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► **To cite this version:**

Guillaume Guinot, Lionel Hautier, Bernard S Sambou, Raphaël Sarr, Jeremy E Martin. The Upper Cretaceous elasmobranch fauna from Senegal. *Cretaceous Research*, 2023, 146, pp.105480. 10.1016/j.cretres.2023.105480 . hal-04192697

**HAL Id: hal-04192697**

**<https://hal.science/hal-04192697v1>**

Submitted on 31 Aug 2023

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1                   **The Upper Cretaceous elasmobranch fauna from Senegal**

2

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4

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11 **Abstract.** Three successive horizons were sampled by bulk-sampling across the Campanian–  
12 Maastrichtian marine succession at the Cap de Naze cliff, South of Popenguine, Senegal. The material  
13 collected includes several hundreds of elasmobranch micro-remains as well as surface-collected  
14 specimens that are described in the present work. Twenty-six species are recorded, including three  
15 new genera and eight new batomorph species (*Ptychotrygon nazeensis* sp. nov., *Terangabatis thiami*  
16 gen. et sp. nov., '*Rhinobatos*' *popenguinensis* sp. nov., *Atlantobatis acrodonta* gen. et sp. nov.,  
17 *Sowibatos minimus* gen. et sp. nov., '*Dasyatis*' *reticulata* sp. nov., *Coupatezia casei* sp. nov.,  
18 *Phosphatodon cretaceus* sp. nov.). These new samplings complement previous records based on  
19 surface collection of the Cape de Naze section and bring the number of elasmobranch species for this  
20 fauna to 31. Increasing elasmobranch taxonomic diversity throughout the three successive  
21 assemblages indicates a transition from restricted marine to open coastal settings. This high-diversity  
22 fauna is dominated by necto-benthic batomorphs and is similar in its structure to other Tethyan and  
23 Eastern Atlantic Maastrichtian faunas. The high number of species apparently endemic to the studied  
24 area suggests high habitat differentiation in corresponding marine Maastrichtian settings. The  
25 presence of typical Maastrichtian species in the top of Unit 1 argues against a Campanian age  
26 previously proposed for this unit, while our data support a middle–late Maastrichtian age for the  
27 ferruginous sandstone bed of Unit 3.

28 **Key words:** chondrichthyans, micro-vertebrates, Maastrichtian, Western Africa, biostratigraphy,  
29 palaeoecology.

30

## 31 **1. Introduction**

32 The latest Cretaceous (Campanian-Maastrichtian) represents an all-time diversity peak in the  
33 elasmobranch evolutionary history (Guinot and Cavin, 2016). Campanian-Maastrichtian  
34 elasmobranch assemblages are known from a variety of depositional environments and geographical  
35 areas, although most of the fossil record of this group is based on faunas from North America,  
36 Northern Europe, and Northern Africa. In the eastern Atlantic and southern Tethys, knowledge on  
37 Maastrichtian elasmobranch assemblages is strongly dominated by samplings from Morocco (e.g.  
38 Arambourg, 1952; Noubhani and Cappetta, 1997) and the Middle East (Bardet et al., 2000; Cappetta,  
39 1991a; Cappetta et al., 2000; Lewy and Cappetta, 1989; Signeux, 1959), although the latter often  
40 consists of faunal lists lacking thorough descriptions of the reported taxa. In contrast, records of sub-  
41 Saharan African faunas are scarce. These are restricted to sporadic accounts from Angola and  
42 Democratic Republic of Congo (Antunes and Cappetta, 2002; Darteville and Casier, 1959, 1943) as  
43 well as from Senegal (Cuny et al., 2012), Niger and Nigeria (Cappetta, 1972; Vullo and Courville, 2014;  
44 White, 1934). These reports are mainly based on surface-collections that overlooked micro-remains  
45 and do not allow a clear picture of the regional diversity distribution of Maastrichtian elasmobranchs  
46 in this area.

47 When reporting on the surface-collected elasmobranch macro-remains from the Late Campanian-  
48 Maastrichtian section of Popenguine (Senegal), Cuny *et al.* (2012) found strong similarities between  
49 the Senegalese assemblages and others from Morocco and the Near East, and underlined the  
50 potential of this West African section for sampling of elasmobranch micro-remains. Here, we present  
51 a detailed account of the elasmobranch fauna from the Popenguine section based on bulk-sampling  
52 and additional surface prospections from three successive horizons. Biostratigraphic implications and  
53 geographic distribution of the elasmobranch communities in the eastern Atlantic and southern  
54 Tethys areas are discussed in light of the newly described fauna.

55

## 56 **2. Geological and Geographical Settings**

57 Sedimentary levels producing marine vertebrates described here crop out in the area surrounding  
58 the village of Popenguine along the Atlantic coastline of Senegal (Figure 1A), and span the uppermost  
59 Cretaceous–early Paleocene interval (Cuny et al., 2012; Jacquet, 1936; Martin et al., 2019; Sarr, 1995;  
60 Sow, 1992). The Cap de Naze cliff, located South of Popenguine is a topographic height, which  
61 consists of a stack of Late Cretaceous argilites and siltstones from the Paki and Cap de Naze  
62 Formations from the Campanian-Maastrichtian interval that is subjected to the weathering action of  
63 the waves. Detailed geological information is available from Tessier (1952), Khatib et al. (1990), Sow

64 (1992), Sarr (1995) and has recently been summarized in Cuny *et al.* (2012). A slight southward  
65 dipping of the lithographic succession allows access to the oldest, mostly argillaceous, levels (Units 1  
66 and 2) in the northern area of the section, whereas younger levels dominated by siltstones (Units 3  
67 and 4), are located in the cliff area (Figure 1B-C). Unit 1 (Paki Formation) comprises grey silty argillites  
68 (12.50 m thick) underlying yellow siltstone (30 cm thick) that is topped by a yellow calcareous  
69 sandstone bed (20 cm thick). Within the Cap de Naze Formation, Unit 2 is composed of a 12 m thick  
70 series of argillites and siltites topped by a fine sandstone level, while Unit 3 is thicker (24 m) and  
71 includes basal variegated clayey siltstones (8 m) overlain by a massive set of medium-fine sandstones  
72 (16 m) with variegated siltstone. The top of Unit 3 comprises a fine to medium silty sandstone with  
73 ferruginous cement and has produced a diverse assemblage of surface-collected invertebrate and  
74 vertebrate remains (Cuny *et al.*, 2012; Hyžný *et al.*, 2016b, 2016a). This is no longer accessible due to  
75 the recent collapse of parts of the cliff. Planktonic foraminifera were used to establish the  
76 chronostratigraphic succession for the lower units at Cap de Naze with Unit 1 corresponding to the  
77 uppermost Campanian and Unit 2 to the lower to middle Maastrichtian (Khatib *et al.*, 1990; Sarr,  
78 1995; Sow, 1992). Units 3 and 4 are devoid of foraminifera. However, the elasmobranch taxa  
79 reported by Cuny *et al.* (2012) from Unit 3 support a Maastrichtian age for this unit. Unit 4 yielded an  
80 ammonite assemblage reported by Tessier (1952) from the calcareous sandstone at the base of this  
81 unit on the Popenguine beach, which suggests an upper Maastrichtian assignment.

82 **FIGURE 1 HERE**

83

### 84 **3. Material and Methods**

85 The specimens reported here were bulk-sampled and surface-collected from three horizons within  
86 the Paki and Cap de Naze Formations. In Unit 1 of the Paki Formation, one sample (sample 1; Figure  
87 1B-C) consisted of 9.7 kgs from the grey silty argillites (about 8 meters below the calcareous  
88 sandstone), which were processed using diluted (3%) hydrogen peroxide. Another sampling within  
89 Unit 1 consisted of 6.5 kgs of rock from the yellow calcareous siltstone (sample 2; Figure 1B-C) and  
90 was acid processed using diluted (7%) formic acid buffered with 30% of calcium formate solution.  
91 Sampling from the summit of Unit 3 within the Cap de Naze Formation (sample 3; Figure 1B-C)  
92 consisted of about 20 kgs of ferruginous sandstone that were processed using diluted (7%) formic  
93 acid buffered with 30% of calcium formate solution. All residues were sieved down to 0.35 mm mesh  
94 size. In total, 331 identifiable isolated elasmobranch specimens were studied (of which only 18 were  
95 surface-collected from sample 2), along with several fragmentary teeth and isolated scales. Sample 2  
96 produced abundant isolated actinopterygian remains (teeth, vertebrae) and scarce fragmentary

97 decapod remains, while sample 1 yielded a few bivalve fragments and no associated fauna was  
98 recovered in sample 3.

99 The specimens described here are currently under study at the University of Montpellier and will be  
100 housed in the Laboratoire de Sédimentologie et de Biostratigraphie, Département de Géologie,  
101 Université Cheikh Anta Diop, Dakar, Senegal.

102 The present work is registered in ZooBank under the following Life Science Identifier (LSID):  
103 urn:lsid:zoobank.org:pub:2E7AEE55-E41D-440B-82EB-5CFFFBE0755D, and the LSIDs of new species  
104 names are provided in the Systematic Palaeontology section, below.

105

#### 106 **4. Systematic Palaeontology**

107 The systematics and terminology used here largely follow those of Cappetta (2012).

108

109 Order Orectolobiformes Appelgate, 1972

110 Family Hemiscylliidae Gill, 1862

111 Genus *Chiloscyllium* Müller & Henle, 1837

112 *Chiloscyllium* sp.

113 Fig. 2A-B

114 Material. Two teeth (SN2012-41-42) from Unit 3, Cap de Naze Formation.

115 Description. The crown is smooth and less than 1.2 mm high. The main cusp is triangular, biconvex  
116 and slightly inclined toward the commissure. The main cusp is flanked by a pair of low, broad and  
117 triangular cusplets with the mesial one being more reduced than the distal one. The faint cutting  
118 edges are observable in the lower third of the main cusp and run continuously until the base of the  
119 cusplets. The cusplets are diverging and located more labially than the main cusp. The apron is  
120 developed and broad with a narrow medio-labial concavity. The labial face of the cusplets displays a  
121 slight bulge that runs over the labial outline of the apron and only tapers near its median concavity.  
122 The median uvula and root are missing on both specimens.

123 Remarks. Dental remains of *Chiloscyllium* have been so far reported from the Maastrichtian of the  
124 Tethys (Bardet et al., 2000; Cappetta et al., 2014; Cappetta and Corral, 1999) but these were not  
125 illustrated and it is therefore impossible to compare our specimens with them. The teeth described

126 here differ from those reported as *Chiloscyllium* sp. from the Maastrichtian of New Jersey (Case et  
127 al., 2001) by their less developed cusplets and apron with narrower labial concavity. The Senegalese  
128 specimens can be differentiated from *C. frequens* Guinot, Underwood, Cappetta and Ward, 2013  
129 known from the Santonian and Campanian of France, England and Germany (Guinot et al., 2013) by  
130 their smaller size, bulged labial outline of the cusplets and apron, less developed cutting edges and  
131 narrow medio-lingual concavity in the apron. Teeth of *C. salvani* Noubhani and Cappetta, 1997 from  
132 the Paleocene of Morocco display a convex labial crown face and an apron demarcated by marginal  
133 convexities in labial view.

134

135 Genus *Hemiscyllium* Müller & Henle in Smith 1837

136 *Hemiscyllium* sp.

137 Fig. 2C-D

138 Material. One tooth (SN2012-43) from Unit 3, Cap de Naze Formation.

139 Description. The single tooth found is about 0.6 mm wide and lacks the apex of the main cusp and  
140 most of the root. The labial crown face is flat whereas the lingual face of the main cusp is convex. The  
141 apron is wide with a regular and curved lower edge with no demarcation. Very faint cutting edges are  
142 present at the base of the main cusp, in labial position, and taper when reaching the heels. The distal  
143 heel is horizontal in labial view, whereas the mesial heel is oblique. The margino-lingual crown faces  
144 are high and abrupt, the distal one being less laterally expanded and is overhung by the heel in labial  
145 view. The uvula is rather wide, broadly united to the margino-lingual face and is slightly mesially  
146 oriented.

147 Remarks. Teeth of *Hemiscyllium* are known from several Maastrichtian and Paleocene assemblages  
148 including *H. hermani* Müller, 1989 from the Campanian and Maastrichtian of Germany (Herman,  
149 1982; Müller, 1989) as well as from the Maastrichtian and Danian of Denmark (Adolfsson and Ward,  
150 2015, 2014) and a few unnamed species (Kriwet et al., 2007; Noubhani and Cappetta, 1997). The  
151 tooth described here differs from those of other *Hemiscyllium* species in being of smaller size and not  
152 mesio-distally expanded with a weakly demarcated apron.

153

154 Family Ginglymostomatidae Gill, 1862

155 Genus *Plicatoscyllium* Case & Cappetta, 1997

156

*Plicatoscyllium youssoufiaense* Noubhani & Cappetta, 1997

157

Fig. 2E-M

158

1997 *Plicatoscyllium youssoufiaense* Noubhani & Cappetta; p. 43, pl. 16, figs 1-10.

159

2014 *Plicatoscyllium youssoufiaense* Noubhani & Cappetta; Cappetta et al., Table 1.

160

Material. Four teeth (SN2012-44-47) and several crown fragments from Unit 3, Cap de Naze

161

Formation.

162

Description. Anterior teeth (Fig. 2F-H) are higher than wide and not exceeding 1.5 mm high. The

163

crown comprises of a triangular and rather developed main cusp with a broad lower region that is

164

flanked by a pair of elongate and weakly divergent cusplets as well as a second external pair of low

165

and incipient cusplets. The cutting edges run continuously from the main cusp to the marginal angles

166

of the crown although notches separate the main cusp and cusplets. The lower region of the labial

167

crown face displays a rather short, weakly developed and bifid apron with slightly concave marginal

168

edges. The labial crown face bears ornament made of a single vertical ridge on the main cusp that

169

bifurcates in its lower region where it is accompanied by several irregular vertical ridges of variable

170

sizes that occupy a triangular area on the apron, but do not reach the cusplets nor the lower edge of

171

the apron. The lingual crown face is smooth and concave in profile view and displays a developed

172

lingually-projected uvula. The hemiaulacorhize root projects lingually and is heart-shaped in basal

173

view with nearly flat to concave basal face that is pierced by a large central foramen. The root

174

branches are oriented labially and the moderately developed lingual protuberance displays a rather

175

large median foramen in basal position. A pair of large oval-shaped margino-lingual foramina is

176

present in the concavities between the marginal faces and the lingual protuberance. Some teeth

177

display a second, smaller foramina on the mesial marginal face, in a more labial position than the

178

other. Teeth from lateral and latero-posterior files (Fig. 2E, I-M) are strongly asymmetrical, the main

179

cusp and cusplets being bent toward the commissure. There are two pairs of cusplets of decreasing

180

size marginally as well as a third incipient mesial cusplet that is reduced to a protuberance. The apex

181

of the cusplets is bent toward to main cusp. The apron is short and weakly bifid. The labial crown

182

ornament consists of a vertical ridge on the main cusp that does not divide before reaching the base

183

of the cusp where several subvertical folds of various sizes are present. The density of the labial

184

ornament decreases towards the posterior files where it is limited to few large and short folds below

185

the cusplets. The root is strongly asymmetrical with a longer mesial branch and the medio-lingual

186

foramen is narrower than in anterior teeth.



187 Remarks. The teeth described here display typical features of members of the genus *Plicatoscyllium*,  
188 which included seven species so far, all represented in the Maastrichtian. The Senegalese specimens  
189 differ from those of *P. globidens* (Cappetta and Case, 1975) from the Maastrichtian of the USA and of  
190 *P. lehneri* (Leriche, 1938) from the Maastrichtian of Morocco, the Democratic Republic of Congo,  
191 Trinidad and Tobago, and Spain by the presence of well-developed main cusp and cusplets. Among  
192 species represented by teeth with developed cusplets, teeth of *P. antiquum* Case and Cappetta,  
193 1997, *P. derameei* Case and Cappetta, 1997 and *P. gharbii* Noubhani and Cappetta, 1997 can be  
194 separated from the Senegalese specimens by their much weaker labial ornamentation.  
195 *Plicatoscyllium youssoufiaense* Noubhani and Cappetta, 1997 from the Maastrichtian of Morocco and  
196 *P. minutum* (Forir, 1887) from the Maastrichtian of Morocco, Netherlands, and Belgium are species  
197 with moderate to strong labial crown ornamentation, respectively. The specimens described here are  
198 much closer to *P. youssoufiaense* in that they display characteristic features of the species: small size,  
199 two to three cusplets, short but wide apron that is bifid in anterior teeth, and moderately developed  
200 lingual root protuberance. Some anterior teeth from Senegal present a slightly more developed labial  
201 ornament than in the specimens from the type series (Upper Maastrichtian of the Ganntour Basin)  
202 that is attributed to intraspecific variability.

203 **[FIGURE 2 HERE]**

204 Order Lamniformes Berg, 1958

205 Family Anacoracidae Casier, 1947

206 Genus *Squalicorax* Whitley, 1939

207 *Squalicorax pristodontus* (Agassiz, 1843)

208 Fig. 3A-B

209 For synonymy, see Hoganson et al. (2019), and add:

210 2012 *Squalicorax pristodontus* (Agassiz); Cuny et al., p. 111, Fig. 3P-R, V-X.

211 2014 *Squalicorax pristodontus* (Agassiz); Cappetta et al., p. 221, fig. 7F-I.

212 2017 *Squalicorax pristodontus* (Agassiz); Case et al., p. 70, fig. 3G.

213 Material. A single incomplete tooth (SN2012-48) from the yellow calcareous sandstone bed of Unit 1,  
214 Paki Formation.

215 Description. This robust lateral tooth is triangular in labial view with straight distal and convex mesial  
216 cutting edges. The mesial heel is reduced and inclined basally while the distal heel is incipient.

217 Serrations are strong and deep, being coarse in the upper half of the crown and decreasing in size  
218 toward the heels. The labial crown face is flat to slightly concave in its centre and overhangs the root  
219 in the areas situated below the heels. Several coarse vertical folds are present above the crown/root  
220 edge, being more developed in the centre of the crown. The lingual crown face is strongly convex.  
221 The lingual crown/root edge is triangular with a marked collar. The basal root face displays a wide  
222 medio-central foramen. Numerous oval-shaped foramina are present on the labial face, immediately  
223 below the crown. The root lobes are lacking.

224 Remarks. The crown morphology, size, and serration pattern comply with those of *S. pristodontus*  
225 (see Darteville and Casier, 1943 and Arambourg, 1952 for illustrations). This species has a worldwide  
226 distribution, is common in early Campanian to late Maastrichtian faunas, and was previously  
227 reported from Senegal by Cuny et al. (2012) from the Unit 3 of the Cap de Naze Formation.

228

229 Family Carchariidae Müller & Henle, 1838

230 Genus *Carcharias* Rafinesque, 1810

231 *Carcharias* sp.

232 Fig. 3C-F

233 Material. Two anterior teeth (including SN2012-50) from the yellow calcareous sandstone bed of Unit  
234 1, and one (SN2012-49) from the grey silty argillites of Unit 1, Paki Formation.

235 Description. The teeth are higher than wide and can reach up to 30 mm in total height. The main  
236 cusp is elongate, smooth, and bent lingually. The lingual crown face is strongly convex, whereas the  
237 labial face is flatter and bears a marked vertical convexity that broadens towards its basal crown  
238 edge. A short collar is present at the base of the lingual crown face. In labial view, the heels are  
239 elongate and strongly oriented basally. The basal edge of the labial crown face strongly overhangs  
240 the root from the medio-labial region towards the extremities of the heels. The medial overhang is  
241 narrow and triangular and can bear enameloid folds. A pair of triangular cusplets is present, lingually  
242 oriented with sharp and developed cutting edges. The main cusp bears well-developed cutting edges  
243 that taper before reaching the cusplets, from which they are separated by a marked notch. The root  
244 displays a marked and somewhat wide lingual protuberance, which bears a nutritive groove where a  
245 large central foramen opens. The root branches are elongate and thin, with compressed extremities.  
246 Several small foramina are present below the lingual collar as well as immediately below the labial  
247 crown bulge, and reach larger sizes in the medio-labial area.

248 Remarks. These anterior teeth resemble those of *Odontaspis samhamera* Cappetta & Case, 1975 but  
249 differ from the latter in the morphology of the cusplets, their more elongate crown heels and labial  
250 crown face with strong and narrow labial bulge. The same characteristics differentiate the  
251 Senegalese specimens from *Odontaspis holmdelensis* Cappetta and Case, 1975 and *Odontaspis*  
252 *hardingi* Cappetta and Case, 1975, along with their smooth lingual face. The specimens described  
253 here also bear resemblances with anterior teeth of *Serratolamna serrata* (Agassiz, 1843) (see  
254 Arambourg, 1952), but differ from the latter in being more symmetrical and gracile with more  
255 slender and elongate root branches. The three anterior teeth reported here most closely resemble  
256 those of *Carcharias heathi* Case and Cappetta, 1997. However, the latter differ in being more robust  
257 with a flat labial crown face, while the Senegalese specimens display a marked vertical convexity.  
258 Cuny et al. (2012) reported two teeth as *Carcharias cf. heathi*, but these show no marked labial  
259 crown bulge and display a flat labial crown face.

260

261 Family Otodontidae Glickman, 1964

262 Genus *Cretolamna* Glickman, 1958

263 *Cretolamna maroccana* (Arambourg, 1935)

264 Fig. 3G-J

265 For synonymy, see Case and Cappetta (1997), and add:

266 2014 *Cretolamna maroccana* (Arambourg); Cappetta et al., fig. 6I-K.

267 2017 *Cretolamna maroccana* (Arambourg); Case et al., p. 69, fig. 3E.

268 Material. Two teeth (SN2012-51-52) from the yellow calcareous sandstone bed of Unit 1, Paki  
269 Formation.

270 Description. The lower anterior tooth (Fig. 3G-H) displays a triangular main cusp flanked by a pair of  
271 lateral cusplets and an additional outer pair of incipient cusplets. The main cusp is biconvex, the  
272 lingual face being more developed. The apical region of the main cusp is missing. Strong sharp cutting  
273 edges are present on the main cusp and are separated from the less marked cutting edges of the  
274 cusplets by a deep but narrow notch. The cusplets are broad, triangular and diverging, the distal one  
275 being more bent marginally. The pair of incipient outer cusplet is poorly separated from the inner  
276 cusplets by a shallow notch. The cusplets are positioned in a more labial position than the main cusp  
277 and extend over the basal end of the cutting edges of the main cusp, forming a large notch in labial  
278 view. The base of the labial crown face shows a bulge that is more marked in the central region,

279 where the basal outline of the crown is concave and bears numerous short vertical folds. The root is  
280 robust with root branches oriented labially. The distal branch is slightly shorter and thinner than the  
281 mesial one. A shallow and short nutritive notch is present but damaged in the area of the central  
282 foramen. Numerous oval foramina of varying sizes are present immediately below the basal bulge of  
283 the labial crown face. The lower lateral tooth (Fig. 3I-J) differs from the anterior in being lower, more  
284 robust, and more mesio-distally developed. The root is mesio-distally expanded, labio-lingually  
285 compressed in its mesial and distal extremities, and the surface of the basal face is irregular. The  
286 margino-labial angle of the root is slightly acute in basal view and oriented lingually.

287 Remarks. This species is restricted to the Maastrichtian and was reported from Morocco (Arambourg,  
288 1952, 1935; Cappetta et al., 2014; Noubhani and Cappetta, 1997), the Democratic Republic of Congo  
289 (Darteville and Casier, 1943), United States (Case et al., 2017; Case and Cappetta, 1997; Welton and  
290 Farish, 1993), and Madagascar (Gottfried et al., 2001). Among previous records, those based on fine  
291 stratigraphic framework suggest that this species might be restricted to the Upper Maastrichtian  
292 (Case and Cappetta, 1997). Its occurrence in the lower Maastrichtian of Israel as *Cretalamna*  
293 *biauriculata maroccana* is not supported by illustrations (Lewy and Cappetta, 1989).

294

295 Family Serratolamnidae Landemaine, 1991

296 Genus *Serratolamna* Landemaine, 1991

297 *Serratolamna serrata* (Agassiz, 1843)

298 Fig. 3K-T

299 For synonymy, see Hoganson et al. (2019), and add:

300 ? 2012 *Cretalamna* cf. *C. biauriculata* (Wanner, 1902); Cuny et al., p. 108, Fig. 3A-I.

301 Material. Seven teeth (including SN2012-53-57) from the yellow calcareous sandstone bed of Unit 1,  
302 Paki Formation.

303 Description. Anterior teeth (Fig. 3M-N) are higher than broad and can reach 25 mm in total height.  
304 The main cusp is triangular and biconvex, although this convexity is more marked in the lingual face.  
305 A pair of broad, triangular, and diverging cusplets is present, separated from the sharp cutting edges  
306 of the main cusp by a narrow notch. The basal edge of the lingual crown face displays a distinct  
307 collar. The basal edge of the labial crown face is developed and strongly overhangs the root,  
308 especially in the medio-labial area where the depression of the basal edge is acute. The root is  
309 strongly asymmetrical with the distal lobe being broad and distally oriented with squared extremity,

310 whereas the mesial lobe is short, basally oriented with an acute extremity. Both lobes are separated  
311 by a broad concavity of the basal root edge. Several foramina open below the labial bulge, the largest  
312 and most oval-shaped one being restricted to the medio-labial region. The lingual root face is low  
313 and can overhang the crown at the level of the cusplets in basal view. A moderate lingual  
314 protuberance is present with a distinct nutritive groove. Teeth from lateral files (Fig. 3K-L, O-T) are  
315 more mesio-distally developed and more asymmetrical than anterior ones. Up to three pairs of  
316 cusplets can be observed, the distal ones being more developed and more diverging. The root lobes  
317 are mesio-distally oriented with squared extremities. A notch is frequently present near the distal  
318 and mesial extremities of the basal edge of the lingual face.

319 Remarks. This species has a wide palaeogeographical range but is restricted to the Maastrichtian  
320 (Hoganson et al., 2019). In Senegal, *S. serrata* was previously reported from Unit 3 of the Cap de Naze  
321 Formation based on a single tooth (Cuny et al., 2012) and the specimens described here extend the  
322 stratigraphic range of this species to Unit 1 (Paki Formation). However, some additional specimens  
323 reported by Cuny et al. (2012) from Unit 3 were tentatively assigned to juvenile individuals of  
324 *Cretolamna* cf. *biauriculata*, although the authors noted the strong resemblances with *S. serrata*,  
325 differing only in being more symmetrical with a less slender main cusp. Arambourg (1952; pl. 16, figs  
326 31-32, 37-40) illustrated small-sized *S. serrata* specimens from Morocco that display similar  
327 morphologies and symmetry to the specimens from Senegal reported by Cuny et al. (2012). It is  
328 therefore likely that the small teeth reported from Unit 3 by Cuny et al. (2012) actually represent  
329 juvenile teeth of *S. serrata*.

330 **[FIGURE 3 HERE]**

331

332 Super-order Batomorphii Cappetta, 1980

333 Order Rajiformes Berg, 1940

334 Sub-Order Sclerorhynchoidei Cappetta, 1980

335 Family Sclerorhynchidae Cappetta, 1974

336 Genus *Dalpiazia* Checchia-Rispoli, 1933

337 *Dalpiazia stromeri* Checchia-Rispoli, 1933

338 Fig. 4A-J

339 1902 *Problematicum*, Quaas, p. 320, pl. 28, fig. 15.

- 340 1933 *Dalpiazia stromeri* Checchia-Rispoli, p. 7, pl. 1.
- 341 1935 *Onchosaurus maroccanus* Arambourg, p. 421, pl. 19, fig. 8.
- 342 1940 *Onchosaurus maroccanus* Arambourg; Arambourg, p. 143, pl. 3, figs. 2-5.
- 343 1943 *Onchosaurus manzadinensis* Darteville & Casier, p. 166, pl. 14, figs. 1-8, text-fig. 55.
- 344 1952 *Onchosaurus (Ischyrhiza) maroccanus* Arambourg; Arambourg, p. 191, pl. 19, figs. 34-43.
- 345 1972 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 198, pl. 4, fig. 8 and pl. 13, figs. 11-12.
- 346 1987 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 147, p. 148, fig. 125.
- 347 1991a *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 23, pl. 4, fig. 1-8.
- 348 1997 *Dalpiazia stromeri* Checchia-Rispoli; Noubhani & Cappetta, p. 138, Tab. 4 (name only).
- 349 1999 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta & Corral, p. 362, pl. 3, fig. 9.
- 350 2000 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta et al., p. 85 (name only).
- 351 2000 *Dalpiazia stromeri* Checchia-Rispoli; Bardet et al., p. 273, Tab. 1 (name only).
- 352 2012 *Dalpiazia stromeri* Checchia-Rispoli; Cappetta, p. 375, fig. 363.

353 Material. Eight teeth (including SN2012-58-60) from Unit 3, Cap de Naze Formation.

354 Description. Teeth of this species are higher than wide, not exceeding 0.7mm in height and show a  
355 strong degree of heterodonty. Possible anterior teeth (Fig. 4A-D) are symmetrical and strongly  
356 cuspidate. The crown bears a wide and strongly lingually-oriented main cusp bearing incipient cutting  
357 edges that become more marked in its basalmost region and run continuously over the heels until  
358 the marginal angles. The heels are rather developed laterally, lingually oriented and only slightly  
359 inclined basally. The labial crown face displays a marked but somewhat narrow vertical medio-labial  
360 protuberance that develops basally below the basal edge of the heels and overhangs the crown/root  
361 edge in occlusal view. The medio-labial protuberance bears a vertical ridge that originates in the  
362 lower half of the main cusp and tapers before reaching the basal edge of the labial crown face. The  
363 lingual crown face is smooth and slightly protrudes medially where it is nearly flat. The crown/root  
364 edge is narrow but the basal region of the root is flared at all points in occlusal view. The crown is  
365 high and labio-lingually elongated. In basal view, the root lobes are separated by a groove that is  
366 partially closed in the median region but broadens towards the lingual and labial edges, forming a  
367 wide triangular notch in the latter. A wide central foramen opens lingually at the bottom of the  
368 nutritive groove. In basal view, the root lobes are more mesio-distally developed in their labial half

369 than in their lingual region. In the latter, the basal face is inclined basally whereas this inclination only  
370 involves the margino-labial edges of the labial region, which is otherwise flat. The medio-lingual root  
371 protuberance is moderate and wide. Both the labial and lingual root faces are concave. Up to two  
372 foramina are present on the flared area of each margino-lingual face, the foramina placed in  
373 lingualmost position being larger. Teeth from supposed more lateral files (Fig. 4E-J) are smaller with a  
374 shorter triangular main cusp. The heels are less laterally expanded, more strongly inclined basally  
375 and broadly united to the main cusp. The medio-labial protuberance of the crown is absent or  
376 residual and the medio-lingual crown protuberance is faint. Labial crown ornament is stronger and  
377 consists of several vertical ridges that originate at the base of the main cusp and do not reach the  
378 basal crown edge. The root has a wider mesial lobe in basal view and wider nutritive groove.

379 Remarks. The genus *Dalpiazia* includes the Maastrichtian type species *D. stromeri* as well as *D. indica*  
380 (Chiplonkar and Ghare, 1977), which is known from a single rostral denticle from the Cenomanian–  
381 Turonian Bagh Beds of NW India. Although *D. stromeri* is common in Tethyan and Eastern Atlantic  
382 deposits (RDC, Niger, Morocco, Libya, Egypt, Jordan, Syria, Spain), these occurrences are mostly  
383 based on rostral denticles. Some of these were referred to different species (*Onchosaurus*  
384 *maroccanus* Arambourg, 1935 and *Onchosaurus nzadinensis* Darteville and Casier, 1943), but these  
385 should be considered junior synonyms of *D. stromeri* (Cappetta, 2006, 1972). Oral teeth have only  
386 been described in detail by Cappetta (1991a) based on specimens from the Maastrichtian of Egypt  
387 and on the co-occurrence of oral sclerorhynchiform teeth with *D. stromeri* rostral denticles in a lower  
388 Maastrichtian assemblage from Oued Erguita (Morocco). Cappetta (1991a) noted that the crown  
389 morphology of teeth from Egypt display a stronger variability (medio-lingual protuberance present or  
390 absent and varying degree of labial ornament) than the specimens from Morocco, which constantly  
391 bear a medio-lingual protuberance and no labial folds. In addition, the lingual crown face of  
392 specimens from Egypt is characterized by a pair of short but sharp vertical ridges on each sides of the  
393 base of the main cusp, a feature that is not present in the Moroccan specimens, according to  
394 Cappetta (1991a). The specimens reported here, albeit few, comprise some teeth with a smooth  
395 crown and marked medio-lingual protuberance bearing a single vertical ridge as well as teeth devoid  
396 of a medio-lingual crown protuberance and numerous vertical folds of the labial face. This suggests  
397 that the variation observed among and between the populations from Egypt, Morocco, and Senegal  
398 correspond to a single species with high variation in tooth morphology. However, no rostral denticles  
399 were recovered in our samplings and therefore we cannot confirm the attribution of the oral teeth of  
400 the morphology described here and in Cappetta (1991a) to *D. stromeri*, although the arguments  
401 provided by Cappetta (1991a) are convincing and are followed here pending additional data.

402

403 Genus *Ctenopristis* Arambourg, 1940

404 *Ctenopristis nougareti* Arambourg, 1940

405 Fig. 4K-L

406 1940 *Ctenopristis nougareti* Arambourg, p. 137, fig. 11, p. 138, fig. 12, pl. 4, figs 4-5, 7.

407 1952 *Ctenopristis nougareti* Arambourg; Arambourg, p. 194, pl. 29, figs 3-11.

408 1959 *Ctenopristis nougareti* Arambourg; Darteville & Casier, p. 324, pl. 32, figs 1-4.

409 1959 *Ctenopristis nougareti* Arambourg; Signeux, p. 237, pl. 9, fig. 16.

410 1987 *Ctenopristis nougareti* Arambourg; Cappetta, p. 147, fig. 124.

411 2012 *Ctenopristis nougareti* Arambourg; Cappetta, p. 373, fig. 362.

412 Material. Four incomplete rostral denticles (including SN2012-61) from Unit 3, Cap de Naze  
413 Formation.

414 Description. The less damaged specimen preserves a cap lacking most of the cusp that bears  
415 numerous silica grains embedded in the enameloid. The cap is strongly posteriorly oriented and  
416 dorso-ventrally compressed. The crown base is antero-posteriorly elongated with triangular dorsal  
417 and ventral margins in apical view, which confer a lozenge shape to the crown in apical view. The  
418 edges of the basal dorsal and ventral margins are irregular and markedly curved apically to form  
419 ridges, especially in the anterior region. Their posterior, uncurved, region can display a few slight  
420 enameloid protuberances. The anterior angle of the basal crown edge is sharp and connects the  
421 anterior face of the cusp by a very salient cutting edge that is straight to slightly convex in  
422 ventral/dorsal view. The posterior edge of the crown is concave in ventral/dorsal view.

423 Remarks. Although incomplete, these rostral denticles are identical to the type specimens of *C.*  
424 *nougareti* described by Arambourg (1952, 1940) from the Maastrichtian of Morocco. This species has  
425 also been reported from Maastrichtian localities in the Democratic Republic of Congo and Cabinda  
426 enclave (Darteville and Casier, 1959). Although original description and subsequent reports were  
427 based on rostral denticles, teeth were subsequently attributed to this species based on samplings  
428 from Morocco (Herman, 1973). The genus *Ctenopristis* also includes the species *C. jordanicus*  
429 Mustafa, Case and Zalmout, 2002, which was described from the Santonian of Jordan and  
430 subsequently reported from the Coniacian-Santonian of Turkey (Yilmaz et al 2018). This species is  
431 only known by teeth and it is therefore impossible to compare the rostral denticles of *C. nougareti*.  
432 Numerous other reports of *Ctenopristis* rostral denticles and/or teeth have been made, especially



433 from the Maastrichtian (Bardet et al., 2000; Cappetta, 1991a; Cappetta et al., 2000; Signeux, 1959)  
434 and Campanian (Lewy and Cappetta, 1989) of the Middle East. However, these reports did not  
435 provide illustrations of the specimens and it is therefore impossible to compare them with the type  
436 series of Arambourg (1940).

437 **[FIGURE 4 HERE]**

438

439 Subfamily Schizorhizinae Kirkland & Aguilón-Martinez, 2002

440 Genus *Schizorhiza* Weiler in Stromer & Weiler, 1930

441 *Schizorhiza stromeri* Weiler in Stromer & Weiler, 1930

442 Fig. 5A-O

443 1930 *Schizorhiza stromeri* Weiler in Stromer & Weiler, p. 20-23, pl. 2, figs. 1-8, pl. 4, figs 2-4.

444 1933 *Schizorhiza weileri* Serra, p. 103-108, figs 1-7.

445 1934 *Schizorhiza stromeri* Weiler; White, pl. 3, figs 2-4 *non* figs 5-6.

446 1940 *Schizorhiza* aff. *weileri* Serra; Arambourg, p. 143, pl. 3, fig. 10-12 et p. 132, fig. 6.

447 1943 *Schizorhiza stromeri* Weiler; Darteville & Casier, p. 168, pl. 14, figs 10-16.

448 1948 *Schizorhiza* cf. *weileri* Serra; Dunkle, p. 174-175, fig. 2.

449 1952 *Schizorhiza stromeri* Weiler; Arambourg, p. 193-194, pl. 29, figs 12-20.

450 1959 *Schizorhiza stromeri* Weiler; Signeux, p. 237, pl. 9, fig. 17.

451 1972 *Schizorhiza stromeri* Weiler; Cappetta, p. 199, pl. 4, figs 9-10

452 1987 *Schizorhiza stromeri* Weiler; Cappetta, p. 155, fig. 133.

453 1991a *Schizorhiza stromeri* Weiler; Cappetta, p. 24, pl. 5, figs 1-6.

454 1991b *Schizorhiza* aff. *stromeri* Weiler; Cappetta, p. 436, fig. 1.

455 1993 *Schizorhiza* aff. *stromeri* Weiler; Gayet et al., fig. 6E.

456 1993 *Schizorhiza* cf. *weileri* Serra; Welton & Farish, p. 145, figs 1, 2.

457 2000 *Schizorhiza stromeri* Weiler; Cappetta et al., p. 85 (name only).

458 2000 *Schizorhiza stromeri* Weiler; Bardet et al., Tab. 1 (name only).

459 2002 *Schizorhiza stromeri* Weiler; Kirkland & Aguillon-Martinez, p. 22, figs 2, 5-11.

460 2006 *Schizorhiza cf. stromeri* Weiler; Becker et al., p. 709, figs 4.17-4.19.

461 2007 *Schizorhiza stromeri* Weiler; Knight et al., p.88, fig. 1A-B.

462 2012 *Schizorhiza stromeri* Weiler; Cappetta, p. 388, figs 376-377.

463 2012 *Schizorhiza stromeri* Weiler; Cuny et al., p. 111, fig. 3Y-AA.

464 2014 *Schizorhiza stromeri* Weiler; Cappetta et al., p. 224, tab. 1 (name only).

465 Material. Three fragmentary rostral denticles and eight teeth (including SN2012-62-65) from Unit 3,  
466 Cap de Naze Formation, and one rostral denticle (SN2012-66) from the yellow calcareous sandstone  
467 bed of Unit 1, Paki Formation.

468 Description. The teeth are higher than broad, do not exceed 2 mm high and show some degree of  
469 heretodonty. The cuspidate crown is triangular in labial view and strongly bent lingually. In anterior  
470 teeth (Fig. 5A-D), the labial crown face slightly overhangs the root and is strongly convex in profile  
471 view. The basal region of the labial crown face can bear a pair of slight oblique folds situated below  
472 the marginal angles or a single median vertical ridge. The lingual crown face is smooth and strongly  
473 concave in profile view. The cutting edges are variably present in the upper half of the main cusp but  
474 are consistently present in its lower part where they diverge and become more developed to form  
475 incipient and abrupt heels. The heels of one specimen display a pair of short and broad incipient  
476 cusplets with the distal one being slightly more developed. The root is moderately high with strongly  
477 convex basal face and flared lingual and marginal regions, whereas the labial face is nearly flat. The  
478 root is anaulacorhize with a very shallow nutrient canal except near the labial and lingual edges of  
479 the basal face. The nutrient canal opens labially into a wide circular median foramen and lingually  
480 into a large oval-shaped and rather high median foramen. Lateral teeth (Fig. 5E-J) are less mesio-  
481 distally compressed, with cutting edges of regular development from the apex to the base of the  
482 cusp and no demarcated heels. These teeth further show a less marked constriction of at the  
483 crown/root edge and less marked bulge of the labial crown face.

484 The rostral denticle displays a strongly dorsoventrally compressed and lozenge-shaped crown in  
485 dorsal/ventral view. The crown is lower than the root, with sharp and rectilinear cutting edges. The  
486 root is bilobate with lobes (one lacking) separated by a deep V-shaped notch. The root is narrower in  
487 its upper region below the crown than in its lower region, where vertical undulations are present.

488 Remarks. *Schizorhiza* is a monospecific genus that was only known by its highly characteristic rostral  
489 denticles until Cappetta (1991a, 1991b) associated teeth of *S. stromeri* to rostral denticles based on

490 material from Bolivia and Egypt. Since then, rostral denticles of *S. stromeri* have been reported from  
491 numerous Maastrichtian localities worldwide but teeth were not recorded. Additionally, Kirkland and  
492 Aguilòn-Martínez (2002) reported a fragmentary rostrum with associated denticles from the  
493 Uppermost Campanian Cerro de Pueblo Formation, Mexico. The morphology of the teeth described  
494 here complies with that of teeth reported from Egypt and only differ in the presence of incipient  
495 cusplets on one tooth, which probably falls within the intraspecific morphological variation of this  
496 species. Two rostral denticles were reported by Cuny et al. (2012) from the Unit 3 of the Cap de Naze  
497 Formation. The teeth reported here from the Unit 3 add to the description of the Senegalese  
498 population of this species from Unit 3, and the rostral denticle from Unit 1 extends the stratigraphic  
499 distribution of this species lower in the Cap de Naze series.

500

501 Family Ptychotrygonidae Kriwet, Nunn and Klug, 2009

502 Genus *Ptychotrygon* Jaekel, 1894

503 *Ptychotrygon nazeensis* sp. nov.

504 LSID: urn:lsid:zoobank.org:act:31ABD242-4463-43BE-B9EA-7D1E5DE247B6

505 Fig. 5P-T

506 Derivation of name. After the Cap de Naze, the name of the type locality.

507 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
508 Maastrichtian.

509 Diagnosis. Ptychotrygonid species with sub-oval to triangular teeth not exceeding 2 mm in width.  
510 Crown low, mesio-distally elongated and devoid of main cusp. Wide and high transverse crest  
511 separating the lingual and labial faces and not reaching the marginal angles. Coarse secondary crest  
512 in the middle of the labial face not reaching the marginal angles nor the extremities of transverse  
513 crest. Acute and triangular labial crown edge with narrow and rounded apron projecting labially and  
514 basally. Few short and coarse ridges between secondary crest and labial crown edge. Upper region of  
515 lingual crown face concave and inclined; flat and abrupt lower region. Marked horizontal lingual ridge  
516 not reaching marginal angles. Wide and rather short uvula with rounded lower edge. Root  
517 holaulacorhize, moderately high with triangular, inclined and slightly flared basal lobe faces. Wide  
518 nutritive groove with central foramen. Pair of margino-lingual foramina and slightly scalloped basal  
519 edge lingual root face.

520 Material. One tooth (SN2012-67, holotype) from Unit 3, Cap de Naze Formation.

521 Description. This low-crowned tooth is mesio-distally elongated with a sub-oval and slightly  
522 asymmetrical outline in occlusal view. The crown overhangs the root at all points and displays a wide  
523 and high transverse crest that separates the lingual and labial faces. The extremities of the transverse  
524 crest are slightly curved labially towards the wide marginal angles, where they taper. A secondary  
525 crest is present on the middle of the labial face and is curved labially towards the apron in occlusal  
526 view. The extremities of the secondary crest do not reach the marginal angles and taper before  
527 reaching the extremities of the transverse crest. The labial crown edge is acute and triangular in  
528 occlusal view. A narrow and rounded apron projects labially and basally. Few short and coarse ridges  
529 connect the secondary crest with the labial crown edge. In profile view, the lingual crown face is  
530 divided into a concave and inclined upper region and a flat and abrupt lower region by a marked  
531 horizontal ridge that does not reach the marginal angles. The lower region of the lingual crown face  
532 bears a wide but rather short uvula with a rounded lower edge that is slightly oriented distally. The  
533 uvula is only slightly demarcated from the rest of the crown with wide and shallow concavities in  
534 lingual view. The holaulacorhize root is moderately high with triangular and slightly flared basal faces  
535 of the root lobes, which are somewhat inclined. The lobes are separated by a wide nutritive groove in  
536 the middle of which opens a foramen. The margino-lingual faces bear a foramen and the basal edge  
537 of the lingual root face is slightly scalloped. Several foramina open on the basal root face, close to the  
538 labial edge and marginal-angles.

539 Remarks. *Ptychotrygon* is a genus of sclerorhynchiform skates with denticle-free rostra (Villalobos-  
540 Segura et al., 2021, 2019) that includes over 20 named species and ranges from the Albian to the  
541 Maastrichtian of Europe, Africa and the Near East as well as N. America, where most Campanian-  
542 Maastrichtian records originate. Teeth of *Ptychotrygon nazeensis* sp. nov. differ from those of other  
543 *Ptychotrygon* and ptychotrygonid taxa (*Texatrygon* Cappetta & Case, 1999, *Asflapristis* Villalobos-  
544 Segura, Underwood, Ward and Cleason, 2019, *Ptychotrygonoides* Landemaine, 1991, *Iberotrygon*  
545 Kriwet, Nunn and Klug, 2009) in exhibiting the following combination of characters: non-cuspidate  
546 crown with low and flat labial face and very weakly ornamented crown. Teeth of *Erguitaia misrensis*  
547 Cappetta, 1991a from the Maastrichtian of Egypt display resemblances with *Ptychotrygon nazeensis*  
548 sp. nov. but differ in having a much higher uvula, a more developed apron, more ornamented lingual  
549 and labial crown faces and no secondary crest. The Cenomanian species *Libanopristis hiram* (Hay,  
550 1903) is known from articulated skeletons with denticle-bearing rostra from Lebanon (Cappetta,  
551 1980), and its teeth display several similarities with those of *Ptychotrygon nazeensis* sp. nov.  
552 However, teeth of the Lebanese species are more cuspidate with a blunt labial crown edge, whereas  
553 it exhibits a ridge in *Ptychotrygon nazeensis* sp. nov. The genus *Ptychotrygon* has been reported from  
554 Maastrichtian deposits of Morocco, Jordan and Egypt (Cappetta, 1991a; Cappetta et al., 2000;

555 Noubhani and Cappetta, 1997) but corresponding specimens have not been illustrated. However,  
556 *Ptychotrygon nazeensis* sp. nov. is likely present in the Upper Maastrichtian assemblage from Imin  
557 Tanout, Morocco (GG pers. obs.).

558 **[FIGURE 5 HERE]**

559

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

561 Suborder Rhinobatoidei Fowler, 1941

562 Family Rhynchobatidae Garman, 1913

563 Genus cf. *Rhynchobatus* Müller & Henle, 1837

564 cf. *Rhynchobatus* sp.

565 Fig. 6A-B

566 Material. One tooth (SN2012-68) from Unit 3, Cap de Naze Formation.

567 Description. This tooth preserves the crown and a small part of the root. The crown is 2 mm wide and  
568 displays a large and slightly convex labial face with an abrupt labial edge in profile view. The labial  
569 face is separated from the lingual one by a rather wide and shallow transverse crest. The crest is  
570 lingually convex and reaches the marginal angles of the crown. Below the crest, the upper region of  
571 the lingual crown face is triangular flat and oblique. The lower region of the lingual crown face is  
572 concave in profile view and made of a wide and moderately elongate median uvula and rather high  
573 margino-lingual faces. In lingual view, the mesial and distal edges of the margino-lingual faces are  
574 slightly concave. The median uvula is triangular and projects lingually relatively to the margino-  
575 lingual faces. A pair of margino-lingual foramina is present.

576 Remarks. Although incomplete, this tooth displays a combination of crown characters that is typical  
577 of teeth of living and fossil *Rhynchobatus* species: convex labial face, transverse crest, triangular  
578 oblique and flat upper lingual face region, lower region with moderately developed median uvula, no  
579 marginal uvulae. However, the tooth described here departs from those of *Rhynchobatus* species by  
580 its much wider uvula and absence of crown ornament, whereas *Rhynchobatus* teeth display a typical  
581 ornamentation on the labial and upper lingual region. This specimen likely represents a new  
582 rhynchobatid genus and species. This taxon would represent the oldest record of the family  
583 Rhynchobatidae, which was so far unknown prior to the Ypresian (Cappetta, 2012), although the

584 genus *Rhynchobatus* has been reported without illustrations from the Maastrichtian of Morocco  
585 (Noubhani and Cappetta, 1997).

586

587 Family Rhinobatidae Garman, 1913

588 Genus *Terangabatis* gen. nov.

589 Type species. *Terangabatis thiami* gen. et sp. nov.

590 Derivation of name. From the Wolof word “Teranga” (hospitality in Wolof, a word that is often used  
591 to define the Senegalese lifestyle and philosophy) and *batis* (ray/skate in ancient Greek).

592 Diagnosis. Rhinobatid with teeth showing moderate degree of monognathic heterodonty. Non-  
593 cuspidate teeth broader than long; crown with transverse crest separating lingual and labial crown  
594 faces. Transverse crest slightly convex lingually reaching the marginal angles. Crown bulged in the  
595 median area of the crest. Labial crown face concave near the transverse crest, convex near the  
596 developed labial crown margin. No apron differentiated. Marginal angles wide and obtuse. Lingual  
597 crown face very abrupt; reduced margino-lingual faces; slightly lingually protruding median region  
598 extended basally into a uvula. Median region of lingual crown face with vertical depression bordered  
599 by bulged and V-shaped margins of uvula. Uvula wide and triangular not reaching the basal root face.  
600 Root holaulacorhize, less than half the total tooth height and overhung by the crown. Pair of large  
601 oval margino-lingual foramina; additional foramina occasionally present.

602 Remarks. The tooth morphology of this taxon can be separated from that of other rhinoprists and  
603 rhinopristsiforms by the following combination of characters: mesio-distally elongate and labio-  
604 lingually compressed crown, non-cuspidate crown, flat to concave lingual crown face, median uvulae  
605 wide with vertical concavity and broadly attached to marginal faces (no notches), reduced margino-  
606 lingual faces with no developed marginal uvulae.

607

608 *Terangabatis thiami* gen. et sp. nov.

609 LSID: urn:lsid:zoobank.org:act:FF66D7CE-641F-4A75-BDEF-5B789CC486D0

610

Fig. 6C-K

611 Derivation of name. After Dr. Mouhamadou Moustapha Thiam (Institut des Sciences de la Terre,  
612 Cheikh Anta Diop University, Dakar) for his participation in the fieldwork.

613 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
614 Maastrichtian.

615 Diagnosis. As for genus.

616 Material. Four teeth (SN2012-69-72) from Unit 3, Cap de Naze Formation.

617 Description. Teeth from anterior jaw positions (Fig. 6C-I) are broader than long and do not exceed 2  
618 mm in width. The crown exhibits a transverse crest that separates the lingual and labial crown faces  
619 and reaches the marginal angles. The transverse crest is slightly convex lingually in labial view and  
620 the crown is bulged in the median area of the crest. In profile view, the labial crown face is concave  
621 in the vicinity of the transverse crest and convex near the labial margin of the crown, which is devoid  
622 of apron. The labial crown edge is rounded and strongly overhangs the root in profile view. The  
623 marginal angles are wide and obtuse in labial view. The lingual crown face is overall abrupt and made  
624 of reduced margino-lingual faces and a slightly lingually protruding median region extended basally  
625 into a uvula. The lateral edge of the margino-lingual faces is convex, while their lower margin is  
626 straight to slightly convex in lingual view. The median region of the lingual crown face displays a  
627 vertical depression that is bordered by bulged and V-shaped edges of the uvula, which diverge and  
628 taper towards the margino-lingual faces. The uvula is wide and triangular and does not reach the  
629 basal root face. The uvula is separated from the lower edges of the margino-lingual faces by wide  
630 and shallow concavities. The root is holaulacorhize and accounts for less than half the total height of  
631 the tooth. The root is positioned lingually and is overhung by the crown at all points in occlusal view.  
632 The marginal root edges are straight and slightly diverging basally in lingual view. In basal view, the  
633 root lobes are L-shaped with lingually and labially developed branches, with concave margino-lingual  
634 faces. The basal face of each root lobe is flat to lightly convex and oblique. The lobes are separated  
635 by a large nutritive groove, which hosts a central foramen. Each margino-lingual root faces are  
636 pierced by a large and oval foramen situated below the concavity of the lower crown edge.  
637 Additional small margino-lingual foramina can be present below the margins of the uvula. Teeth from  
638 more lateral jaw positions (Fig. 6J-K) display a similar morphology but show a more convex transverse  
639 crest with a less bulged median region.

640 Remarks. The teeth of this taxon exhibit a peculiar morphology, which makes their identification  
641 easy. Some superficial resemblances can be noted with teeth of species of the Cenomanian genus  
642 *Rhombopterygia* Cappetta, 1980. However, species of the latter genus differ in having a more  
643 lingually protruding and convex medio-lingual crown region, a moderately developed cusp as well as  
644 a convex labial crown face and incipient lateral uvulae. Teeth of some species of the mid to late  
645 Cretaceous *Squatirhina* Casier, 1947 can be easily separated from those of *T. thiami* gen. et sp. nov.

646 by their stronger heterodonty, developed main cusp, ornamented crown and developed apron.  
647 *Terangabatis thiami* gen. et sp. nov. is so far restricted to the type locality.

648 **[FIGURE 6 HERE]**

649

650 Genus *Rhinobatos* Link, 1790

651 '*Rhinobatos*' *popenguinensis* sp. nov.

652 LSID: urn:lsid:zoobank.org:act:62E0D86F-1855-45F8-AD59-6991ADF88B58

653 Fig. 7

654 Derivation of name. After Popenguine, a locality close to the Cape de Naze cliff.

655 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
656 Maastrichtian.

657 Diagnosis. Small rhinopristiform species showing a weak degree of monognathic and possibly sexual  
658 dimorphism. Teeth slightly higher than wide. Crown lozenge-shaped in occlusal view with acute  
659 marginal and medio-labial angles. Transverse crest convex lingually, reaching the marginal angles and  
660 projecting lingually above median uvula. Occasional presence of incipient cusp. Margino-lingual faces  
661 reduced. Short and lingually protruding lateral uvulae. Median uvula strongly lingually projected not  
662 reaching the basal root edge. Profile of median uvula convex medially and near its basal tip; concave  
663 profile below the transverse crest and between the two convexities. Median uvula triangular with  
664 convex lateral margins and a sharp lower extremity; slight flaring of the media uvula below the  
665 notches separating the lateral uvulae in some teeth. Labial visor strongly overhanging the root with  
666 strong and rounded median process. Margino-labial crown edges straight to slightly concave in  
667 occlusal view. Root lingually projected and narrower than the crown. Basal face of root lobes convex  
668 and L-shaped with short marginal projections. Wide nutritive groove with large labial foramen.

669 Material. Twenty-six teeth (including SN2012-73-78) from Unit 3, Cap de Naze Formation.

670 Description. Teeth of this species are slightly higher than wide and do not exceed 1 mm. The crown is  
671 rather low and comprises a developed labial face, a developed median uvula, and reduced lateral  
672 uvulae. The crown is lozenge-shaped in occlusal view with acute marginal and medio-labial angles. A  
673 marked transverse crest separates the lingual and labial crown faces. The crest is convex lingually,  
674 reaches the marginal angles and can project in its median region into an incipient cusp in putative  
675 male individuals. The margino-lingual faces are reduced with oblique marginal edges converging



676 basally as well as very short and lingually protruding lateral uvulae. The lateral uvulae are separated  
677 from the median uvula by a broad notch. The median uvula is strongly lingually projected and does  
678 not reach the basal root edge. In profile view, the median uvula displays a marked medial convexity  
679 separated from the convex basal region by a concavity. The region immediately below the transverse  
680 crest and the medial convexity is also markedly concave in profile view. The median uvula is  
681 triangular in lingual view with convex lateral margins and a rather sharp lower extremity. In some  
682 teeth, there is a slight flaring of the uvula just below the notches separating the lateral uvulae. Most  
683 of the labial crown face is slightly concave in profile view, except its labial visor, which is flat to  
684 convex. The labial visor strongly overhangs the root and displays a strong and rounded median  
685 process that projects both basally and labially. The margino-labial crown edges are straight to  
686 somewhat concave in occlusal view. The root is lingually projected and narrower than the crown. The  
687 labial root face is oblique and the convex basal face of the root lobes is L-shaped with short marginal  
688 projections. The root lobes are separated by a wide nutritive groove at the labial edge of which a  
689 large foramen opens. The depressed margino-lingual root faces host a moderately wide and rounded  
690 foramen. Anterior teeth tend to display a more marked lingual projection of the median uvula,  
691 whereas lateral teeth are slightly lower and more mesio-distally expanded.

692 Remarks. A number of Campanian-Maastrichtian species have been referred to the genus  
693 *Rhinobatos*. However, the tooth morphology of living rhinopristiform species is imperfectly known  
694 (Guinot et al., 2018) and many Cretaceous species included in this genus might belong to new genera  
695 (Cappetta, 2012). Among described *Rhinobatos* species, teeth of '*R.*' *popenguinensis* sp. nov. are  
696 morphologically close to those of *R. ibericus* Cappetta and Corral, 1999 from the Maastrichtian of  
697 Spain but differ from the latter by their more acute marginal angles of the crown, sharper and more  
698 protruding apron as well as broader and more triangular uvula. '*Rhinobatos*' *popenguinensis* sp. nov.  
699 differs from *Rhinobatos echavei* Cappetta and Corral, 1999 from the Maastrichtian of Spain by its  
700 teeth with more acute marginal angles of the crown, transverse crest with short cusp, sharp apron,  
701 marginal edges of margino-lingual faces oblique and converging basally, and smaller size. Teeth of  
702 the new Senegalese species can be separated from numerous *Rhinobatos* species with developed  
703 lateral uvulae (e.g., *R. casieri* Herman in Cappetta and Case, 1975; *R. ladoniaensis* Cappetta and Case,  
704 1999) by their reduced lateral uvulae, triangular labial crown edge and much smaller size. Teeth of *R.*  
705 *craddocki* Case and Cappetta, 1997 differ in having a lower lingual crown face with shorter uvula that  
706 is more broadly united to the margino-lingual faces, more flared and labially oriented margino-lingual  
707 crown faces, more mesio-distally developed crown, less lingually projected medio-lingual region.  
708 Teeth of *R. uvulatus* Case and Cappetta, 1997 can be separated from those of '*R.*' *popenguinensis* sp.  
709 nov. by their uncuspidate crown with more rounded marginal angles and labial crown edge, and less

710 protruding central uvula with a rectilinear profile. *Rhinobatos mariannae* Bor, 1983 differs by its  
711 teeth with higher margino-lingual faces, less marked transverse crest with convex extremities near  
712 the marginal angles, less acute and oblique marginal angles, presence of lingual ornament and more  
713 rounded extremity of uvula. Teeth of 'R.' *popenguinensis* sp. nov. differ from those of  
714 *Rhombopterygia* in having a lozenge-shaped labial face, straight margino-labial crown edges, convex  
715 medio-lingual region in profile view, acute marginal angles of the crown. '*Rhinobatos*' *popenguinensis*  
716 sp. nov. is possibly closely related to *R. ibericus* and probably belongs to a new rhinobatid genus, but  
717 more knowledge is needed on living rhinobatid taxa before drawing such conclusions.

718 **[FIGURE 7 HERE]**

719

720

Rhinopristiformes *incertae familiae*

721

Genus *Atlantobatis* gen. nov.

722

Derivation of name. After the geographic distribution of species of this genus.

723

Type species. *Hamrabortis weltoni* Case & Cappetta, 1997.

724

Diagnosis. Same as for type species.

725

Remarks. *Hamrabortis weltoni* was described from the Late Maastrichtian (Navarroan), Kemp Clay

726

Formation in Texas (South Sulphur River, near Commerce, Hunt County). This species was referred to

727

the genus *Hamrabortis* based on superficial resemblances with *H. ornata* Cappetta, 1991a, the type

728

species of the genus. However, the morphology of the type specimens of *Hamrabortis weltoni* departs

729

from that of *H. ornata* teeth in having a more developed labial protuberance of the labial crown

730

margin, a higher crown, much higher occlusal face, higher lingual crown face, crown with irregular

731

ornament not reticulate nor alveolate, less acute marginal angles, more constricted root near the

732

crown, and no margino-lingual foramina. Teeth of *Archingeayia* Vullo, Cappetta and Néraudeau,

733

2007 share similar crown characters with *Atlantobatis* gen. nov., but differ by the absence of labial

734

ornament, different lingual ornament, lingual occlusal region and lingual crown faces abrupt and in

735

the same plane in profile view, lingual face much shorter and restricted to a bulge-like lingual crest,

736

and more developed cusp. The genus *Hamrabortis* should now be restricted to the type species from

737

the Maastrichtian of Egypt and *H. bernardezi* Vullo, Cappetta and Néraudeau, 2007 from the

738

Cenomanian of France and Spain. A putative additional, unnamed *Hamrabortis* species with a weakly

739

ornamented crown is probably present in the Maastrichtian of Syria (Bardet et al., 2000). The genus

740 *Atlantobatis* gen. nov. described here includes the type species as well as a new species described  
741 below, and is so far restricted to the Maastrichtian of the Atlantic Ocean.

742

743 *Atlantobatis acrodonta* gen. et sp. nov.

744 LSID: urn:lsid:zoobank.org:act:4D98EAFC-1DCA-4D59-A339-A3691C6FB81F

745 Fig. 8

746 Derivation of name. After the high-crowned teeth of this species.

747 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
748 Maastrichtian.

749 Diagnosis. Teeth broader than high; triangular crown in occlusal view with elliptical occlusal crown  
750 face. Thick transverse crest, sub-horizontal or convex in its medial region, situated below the  
751 marginal angles in lingual view. Lingual crown face high, abrupt, and concave in profile view with  
752 marked median articular concavity and faint median uvula. Occlusal face is high, labio-lingually  
753 compressed, and triangular in lingual view. Sharp and lingually-projected occlusal crest connecting  
754 the transverse crest lingually and separating the occlusal face into lingual and labial areas. Lingual  
755 area concave with light irregular ornament. Labial area of occlusal face convex with short and rather  
756 coarse vertical folds near basal edge. Coarsely ornamented labial crown face separated from occlusal  
757 face by an irregular secondary crest. Labial crown face with very developed median protuberance.  
758 Root low, bilobate and narrower near the crown. Root lobes triangular with rounded angles in basal  
759 view. Root lobes varying from as broad as long to mesio-distally expanded. Nutritive groove wide and  
760 rather deep with central foramen in labial position.

761 Material. Forty-one teeth (including SN2012-79-86) from Unit 3, Cap de Naze Formation.

762 Description. These teeth are broader than high and do not exceed 1.5 mm in width. In occlusal view,  
763 the crown is triangular and overhangs the root at all points. The occlusal crown face is elliptical and  
764 bordered lingually by a marked and thick transverse crest situated below the marginal angles in  
765 lingual view. The crest can be sub-horizontal or convex in its medial region, and its marginal  
766 extremities are oblique as they reach the marginal angles. This crest is in continuity with the sharp  
767 ridge that runs along the labial crown edge. The marginal angles are rounded and rather wide. Below  
768 the transverse crest, the lingual crown face is well developed, abrupt, and concave in profile view. A  
769 marked median articular concavity is present and the basal edge of the lingual crown face is  
770 triangular with a faint uvula that is individualized from the rest of the basal edge by broad

771 concavities. The occlusal face is very high, labio-lingually compressed, and triangular in lingual view.  
772 The occlusal face bears a sharp and lingually-projected occlusal crest that is slightly lingually  
773 positioned. The extremities of the occlusal crest are lingually oriented and connect the transverse  
774 crest on the lingual face, just before the marginal angles. The occlusal crest separates the occlusal  
775 face into two areas linguo-labially. The lingual area is concave in profile view, excepted medially  
776 where it is flat, and bears light irregular ornament that tend to arrange into apico-basally oriented  
777 wrinkles near the basal edge. The labial area of the occlusal face is convex in occlusal view and  
778 displays short and rather coarse vertical folds in its basal edge. This ornament is coarser on the labial  
779 crown face, which can be separated from the occlusal face by an irregular secondary crest. This  
780 secondary crest, when present, bifurcates from the labial ridge that runs along the labial crown edge.  
781 In occlusal view, the labial crown face is weakly inclined basally and weakly developed in its marginal  
782 areas but bears a very developed median protuberance. The median protuberance is well  
783 demarcated from the rest of the crown by concave margino-labial edges in occlusal view. The median  
784 protuberance is developed both labially and basally. The labial crown edges are blunt with no  
785 articular facets. The root is rather low and constricted near the crown. In basal view, the root lobes  
786 are triangular with rounded angles. The basal face of the root lobes is flat to slightly convex and  
787 inclined towards the nutritive groove. The root lobes vary from being as broad as long to mesio-  
788 distally expanded. Some teeth display a short lingual projection of the root lobes. The nutritive  
789 groove is wide and rather deep and bears a central foramen in labial position. There are no margino-  
790 lingual foramina.

791 Remarks. Teeth of this species are morphologically close to those of *A. weltoni* comb. nov. This  
792 species was described based on two illustrated specimens from the Late Maastrichtian of Texas (Case  
793 and Cappetta, 1997), which did not provide a complete overview of the intraspecific morphological  
794 variation. Study of numerous specimens of *A. weltoni* comb. nov. from the type locality housed in the  
795 collections of the University of Montpellier (G.G. perso. obs.) and comparison with the specimens  
796 from Senegal allowed the identification of several differences between teeth of *A. weltoni* comb.  
797 nov. and those of the Senegalese species. Teeth of the latter display a less marked lingual ornament,  
798 denser and finer labial ornament, presence of a marked labial crest, and less high lingual crown face.

799 **[FIGURE 8 HERE]**

800

801

Genus ? *Microbatis* Cappetta, 1993

802

? *Microbatis* sp.

803

Fig. 9A-J

804 Material. Four teeth (SN2012-87-90) from Unit 3, Cap de Naze Formation.

805 Description. Teeth of this species are higher than broad and minute-sized (less than 1 mm wide). The  
806 crown is asymmetrical, smooth and cuspidate. The labial crown face is flat to slightly concave in  
807 profile view, with a convex labial edge strongly overhanging the root. The labial visor is convex and  
808 connects the labial crown face in a sharp angle in profile view. The marginal angles are blunt in  
809 anterior teeth, while more lateral teeth have a more marked distal marginal angle. The lingual crown  
810 face displays a moderately developed conical cusp that is oriented lingually. Blunt and thick cutting  
811 edges originate at the base of the main cusp, in labial position, the mesial one being more developed.  
812 The cutting edges taper just before reaching the marginal angles. The lingual crown face is strongly  
813 concave in profile view. A short and rather wide median uvula is present below the main cusp and  
814 separated from the margino-lingual faces by wide concavities. The margino-lingual faces are reduced,  
815 abrupt and labially oriented. The marginal uvulae are very short, being reduced to fine blades  
816 oriented mesio-distally and more marked mesially. The root, although incomplete in all specimens, is  
817 very low, bilobate, and lingually positioned. A wide nutritive groove is present where a broad central  
818 foramen opens.

819 Remarks. The combination of characters present in teeth of this taxon and their size compare well  
820 with those of *Microbatis sabatieri* Cappetta, 1993, which was described from the Thanetian of  
821 Morocco and is the only known species of the genus *Microbatis*. However, the specimens described  
822 here differ from in having a more demarcated, although short, median uvula, very reduced and more  
823 labio-lingually oriented margino-lingual faces, and by the presence of very short marginal uvulae.  
824 *Microbatis sabatieri* is supposedly moderately heterodont and most specimens from the type series  
825 lack the root. Considering the small number and poor preservation of the specimens sampled  
826 described here, they cannot be assigned to the genus *Microbatis* with certainty.

827

828 Genus *Sowibatos* gen. nov.

829 Derivation of name. After Prof. El Hadji Sow, who greatly facilitated the organization of the field  
830 sessions.

831 Type species. *Sowibatos minimus* gen. et sp. nov.

832 Diagnosis. Teeth broader than high not exceeding 0.8 mm wide. Crown lozenge-shaped in occlusal  
833 view; labial visor strongly overhanging the root with median labial expansion separated by straight to

834 concave margino-labial edges. Marginal angles wide and bevelled labially. Transverse crest high,  
835 wide, and acute, separating the lingual and labial faces. Transverse crest straight to curved labially,  
836 tapering before reaching the margino-lingual edges, anterior to the marginal angles. Occlusal region  
837 flat and oval to triangular in shape. Lower lingual region abrupt, moderately developed and concave  
838 in profile view with flared basal edge. Median uvula short, wide and triangular, demarcated from  
839 margino-lingual faces by a slight concavity. Holaulacorhize root low and lingually positioned with  
840 concave lingual face and flat to convex and oblique labial face. Root lobes with triangular basal faces;  
841 wide nutritive groove with rounded central foramen positioned slightly labially.

842

843 *Sowibatos minimus* gen. et sp. nov.

844 LSID: urn:lsid:zoobank.org:act:3950016E-24C0-4F95-81AF-4417ED802685

845 Fig. 9K-U

846 Derivation of name. After the small size of teeth of this species.

847 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
848 Maastrichtian.

849 Diagnosis. As for genus.

850 Material. 37 teeth (including SN2012-91-94) from Unit 3, Cap de Naze Formation.

851 Description. Teeth of this species are broader than high and do not exceed 0.8 mm in width. The  
852 crown is smooth, low and more developed mesio-distally than labio-lingually. In occlusal view, the  
853 crown is lozenge-shaped, although the lingual edge tends to be less developed than the labial one in  
854 some specimens. The lingual edge is convex, whereas the labial visor strongly overhangs the root and  
855 displays a wide median labial expansion, which is demarcated by margino-labial edges that vary from  
856 being slightly concave in anterior teeth to more strongly concave in laterals. The marginal angles are  
857 rather wide and blunt, except in their labial region where the concavity of the margino-labial edges  
858 confers an acute outline to this area, especially in lateral teeth. The labial face is convex, both labio-  
859 lingually and mesio-distally. The labial and lingual faces are separated by a high, wide, and acute  
860 transverse crest. This transverse crest varies from being strongly curved labially to nearly straight in  
861 anterior teeth. The crest orientates slightly labially and tapers before reaching the margino-lingual  
862 edges, slightly anterior to the marginal angles. The lingual crown face is separated into two regions.  
863 One, on occlusal position, is delimited labially by the transverse crest and lingually by the angle with  
864 the lower and oblique lingual region. This occlusal region is oval to triangular in shape and flat. The

865 abrupt, lower lingual region is moderately developed and concave in profile view. The basal edge of  
866 this face is slightly flared and flanked by obtuse margino-lingual angles that are overhung by the  
867 marginal angles, which they join by a slightly concave edge in lingual view. No individualized marginal  
868 uvulae are present but a short and wide triangular median uvula is demarcated from the margino-  
869 lingual faces by a slight concavity. The median uvula can be slightly bent distally in lateral teeth. The  
870 crown is devoid of ornamentation, but its surface can be irregular on the occlusal region of the  
871 lingual face and on the labial face. The holaulacorhize root is low and positioned lingually. In profile  
872 view, the lingual root face is strongly concave, whereas the labial face is flat to concave, and oblique  
873 lingually. The basal edge of the lingual crown face is flared with an irregular outline and is as  
874 developed as the lingual crown face in profile view. A pair of margino-lingual foramina is present  
875 below the concavities separating the median uvula from the margino-lingual crown faces. The basal  
876 face of the root lobes is triangular with a slight projection of the median region, close to the nutritive  
877 groove, which is wide, circular in cross section, and more open in its labial part. The large circular  
878 central foramen opens in the nutritive groove, in labial position. One tooth, probably originating from  
879 a parasymphyseal file, differs from the morphology described above in being much more mesio-  
880 distally compressed and more asymmetrical with straight mesial marginal angle, more developed  
881 margino-lingual crown faces and more elongate median uvula.

882 Remarks. Teeth of this species differ from those of species referred to the genus *Hamrabatis* (see  
883 above) including *H. ornata* and *H. bernardezi* in having a smooth crown, thicker transverse crest, no  
884 lingual crest, less concave lower lingual crown face, more mesio-distally developed root lobes, and  
885 no labial foramina. The crown morphology of *S. minimus* gen. et sp. nov. tends to superficially  
886 resemble that of some rynchobatids but the Maastrichtian species differs by its smooth and more  
887 mesio-distally elongate crown, shorter median uvula, no or incipient lingual projection of the root  
888 and more marked transverse crest not reaching the marginal angles.

889 **[FIGURE 9 HERE]**

890

891 Order Myliobatiformes Compagno, 1973

892 Superfamily Dasyatoidea Whitley, 1940

893 Family Dasyatidae Jordan & Gilbert, 1879

894 Genus '*Dasyatis*' Rafinesque, 1810

895 '*Dasyatis*' *reticulata* sp. nov.

896

LSID: urn:lsid:zoobank.org:act:99EFCA2B-A3C9-44D6-8A51-78E8A6D02AC6

897

Fig. 10

898 Derivation of name. After the reticulate ornamentation on the crown of teeth of this species.

899 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
900 Maastrichtian.

901 Diagnosis. Dasyatid showing gradient monognathic and possibly gynandric heterodonty. Non-  
902 cuspidate teeth higher than wide (anterior) to wider than high (laterals/posterior). Crown with fine  
903 reticulate ornamentation on occlusal face and upper part of labial face, occasionally on basal region  
904 of labial face. Occlusal face bulged in anterior, flat in laterals/posterior. Labial face concave in  
905 profile view; labial visor strongly flared with a developed, convex, and smooth lower face. Lingual  
906 crown face high, smooth, with depressed margino-lingual faces separated by a broad medio-lingual  
907 crest; marked transverse depression on lingual crown face; margino-lingual faces concave; lingual  
908 visor developed and triangular. Cuspidate teeth high and labio-lingually developed. Cusp strongly  
909 bent lingually with blunt and curved margins reaching the marginal angles. Median vertical  
910 depression on labial crown face from the apex to the labial visor. Labial visor flared with concave  
911 margins. Lingual face high with two concave and basally flared margino-lingual faces separated by  
912 broad medio-lingual crest. Elongated and strongly lingually-projected lingual visor. Reticulate crown  
913 ornament on labial face and occasionally on upper part of lingual face. Root holaulacorhize, lingually  
914 positioned. Root lobes triangular in basal view and lingually-projected. Developed labial root face  
915 with several foramina.

916 Material. 74 teeth (including SN2012-95-107) from unit 3, Cap de Naze Formation.

917 Description.

918 *Non-cuspidate morph (Fig. 10A-A')*. Anterior teeth are higher than wide and do not exceed 2mm in  
919 height. In occlusal view, the crown outline is overall lozenge-shaped with sharp marginal and medio-  
920 lingual angles, but with a blunt medio-lingual angle. The occlusal face is strongly bulged in profile  
921 view, and bears a marked and fine reticulate ornamentation. The marginal angles are marked and  
922 reach the labial visor by a labially inclined and thick bulge. The labial crown face displays two  
923 depressed margino-labial faces separated by a wide medio-labial bulge originating from the occlusal  
924 face toward the medio-labial angle of the visor. In profile view, this median bulge can be straight and  
925 oblique to convex. In occlusal view, the marginal edges of the labial visor are straight to slightly  
926 concave. The labial crown face is generally devoid of ornamentation, excepted in its upper region  
927 where the reticulate ornament of the occlusal face tapers. Some specimens occasionally bear coarse



928 but shallow ridges in the lower region of the labial crown face. The labial visor is strongly flared with  
929 a developed, convex, and smooth lower face. The lingual crown face is high and smooth with  
930 depressed margino-lingual faces separated by a broad medio-lingual crest. No marked transverse  
931 crest is observable. In profile view, a strong transverse depression separates the vertical upper region  
932 of the lingual face from the oblique lower region. Both the upper and lower regions display a convex  
933 profile. The margino-lingual edges are oblique and the lingual visor is triangular with a rounded lower  
934 extremity. The holaulacorhize root is positioned lingually and shows a constriction just below the  
935 crown/root edge. The root lobes are triangular in basal view and project lingually where they barely  
936 overtake the basal edge of the lingual visor of the root in profile view. The lingual and labial root  
937 faces are transversally convex. The nutritive groove is wide and bears a broad central foramen.  
938 Several labial foramina of varying sizes open below the crown/root edge, whereas there are no  
939 lingual foramina. Teeth from more lateral jaw positions are lower and generally broader than high,  
940 with some lateral teeth being very large (Fig. 10E-H). Posterior teeth are very low-crowned. The  
941 occlusal face gradually becomes flat and the lingual crown face is reduced with a more marked  
942 transverse depression. A blunt transverse crest marks the limit between the occlusal and lingual  
943 crown faces. The lingual visor is proportionally shorter than in anterior teeth. The medio-lingual and  
944 medio-labial angles are blunt or absent in posterior-most teeth. The labial depression of the crown is  
945 present and can bear a reticulate ornament similar to that of the occlusal face. The marginal angles  
946 are blunt in posterior teeth. The root displays similar features to those observed in anterior teeth,  
947 but differ in being lower with wider root lobes.

948 *Cuspidate morph (Fig. 10B'-S')*. Teeth of this morph are of similar size to those of the non-cuspidate  
949 morph but differ in being higher, more labio-lingually developed, and in bearing an elongate but  
950 broad cusp. In profile view, the cusp is strongly bent lingually with blunt and curved margins reaching  
951 the marginal angles. The labial crown face displays a median vertical depression that runs from the  
952 apex of the cusp to the labial visor, which is bifid in its median region. In some teeth, the vertical  
953 depression bears a broad median vertical ridge, which connects a medio-labial angle. In profile view,  
954 a transverse depression separates the convex labial face of the cusp from the flared labial visor,  
955 which is demarcated from the rest of the labial face by concave edges in basal view. The lower face  
956 of the labial visor is very developed, smooth, and convex. The lingual face is high with two concave  
957 margino-lingual faces separated by a broad medio-lingual crest, which is concave in profile view. The  
958 lingual visor is elongated and strongly projects lingually. The basal edges of the margino-lingual  
959 crown faces are markedly flared. The extent of the crown ornamentation is variable, but is generally  
960 present as a reticulate pattern on the labial face of the main cusp and often develops over the labial

961 visor. Some teeth bear such an ornamentation on the upper half of the lingual crown face as well  
962 (Fig. 10Q'-S'). The root displays the same features as in teeth of the non-cuspidate morph.

963 Remarks. The general morphology and heterodonty of these teeth agree with those of extant and  
964 extinct dasyatids. Fossil dasyatid species have been commonly assigned to the genus '*Dasyatis*' as  
965 their tooth morphology was closer to that of some extant *Dasyatis* species than to other dasyatid  
966 genera, but knowledge on tooth morphology of extant dasyatid species is very limited (Guinot et al.,  
967 2018). However, the systematics of extant dasyatids has been deeply modified (Last et al., 2016) and  
968 while the genera *Himantura* and *Dasyatis* used to gather most dasyatid species, the latter have been  
969 split into several genera. Therefore, considering the lack of knowledge on the tooth morphology of  
970 extant dasyatids and uncertainties on the systematic position of fossil representatives of this clade, it  
971 is preferred to refer the species described here to '*Dasyatis*'. Several *Dasyatis*-like fossil species have  
972 been reported from various Campanian-Maastrichtian and Paleocene localities. Among them, few  
973 display the reticulate crown ornamentation observed in teeth of the new Senegalese species.  
974 Comparable crown ornamentation occurs in teeth of the Maastrichtian *D. commercensis* Case and  
975 Cappetta, 1997 and of the Danian *D. martini* Noubhani and Cappetta, 1997, *D. tetraedra* Arambourg,  
976 1952, *D. hexagonalis* Arambourg, 1952, *D. ponsi* Noubhani and Cappetta, 1997, *D. alveolata* (Leriche,  
977 1942), *Palaeodasyatis hermani* Halter, 1989 (pl. 1-2 non pl. 3) and *D. puerensis* Williamson and  
978 Lucas, 1993. Teeth of '*D.*' *reticulata* sp. nov. differ from these species excepted *D. commercensis* and  
979 *D. hexagonalis*, by the combined presence in non-cuspidate teeth of a strongly bulged occlusal face,  
980 developed and markedly depressed margino-labial crown faces, and high lingual crown face. The new  
981 species described here further differs from *D. commercensis* by the absence of marked transverse  
982 crest, more developed labial crown face, longer lower face of the labial visor, and more marked  
983 transverse depression of the lingual crown face. Teeth of *D. hexagonalis* and *P. hermani* are larger  
984 with finer and denser crown ornamentation, and display labio-lingually developed, non-triangular  
985 root lobes that characteristically separate these species from '*D.*' *reticulata* sp. nov. In addition, teeth  
986 of *D. hexagonalis* possess a median vertical depression on the lingual crown face bordered by two  
987 vertical wrinkles that further differentiates this species from '*D.*' *reticulata* sp. nov. Large lateral teeth  
988 of the non-cuspidate morph of '*D.*' *reticulata* sp. nov. might suggest the presence of protrusions in  
989 the dentition of this species, as seen in some modern dasyatids (e.g., *Urogymnus*, *Hypanus*).

990 **[FIGURE 10 HERE]**

991 Family Dasyatoidea incert. fam.

992 Genus *Coupatezia* Cappetta, 1982

993 *Coupatezia casei* sp. nov.

996 Derivation of name. After Gerard R. Case, for his contribution to the knowledge on Cretaceous  
997 elasmobranchs.

998 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
999 Maastrichtian.

1000 Material. 86 teeth (including SN2012-108-126) from Unit 3, Cap de Naze Formation; two teeth from  
1001 the yellow calcareous sandstone bed of Unit 1, Paki Formation.

1002 Diagnosis. Dasyatoid species with moderate degree of monognathic heterodonty and strong sexual  
1003 heterodonty. Teeth varying from broader than high to as high as broad, not exceeding a maximum  
1004 size of 1.5 mm. Holaulacorhize root low and wider than the crown but constricted below the crown.  
1005 Root lobes triangular projecting lingually with flat and strongly inclined basal face. Broad and deep  
1006 nutritive groove wider in its central region with wide central foramen. Labial root face sub-vertical  
1007 with one to three large foramina. Non-cuspidate anterior teeth of trapezoidal occlusal outline,  
1008 broader labially than lingually; rectangular in laterals. Marginal angles are obtuse and blunt. Margino-  
1009 labial angles very developed, acute and strongly projecting labially as well as laterally in anteriors.  
1010 Marked median concavity of the labial crown edge between the margino-labial angles. Oblique and  
1011 lingually-protruding transverse region separating the lingual and labial faces with oval to rectangular  
1012 depression. Labial edge of transverse depression weakly convex with irregular crest of varying  
1013 sharpness. Lingual edge of transverse depression with granulose enamelled ornament that can form  
1014 a sharp irregular crest. Crest on labial face that may or may not reach the marginal edges of the base  
1015 of the margino-labial angles. Fine and irregular transverse ridge between the crest and the labial  
1016 crown edge. Labial ornament coarse and irregular represented by tubercles, short ridges or cupulas.  
1017 Lingual face is high and concave in profile view, divided into two depressed margino-lingual faces by  
1018 a wide hourglass-shaped vertical ridge. Marginal edges of lingual crown face vertical and straight.  
1019 Lower edge of lingual crown face concave in its centre. Cuspidate teeth cordiform in occlusal view  
1020 with concave labial edge. Rounded, broad and both labially and laterally (in anteriors) projected  
1021 margino-labial angles. Labial crown face oblique and bordered labially by a sharp ridge. Base of labial  
1022 crown face depressed, upper profile convex. Very coarse labial ornament of broad tubercles  
1023 occasionally arranged into vertical ridges. Main cusp short, narrow, triangular, and lingually curved.  
1024 Lingual crown face high with weakly depressed margino-lingual faces and vertical medial convexity.  
1025 Lingual face with concave marginal and lower edges.

1026 Material. 85 teeth (of which nine belong to the cuspidate morph) from Unit 3, Cap de Naze  
1027 Formation; two uncuspidate teeth from the sandstones of Unit 1, Paki Formation.

1028 Description.

1029 *Non-cuspidate morph (Fig. 11A-C')*. Anterior teeth are as high as broad or slightly broader than high  
1030 with a trapezoidal occlusal outline that is broader labially than lingually. The margino-labial angles  
1031 are very developed, acute and strongly project both labially and laterally. The margino-labial angles  
1032 are separated by a marked median concavity of the labial crown edge in occlusal view. The marginal  
1033 angles are obtuse and blunt and connect the margino-labial angles by slightly concave, sharp, and  
1034 diverging edges. The transverse region separating the lingual and labial faces is oblique, protruding  
1035 lingually and occupied by an oval to rectangular depression in lingual view. In occlusal view, the labial  
1036 edge of this transverse depression is weakly convex, almost straight and can bear in its central region  
1037 a blunt and irregular crest. The lingual edge of the transverse depression is made of a blunt and  
1038 concave projection that reaches the marginal angles and bears irregular and granulose enamelled  
1039 ornament that can join each other to form a sharp but irregular crest. The labial face displays a crest  
1040 that may or may not reach the marginal edges of the base of the margino-labial angles. Another very  
1041 fine and irregular crest can be present between the latter and the labial crown edge. The labial  
1042 ornament is coarse and irregular in the concave area between the labial crest and the transverse  
1043 depression, where it can be represented by tubercles, short ridges or cupulas. The lingual face is high  
1044 and concave in profile view and is overhung by the transverse region. The lingual face is divided into  
1045 two strongly depressed margino-lingual faces by a wide hourglass-shaped vertical ridge that connects  
1046 the basal edge of the lingual face and the lingual edge of the transverse depression. The marginal  
1047 edges of the lingual face are vertical and straight as is its lower edge, excepted below the hourglass-  
1048 shaped vertical ridge where it is concave. The root is positioned lingually, low and wider than the  
1049 crown in lingual view. A strong and somewhat high constriction of the root is present below its  
1050 contact with the crown. The lobes are triangular in basal view and project lingually with a flat basal  
1051 face that is strongly inclined. The lobes are separated by a broad and deep groove that tends to be  
1052 wider in its central region and at the bottom of which a wide central foramen opens. The labial face  
1053 is sub-vertical and generally displays from one to three large foramina. Other small labial foramina  
1054 can be present just below the crown. Teeth from more lateral jaw positions display the same general  
1055 morphology but differ in being more labio-lingually compressed and broader than high with a  
1056 rectangular outline in occlusal view. The margino-labial angles are wider and developed labially but  
1057 not laterally. The labial ornament displays the same pattern as in anteriors but is generally sharper.  
1058 Both the upper and lower edges of the transverse depression are sharper, although irregular. The  
1059 lingual face is wide with a less marked vertical separation between the margino-lingual faces. The

1060 root is of comparable morphology to that of anteriors, but is lower with more labio-lingually  
1061 compressed and mesio-distally developed lobes.

1062 *Cuspidate morph (Fig. 11D'-V')*. Anterior teeth of this morph are cordiform in occlusal view with a  
1063 strongly marked concavity of the labial crown edge separating the rounded margino-labial angles.  
1064 The margino-labial angles are broad and projected both labially and laterally. The labial crown face is  
1065 oblique and bordered labially by a sharp ridge that can be very developed in some teeth. The lower  
1066 edge of the labial crown face is thick and convex in profile view. The labial crown face is depressed  
1067 between this basal labial ridge and the rest of the labial crown face, which is mainly convex in profile  
1068 view. The labial ornament is very coarse and consists of broad tubercles that tend to be arranged into  
1069 vertical ridges in some teeth. The main cusp is rather short, narrow, triangular, and curved lingually.  
1070 The marginal angles are wide and faint and bear a fine ridge that runs continuously from the labial  
1071 edge of the margino-labial angles to the base of the cusp. The lingual crown face is high with weakly  
1072 depressed margino-lingual faces separated by a vertical medial convexity. The margino-lingual faces  
1073 are concave in lingual view as is the lower edge of the lingual face. The root is of similar morphology  
1074 to that of non-cuspidate teeth. Lateral cuspidate teeth are more mesio-distally developed and more  
1075 asymmetrical, with less deep and broader concavity of the basal edge of the labial face.

1076 Remarks. Teeth of *Coupatezia casei* sp. nov. differ from those of most congeneric species by their  
1077 strong, coarse and non-reticulated labial ornament, which is also present in teeth of *C.*  
1078 *ambroggii* Noubhani and Cappetta, 1997 and *C. reniformis* Noubhani and Cappetta, 1997 from the  
1079 Maastrichtian of Morocco (Noubhani and Cappetta, 1997). Teeth of *Coupatezia casei* sp. nov. can be  
1080 separated from those of *C. ambroggii* by their higher lingual face, presence of transverse depression  
1081 between lingual and labial faces, less numerous transverse ridges on labial face, granular ornament  
1082 on lingual face, no secondary reticulate ornament in cupulas, and large labial foramina. The  
1083 Senegalese species differs from *C. reniformis* by its teeth with less oblique labial face in profile view,  
1084 stronger labial ornament, wider and more oblique transverse depression, lower root, less flared basal  
1085 root lobe face, and wider nutritive groove less constricted lingually. This is the sixth nominal  
1086 Maastrichtian *Coupatezia* species known so far.

1087 **[FIGURE 11 HERE]**

1088 *? Coupatezia* sp.

1089 Fig. 12A-C

1090 Material. One tooth (SN2012-127) from Unit 3, Cap de Naze Formation.

1091 Description. This tooth is broader than high and roughly triangular in occlusal view. The transverse  
1092 region separating the lingual and labial faces is devoid of crest but bears a marked bulge that is  
1093 thicker and nearly rounded in its median region. Several faint and irregular vertical folds originate  
1094 from the lingual side of this bulge. The lingual crown face is divided into an upper, oblique region  
1095 situated below the transverse bulge and a lower, abrupt region. The upper area is concave in profile  
1096 view and separated from the lower region by a faint ridge made of fine reticulate ornament that  
1097 reaches the transverse bulge on the margino-lingual angles. The lower part of the lingual face is  
1098 mostly damaged but appears made of concave margino-lingual faces separated by a flat vertical band  
1099 of enameloid. The basal edge of the lingual crown face is convex. The labial crown face is concave in  
1100 profile view and displays wide margino-labial angles connected to the margino-lingual angles by  
1101 oblique and irregular marginal edges. The labial crown edge is wider than the lingual and the former  
1102 shows a median convexity delimited from the margino-labial angles by shallow and broad  
1103 convexities. The labial crown ornament is made of irregular and finely anastomosed ridges that are  
1104 mainly situated near the labial edge of the labial face. The root is damaged but is at the  
1105 holaulacorhize stage with a central foramen and margino-labial foramina.

1106 Remarks. This tooth, although incomplete, bears crown characters typical of the genus *Coupatezia*  
1107 but differ in having a marked transverse bulge that is nearly rounded in its median region. However,  
1108 teeth of the Thanetian species '*Dasyatis russelli* Cappetta, 1972, which should most likely be  
1109 assigned to the genus *Coupatezia*, tend to develop such a median bulge, although they differ from  
1110 the specimens described here by a much stronger crown ornament

1111

1112 Superfamily Myliobatoidea Compagno, 1973

1113 Family Rhombodontidae Cappetta, 1987

1114 Genus *Rhombodus* Dames, 1881

1115 *Rhombodus binkhorsti* Dames, 1881

1116 Fig. 12D-H

1117 Material. Four teeth (including SN2012-128) from the yellow calcareous sandstone bed of Unit 1, Paki  
1118 Formation.

1119 Description. Teeth of this species are large, reaching up to about 15 mm in total width. The crown is  
1120 thick, lozenge-shaped in occlusal view, and much higher than the root. The occlusal surface is flat and  
1121 bears a shagreened ornament observable on teeth with a low degree of wear. The margino-labial

1122 faces are slightly concave in profile view and bear vertical to sub-vertical folds and grooves that are  
1123 mainly located on their lower two-thirds. These margino-labial faces bear a shagreened ornament  
1124 that is comparable to that of the occlusal face, but can change to a honeycombed ornamentation in  
1125 their upper part. A very prominent ridge marks the limit between the margino-labial faces and the  
1126 lower edge of the labial visor. The latter is smooth, oblique and concave in profile view. The margino-  
1127 lingual faces are abrupt, sometimes slightly convex in profile view, and bear large sub-vertical folds  
1128 and grooves that are smooth and bifurcating in the upper third of the lingual face. A strong bulge  
1129 borders the basal edge of the margino-lingual faces and is separated from the rest of the margino-  
1130 lingual faces by a deep but narrow transverse depression. This bulge is smooth, slightly concave on  
1131 the margino-lingual faces but convex in the medio-lingual region although not developing into a  
1132 marked uvula. The marginal angles are blunt, forming narrow marginal faces with weaker ornament  
1133 than on the margino-lingual faces. The root is robust, slightly narrower than the crown, and  
1134 somewhat offset lingually. The lobes are trapezoidal in basal view and separated by a wide and deep  
1135 furrow where foramina of variable number and position open. Short branches bordering the furrow  
1136 develop lingually, which confers a concave outline of the lingual crown face in basal view. The labial  
1137 face is slightly higher than the lingual. The labial and lingual root faces are abrupt to slightly oblique  
1138 towards the basal face. Several small round to oval foramina are aligned just below the crown on all  
1139 root faces, and additional larger foramina are present on the margino-labial root faces. The basal  
1140 root face also bears numerous foramina of variable size and shape.

1141 Remarks. Teeth reported here can be attributed to the genus *Rhombodus* by the lozenge-shaped  
1142 occlusal outline of the crown, the holaulacorhize root of lozenge-shape basal outline with deep and  
1143 large median notch separating large root lobes. Seven valid nominal species of *Rhombodus* are  
1144 known so far, spanning the Campanian-Maastrichtian interval (see Cicimurri and Ebersole, 2020). The  
1145 specimens reported here display a combination of characters (crown much higher than the root with  
1146 strong labial and lingual vertical wrinkles, flat occlusal crown face, moderately developed basal bulge  
1147 on lingual crown face with median convexity, slightly concave labial crown face in profile view)  
1148 reminiscent of teeth of *R. binkhorsti*, the type species of the genus. This species has a large  
1149 geographical range (North and South America, Western Europe, Northern and Western Africa, and  
1150 Middle East), but is restricted to the Maastrichtian (Cicimurri and Ebersole, 2020). *Rhombodus*  
1151 *binkhorsti* has been reported from the Unit 3, Cap de Naze Formation (Cuny et al., 2012), but is  
1152 reported from Unit 1 for the first time.

1153

1154

*Rhombodus* sp.

1155

Fig. 12I-M

1156 ? 2012 *Rhombodus* sp.; Cuny et al., p. 113, fig. 5.

1157 Material. One tooth (SN2012-129) from the yellow calcareous sandstone bed of Unit 1, Paki  
1158 Formation.

1159 Description. This tooth does not exceed 1 mm in width and 6 mm high, the (worn) crown being much  
1160 lower than the root. The crown is rhombic in occlusal view. The margino-lingual faces are low with  
1161 thick residual vertical folds. A well-developed and smooth basal bulge is present on the lingual crown  
1162 face, with a straight margino-lingual outline and reduced median convexity. The margino-labial faces  
1163 are very low and smooth. The lower edge of the labial visor is strongly oblique and slightly concave in  
1164 profile view. The marginal angles are blunt. The root is high and narrower than the crown. The root  
1165 lobes are trapezoidal in occlusal view and separated by a deep and wide furrow where several large  
1166 foramina open. The margino-lingual root faces are convex and slightly oblique basally. The margino-  
1167 labial root faces are concave in profile view. Large foramina are present below the labial visor,  
1168 whereas only few small foramina open just below the lingual crown bulge.

1169 Remarks. This tooth differs from the co-occurring teeth of *R. binkhorsti* by its more developed basal  
1170 bulge on the lingual crown face with straight margino-lingual outline, less developed median  
1171 convexity of the bulge, higher and more oblique lower edge of the labial visor, absence of labial  
1172 crown ornament, higher root, absence of incipient lingual root branches, and concave margino-labial  
1173 root faces. The specimen described here further differs from the Maastrichtian species *R. andriesi*  
1174 Noubhani and Cappetta, 1994 reported from Unit 3 of Cap de Naze Formation by Cuny et al. (2012)  
1175 by its higher root, basal bulge with straight margino-lingual outline and reduced median convexity,  
1176 and more labio-lingually developed root. A specimen (SN235) reported as *Rhombodus* sp. by Cuny et  
1177 al. (2012) from the same horizon in Unit 1 of the Paki formation displays similarities in both size and  
1178 morphology with the tooth described here. However, both SN235 and the tooth described here are  
1179 imperfectly preserved and there are no basal views available for SN235, which precludes detailed  
1180 comparison of crown ornament and root morphology. Nevertheless, SN235 displays higher margino-  
1181 lingual crown faces, possibly less ornamented lingual crown face, and less robust root branches  
1182 showing an oblique labial face while it is vertical in the specimen described here. Although both  
1183 specimens might be conspecific, the above-mentioned differences suggest that more material is  
1184 needed to better assess this tooth morphology.

1185 Cuny et al. (2012) reported a myliobatiform caudal spine from Unit 3 that was assigned to  
1186 *Rhombodus* arguing that this genus was the only myliobatiform present in Unit 3, although the size of  
1187 the spine was considered very small in comparison to teeth of *Rhombodus*. Our new samplings



1188 indicate that at least four myliobatiform genera were present in Unit 3 (*Dasyatis*, *Coupatezia*,  
1189 *Rhombodus*, and *Phosphatodon*). Consequently, the generic attribution of the caudal spine reported  
1190 in Cuny et al. (2012) is unknown.

1191

1192 *Myliobatiformes incertae familiae*

1193 *Phosphatodon* Cappetta, 2012

1194 *Phosphatodon cretaceus* sp. nov.

1195 LSID: urn:lsid:zoobank.org:act:C97061D2-C44F-447E-BA31-E6DF5ECA9E5F

1196 Fig. 12N-Q

1197 Derivation of name. From the Cretaceous occurrence of this genus, which was previously restricted  
1198 to the Paleogene.

1199 Type stratum. Ferruginous sandstone on top of Unit 3, Cap de Naze Formation, middle–upper  
1200 Maastrichtian.

1201 Diagnosis. Teeth very high with crown broader than root. Lingual face abrupt and concave in profile  
1202 view. Margino-lingual faces slightly depressed, separated by a wide and faint central vertical bulge  
1203 the upper region of lingual face. Central uvula wide, short, and triangular, separated from the  
1204 margino-lingual faces by shallow and broad concavities. Occlusal face inclined lingually and convex  
1205 both. Lingual crown edge of occlusal face convex, labial outline with concave margino-labial edges  
1206 and marked medio-labial bulge. Labial crown face is as high as lingual face with labially projected  
1207 median region. Margino-labial faces flat to slightly concave. Lower edge of labial crown face  
1208 scalloped with broad and triangular medio-labial protuberance. Crown not ornamented although of  
1209 irregular surface or rough lingually. Root very high, narrow, and oval in cross-section and constricted  
1210 above the deep nutritive groove. Root lobes moderately high and mesio-distally compressed. Medio-  
1211 lingual foramen in a depression located labially to the groove. Several margino-lingual and labial  
1212 foramina below the crown/root edge and above the root constriction.

1213 Material. One tooth (SN2012-130, holotype) from Unit 3, Cap de Naze Formation.

1214 Description. The holotype is an anterior tooth that is much higher than broad and about 3 mm high.  
1215 The crown only slightly overhangs the root in occlusal view and is as high as broad. The lingual face is  
1216 abrupt and somewhat concave in profile view with straight marginal edges in lingual view. The  
1217 margino-lingual faces are slightly depressed and separated by a wide and faint central vertical bulge

1218 restricted to the upper region of the lingual face. The lower edges of the margino-lingual faces are  
1219 oblique and straight, although irregular. These converge medially into a wide, short, and triangular  
1220 central uvula that is separated from the margino-lingual faces by shallow but broad concavities. The  
1221 lingual face is not ornamented, although its surface is irregular and weakly rough. The occlusal face is  
1222 inclined lingually and convex both mesio-distally and labio-lingually. The lingual crown edge of the  
1223 occlusal face is convex and blunt due to functional wear, whereas the labial outline displays concave  
1224 margino-labial edges that connect into a marked medio-labial bulge with a straight edge. The  
1225 marginal angles are rounded and about 90°. The labial crown face is as high as the lingual face. The  
1226 median region of the labial face is broad and labially projected, whereas the margino-labial faces are  
1227 flat to slightly concave. The lower edge of the labial crown face is scalloped and develops medially  
1228 into a broad, triangular, and rather long medio-labial protuberance that is somewhat depressed in its  
1229 median region. The surface of the labial crown face is irregular but devoid of ornament. The root is  
1230 very high, relatively narrow, and oval in cross-section. A constriction is present at mid-height of the  
1231 crown, above the nutritive groove. Below the constriction, the margino-labial root faces are flat. The  
1232 root lobes are moderately high, mesio-distally compressed and separated by a wide groove. A  
1233 foramen is present in a depression located labially to the groove. Several margino-lingual and labial  
1234 foramina are present just below the crown/root edge, others scarce foramina open lingually and  
1235 labially above the constriction.

1236 Remarks. The morphological features observed in this new species include a very high and narrow  
1237 root, crown with high lingual and labial faces bearing broad and short median uvula and marked  
1238 labial bulge, constriction of the root and mesio-distally compressed root lobes. These dental features  
1239 are uncommon among elasmobranchs and are unique to the genus *Phosphatodon* (originally  
1240 *Prosopodon*, see Cappetta, 2012). So far, the genus *Phosphatodon* was restricted to a single species,  
1241 *P. asafai* (Noubhani and Cappetta, 1995), known from the Danian of Morocco and Europe. Teeth of  
1242 this species show a strong degree of monognathic heterodonty with a decrease in tooth height  
1243 towards lateral files, where teeth have lower lingual and labial crown faces, a reduced median uvula  
1244 and no medio-labial protuberance. This morphology led Noubhani and Cappetta (1995) to include  
1245 the genus *Phosphatodon* in the Dasyatoidea. Considering its extremely derived morphology, this  
1246 genus might be better regarded as Myliobatiformes of uncertain affinities. Despite the strong  
1247 resemblances between the Paleocene and the Maastrichtian species, anterior teeth of *P. cretaceus*  
1248 sp. nov. can be separated from those of *P. asafai* by the following characters: no marked crown  
1249 ornament, scalloped basal crown edge of labial face, wider labial bulge of the crown that is more  
1250 developed labially, concave lingual face, convex labial face with no demarcated labial visor, more  
1251 developed medio-labial protuberance that almost reaches the level of the lower edge of the median

1252 uvula, convex profile of the labial face, lower constriction of the root, and smaller size. The species  
1253 described here extends the stratigraphic range of the genus back into the Mesozoic.

1254

1255 *Batomorphii incertae sedis*

1256 *Batomorphii* indet. 1

1257 Fig. 12R-V

1258 Material. One tooth (SN2012-131) from Unit 3, Cap de Naze Formation.

1259 Description. This tooth is as high as broad and displays a hexagonal outline in occlusal view. The labial  
1260 crown face is separated from the lingual face by a wide and blunt transverse crest that is sharper  
1261 near the acute marginal angles. This crest projects lingually and overhangs the lingual crown face in  
1262 occlusal view. The margino-labial regions of the labial face are strongly depressed and concave in  
1263 labial view. These depressed area do not reach each other labially and are separated by a thin labial  
1264 band of occlusal surface projecting labially, which ends into a short and flat labial visor. The margino-  
1265 labial edge of the crown is straight. The lingual crown face is concave in profile view and separated  
1266 into a median and two margin-lingual faces that are flat. The broad and moderately long median  
1267 uvula is weakly demarcated from the margino-lingual edges by shallow and wide concavities. The  
1268 root is worn but shows two labio-lingually compressed lobes placed lingually and separated by a  
1269 nutritive groove where a central foramen opens. A strong constriction of the root is present,  
1270 immediately below the crown.

1271 Remarks. The overall crown morphology of this specimen is reminiscent of that of some extant and  
1272 extinct dasyatoids such as *Aturobatis* and *Pastinachus*. The labial crown morphology is particularly  
1273 close to that of anterior teeth of the extant *Pastinachus sephen* (see Cappetta 2012), which display a  
1274 marked degree of tooth interlocking. Nonetheless, the Senegalese specimen differs from anteriors of  
1275 *P. sephen* in the presence of a uvula basal edge of lingual crown face. However, teeth of some  
1276 rhinobatoid taxa (e.g., *Atlantobatis* gen. nov. and, to a lesser extent *Phosphatobatis*) have  
1277 comparable lingual crown face morphology. In the absence of knowledge on its heterodonty and  
1278 tooth histology, the taxon represented by the specimens described here cannot be positively  
1279 assigned to any higher taxonomic rank

1280

1281 *Batomorphii* indet. 2

1282 Fig. 12W-Z

1283 Material. One tooth (SN2012-132) from Unit 3, Cap de Naze Formation.

1284 Description. This tooth is labio-lingually compressed (0.5 mm) and mesio-distally expanded (1 mm).  
1285 The crown is low and oval-shaped in occlusal view. A rather wide and blunt transverse crest  
1286 separates the labial and lingual faces. The transverse crest is rectilinear in occlusal view but its  
1287 extremities are slightly oriented lingually when reaching the rounded marginal angles. The labial face  
1288 is oblique and concave in profile view and bounded labially by an incipient but broad and irregular  
1289 ridge that follows the labial edge of the labial face. The labial visor overhangs the root in occlusal  
1290 view and displays a basally projected median process, which is triangular in labial view. The upper  
1291 third of the lingual face is flat and oblique, and demarcated from the lower part, which is abrupt and  
1292 concave in profile view. The basal edge of the lingual crown face bears a wide but short and rounded  
1293 median uvula. The uvula is separated from the rest of the crown by faintly concave margins. The  
1294 whole crown has an irregular surface made of very fine pits. The holaulacorhize root is high and  
1295 strongly labio-lingually compressed. In basal view, the root lobes are mesio-distally developed with  
1296 straight to slightly convex labial and lingual margins with their mesial and distal edges are rather  
1297 wide and rounded. The basal faces of the lobes are flat and strongly oblique. The nutritive groove is  
1298 deep and relatively wide, in the centre of which opens a labio-lingually compressed median foramen.  
1299 The root displays no lingual or labial foramina.

1300 Remarks. The morphology of this tooth recalls that of some dasyatoid or rhinopristid taxa with  
1301 crushing dentition but the combination of crown and root characters observed in the Senegalese  
1302 specimen have not been reported previously. Additional material is needed to better assess the  
1303 systematic position of this probable new taxon.

1304

1305 *Batomorphii* indet. 3

1306 Fig. 12A'-B'

1307 Material. Two teeth (SN2012-133-134) from Unit 3, Cap de Naze Formation.

1308 Description. These teeth are less than 1 mm high and are roughly as broad as high. The crown is high  
1309 with a flat labial face. The lingual face is abrupt and high and slightly project lingually in its median  
1310 region at the base of which a variably developed median uvula is present. One of the specimens is  
1311 damaged on its basal edge of the lingual crown face but seems devoid of marginal uvulae, whereas  
1312 another specimen shows notches separating short marginal uvulae from the central one. The labial  
1313 face displays a curved labial edge and a triangular lingual edge that connect into broad and blunt  
1314 marginal angles. The margino-lingual edges are straight to slightly convex and gently converge

1315 medially. None of the specimens have a preserved root but the preserved elements indicate labio-  
1316 lingually compressed root lobes separated by a notch that bears a central foramen in labial position.

1317 Remarks. These teeth resemble those of the late Cretaceous hypsobatid species *Angolabatis*  
1318 *benguelaensis* (Antunes and Cappetta, 2002) but differ in their rounded labial crown edge, whereas  
1319 this is markedly angular in *A. benguelaensis*. Teeth of the Cenomanian rajoid *Rajorhina epansa*  
1320 (Davis, 1887) show a comparable overall crown morphology but are cuspidate (although less marked  
1321 in lateral teeth) with less developed uvulae. More material is needed to provide a more accurate  
1322 identification and higher taxonomic rank assignment of this taxon.

1323 **[FIGURE 12 HERE]**

1324 **5. Discussion**

1325 *5.1. Biostratigraphical implications*

1326 The geological section and biostratigraphy of the Cap de Naze cliffs were previously studied by  
1327 Tessier (1952), Khatib et al. (1990), Sow (1992), and Sarr (1995). While the oldest works suggested a  
1328 Maastrichtian age for the Cretaceous series (Faye, 1983; Tessier, 1952), Khatib et al. (1990) reported  
1329 samplings made in the marls of Unit 2, just above the calcareous sandstone bed of Unit 1, which  
1330 yielded the species *Globotruncanita cf. calcarata* (Cushman). According to Khatib et al. (1990), this,  
1331 along with other taxa that would suggest the presence of the biozones *G. calcarata* to *G. aegyptiaca*,  
1332 would indicate the uppermost Campanian. However, the assemblage of planktonic foraminifera from  
1333 the calcareous siltstone bed of Unit 2 (*Globotruncana aegyptiaca* and *Gansserina gansseri* biozones)  
1334 suggests an early to middle Maastrichtian age (Khatib et al., 1990). Consequently, Khatib et al. (1990)  
1335 placed the Campanian-Maastrichtian boundary at the base of Unit 2, one meter above the calcareous  
1336 sandstone bed of Unit 1 (sampling 2, here), and assigned a Campanian age to the gypsum-rich clays  
1337 of the base of Unit 1 (sampling 1, here).

1338 The gypsum-rich clays yielded a single elasmobranch tooth attributed here to *Carcharias* sp., which  
1339 does not provide any valuable biostratigraphic information. However, eight elasmobranch taxa were  
1340 recovered from the calcareous sandstone bed of Unit 1 (Table 1): one (*Rhombodus* sp.) reported by  
1341 Cuny et al. (2012) and seven reported in the present work (*Squalicorax pristodontus*, *Carcharias* sp.,  
1342 *Cretolamna maroccana*, *Serratolamna serrata*, *Schizorhiza stromeri*, *Coupatetia casei* sp. nov., and *R.*  
1343 *binkhorsti*). Among the nominal elasmobranch species sampled in this work, a single one (*S.*  
1344 *pristodontus*) spans the Campanian-Maastrichtian interval. However, this horizon yielded three  
1345 geographically widespread and exclusively Maastrichtian elasmobranch species (*C. maroccana*, *R.*  
1346 *binkhorsti*, and *S. serrata*). The presence of these species strongly argues against a Campanian age for  
1347 the calcareous sandstone bed, and rather suggests that this horizon is Maastrichtian in age. These  
1348 new findings potentially have important implications because this calcareous sandstone bed may be  
1349 laterally equivalent to the one that yielded fossil remains of diverse groups including bivalves,  
1350 brachiopods, fruits (Monteillet and Lappartient, 1981), fish teeth, and remains of a pterosaur  
1351 (Monteillet and Lappartient, 1982) in the Paki area.

1352 Unit 3 is devoid of microfossils but has been assigned a middle to late Maastrichtian age due to its  
1353 position between the underlying early to middle Maastrichtian Unit 2 and overlying Unit 4, which  
1354 was assigned a late Maastrichtian age based on ammonites (Tessier 1952). This middle-late  
1355 Maastrichtian age was supported by the elasmobranch fauna reported from the ferruginous  
1356 sandstone bed of Unit 3 by Cuny et al. (2012), who described several exclusively Maastrichtian, and

1357 possibly late Maastrichtian, taxa (Table 1). Cuny et al. (2012) reported the species *Cretolamna* cf.  
1358 *biauriculata* from Unit 3, which would argue against an Upper Maastrichtian age, since this species  
1359 seems restricted to the early Maastrichtian. However, this material should rather be considered  
1360 juveniles of *S. serrata* (see above, Systematics section), which is common in late Maastrichtian  
1361 faunas. Additional elasmobranch species described here (*Plicatoscyllium youssoufiaense*, *Dalpiazia*  
1362 *stromeri*, and *Ctenopristis nougareti*) further support the proposed middle-late Maastrichtian age for  
1363 the ferruginous sandstone bed of Unit 3.

1364

## 1365 5.2. Palaeoenvironmental and palaeogeographical implications

1366 Previous works on the geological section at Cap de Naze provided sedimentological and  
1367 micropalaeontological arguments that suggest several successive short-term regressive cycles, which  
1368 make part of a long-term transgressive phase (Khatib et al., 1990; Sow et al., 1994). The gypsum-rich  
1369 clays of Unit 1 (sample 1) represent the base of a regressive cycle reaching a lowstand located in the  
1370 sandstones of Unit 1. This is followed by a transgressive event right above the yellow calcareous  
1371 sandstone bed (sample 2), at the top of Unit 1. The ferruginous sandstone (sample 3) would  
1372 correspond to a lowstand that follows the second regressive event recorded in the lower siltstones of  
1373 Unit 3. Both sampled horizons 2 and 3 were interpreted as representing nearshore  
1374 palaeoenvironments (Khatib et al., 1990; Sow et al., 1994).

1375 The elasmobranch assemblage from the yellow calcareous sandstone bed contains exclusively  
1376 lamniforms (*S. pristodontus*, *Carcharias* sp., *C. maroccana*, and *S. serrata*) and batomorphs (*S.*  
1377 *stromeri*, *Coupatazia casei* sp. nov., *Rhombodus* sp., and *R. binkhorsti*). The assemblage from the  
1378 ferruginous sandstone differs in its much higher taxonomic diversity (28 species). Only two species  
1379 among those recorded in the lower yellow calcareous sandstone bed (the lamniforms *Carcharias* sp.  
1380 and *C. maroccana*) were not recovered in the Unit 3, which instead yielded the species *Carcharias* cf.  
1381 *heathi* and *Carcharias* sp. 1 reported by Cuny et al. (2012). The sampled assemblage from Unit 3  
1382 further differs from that of the yellow calcareous sandstone in the presence of three orectolobiforms  
1383 (*Chiloscyllium* sp., *Hemiscyllium* sp., and *Plicatoscyllium youssoufiaense*) and much more diverse  
1384 batomorphs (21 species). The increasing species diversity toward the top of the section (one species  
1385 in sample 1, eight in sample 2, and 28 in sample 3) suggests a transition from restricted marine  
1386 (Sample 1) to more open coastal conditions (Sample 3), and is in line with an increasing opening of  
1387 the marine setting reported previously (Khatib et al., 1990).

1388 The fauna reported here is typical of Cretaceous nearshore tropical/sub-tropical settings and the  
1389 dominance of sclerorhynchoids, rhinopristiforms, myliobatiforms, lamniforms, and orectolobiforms

1390 compares well with other Maastrichtian Tethyan and Eastern Atlantic faunas known so far from  
1391 Morocco (Noubhani and Cappetta, 1997), Egypt (Cappetta, 1991a), Niger (Cappetta, 1972), Syria  
1392 (Bardet et al., 2000), Jordan (Cappetta et al., 2000), and Spain (Cappetta and Corral, 1999; Corral et  
1393 al., 2016). It also contrasts with other Maastrichtian assemblages from the Western Interior Seaway  
1394 (Case and Cappetta, 1997; Cook et al., 2014; Estes, 1964), NW Atlantic (Cappetta and Case, 1975), as  
1395 well as with assemblages from Niger and Algeria in the absence of hybodonts, despite the coastal  
1396 palaeoenvironment of the Senegalese assemblages. Most of the previously known species recorded  
1397 from the Popenguine fauna are represented by cosmopolitan taxa (*S. pristodontus*, *C. maroccana*, *S.*  
1398 *serrata*, *D. stromeri*, and *R. binkhorsti*) as well as *S. stromeri*, a species largely distributed in sub-  
1399 tropical Tethyan and Eastern Atlantic neritic environments in the Maastrichtian (Cappetta, 2012).  
1400 Some species with a more restricted distribution include *P. youssoufiaense* (Unit 3) previously limited  
1401 to the Maastrichtian of Morocco (Noubhani and Cappetta, 1997), *R. andriesi* (Unit 3) known from the  
1402 Maastrichtian of Morocco and Spain (Cappetta and Corral, 1999; Noubhani and Cappetta, 1997), and  
1403 possibly *C. heathi* previously reported from Morocco, Spain, and the USA (Cappetta and Corral, 1999;  
1404 Case and Cappetta, 1997; Noubhani and Cappetta, 1997). Although similarities with the  
1405 Maastrichtian Moroccan fauna are expected, these are few. More striking, however, is the large  
1406 number of new taxa recorded in the Popenguine fauna. These newly described taxa are mainly  
1407 represented by necto-benthic species and suggests a strong degree of endemism in marine coastal  
1408 vertebrate assemblages from eastern Atlantic environments, as these taxa were not reported from  
1409 Niger (Cappetta, 1972), Morocco (Noubhani and Cappetta, 1997), or Angola (Antunes and Cappetta,  
1410 2002), where fine sieving for micro-vertebrates was carried out. Although several published  
1411 Maastrichtian faunas from the Tethys have not been formally described (Cappetta et al., 2000; Lewy  
1412 and Cappetta, 1989), some known assemblages (e.g., from Egypt, Syria) indicate a similar degree of  
1413 endemism (Bardet et al., 2000; Cappetta, 1991a). This strong degree of endemism among necto-  
1414 benthic species likely reflects high habitat differentiation in tropical to sub-tropical marine  
1415 Maastrichtian settings, which probably mediated the all-time diversity peak in the elasmobranch  
1416 evolutionary history (Guinot and Cavin, 2016) that preceded the Cretaceous/Paleogene extinction  
1417 event.

1418

## 1419 **6. Conclusions**

1420 Additional fieldwork was carried out in the late Cretaceous geological section at Cap de Naze near  
1421 Popenguine. Surface collecting and bulk-sampling allowed to largely complement the previous report  
1422 on the elasmobranch fauna (Cuny et al., 2012) by the addition of 22 species and to improve



1423 knowledge on the stratigraphic distribution of the elasmobranch taxa along the section. Three new  
1424 genera and eight new species are described, all being represented by small-sized teeth, which  
1425 highlights the importance of bulk-sampling and fine sieving techniques in the understanding of past  
1426 elasmobranch communities. Our findings suggest a Maastrichtian age for the calcareous siltstone at  
1427 the top of Unit 1 (Paki Fm.), based on the presence of three exclusively Maastrichtian elasmobranch  
1428 species (*C. maroccana*, *R. binkhorsti*, and *S. serrata*). This challenges previous works based on  
1429 microfossil analysis. Samplings from Unit 3 (Cap de Naze Fm.) is in agreement with the middle-late  
1430 Maastrichtian age proposed based on the previous account on elasmobranchs (Cuny et al., 2012).  
1431 Increasing taxonomic diversity throughout the three successive assemblages indicates a transition  
1432 from restricted marine to open coastal settings. This high-diversity fauna is dominated by necto-  
1433 benthic batomorphs and is similar in its structure to other Tethyan and Eastern Atlantic  
1434 Maastrichtian faunas. The high number of species apparently endemic to the studied area suggests  
1435 high habitat differentiation in corresponding marine Maastrichtian settings.

1436

#### 1437 **Acknowledgements**

1438 This work benefited from the support of the Geology Department of the University Cheikh Anta Diop  
1439 (Prof. E. Sow and Dr. Faaye Cisse S.). We express our gratitude to the Keur Cupaam camp for their kind  
1440 welcoming. M. Thiam, R. Tabuce, S. Adnet and F. Lihoreau are thanked for their help in the field and  
1441 for preliminarily sieving the sediment of Unit 1 during the 2011 field campaign. We wish to thank the  
1442 editor (E. Koutsoukos), Jürgen Kriwet, and an anonymous reviewer for providing useful comments on  
1443 a previous version of the manuscript. This research is part of the PaleoSen project  
1444 ([www.paleosen.com](http://www.paleosen.com)) and was supported by the French ANR-PALASIAFRICA Program (ANR-08-JCJC-  
1445 0017), the CNRS PICS Grant, the International Exchange Scheme of the Royal Society, the National  
1446 Geographic Society's Global Exploration Fund (Northern Europe), the Sidney Sussex College  
1447 (Cambridge, UK) and the IRD.

1448

#### 1449 **Author contributions**

1450 LH, RS, JM and GG conceived the study; LH, JM, RS, and BS did the fieldwork and sampling; GG  
1451 drafted the manuscript and illustrations with inputs from all authors; all authors reviewed the  
1452 manuscript.

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1719 **Figure Captions**

1720 **Figure 1.** Geographical and geological setting of the sampled locality. **A)** geographical situation of the  
1721 Cap de Naze cliffs (black star), the grey-shaded area represents the extent of Campanian-  
1722 Maastrichtian series. **B)** geological section at the Cap de Naze cliffs (after Khatib *et al.* 1990), stars  
1723 indicate the sampled horizons. **C)** view of the northern part of the Cap de Naze area (November  
1724 2018), showing the three sampled horizons (stars).

1725 **Figure 2.** Orectolobiform sharks from the Unit 3, Cap de Naze Fm. **A-B: *Chiloscyllium* sp.** A: tooth  
1726 (SN2012-41) in labial view; B: tooth (SN2012-42) in labial view. **C-D: *Hemisycyllium* sp.** tooth (SN2012-  
1727 43) in C, labial and D, lingual views. **E-M: *Plicatoscyllium youssoufiaense*.** E: latero-posterior tooth  
1728 (SN2012-44) in labial view; F-H: anterior tooth (SN2012-45) in F, labial, G, lingual and H, basal views;  
1729 I: lateral tooth (SN2012-46) in labial view; J-M: lateral tooth (SN2012-47) in J, lingual, K, labial, L,  
1730 oblique basal and M, basal views. Scale bars 500  $\mu$ m (AB and C-D) and 1mm (E-M).

1731 **Figure 3.** Lamniformes from the Unit 1, Paki Fm. **A-B: *Squalicorax pristodontus*** tooth (SN2012-48) in  
1732 A, lingual and B, labial views, yellow sandstone (Unit 1). **C-F: ? *Carcharias* sp.** C-D: anterior tooth  
1733 (SN2012-49) in C, labial and D, lingual views, argillites (Unit 1); E-F: anterior tooth (SN2012-50) in E,  
1734 labial and F, lingual views, yellow sandstone (Unit 1). **G-J: *Cretolamna maroccana*,** yellow sandstone  
1735 (Unit 1). G-H: anterior tooth (SN2012-51) in G, lingual and H, labial views; I-J: lower lateroposterior  
1736 tooth (SN2012-52) in I, lingual and J, labial views. **K-T: *Serratolamna serrata*,** yellow sandstone (Unit  
1737 1). K-L: upper lateral tooth (SN2012-53) in K, lingual and L, labial views; M-N: anterior tooth (SN2012-  
1738 54) in M, lingual and N, labial views; O-P: anterolateral tooth (SN2012-55) in O, labial and P, lingual  
1739 views; Q-R: lateral tooth (SN2012-56) in Q, lingual and R, labial views; S-T: lateral tooth (SN2012-57)  
1740 in S, labial and T, lingual views. All scale bars equal 1cm.

1741 **Figure 4.** Sclerorhynchiforms from the Unit 3, Cap de Naze Fm. **A-J: *Dalpiazia stromeri*.** A-D: anterior  
1742 tooth (SN2012-58) in A, labial, B, basal, C profile and D, lingual views; E-H: lateral tooth (SN2012-59)  
1743 in E, labial, F, basal, G, profile and H, lingual views; I-J: posterior tooth (SN2012-60) in I, lingual and J,  
1744 labial views. **K-L: *Ctenopristis nougareti*,** rostral denticle (SN2012-61) in K, anterior and L, profile  
1745 views. Scale bars equal 1mm.

1746 **Figure 5.** Sclerorhynchiforms from the Paki and Cap de Naze Fm. **A-N: *Schizorhiza stromeri*** teeth  
1747 from the Unit 3, Cap de Naze Fm. A-B: anterior tooth (SN2012-62) in A, labial, B, lingual and C, profile  
1748 views; D-G: anterior tooth (SN2012-63) in D, labial, E, lingual, F, profile, and G, basal views; H-K:  
1749 anterior tooth (SN2012-64) in H, labial, I, profile, J, lingual, and K, basal views; M-N: juvenile anterior  
1750 tooth (SN2012-65) in M, labial and N, occlusal views. **O: *Schizorhiza stromeri*** rostral denticle  
1751 (SN2012-66) from the Unit 1 (yellow sandstone), Paki Fm. **P-T: *Ptychotrygon nazeensis* sp. nov.,**

1752 tooth (SN2012-67, **holotype**) from the Unit 3, Cap de Naze Fm. in O, lingual, P, occlusal, Q, basal, R,  
1753 profile, and S, labial views. Scale bars equals 1 mm, excepted O (5 mm).

1754 **Figure 6.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-B: cf. *Rhynchobatus* sp.**, tooth  
1755 (SN2012-68) in A, lingual and B, profile views. **C-K: *Terangabatis thiami* gen. et sp. nov.** C-D: anterior  
1756 tooth (SN2012-69) in C, lingual and D labial views; E-I anterior tooth (SN2012-70, **holotype**) in E,  
1757 occlusal, F, lingual, G, labial, H, profile, and I, basal views; J: lateral tooth (SN2012-71) in lingual view;  
1758 K: posterior tooth (SN2012-72) in occlusal view. All scale bars equal 1mm excepted K (500  $\mu$ m).

1759 **Figure 7.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-Q: '*Rhinobatos*' *popenguinensis* sp.**  
1760 **nov.** A-D: tooth (SN2012-73) in A, lingual, B, occlusal, C, profile, and D, labial views; E: tooth (SN2012-  
1761 74) in lingual view; F-H: tooth (SN2012-75) in F, lingual, G, basal, and H, profile views; I-J: tooth  
1762 (SN2012-76) in I, occlusal and J, lingual views; K-M: tooth (SN2012-77) in K, labial, L, lingual, and M,  
1763 occlusal views; N-Q: tooth (SN2012-78) in N, lingual, O, occlusal, P, profile, and Q, basal views. All  
1764 scale bars equal 500  $\mu$ m.

1765 **Figure 8.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-Y: *Atlantobatis acrodonta* gen. et sp.**  
1766 **nov.** A-E: tooth (SN2012-79, **holotype**) in A, lingual, B, basal, C, occlusal, D, profile, and E, labial  
1767 views; F-G: tooth (SN2012-80) in F, labial and G, lingual views; H-J: tooth (SN2012-81) in H, occlusal, I,  
1768 lingual, and J, profile views; K-N: tooth (SN2012-82) in K, lingual, L, occlusal, M, profile, and N, basal  
1769 views; O-Q: tooth (SN2012-83) in O, lingual, P, lingual, and Q, basal views; R-T: tooth (SN2012-84) in  
1770 R, lingual, S, occlusal, and T, basal views; U-W: tooth (SN2012-85) in U, labial, V, occlusal, and W,  
1771 lingual views; X-Y: tooth (SN2012-86) in X, lingual and Y, basal views. Scale bar equals 1mm.

1772 **Figure 9.** Rhinopristiforms from the Unit 3, Cap de Naze Fm. **A-J: ? *Microbatis* sp.** A-D: anterior tooth  
1773 (SN2012-87) in A, lingual, B, labial, C, profile, and D, basal views; E-F: anterolateral tooth (SN2012-88)  
1774 in E, lingual and F, basal views; G-H: anterolateral tooth (SN2012-89) in G, lingual and H, labial views;  
1775 I-J: anterolateral tooth (SN2012-90) in I, lingual and J, labial views. **K-U: *Sowibatos minimus* gen. et**  
1776 **sp. nov.** K-L: tooth (SN2012-91) in K, occlusal and L, lingual views; M-O, tooth (SN2012-92) in M,  
1777 lingual, N, basal, and O, occlusal views; P: tooth (SN2012-93) in lingual view; Q-U: tooth (SN2012-94,  
1778 **holotype**) in Q, occlusal, R, basal, S, profile, T, labial, and U, lingual views. Scale bar equals 500  $\mu$ m.

1779 **Figure 10.** Myliobatiforms from the Unit 3, Cap de Naze Fm. **A-A': '*Dasyatis*' *reticulata* sp. nov., non-**  
1780 **cuspidate morph.** A-D: tooth (SN2012-95) in A, lingual, B, profile, C, occlusal, and D, basal views; E-H:  
1781 tooth (SN2012-96) in E, lingual, F, occlusal, G, profile, and H, basal views; I-L: tooth (SN2012-97) in I,  
1782 lingual, J, profile, K, occlusal, and L, basal views; M-P: tooth (SN2012-98) in M, lingual, N, profile, O,  
1783 occlusal, and P, basal views; Q-T: tooth (SN2012-99) in Q, lingual, R, profile, S, occlusal, and T, basal  
1784 views; U-W: tooth (SN2012-100) in U, lingual, V, basal, and W, occlusal views; X-A': tooth (SN2012-

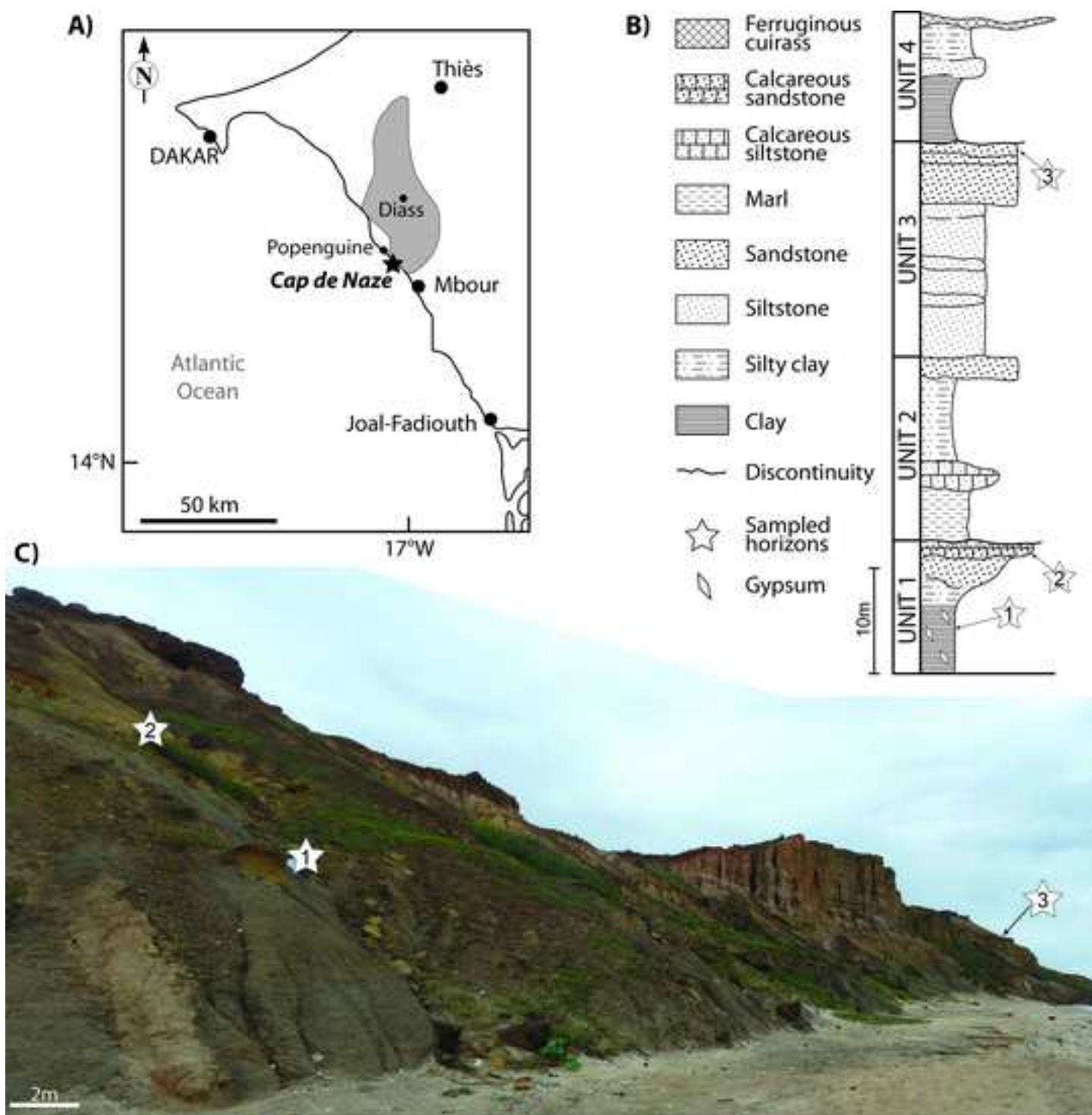
1785 101) in X, lingual, Y, profile, Z, occlusal, and A', basal views; **B'-S'**: '*Dasyatis' reticulata* sp. nov.,  
1786 **cuspidate morph.** B'-C': tooth (SN2012-102) in B', profile and C', occlusal views; D'-F': tooth (SN2012-  
1787 103) in D', profile, E', lingual, and F', basal views; G'-I': tooth (SN2012-104) in G', occlusal, H', profile,  
1788 and I', lingual views; J'-L': tooth (SN2012-105) in J', occlusal, K', profile, and L', basal views; M'-P':  
1789 tooth (SN2012-106) in M', lingual, N', profile, O', occlusal, and P4, basal views; Q'-S': tooth (SN2012-  
1790 107) in Q', profile, R', lingual, and S', labial views. Scale bar equals 2mm.

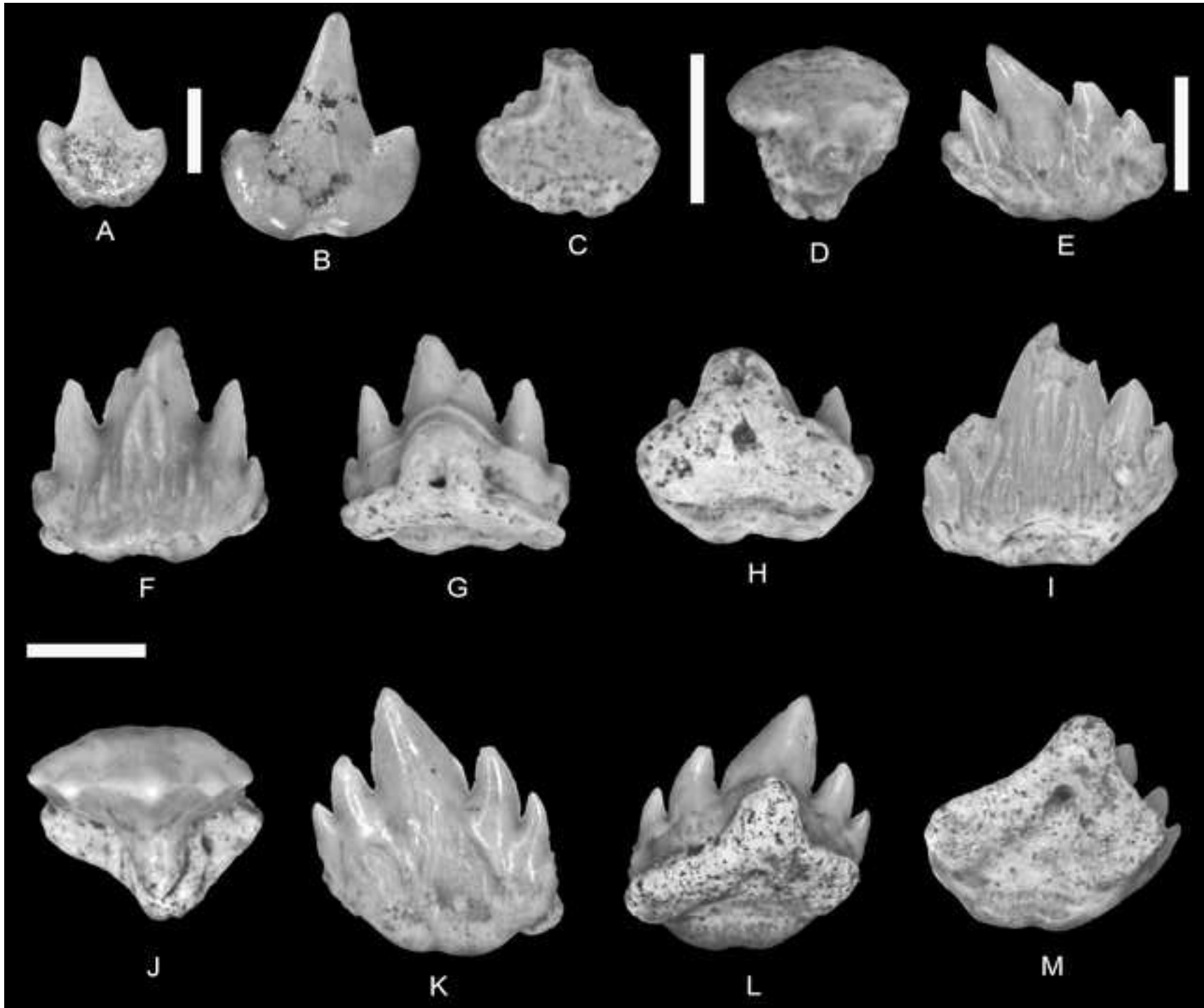
1791 **Figure 11.** Myliobatiforms from the Unit 3, Cap de Naze Fm. **A-C'**: *Coupatezia casei* sp. nov., non-  
1792 **cuspidate morph.** A-D: anterolateral tooth (SN2012-108, **holotype**) in A, lingual, B, basal, C, profile,  
1793 and D, occlusal views; E-F: anterior tooth (SN2012-109) in E, lingual and F, labial views; G-I:  
1794 anterolateral tooth (SN2012-110) in G, lingual, H, profile, and I, basal views; J-L: anterior tooth  
1795 (SN2012-111) in J, lingual, K, basal, and L, occlusal views; M-P: anterolateral tooth (SN2012-112) in  
1796 M, lingual, N, labial, O, basal, and P, occlusal views; Q-R: anterior tooth (SN2012-113) in Q, lingual  
1797 and R, occlusal views; S-U: anterolateral tooth (SN2012-114) in S, lingual, T, basal, and U, occlusal  
1798 views; V-W: anterolateral tooth (SN2012-115) in V, lingual and W, occlusal views; X: lateral tooth  
1799 (SN2012-116) in occlusal view; Y: lateral tooth (SN2012-117) in occlusal view; Z-A': anterolateral  
1800 tooth (SN2012-118) in Z, lingual and A', occlusal views; B'-C': lateral tooth (SN2012-119) in B', lingual  
1801 and C', occlusal views. **D'-V'**: *Coupatezia casei* sp. nov., **cuspidate morph.** D': lateral tooth (SN2012-  
1802 120) in occlusal view; E'-H': lateral tooth (SN2012-121) in E', lingual, F', labial, G', occlusal, and H',  
1803 basal views; I'-J' : anterior tooth (SN2012-122) in I', lingual and J', labial views; K': anterior tooth  
1804 (SN2012-123) in occlusal view; L'-N': anterior tooth (SN2012-124) in L', lingual, M', occlusal, and N',  
1805 labial views; O'-Q': anterior tooth (SN2012-125) in O', occlusal, P', lingual, and Q', labial views; R'-U':  
1806 anterolateral tooth (SN2012-126) in R', occlusal, S', labial, T', lingual, and U', basal views. Scale bar  
1807 equals 1mm.

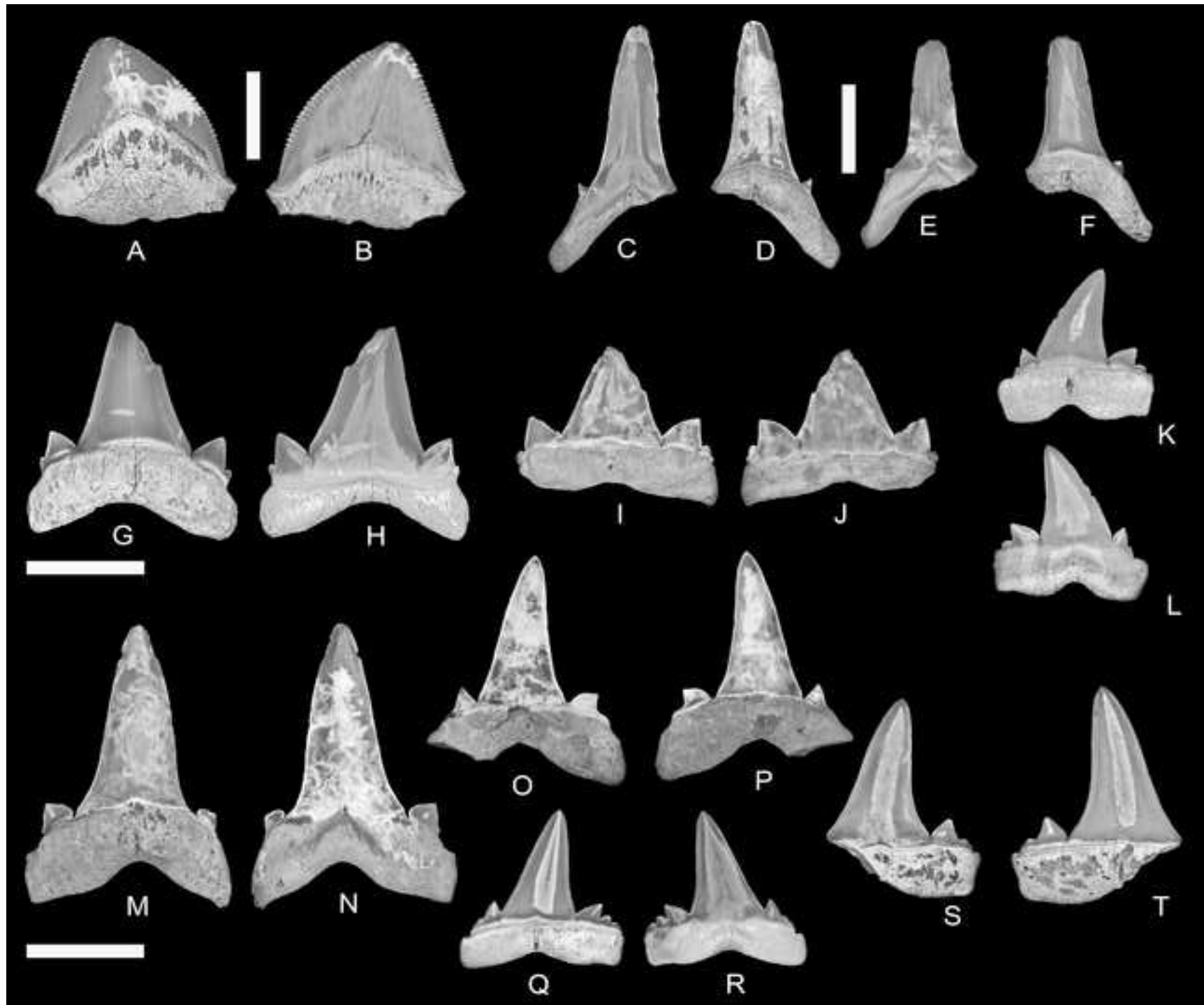
1808 **Figure 12.** Myliobatiforms and Batomorphii *incertae sedis* from the Paki and Cap de Naze Fm. **A-B**: ?  
1809 **Coupatezia** sp. tooth (SN2012-127) from the Unit 3, Cap de Naze Fm. in A, occlusal, B, lingual, and B,  
1810 profile views. **D-H**: *Rhombodus binkhorsti*, tooth (SN2012-128) from yellow sandstone (Unit 1) of the  
1811 Paki Fm. in D, occlusal, E, labial, F, lingual, G, profile, and H, basal views. **I-M**: *Rhombodus* sp., tooth  
1812 (SN2012-129) from yellow sandstone (Unit 1) of the Paki Fm. in I, occlusal, J, labial, K, lingual, L,  
1813 profile, and M, basal views. **N-Q**: *Phosphatodon cretaceus* sp. nov. tooth (SN2012-130, **holotype**)  
1814 from the Unit 3, Cap de Naze Fm. in N, occlusal, O, lingual, P, labial, and Q, profile views. **R-V**:  
1815 **Batomorphii indet. 1** tooth (SN2012-131), from the Unit 3, Cap de Naze Fm. in R, labial, S, profile, T,  
1816 lingual, U; occlusal, and V, basal views. **W-Z**: **Batomorphii indet. 2** tooth (SN2012-132) from the Unit  
1817 3, Cap de Naze Fm. in W, occlusal, X, lingual, Y, labial, and Z, basal views. **A'-B'**: **Batomorphii indet. 3.**

1818 A', tooth (SN2012-133) from the Unit 3, Cap de Naze Fm. in lingual view; B', tooth (SN2012-134, Unit  
1819 3) in lingual view. All scale bars 1mm, excepted D-H (5mm).

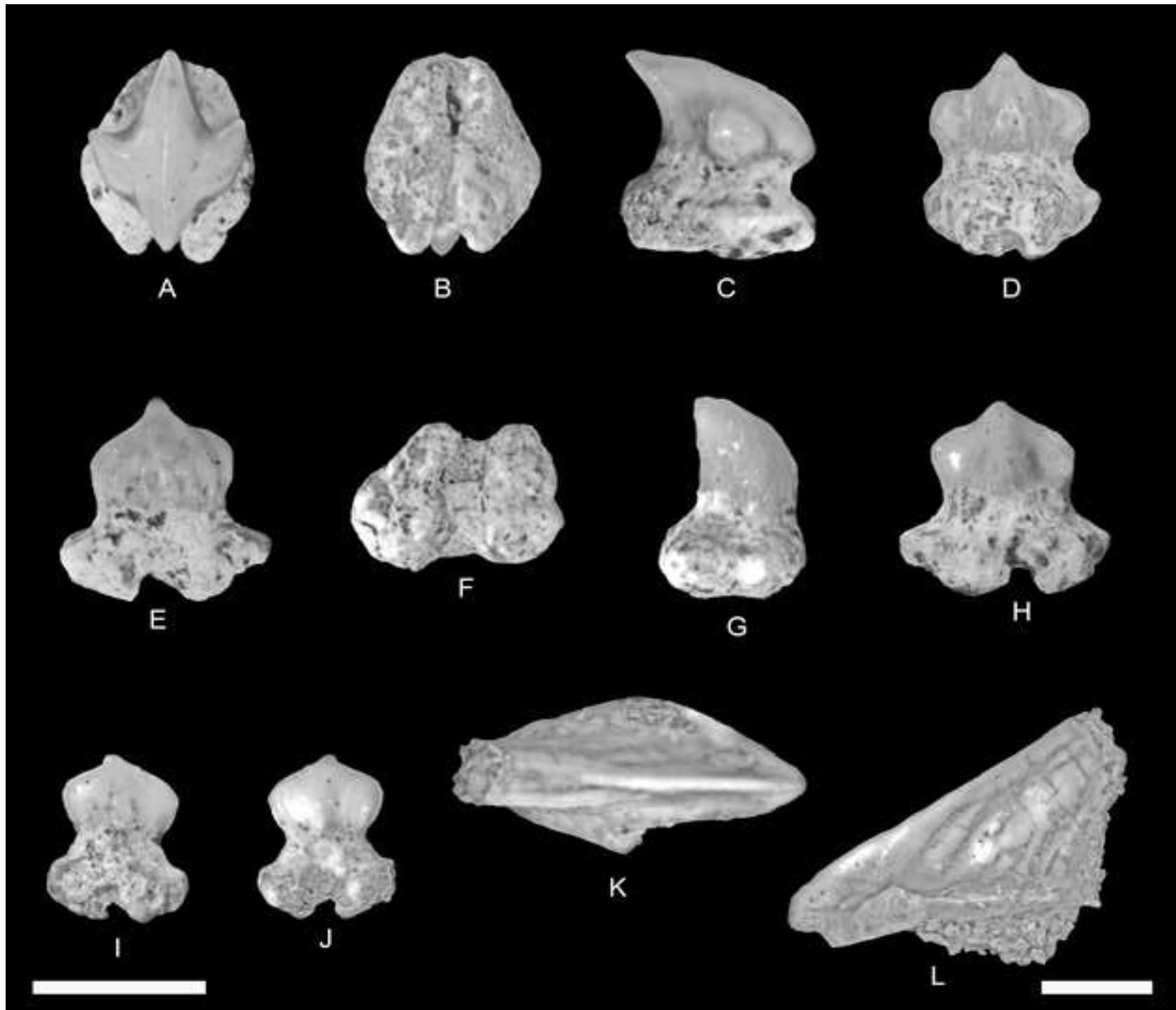
1820 **Table 1.** Faunal list from the Cape de Naze section including previous report of Cuny et al. (2012)  
1821 indicated by letter C, and the news records reported in the present work indicated by letter P. S1  
1822 refers to Sampling 1 (grey silty argillites of Unit 1), S2 refers to Sampling 2 (yellow calcareous  
1823 siltstone of Unit 1), S3 refers to Sampling 3 (ferruginous sandstone of Unit 3).

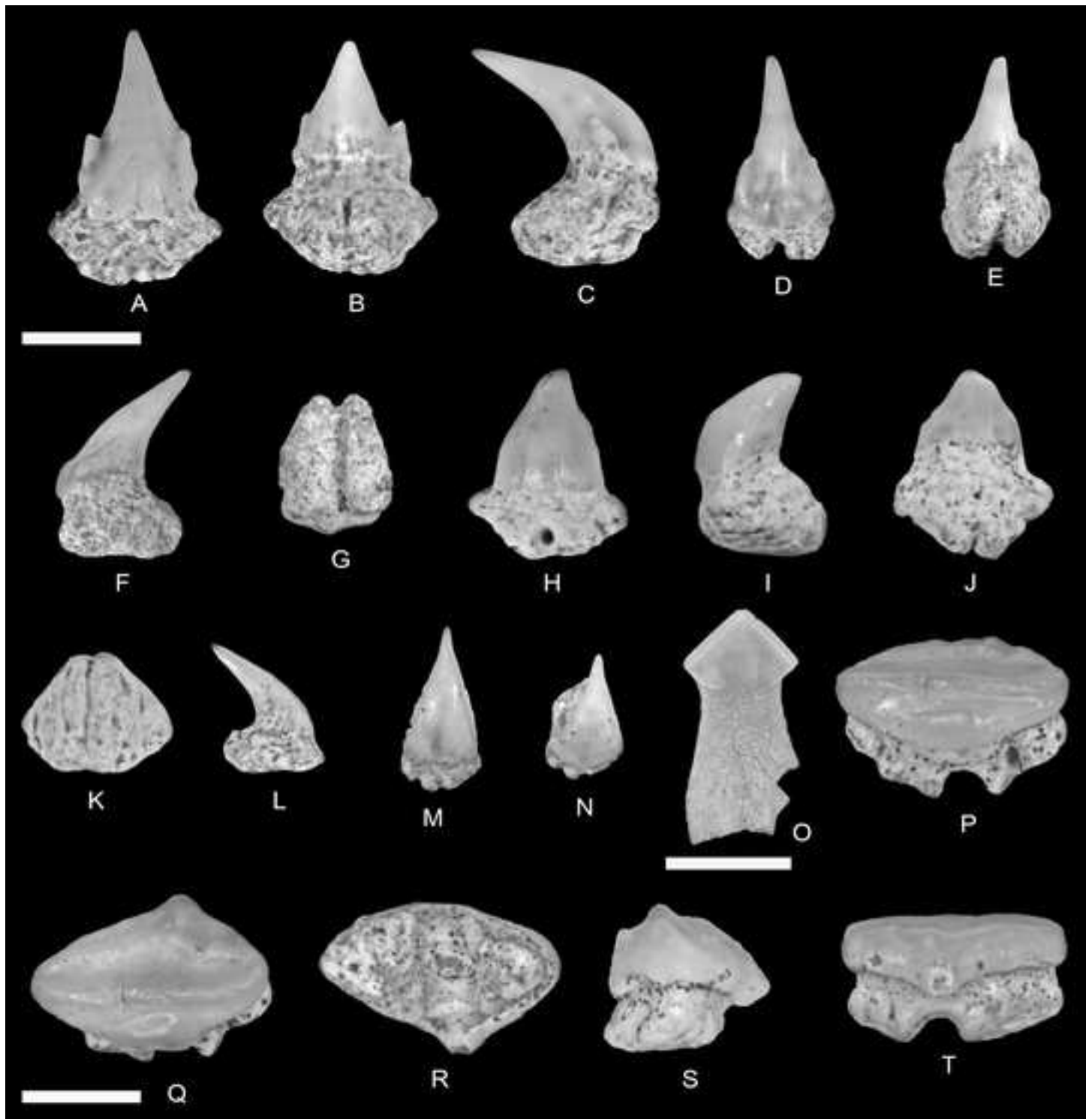


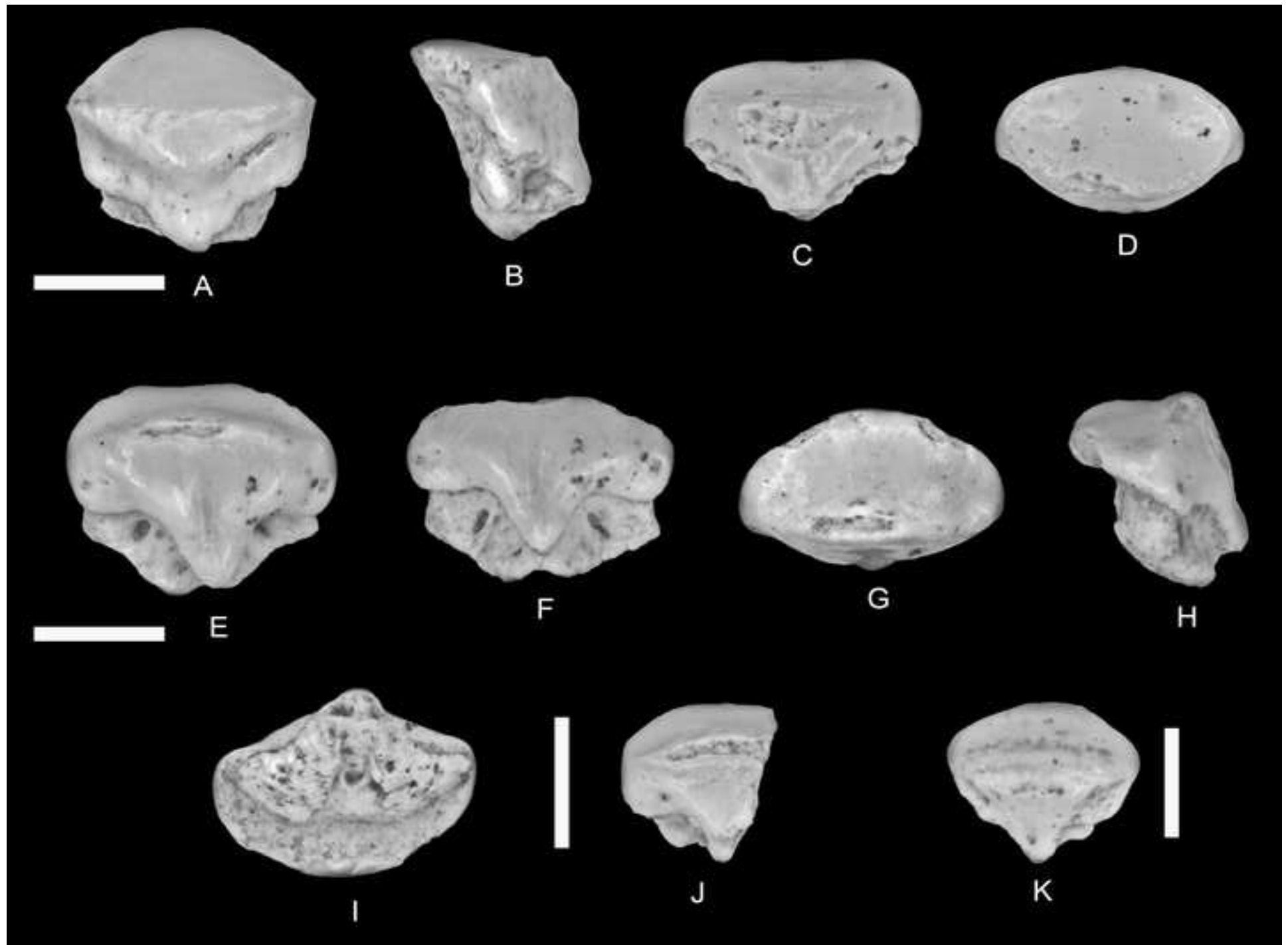


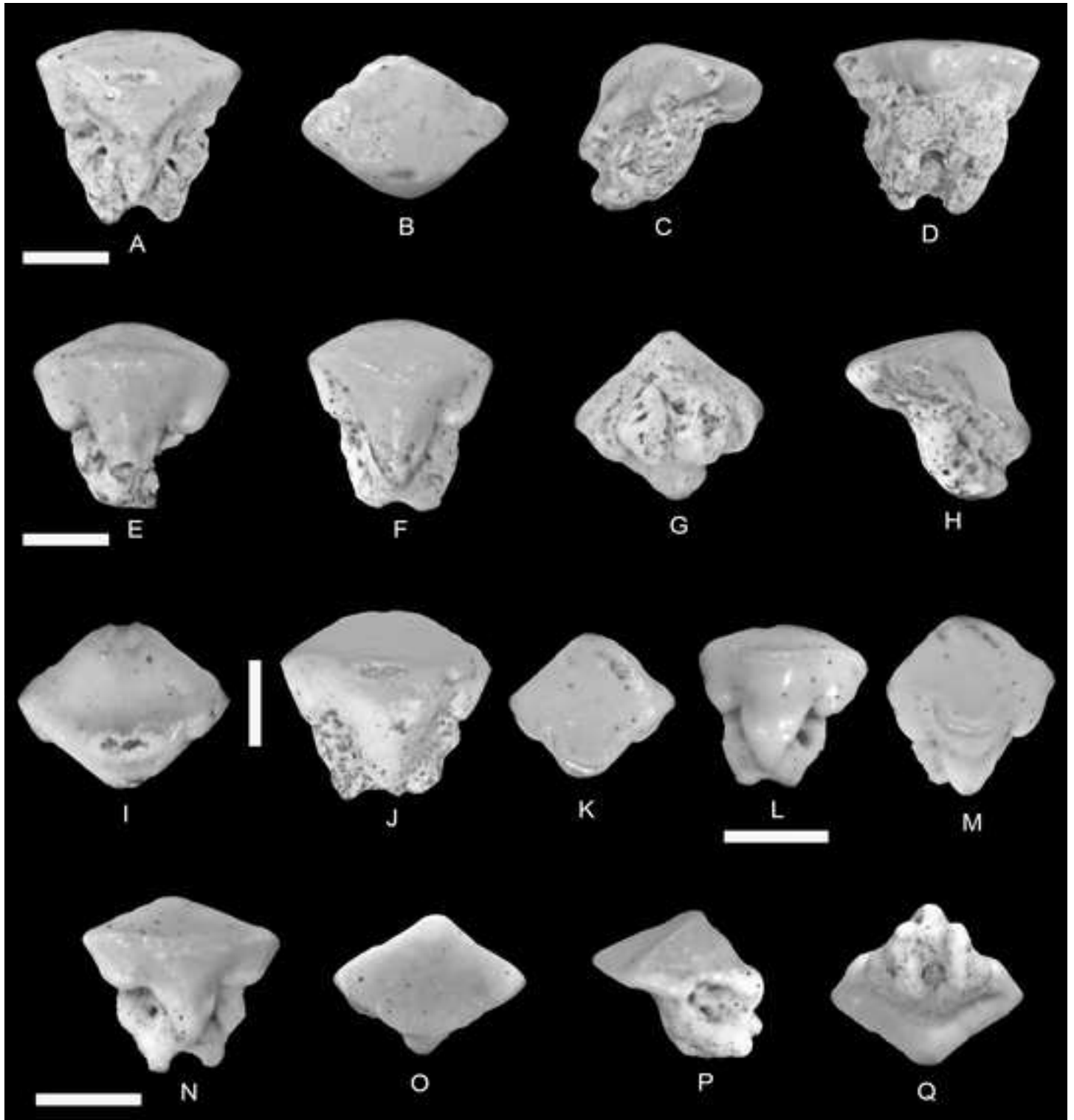


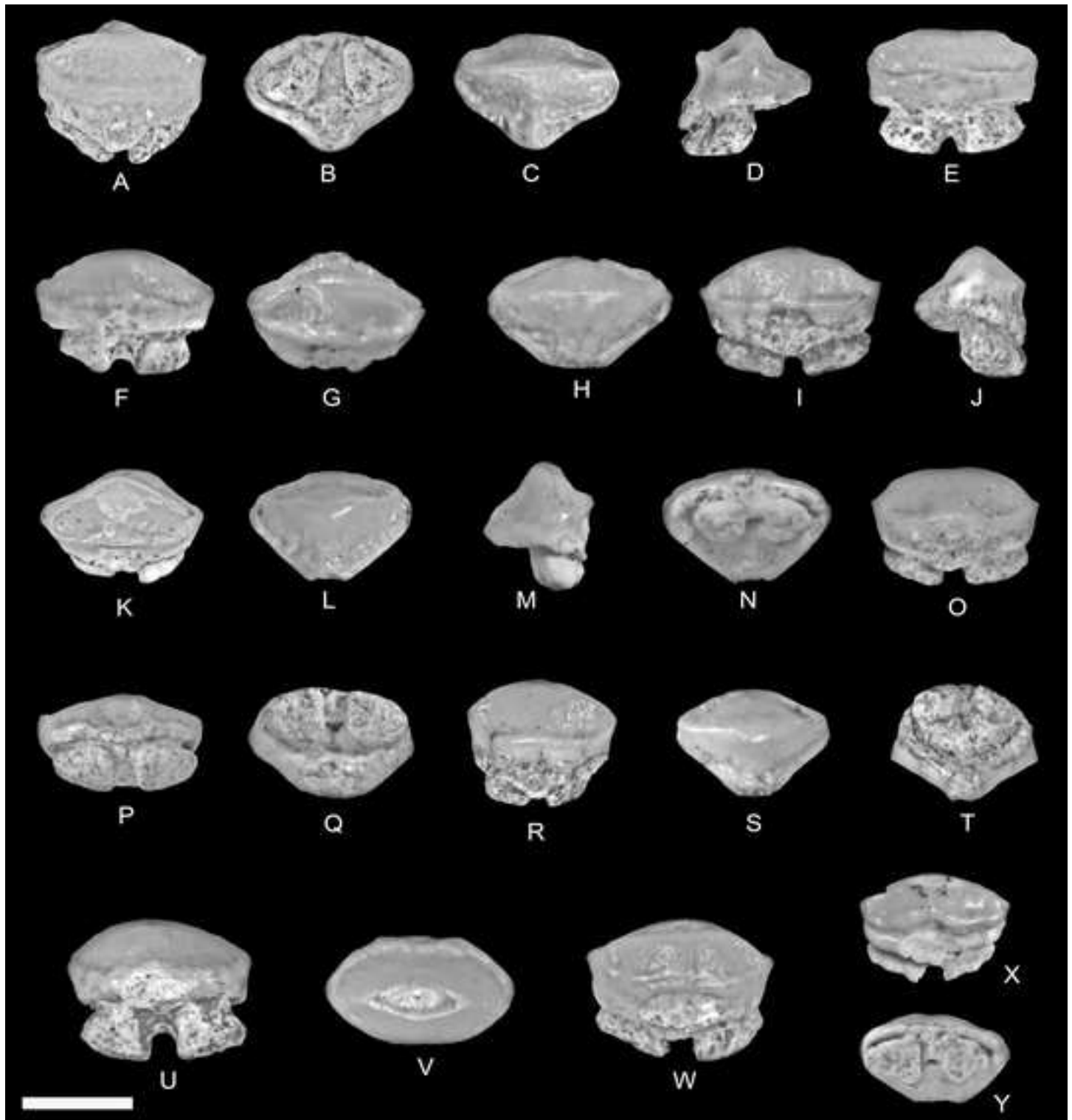




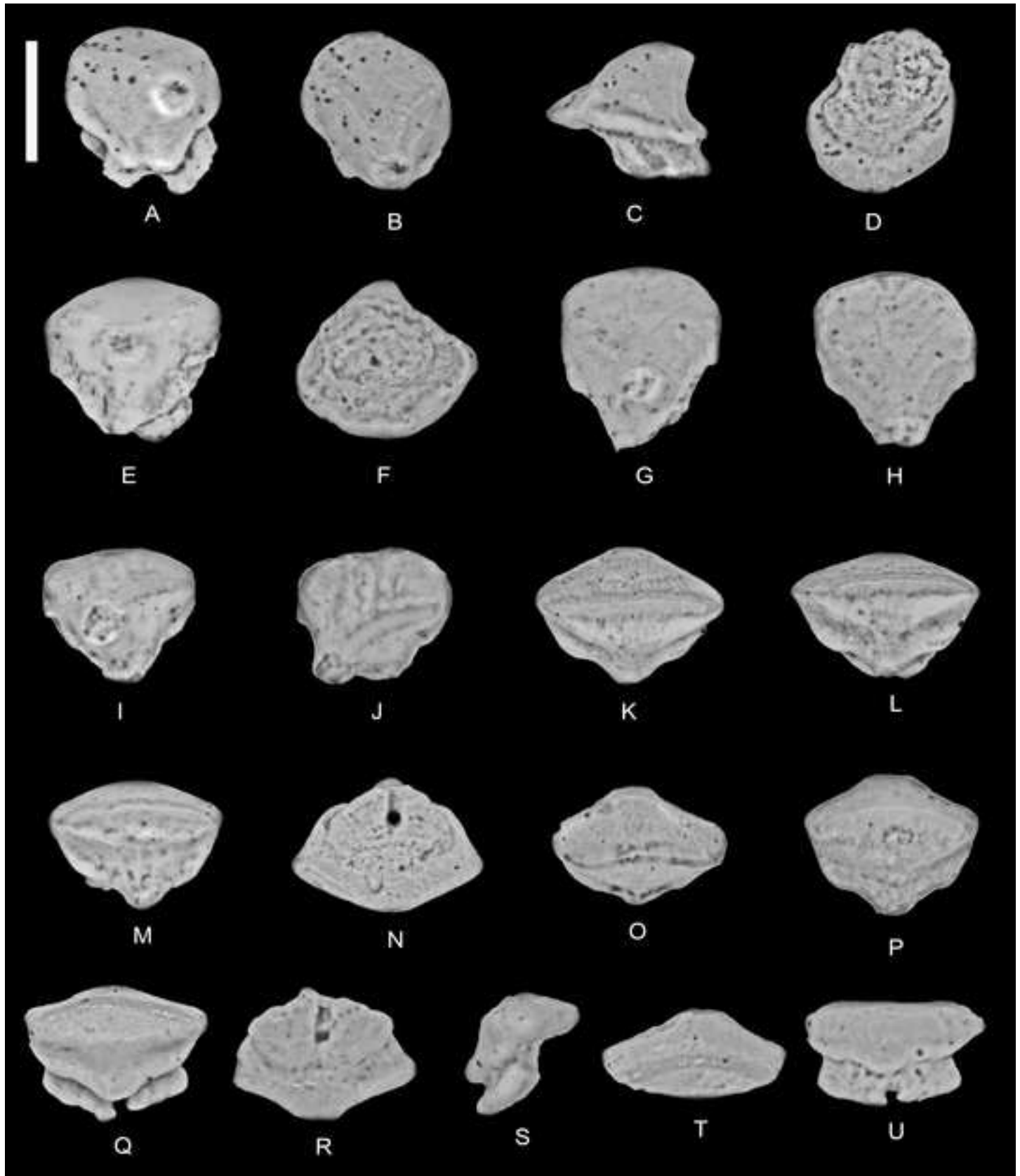


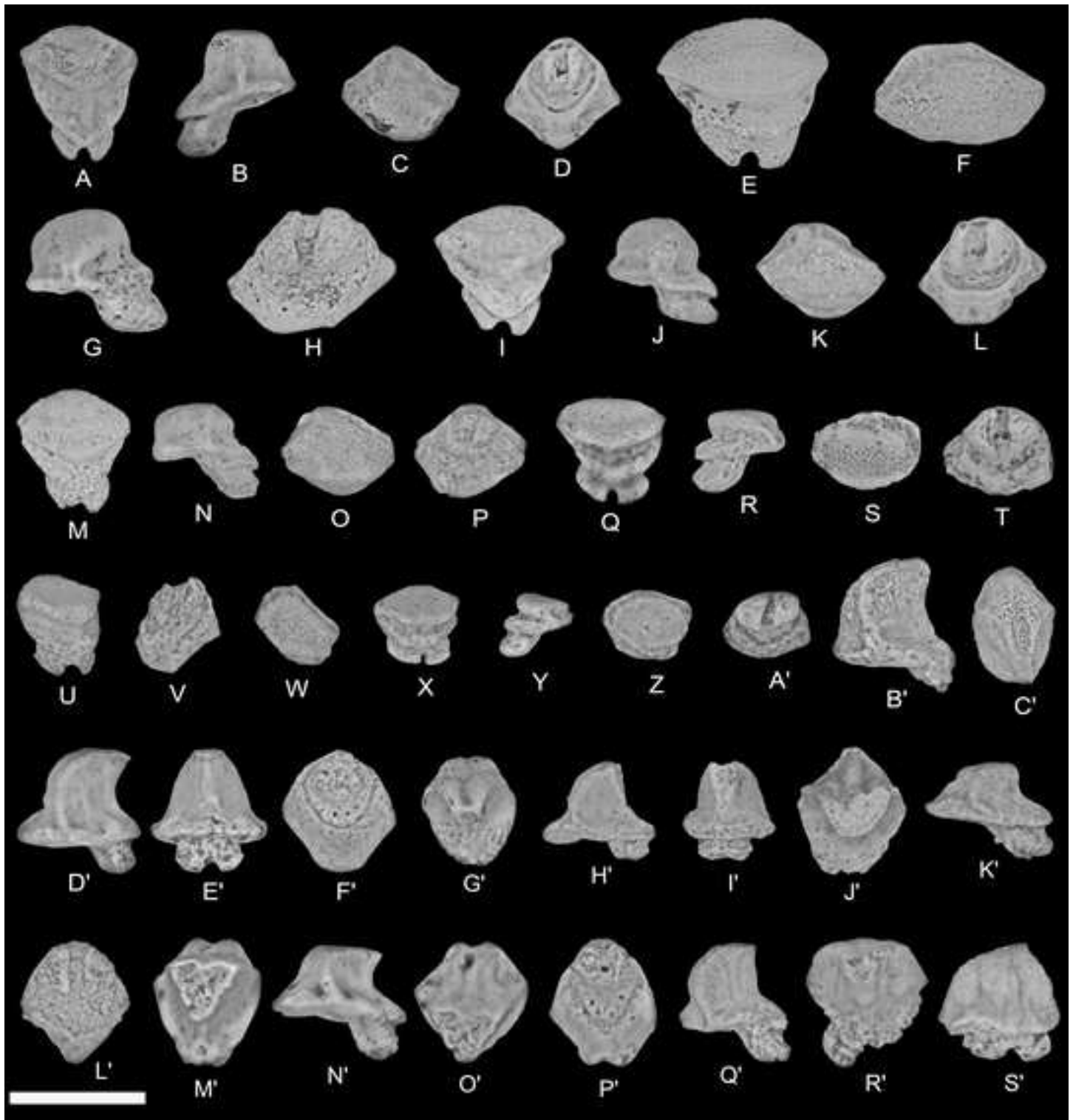


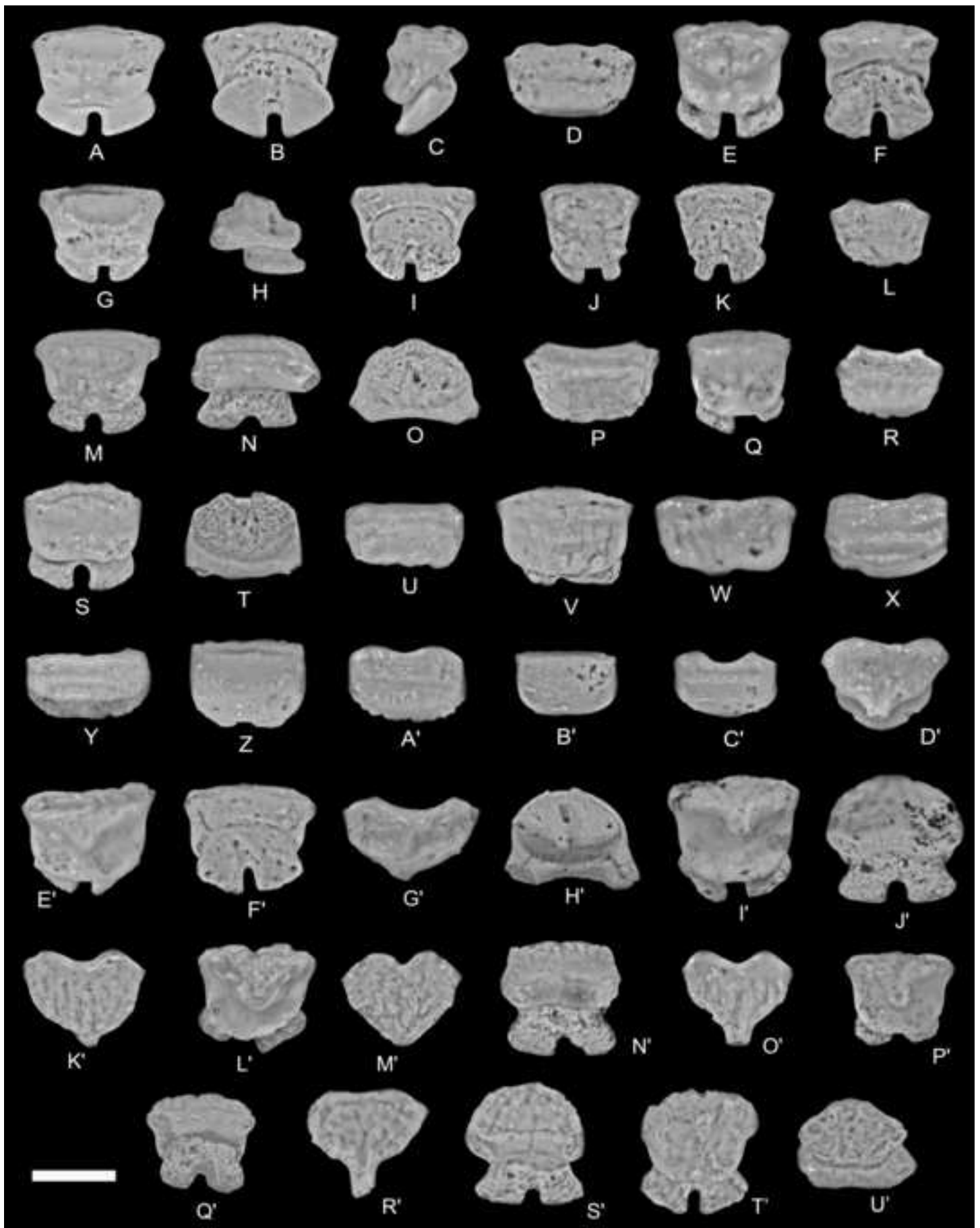




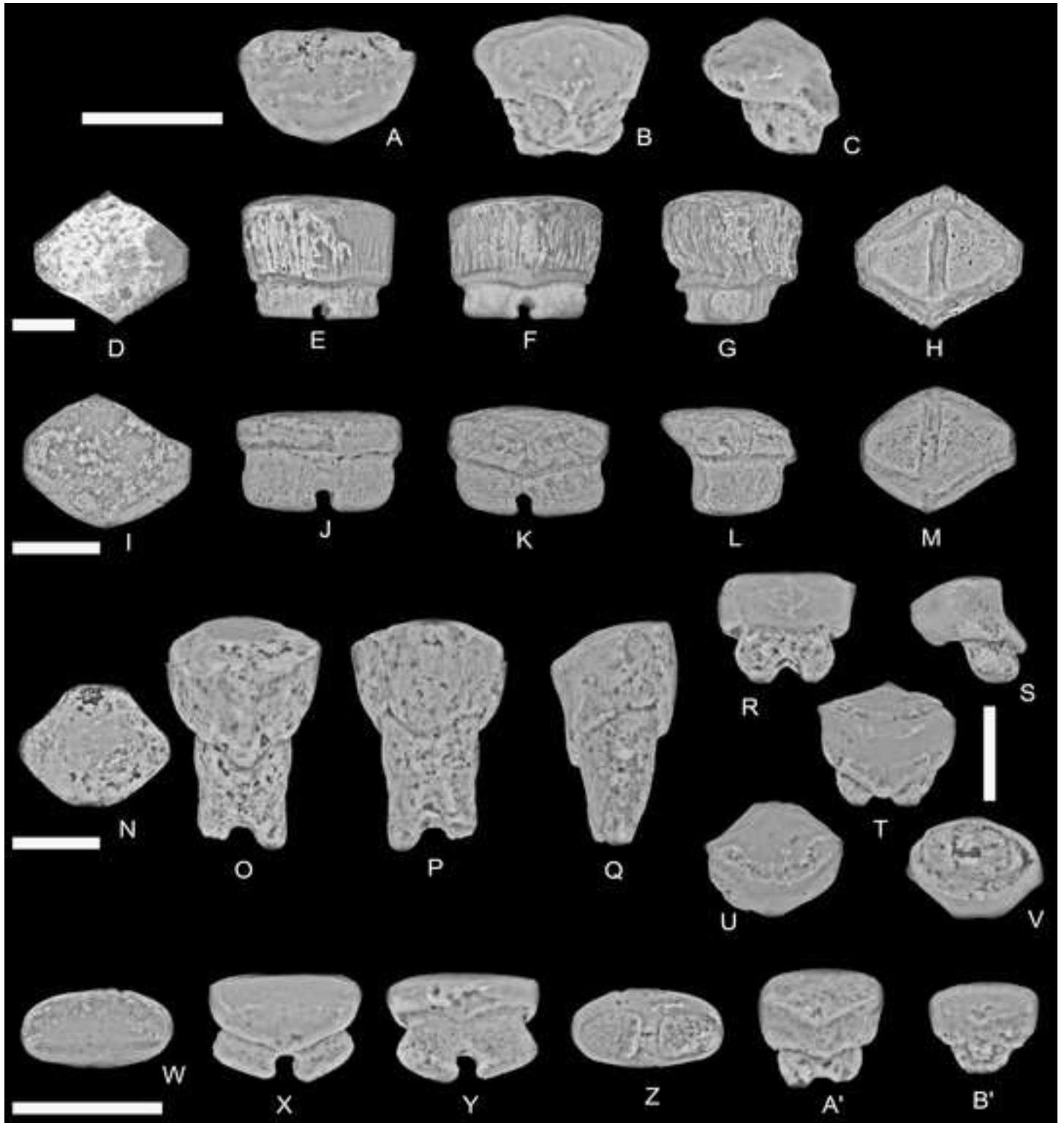


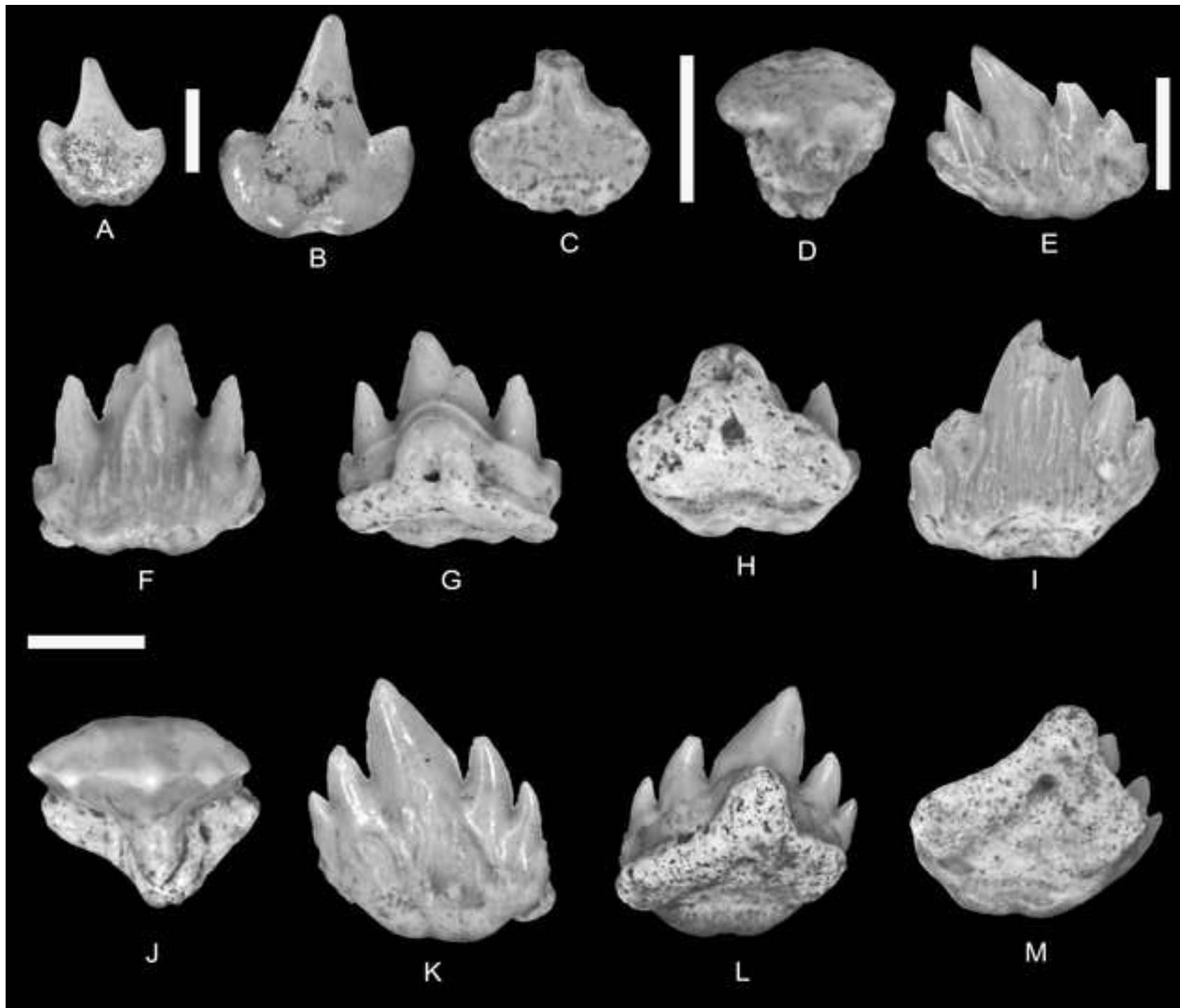












Order	Family	Taxon
Orectolobiformes	Hemiscylliidae	<i>Chiloscyllium</i> sp. <i>Hemiscyllium</i> sp.
Lamniformes	Ginglymostomatidae	<i>Plicatoscyllium youssoufiaense</i>
	Anacoracidae	<i>Squalicorax pristodontus</i>
	Carchariidae	<i>Carcharias</i> cf. <i>heathi</i> <i>Carcharias</i> sp. 1 <i>Carcharias</i> sp. 2
Rajiformes	Otodontidae	<i>Cretalamna maroccana</i>
	Serratolamnidae	<i>Serratolamna serrata</i>
	Sclerorhynchidae	<i>Dalpiazia stromeri</i> <i>Ctenopristis nougareti</i>
	Sclerorhynchidae	<i>Schizorhiza stromeri</i>
Rhinopristiformes	Ptychotrygonidae	<i>Ptychotrygon nazeensis</i> sp. nov.
	Parapalaeobatidae	<i>Parapalaeobates</i> sp.
	Rhynchobatidae	cf. <i>Rhynchobatus</i> sp.
	Rhinobatidae	<i>Terangabatis thiami</i> gen. et sp. nov. <i>Rhinobatos' popenguinensis</i> sp. nov.
	Rhinobatoidei incert. fam.	<i>Atlantobatis acrodonta</i> gen. et sp. nov. ? <i>Microbatis</i> sp. <i>Sowibatos minimus</i> gen. et sp. nov.
Myliobatiformes	Dasyatidae	<i>Dasyatis' reticulata</i> sp. nov.
	Dasyatoidea incert. fam.	<i>Coupatezia casei</i> sp. nov. ? <i>Coupatezia</i> sp.
	Rhombodontidae	<i>Rhombodus binkhorsti</i> <i>Rhombodus andriesi</i> <i>Rhombodus</i> spp.
Batomorphii incert. sed.	Myliobatiformes incert. fam.	<i>Phosphatodon cretaceus</i> sp. nov.
	Batomorphii incert. sed.	Batomorphii indet. sp. 1 Batomorphii indet. sp. 2 Batomorphii indet. sp. 3

\* reported as *Cretalamna* cf. *biauriculata* by Cuny et al. (2012)

S1 (Unit 1)	S2 (Unit 1)	S3 (Unit 3)
		P
		P
		P
	P	C
		C
		C
P	P	
	P	
	P	C*
		P
		P
	P	P, C
		P
		C
		P
		P
		P
		P
	P	P
		P
	P	P, C
		C
	P, C	P
		P
		P
		P
		P

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### **Author contributions**

LH, RS, JM and GG conceived the study; LH, JM, RS, and BS did the fieldwork and sampling; GG drafted the manuscript and illustrations with inputs from all authors; all authors reviewed the manuscript.