral tooth (TAB3-2) in labial view, **X**: anterior  
1486 tooth (TAB3-3) in labial view. **Y-A'**: *Galeorhinus* sp. **Y-Z**: lateral tooth (TAB2-56) in **Y**,  
1487 lingual and **Z**, labial views, **A'**: anterior tooth (TAB2-57) in labial view. Scale bars equal 1  
1488 mm except A-D and S-V (500  $\mu\text{m}$ ).

1489  
1490 **Figure 7.** Carcharhiniformes and Rhinopristiformes. **A-C**: *Triakis* sp. **A**: anterior tooth  
1491 (TAB2-58) in labial view, **B**: anterior tooth (TAB2-59) in labial view, **C**: lateral tooth (TAB2-  
1492 60) in labial view. **D-J**: *Triakidae* ? indet. **D-E**: lateral tooth (TAB2-61) in **D**, labial and **E**,  
1493 occlusal views, **F**: lateral tooth (TAB2-62) in labial view, **G**: lateral tooth (TAB2-63) in labial  
1494 view, **H-I**: lateral tooth (TAB2-64) in **H**, lingual and **I**, labial views, **J**: lateral tooth (TAB2-  
1495 65) in occlusal view. **K-T**: *Abdounia africana*. **K**: symphyseal tooth (TAB2-66) in labial view,  
1496 **L-M**: latero-posterior tooth (TAB2-67) in **L**, labial and **M**, lingual views, **N-O**: anterior tooth  
1497 (TAB2-68) in **N**, lingual and **O**, labial views, **P-Q**: anterior tooth (TAB2-69) in **P**, basal and  
1498 **Q**, labial views, **R-S**: lateral tooth (TAB2-70) in **R**, labial and **S**, lingual views, **T**, latero-  
1499 posterior tooth (TAB2-71) in labial view. **U-Y**: *Physogaleus* sp. **U-V**: lateral tooth (TAB2-72)  
1500 in **U**, labial and **V**, lingual views, **W-X**, lateral tooth (TAB2-73) in **W**, labial and **X**, lingual  
1501 views, **Y**: lateral tooth (TAB2-74) in labial view. **Z-B'**: *Pseudobatos matzensis* comb. nov. **Z**-  
1502 **A'**: anterior tooth (TAB3-4) in **Z**, lingual and **A'**, basal views, **B'**: posterior tooth (TAB2-75)  
1503 in lingual view. Scale bars: 1 mm (D-E, N-Y), 500  $\mu\text{m}$  (A-C, F-M, Z-A') and 200  $\mu\text{m}$  (B').

1504  
1505 **Figure 8.** Batomorphii. **A**: *Arechia* sp., tooth (TAB2-76) in lingual view. **B-H**: *Coupatezia* sp.  
1506 **B-D**: non-cuspidate tooth (TAB2-77) in **B**, lingual, **C**, occlusal and **D**, basal views, **E-F**: non-

1507 cuspidate tooth (TAB2-78) in **E**, lingual and **F**, occlusal views, **G-H**: cuspidate tooth (TAB2-  
1508 79) in **G**, occlusal and **H**, lingual views. **I-N**: '*Dasyatis*' *sudrei*. **I**: tooth (TAB2-80) in labial  
1509 view, **J**: tooth (TAB2-81) in lingual view, **K-L**: tooth (TAB2-82) in **K**, lingual and **L**, basal  
1510 views, **M-N**: posterior tooth (TAB2-83) in **M**, labial and **N**: basal views. **O-Q**: '*Dasyatis*' sp.  
1511 **O**: non-cuspidate tooth (TAB2-84) in lingual view, **P**: non-cuspidate tooth (TAB2-86) in  
1512 occlusal view, **Q**: cuspidate tooth (TAB2-85) in occlusal view. **R-T**: *Archaeomanta* sp., tooth  
1513 (TAB2-87) in **R**, profile, **S**, labial and **T**, profile views. **U-W**: *Burnhamia* sp., tooth (TAB2-  
1514 88) in **U**, occlusal, **V**, labial and **W**, lingual views. **X-Z**: *Myliobatis dixonii*, tooth (TAB2-89)  
1515 in **X**, basal, **Y**, occlusal and **Z**, lingual views. **A'-C'**: *Rhinoptera* cf. *raeburni*, tooth (TAB2-  
1516 90) in **A'**, occlusal, **B'**, basal and **C'**, lingual views. **D'-F'**: *Aetomylaeus* sp., tooth (TAB3-5)  
1517 in **D'**, lingual, **E'**, labial and **F'**, occlusal views. Scale bars: 500  $\mu$ m (A, G-H, I-T), 1 mm (B-  
1518 F), 3 mm (U-C'), 1 cm (D'-F').

1519

















