



Contribution to the reappraisal of the mid Paleogene ichthyofauna of Western Africa with three new enigmatical elasmobranchs from Thanetian–Lutetian of Senegal

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**Contribution to the reappraisal of mid Paleogene ichthyofauna of Western Africa with
three new enigmatical elasmobranchs from Thanetian-Lutetian of Senegal.**

**Contribution à la réévaluation de l'ichtyofaune du Paléogène moyen en Afrique de
l'Ouest avec trois nouveaux élasmodontes énigmatiques du Thanétien-Lutétien du
Sénégal.**

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Abstract.

We report here three new elasmobranch fossil taxa from Thanetian-Lower Lutetian nearshore marine deposits of northeastern (Matam region) and central-western (Sine-Saloum region) Senegal. These three new taxa represent the oldest species of the enigmatical elasmobranch *Odontorhysis*, the oldest putative representatives of marine potamotrygonid, and an uncertain dasyatoid genus with the smallest grinding dentition ever described. These new taxa, representing the second Cenozoic elasmobranch remains formally described from Senegal, broaden our understanding of their evolutionary and biogeographic history in the equatorial Eastern Atlantic during this time period. Their occurrences confirm hypothesised stratigraphically correlations between the top of Matam Fm. and the base of Lam Lam Fm., refine the marine connections between these two Senegalese regions, and suggest that these genera were broadly distributed within the shallow marine settings of the equatorial Eastern Atlantic during latest Paleocene – early Middle Eocene.

Keywords: Elasmobranch, new taxa, Paleogene, Senegal.

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48 **Résumé.**

49 Nous rapportons ici trois nouveaux taxa de fossiles d'élasmobranches des dépôts marins
50 littoraux du Thanétien-Lutétien inférieur du Nord-Est (région de Matam) et du Centre-Ouest
51 (région du Sine-Saloum) du Sénégal. Ces trois nouveaux taxa représentent les espèces les plus
52 anciennes d'élasmobranches énigmatiques appartenant au genre *Odontorhynchus*, aux
53 potamotrygonides marins et à un dasyatoïde avec la plus petite denture broyeuse jamais
54 décrite. Ces nouveaux taxa, complétant l'unique description d'élasmobranches cénozoïques
55 nouveaux au Sénégal, élargissent notre compréhension de leur histoire évolutive et
56 biogéographique de l'Atlantique Est équatorial au cours de cette période. Leurs occurrences
57 confirment des corrélations stratigraphiques hypothétiques entre le sommet de la Formation
58 de Matam et la base de la Formation de Lam Lam. Celles-ci affinent aussi les liens marins
59 entre ces deux régions sénégalaises et leur comparaison avec des occurrences reconnues en
60 Afrique du Nord et de l'Ouest suggèrent que ces genres étaient largement répartis et
61 diversifiés dans les environnements marins peu profonds de l'Atlantique Est équatorial au
62 cours du Paléocène terminal et du début de l'Éocène moyen.

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64 **Mots-clés:** Elasmobranch, nouveaux taxa, Paléogène, Sénégal.

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Introduction

Biogeographic origins of African modern vertebrates have been the focus of considerable research since last decade in warm Paleogene period of West Africa. Among them, elasmobranch fossil record devoted to mid Paleogene was very partial with a unique description of taxa such as *Lophobatis* Cappetta, 1986, preliminary reports (Pascal, 1987; Cappetta and Traverse, 1988; Stevens et al., 2011), and/or ancient works that (e.g. Strömer, 1910, White, 1926, 1934, 1955). Biogeographic interpretations of past elasmobranch diversity in Central Western Atlantic during Paleogene have been mainly evidenced based on the richer northwestern (e.g. Morocco) and southwestern (e.g. Angola) African deposits (e.g. Arambourg, 1952; Noubhani and Cappetta, 1997; Darteville and Casier, 1943, 1959; Solé et al., 2018). However, a corresponding body of research is largely lacking for the Paleogene equatorial Eastern Atlantic elasmobranchs, despite the fact that nearly all of the known Cenozoic rocks along the West African coast are marine, especially near the Guinean Gulf. Indeed, reappraisal of the mid Paleogene Western African faunas is essential to better understand the elasmobranch evolution in the equatorial paleo-Atlantic. Currently, the Senegalese elasmobranch Cenozoic fossil record is only represented by mid Paleogene taxa from the phosphate ores of Matam (Pascal, 1987; Sambou et al., 2018; Sambou 2018) and Taïba (Hautier et al., 2012, 2014). Other associated marine vertebrate, including bony fish like amiid or scombrid (O-Leary et al. 2012, Cleason et al. 2015), sea cows and whales (Hautier et al., 2012) are recovered in Early-Middle Eocene from same or different localities (e.g. Gossas, Bargny). We report here, three new taxa of elasmobranchs with unambiguous dental morphologies that support biostratigraphical correlations between Formations from two

main Senegalese areas: Matam (Pascal, 1987; Sambou et al., 2017; Sambou, 2018) and Kaolack in Sine-Saloum region (Tabuce et al., 2019). These new taxa contribute to the reappraisal of mid Paleogene fauna of Western Africa and improve understanding the diversification of modern elasmobranchs.

Geological setting, material and methods.

Most of the specimens were found in the phosphate ore of Ndendouri-Ouali Diala near Matam (sub-prefecture of Orkadiéré, Matam region, approximatively 15°18'N, 13°01'W, see Sambou et al., 2017 for details) located on the left riverbank of the Senegal River, northeastern part of Senegal (Fig. 1). The studied material was collected in water-well cuttings during ancient campaigns of M. Pascal (see Pascal, 1987) that allowed to collect an amount of 450 kg of phosphatic sediment and 50 kg of sandy sediment in a series of wells (collecting H.C.) and from recent wells drilled manually in the subsoil of Ndendouri-Ouali Diala (collecting B.S.) and following a NW direction (see Sambou, 2018). Sambou et al. (2017) recently revised the faunas from the Gorgol and Matam Fm. outcropping in the phosphate ore of Matam as previously reported in Pascal (1987). 38 species of elasmobranch have been recognized in the different levels of the 20 well-drilling and 33 different samples along the Matam series (see Sambou et al., 2017 : Tab.1 for details). These faunas include several determined and undetermined species of *Brachycarcharias*, "*Cretolamna*", *Protoginglymostoma*, *Ginglymostoma*, *Nebrius*, *Rhizoprionodon*, *Physogaleus*, *Triakis*, *Foumtizia*, *Rhynchobatus*, *Pristis*, *Anoxypristis*, *Eotorpedo*, *Lophobatis*, *Myliobatis*, *Rhinoptera*, *Leidybatis*, *Garabatis*, *Coupatezia*, *Ouledia* and the three new taxa reported here. From these, five fossiliferous associations were identified along the available sedimentological successions (see Fig. 1), and confirmed the late Thanetian age of the top of the Gorgol Fm. (association 1 – lithological Unit 0), the Ypresian age of the phosphate

deposits belonging to Matam Fm (rich associations 2-4, lithological Units 1-3), and the Lutetian age of the higher clay-limestone unit of Matam Fm. (association 5, lithological Unit 4).

The other specimens come from the water-well cuttings located at Sanghaye Bele village (14°16'55.5"N, 16°6'14.01"W, Fig. 1), north of Kaolack in the Sine-Saloum region (central-western part of Senegal, see Tabuce et al., 2019 for details). The fossiliferous deposits attributed to the Lam Lam Fm. correspond to coquina limestone and yellow to white clayey limestone alternating with marls. Material was recovered by soft acid attack (acetic 8%) of 30 kg of sediments (see also Tabuce et al. 2019 for details). If the base of the Lam-Lam Formation is E8 in age (lower Lutetian), the top of the formation (Lam-Lam marls) yielded a rich planktonic foraminifera association that indicates the E9 biozone (top of lower Lutetian) (Flicoteaux 1974, Roger et al. 2009). These regional correlations indicate a confident lower Lutetian age (E8-E9 biozones, 49 to 45,8 Ma ~44 M.a., Vandenberghe et al. 2012) for the fossiliferous level in water-well of Sanghaye Bele (see Tabuce et al. 2019 for correlations). Some elasmobranch remains were collected in the 30 kg of limestone and include for instance some teeth of *Chiloscyllium* sp., *Nebrius* cf. *obliquus*, ?*Rhizoprionodon* sp., *Physogaleus* sp., *Rhynchobatus* sp., *Rhinobatos* sp., *Ouledia* sp., ?*Jacquhermania attiai*, *Arechia* sp., *Dasyatoid* indet., *Coupatezia* sp. as well as two of the three new taxa described here. The elasmobranch assemblage from the coquina limestone of the Lam Lam Fm. in Sanghaye Bele would then be contemporaneous with the coquina limestone of the Ngolothie borehole near Kaolack (Tabuce et al. 2019) and most probably sub contemporaneous with the elasmobranch assemblage of the clay-limestone unit ending the Matam Fm. in Sambou et al. (2017).

FIG.1 here

Systematic Palaeontology

143 *Institutional Abbreviations*— Fossil material, including type series, is housed at the
144 University of Montpellier, France (abbreviations SES, MAM) or at the University Cheikh
145 Anta Diop of Dakar, Senegal (abbreviations SNSAN/2011/). Tooth terminology follows
146 Cappetta (2012)

147

148 Class CHONDRICHTHYES Huxley, 1880

149 Subclass ELASMOBRANCHII Bonaparte, 1838

150 SubCohort NEOSELACHII Compagno, 1977

151 Superorder BATOMORPHII Cappetta, 1980

152 Order MYLIOBATIFORMES Compagno, 1973

153 Superfamily DASYATOIDEA Compagno, 1973

154 ?Potamotrygonidae Garman, 1877

155 ?Styracurinae Carvalho et al., 2016

156

157 *Atlantitrygon nov.gen.*

158 **Type species:** *Dasyatis sudrei* Cappetta, 1972

159 **Type material:** Holotype: SES64, Sessao, Thanetian of Niger (Cappetta, 1972 : Plate 6 fig. 3)

160 refigured in figure 2 A ; paratypes SES62-63, 65-67 (Cappetta, 1972 : Plate 6 fig. 1-2,4-6)

161 partially refigured in figure 2 B-D.

162 **Etymology:** simplified Greek “*Atlanti*” refers to the past distribution of representatives,
163 currently limited to tropical Atlantic sea along the western African coast, and Greek “*trygon*”
164 meaning stingray.

165 **Diagnosis:** Dasyatoid genus characterized by gracile medium sized teeth with high crown
166 compared to root, a development in height of the lingual zone and the lingual marginal face of
167 crown (including the transversal keel); a long, slender cusp mesiodistally flattened and
168 highlighted by an occlusal median crest, a junction between the undulating transverse keel
169 and the median crest of cusp forming a three-pointed star in occlusal view ; a narrow lingual
170 face and a concave labial face of crown with finely ornamented enameloid; a root with two
171 sub-triangular lobes elongated transversally.

172 **Occurrence:** from Thanetian (Niger, Togo and Senegal) with *A. sudrei* to lower Lutetian
173 (Senegal) with *A. senegalensis* nov. sp.

174 **Discussion:** Cappetta (1972) described *Dasyatis sudrei* from Sessao, Niger. At that time,
175 diagnosis characters, e.g. the long slender cusp, were evaluated as enough peculiar compared
176 to other species of *Dasyatis* s.l. to justify the creation of a new species (Cappetta, 1972 : p.
177 207). The author suggested that this taxon could be close to genus *Himantura*, unknown at the
178 fossil state in 1972. In fact, a slender long cusp is known in many male teeth belonging to
179 some dasyatidspecies (e.g. *Dasyatis*, *Hypanus*) and many Urotrygonidae (e.g. *Urobatis*) and
180 Urolophidae (e.g. *Urolophus*) but this long cusp is usually rooted on the edge of lingual zone
181 and its top is delimited by the transversal keel that follows the upper borders of cusp. The
182 upper face of cusp, often concave, belongs in fact to the labial face, contrary to what is
183 observed in *Atlantitrygon*. The unique dasyatoid teeth that display a comparable “displaced”
184 cusp are observable in living western Atlantic “*Himantura*” *schmardae* (Werner, 1904 : see
185 Cappetta, 2012, fig. 410) recently attributed to genus *Styracura* Carvalho et al., 2016 which also

includes *S. pacifica* (Beebe and Tee-Van, 1941). Both these marine species, recently included in Potamotrygonidae, are considered more closely related to freshwater potamotrygonins (Carvalho et al., 2016). The inclusion of *Atlantitrygon* in the marine Styraurinae thus remains hypothetic and is only based on global resemblances of the tooth shape and the presence of a displaced main cusp. However, the teeth of *S. schmardae* are easily distinguishable from *Atlantitrygon* nov. gen. by having a straight transversal keel, a second transverse keel, running more or less parallel to main one, a cusp without crest and a ornamentations absent, contrary to the condition seen in teeth of *Atlantitrygon* nov. gen. Finally, the unique combination of characters in *Atlantitrygon* nov. gen. does support the creation of this new fossil genus but its systematic position among the Potamotrygonidae remains nevertheless uncertain, partly because our limited knowledge of the dental variation in living batoid (Guinot et al., 2018).

Atlantitrygon senegalensis nov. sp.

Etymology: Refers to the country where the type series was found

Type material : Holotype Fig. 2 K, MAM-09 (well F0 9.18-9.3m, Unit 2 in Sambou et al., 2017) Ndendouri-Ouali Diala, ?Early Ypresian, Matam Fm.; Paratypes Fig. 2 F-J, MAM-04 to MAM-08 and MAM-10 to MAM-11 (well F0 9.18-9.30m, Unit 2 in Sambou et al., 2017) Ndendouri-Ouali Diala, ?Early Ypresian, Matam Fm

Additional material: a fifteen teeth from Lower Lutetian (E8-E9 biozones, 49 to 45,8 My) of Sine-Saloum region, Senegal and also partially figured Fig. 2 N-Q

Diagnosis: The new species distinguishes from the unique type species of genus by having teeth with higher transversal keel that looks as more protruding, undulated and often marked by three rounded pseudo cusplets in lingual view. Two of these cusplets are located at the

margin while the third one, the highest, is situated in the cusp axis. Compared to the type species, ornamentation of the enameloid of the lingual and labial faces is more finely developed, especially under the transversal keel with an alveolar network shape.

Occurrence: Ypresian to Lower Lutetian of Matam and Lower Lutetian of Sine-Saloum regions, Senegal, possibly in the Ypresian of Mali (Tamaguilet) and Morocco (Ouled Abdoun)

Description: The tooth morphology is consistent with that of dasyatoids, a paraphyletic group that includes many different families of stingrays (e.g. Dasyatidae, Urolophidae, Urotrygonidae, Potamotrygonidae, Plesiobatidae) with no pavement-like arrangement. The dentition is monognathic heterodont with high-crowned teeth (e.g. Fig. 2 I), which decrease in size toward the commissure (e.g. Fig. 2 M, P). The holotype (Fig. 2 K) is a tooth probably located medially along the jaw. It displays a high crown (Fig. 2 K2) with robust cusp (Fig. 2 K2). In occlusal view (Fig. 2 K1), the crown is semi-oval in shape, broader than long, with a long, slender cusp with median crest on its occlusal part. This median crest does not reach the apex of cusp (Fig. 2 K1). The crown has a high, transverse keel, which divides the crown into distinct labial and lingual parts (Fig. 2 K1). The junction between the undulating transverse keel and the median crest of cusp forms a three-pointed star (Fig. 2 K1). The transverse keel is quite salient and forms an erected cutting edge. The upper part of the lingual face (below the transverse keel) and the labial face are fully ornamented. This ornamentation is quite delicate and organized as an alveolar network with larger alveolus on concave basin of the labial face (Fig. 2 K3). The upper part of the ornamented labial visor (labial border of labial face) is reduced to a straight crest that overhangs the lower part of the unornamented labial visor. The lower part of lingual face, also unornamented below the cusp axis, is relatively expanded marginally. The root is narrow in profile (Fig. 2 K2), of holaulacorhizous type with two short lobes separated by a low groove. A large central foramen opens in labial part of the

235 nutritive groove. Tooth variability, in part due to heterodonty, mainly involves the general
236 shape of the crown, which is sometimes subtriangular in shape (e.g. Fig. 2 I) with often a long
237 slender cusp. This cusp is always present in all specimens suggesting no sexual heterodonty.
238 In more anterior files, the crown sometimes displays a very high, undulating transverse keel
239 that forms three pseudo rounded cusplets in lingual view (e.g. Fig. 2 L1, O1, N1). One of
240 them is located at the junction between the transverse keel and the median crest of the cusp.
241 Lingual ornamentations seemingly are absent on the lower part of lingual face and below the
242 cusp axis of all specimens, conversely to the condition seen in the whole labial face and in the
243 narrow band of lingual marginal face just under the transversal keel. In anterior teeth, this
244 ornamented upper part of lingual face is sometimes set apart from the unornamented lower
245 part by rounded transverse keels in lingual view (Fig. 2 L, N). Enameloid ornamentation is
246 quite delicate in the upper part of the lingual face (Fig. 2 H3, L2) and could be organized as
247 an alveolar network with larger alveolus on concave basin of the labial face (Fig. 2 K3, M2).
248 This ornamentation reduces gradually near the keel and crests where it takes the form of lace
249 when not abraded. The labial visor is merely variable, being often reduced to a salient and
250 straight crest delimiting the labial border of the labial face. The basal view of the crown (Fig.
251 2 H2, I1, O2) shows a broad and slightly convex crown rim at the outer part, which gradually
252 narrows down to half of its width at the inner part. The crown–root junction is located in a
253 shallow depression at the centre of the basal surface of the crown. The root is lower than the
254 crown, of holaulacorhizous type with two lobes, which are triangular (fig. 2 I1, H2) to semi-
255 circular in shape (fig. 2 O2) in basal view. The root base has a well-developed and deep
256 median nutritive groove that encloses a single large central foramen (fig. 2 M1, O2). No inner
257 or outer foramina are discernible on the specimens. The lower Lutetian material from Sine-
258 Saloum (fig. 2 N-P) is quite similar to the type series from Matam region (fig. 2 F-M) despite
259 its poorer state of conservation.

Discussion: Compared to *A. sudrei*, the new species *A. senegalensis* nov. sp. displays teeth with similar shape, but its transversal keel is higher, more protruding, undulated and often marked by three rounded pseudo cusplets in lingual view. Two of these cusplets are located at the margin while the third one, the most developed, is situated in the cusp axis at the junction of the three-pointed star. Compared to *A. sudrei*, less salient crests are present on the concave labial face of the crown in *A. senegalensis* nov. sp., as observable in type series (e.g. fig. 2 B). The ornamentation of the enameloid in the band of the lingual marginal face under transversal keel (as those of the labial face) is more finely developed compared to *A. sudrei* with alveolar network shape, except near the keel and crests where they reduce gradually. Only a few specimens of *A. sudrei* have been recovered in the Thanetian of Matam, Senegal (fig. 2 E). It seems more abundant in the Nigerian type locality (Cappetta, 1972) and in Togolese Thanetian deposits (Guinot et al., 2020). Although badly preserved (partial crown with broken cusp), the tooth crown shows that the cusp was mesiodistally flattened and that the junction between the low transverse keel and the cusp formed a three-pointed star in occlusal view. The enameloid of the crown concave labial face is also finely ornamented (fig. 2 E2). Some teeth from Ypresian deposits of Matam (e.g. fig. 2 F, H) show a morphology very close to that of *A. sudrei* teeth with a weak transverse keel. This probably indicates a close filiation between the two chronospecies of the new genus. Similar teeth to *A. senegalensis* were also observed (H.C. pers. observations) in the Ypresian of Morocco (Ouled Abdoun) and Mali (Tamaguilet), which might indicate that *Atlantitrygon* representatives had a wider distribution along the tropical western Atlantic coasts, from Niger to Morocco, during the Thanetian-Ypresian period.

FIG.2 here

284 Superfamily DASYATOIDEA Whitley, 1940

285 Dasyatoidea INCERTAE FAMILIAE

286 *Microtriftis* nov.gen.

287 **Type species:** *Microtriftis matamensis* nov. sp.

288 **Etymology:** From Greek “*triftis*” refers to the rap shape of occlusal surface and “micro”
289 relatively to the small size of teeth.

290 **Diagnosis:** the same that the unique species referred to this new genus.

291 **Occurrence:** Ypresian to Lutetian of Matam and Sine-Saloum region, Senegal

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293

294 *Microtriftis matamensis* nov.sp.

295 **Etymology:** Refers to the Matam area where the type series was found.

296 **Type material:** Holotype Fig. 3 D, MAM-15 (well F0 9.18-9.3m, Unit 2 in Sambou et al.,
297 2017) Ndendouri-Ouali Diala, ?Early Ypresian, Matam Fm.; Paratypes: MAM-12, 13, 14, 16,
298 (well F0 9.18-9.3m, Unit 2 in Sambou et al., 2017), Ndendouri-Ouali Diala, ?Early Ypresian,
299 Matam Fm., Senegal.

300 **Additional material:** about twenty teeth including those figured SNSAN/2011/05 to
301 SNSAN/2011/07 (Fig. 3 F-H) - lower Lutetian (E8-E9 biozones, 49 to 45,8 My) of Sine
302 Saloum region, Senegal.

303 **Diagnosis:** Myliobatoid ray with very small teeth (less than 1.3 mm in size) exhibiting
304 reduced sexual dimorphism in crown morphology. The teeth of presumed breeding males
305 have crown with small, lingually directed cusp, non-cuspidate teeth of presumed females (or
306 from the lateral files of breeding males). The crown is robust, often diamond shaped in

307 occlusal view with depressed visor suggesting a light teeth imbrication or at least a direct
308 contact between alternating teeth. The lingual face of the crown is straight and mainly
309 unornamented, excepted just under the transverse keel where it is slightly concave with an
310 enameloid marked by vertical folders. The labial face is flat, strongly ornamented with sorted
311 micrometric holes piercing the whole surface. The labial visor is medially concave and its
312 ornamentation is less homogeneous compared to labial face. The teeth roots are bilobate,
313 vertically directed, narrower than the crown and relatively high with two pinched lobes
314 separated by large but soft nutritive groove where a unique large foramen opens medially.

315 **Description:** The teeth are very small, not exceeding 1.3 mm in size. They exhibit reduced
316 sexual dimorphism in crown morphology, the crown teeth of presumed breeding males
317 bearing a short cusp lingually directed (fig 3 A-B). The base of cusp is sometimes as wide as
318 the transverse keel or medially centered (fig. 3 A-B). The non-cuspidate teeth of presumed
319 females (conceivably teeth of non-breeding male or teeth from the lateral files of breeding
320 males) display diamond-shaped occlusal outline. The holotype (fig. 3 D) probably belongs to
321 a latero-anterior file of a female jaw. The crown is high with developed lingual face, which is
322 sub-trapezoid in lingual view (fig. 3 D1). The lingual extremity is medially convex under the
323 vertical bulge and the marginal borders are straight to slightly concave near the transverse
324 keel. The enameloid is mainly unornamented except near the transverse keel where several
325 enameloid folders are easily distinguishable (fig. 3 D1). The labial face is flat, its contour is
326 diamond-shaped in occlusal view (fig. 3 D2) and displays many circular holes deeply piercing
327 the enameloid surface (fig. 3 D3). The hole size is relatively homogenous except near the
328 labial visor where the ornamentation is more unstructured. The labial visor is medially
329 concave, which suggests a light imbrication with the lingual face of tooth directly anterior to
330 it. The lower part of labial visor is thick and unornamented. The crown/root junction is
331 located in a shallow depression in the centre of the basal crown surface. The root is narrower

than the crown, of holaulacorrhizous type with two lobes, which are semi-circular in shape in basal view. The root lobes are slightly lingually directed and almost vertical in profile. The root base displays a weak median nutritive groove that encloses a large central foramen. Male teeth (fig. 3 A-B) are similar in shape with a development of the medial cusp that could be high and as large than transversal keel, small (fig. 3 A) or reduced to a slight protuberance of the transverse keel (fig. 3 B2). Such variability is probably due to different file position of the teeth, the higher teeth being possibly located near the symphysis. The female teeth are less variable, their crown being more or less narrow (fig. 3 C-D) or extended mesio-distally (fig. 3 E). The lateral teeth have a mesio-distally extended labial face, a developed labial visor, a transverse keel slightly worn by functional wearing, and an oblique root lobe as in some extant myliobatoid with pavement-like dentition. Despite the limited sample of this minute species, teeth of female (fig. C-H) seem twice as large as those identified as belonging to male, conformably with expected size difference between sexes in most batoid species. No clear dental difference is obvious between specimens from the type series (Ypresian) and those from the Lower Lutetian (fig. 3 F-H).

Discussion: Currently, *Microtriftis* nov. gen. is only affiliated to dasyatoid of *incertae familiae*. If the morphology of isolated teeth (e.g. high crown with narrower root vertically oriented, flat ornamented labial face with concave visor in all files) suggests that each tooth is in contact with its neighbouring teeth to form a pavement-like dentition as observable in living myliobatoid, there are significant difference with their living and fossil representatives. In *Microtriftis* nov. gen., the root is always of holaulacorrhizous type, like many dasyatoid but unlike myliobatoid that present a root of polyhaulacorrhizous type. The imbrication of teeth (assumed here on alternating gridlines) seems light in *Microtriftis* nov. gen., the lingual face of tooth and the labial visor of previous tooth file could not be interlocked, in contrast to the condition observed in myliobatoid jaws. Other Paleogene dasyatoid *incertae sedis* developed

a grinding dentition with joined alternating teeth (e.g. *Heterobatis* Noubhani and Cappetta 1997, *Hypolophodon* Cappetta 1980; *Ishaquia* Noubhani and Cappetta 1997; *Myliodasyatis* Noubhani and Cappetta 1997; *Phosphatodon* Cappetta 2012; *Meridiana* Case 1994). Among them, only *Heterobatis* can be reasonably compared to new genus, the other genera largely differing both in size and tooth morphology. The teeth of *Heterobatis* are also relatively small (until 3mm tooth size) with a flat labial face sharing ornamentation of enameloid. The anterior teeth display a clear dasyatid pattern with a crown face and a root directed lingually whereas the lateral teeth are sometimes very large, of polyhaulacorhizous type, and remind myliobatids.

The teeth of *Microtriftis* nov. gen. recall those of another Paleocene dasyatoid *incertae sedis*, *Delpitia* Noubhani and Cappetta 1997, with similar sexual heterodonty and ornamentation of the labial face. However, *Delpitia* is larger and possess a typical dasyatid root, directed lingually with lobes enlarged basally. No evidence of interconnecting/joining teeth is visible on type species *D. reticulata* (Noubhani and Cappetta 1997: Pl. 68, fig. 1-6). The minute new taxon is only recorded in Ypresian to Lower Lutetian marine deposits of Central and Northeastern Senegal (Sine-Saloum region and Matam) even if some early-middle Eocene specimens collected in well drilling from Guinea Bissau (Prian, 1986, 1987) are very similar (HC pers. observ.).

FIG.3 here

NEOSELACHII Compagno, 1977 *incertae ordinis*

Odontorhynchus Böhm 1926

Type species: *O. pappenheimi* Böhm, 1926

This enigmatical taxon is commonly recovered with other elasmobranchs in Eocene nearshore marine deposits of Africa and central Asia. Considering its uncertain systematic position among sharks, authors generally report its occurrence with some caution. Whatever the final outcome on systematic issues, this taxon could be a significant part of the Eocene nearshore elasmobranch assemblages. Inappropriately attributed to a percoid fish or to a rajid by Priem (1905; 1915 respectively) based on middle-late Eocene Egyptian specimens, Böhm (1926) described similar teeth from Namibia as *Odontorhynchus pappenheimi*, but also considered that it belongs to bony fish of family Lophiidae. Cappetta (1981) definitively attributed this taxon to an undetermined elasmobranch and figured late Ypresian specimens from Ouled Abdoun (Morocco) that he attributed to the unique species *O. pappenheimi* of Böhm. However, and as noted Cappetta (2012 : 326), clear differences can be noted between Thanetian-Ypresian teeth on one side and middle-late Eocene teeth (e.g. *O. pappenheimi* Böhm, 1926) on the other side, asserting than late Ypresian material from Morocco and several other ones, must be likely considered as representatives of a distinct and unnamed species (Cappetta, 1987, 2012)

Odontorhynchus priemi nov. sp.

Rajidae or Scylliidae Priem (1909: fig. 31-35)

Odontorhynchus pappenheimi Cappetta (1981 plate 1 fig. 2-4)

Odontorhynchus sp. Noubhani and Cappetta (1997: text only)

Odontorhynchus sp. Gheerbrant et al. (1993: text only)

Odontorhynchus sp. Cappetta (2012: fig. 313: C-E)

Odontorhynchus sp. Sambou et al. (2017: text only, in part)

Type material: Holotype: fig. 4 C, MAM-19 (well F0, 9.18-9.30 m, Unit 2 in Sambou et al., 2017) – Ndendouri-Ouali Diala, ?Early Ypresian, Matam Fm. ; Paratypes: MAM-18, MAM-20 (well F3, Unit 2 in Sambou et al., 2017) Ndendouri-Ouali Diala, ?Early Ypresian, Matam Fm., Senegal.

Additional material: Sixteen teeth, partially broken, were mainly found in Thanetian (MAM-22 to 24, well P53, Unit 0 in Sambou et al., 2017) and Ypresian levels of Ndendouri-Ouali Diala (Units 1-3 in Sambou et al., 2017). We can include those from Morocco: MYB8-9, DYD1-2 from Mera-el-arech (sillon A-B) and Recette 4 (Sillon D), Ouled Abdoun, Morocco – Late Ypresian, figured in Cappetta (1981 plate 1 fig. 2-4) and Cappetta (2012: fig. 313: C-E).

Etymology: in honours to the French paleoichthyologist F. Priem (1857-1919) who firstly signalled material attributed to this new species.

Diagnosis: New species of *Odontorhynchus* known by isolated teeth exhibiting reduced heterodonty. The new species is mainly characterized by teeth compressed mesio-distally, a fine cusp of sigmoidal profile with lateral cutting edges and marked enameloid folds on both face, a pair of very low lateral cusplets sometimes reduced to minute bulges in small specimens or simply lacking in the largest ones, the lack of lingual barb near the apex, and the lack of a sharp median crest on the crown labial face. The root is of cordiform outline in lingual or labial view, ever larger than crown with large median groove entirely developed on the root depth.

Occurrences: from Thanetian to Ypresian of North and Western Africa (e.g. Mali, Senegal, Morocco and Tunisia).

426 **Description:** The variation of the tooth morphology in this elasmobranch genus is weak and
427 only involved the presence/development of lateral cusplets compared to the overall/absolute
428 size, which prevents any inference on possible developmental heterodonty. The teeth are
429 small to medium in size and laterally compressed. The holotype is of medium size, probably
430 from one of the anterior files (Fig. 4 C). The weakly enamelled cusp is high, pointed, and of
431 sigmoid profile (fig. 4 C2). The crown labial face is rather flat towards the apex of cusp but
432 convex at its base where several fine folds run on its lower half. It extends downward,
433 overlapping the root by an expansion, high and narrow, more or less pinched laterally (fig. 4
434 C1) that may bear a sagittal keel on the probably more anterior teeth (fig. 4 B1, H1). The
435 lingual face of crown is strongly concave and bears parallel and well-marked vertical folds
436 (fig. 4 C3). These folds rarely reach the apex of cusp but a short, sharp medio-sagittal crest is
437 sometimes observable near the apex in some teeth (fig. 4 E1). The lateral cutting edges are
438 well marked on the cusp but do not reach the base of the crown on many teeth, holotype
439 included (fig. 4 C2). At the base of the cusp, a pair of very low lateral denticles is usually
440 visible near the onset of the cutting edges (fig. 4 F-H), one of the denticles can however
441 disappear in some teeth (fig. 4 D) and could be reduced to tiny or inconspicuous bulges on
442 more largest teeth, holotype included (fig. 4 B-C). The root is of cordiform outline in lingual
443 view (fig. 4 B2, C3, E1), without well-differentiated lobes. In labial view, it extends well
444 beyond the crown. Its basal face is very concave in profile (fig. 4 B3, C2, E2); it has a well-
445 marked lingual protuberance below the crown and displays an axial nutritive groove on all
446 surface (fig. 4 C3). This groove is relatively deep at the level of the protuberance where a
447 foramen opens (fig. 4 C3). Usually, the basal face lifts slightly on the edges of the groove (fig.
448 4 E1). Narrow small elliptical foramina open laterally on the labial surface of the root, near
449 the crown-root boundary (fig. 4 C1). Unfortunately, the Thanetian material (Fig 4 F-H) is
450 poorly preserved in comparison to the Ypresian sample (fig. 4 B-E). However, the root

451 morphology of the Thanetian teeth seemly resemble those of Ypresian teeth, but they are
452 smaller, more often cuspidate, and their root outline seems sharper and less thick in profile.

453 **Discussion:** Compared to the middle-late Eocene representatives of genus (including *O.*
454 *pappenheimi*, *O. bahariensis* Salame and Asan, 2019 and possible other unnamed species in
455 Tabuce et al., 2005), the cusp is thinner, strongly bent lingually and of sigmoidal profile in *O.*
456 *priemi* nov. sp. The lateral cutting edges are thin but distinct and always present in *O. priemi*
457 nov. sp. They do not reach the crown base. A pair of very low and sharp lateral cusplets is
458 sometimes present at the base of the cusp, near the beginning of cutting edges. These cusplets
459 can be weak and sometimes be reduced to minute bulges or even absent in some teeth. The
460 crown lingual face bears numerous fine folds that do not reach the apex. Compared to *O.*
461 *priemi* nov. sp., a barb may be present on the lingual side of the apex in the middle-late
462 Eocene specimens (e.g. *O. pappenheimi*, *O. bahariensis*). In the latter, the crown is more
463 strongly mesio-distally compressed and slightly curved distally in labial view. No lateral
464 cutting edge is visible on the cusp nor lateral cusplets at the base of crown. On the other side,
465 an unusual distinct and sharp median crest is present on the cusp labial face, no crest –but
466 similar fine folds– is present on the lingual face, which is transversally convex as observed in
467 *O. priemi* nov. sp.

468 In both group, the root is high with a heart-like outline (particularly in *O. priemi* nov. sp.) but
469 without differentiated lobes. The profile of its basal face is very concave; it shows a well-
470 marked lingual protuberance and bears an axial furrow on its whole surface. This furrow is
471 much deeper at the end of protuberance where some foramina can be observed. The two
472 groups of species differ from each other only by the morphology of the root (as the crown),
473 which is mesio-distally compressed in *O. pappenheimi* and *O. bahariensis* compared to *O.*
474 *priemi* nov. sp. There is an overlap in tooth size between *O. priemi* nov. sp. and *O.*
475 *pappenheimi*/ *O. bahariensis* but the Thanetian-Ypresian species rarely reach more than 7mm

476 in height whereas the middle-late Eocene specimens can easily measure more than 1cm in
477 height (especially in *O. pappenheimi*). Distinction between *O. pappenheimi* and *O.*
478 *bahariensis* remains unclear. Without diagnosis, the latter seems to have smaller gracile teeth
479 than in *O. pappenheimi*, with crown relatively higher with shorter labial cutting edge (Salame
480 and Asan, 2019). Ignoring the ontogenetic heterodonty of this ambiguous neoselachian, *O.*
481 *bahariensis* could in fact represent the youngest specimens of *O. pappenheimi*, usually
482 recovered in the same areas and ages. The new species *O. priemi* nov. sp. is also present in the
483 Ypresian of Mali (Cappetta 1987), Thanetian-Ypresian of Ouarzazate and phosphate of Ouled
484 Abdoun, Morocco (Cappetta, 1981; Gheerbrant et al., 1993; Noubhani and Cappetta, 1997),
485 and in phosphates of Redeyef, Tunisia (Priem, 1909). The second morphotype (including *O.*
486 *pappenheimi* and ?*O. bahariensis*) also occurs in Senegalese deposits (Fig. 4 A) and was
487 recovered in the top level of the Matam phosphate deposits (wells P1A, P1B, R4, I1 et G0 see
488 Sambou et al. 2017) and in Sanghaye Bele water well, Sine-Saloum region. This morphotype
489 is recovered elsewhere in the middle Lutetian of Morocco (Tabuce et al., 2005), in the late
490 Lutetian-early Bartonian of Egypt (Strougo et al., 2007, Underwood et al., 2011, Salame and
491 Asan, 2019) but seems more frequent in the late middle Eocene–late Eocene from
492 southwestern Morocco (Adnet et al., 2010), Tunisia (Merzeraux et al., 2017; Sweydan et al.,
493 2018), Egypt (Priem, 1905 ; Case and Cappetta, 1990 ; Murray et al., 2010; Adnet et al.,
494 2011 ; Underwood et al., 2011 ; Murray et al., 2014), Namibia (Böhm 1926), and Pakistan
495 (Case and West, 1991). Its occurrence in the early Rupelian of Jebel Qatrani–Quarry E,
496 Fayum (Murray et al., 2014) is based on a unique broken tooth and must be confirmed by
497 additional samples. These two species do not overlap in the fossil record, suggesting a
498 replacement of taxa during the late Ypresian or near the Ypresian/Lutetian boundary.
499 However, the youngest representatives of *O. priemi* nov. sp. from Matam (e.g. fig. 4 B) show
500 a seemingly transitional morphology toward those of “*O. pappenheimi* group” in having larger

teeth, more compressed mesio-distally with no lateral cusplets. Murray et al. (2010) suggested that *Odontorythis pappenheimi* as the other elasmobranch elements from BQ-2 locality (Fayum, Egypt) probably represent freshwater-tolerant species. The co-occurrence of *Odontorhynchus* teeth with mammals remains in different localities (e.g. Gheerbrant et al., 1993; Tabuce et al., 2005; Merzeraux et al., 2016; Murray et al., 2010, 2014; Tabuce et al., 2019) seems to confirm this ecological abilities even if the other listed occurrences, including those of Matam or Morocco, testify that it is firstly a marine elasmobranch.

FIG.4 here

Paleobiological and Paleoecological inferences.

Among Potamotrygonidae, which also include the marine Styracurinae (Carvalho et al., 2016), the sister subfamily Potamotrygoninae (South American river stingrays) is the most diverse and famous group of obligate freshwater stingrays. South American fossils of this subfamily drew particular attention this last decade (e.g. Brito and Deynat, 2004; Adnet et al., 2014; Chabain et al., 2017) with evidences that they were abundant in middle Eocene deposits of Peruvian Amazonia. In contrast, the living styracurines (amphi-American whipray) are less abundant. They are currently frequent in the Central eastern Pacific (*Styracura pacifica*) and Central western Atlantic (*S. schmardae*) shallow waters until the Amazon river mouth southward (Last et al., 2016; Bloom and Lovejoy 2017). No fossil representatives of Styracurine (or formally *Himantura*) are known in fossiliferous deposits along the Central Eastern Pacific or Central Western Atlantic coasts (e.g. Landini et al., 2017; Carrillo-Bricenio et al., 2014, 2015, 2016, 2018). However, the styracurines likely inhabited the Eastern Pacific–Caribbean zone since the middle Eocene, which corresponds to the oldest occurrence of their sister taxa, the potamotrygonins (Adnet et al., 2014). The attribution of *Atlantitrygon*

525 to Styracurinae is based on the similar overall shape of the teeth and the presence of a
526 displaced main cusp. Further evidences (as coeval records in Caribbean zone) are needed to
527 confirm such a systematic assumption but *Atlantitrygon* (and mainly the oldest species *A.*
528 *sudrei*) might represent one of the marine–brackish pool species of potamotrygonid.
529 Subsequently, the multiple occurrence of *Atlantitrygon* in Western Africa deposits may
530 indicate that past styracurines were widespread in the Central Atlantic from western to eastern
531 coasts during the warming period of Paleogene.

532 Solving the systematic affinities of *Microtriftis* among dasyatoid is out of scope of this study.
533 The minute teeth seem partially interlocked forming the pavement-like teeth suited for
534 crushing or grinding preys. Ornamented enameloid of labial surface in *Microtriftis* could
535 probably strengthen the grater function of pavement-like teeth as observed in many other
536 living and fossil taxa with such a dentition (e.g. *Myliobatis*, *Rhombodus*, *Coupatetia*,
537 *Dasyatis sensu lato*, *Pastinachus*). Specialization for extreme durophagy, including an
538 extremely robust dentition with pavement-like teeth, is redundant in myliobatiform evolution
539 (e.g. Underwood et al. 2015, 2017). Their teeth can be only partially interlocked to crush
540 preys, or can be strongly interfitted and jointed together thanks to complementary faces of
541 crown to grind hard mollusc as observed in Myliobatidae and Rhinopteridae (grinding type).
542 *Microtriftis* share the same interlocking pattern than many other fossil dasyatoid (e.g.
543 *Aturobatis*, *Heterobatis*, *Hypolophodon*, *Ishaquia*, *Meridiana*, *Myliodasyatis*, *Phosphatodon*),
544 which could also be considered as grinders (high crown, polygonal outline). However, the
545 dentition of *Microtriftis* is unique in its extreme small size. The number of tooth files in
546 *Microtriftis* jaws, as in all grinding taxa with holaulacorhize root (Cappetta 2012), was likely
547 important. If we cannot surely estimate the size of occlusal surface of pavement of both jaws,
548 it unlikely exceeded two centimetres in width considering the individual tooth size (0.5 mm).
549 Living stingrays with interlocking plates of flat, pavement-like teeth are known to grind

molluscs and other hard-shelled prey. *Microtriftis* then represents one of the smallest stingrays with grinding teeth, which raises the question on the type of preys it could predate on.

The Thanetian-Ypresian occurrence of the enigmatical *Odontorythis* completes the fossil record of the genus usually known by the middle-late Eocene. The tooth morphology of its oldest species *Odontorythis priemi* nov. sp. does not clarify its systematic position among Neoselachii. The presence of lateral cutting edges and additional cusplets is more common in shark teeth compared to the unusual morphology observed in Lutetian-Priabonian representatives, including its sister species *O. pappenheimi*. Observations of transitional forms between these two chronospecies *O. priemi* nov. sp. and *O. pappenheimi* and their relatives suggest that they progressively replaced each other during the latest early Eocene in Senegal and elsewhere.

Conclusions.

The Senegalese Paleogene fauna is significantly rich (see Pascal, 1987 and Sambou et al., 2017 for listing) with numerous other taxa recovered elsewhere. The focus on three new taxa described herein confirms the dating of fossiliferous levels of the phosphate series of Ndendouri-Ouali Diala (Matam) and improves the stratigraphical correlations between the phosphate deposits of Matam area and those of Sine-Saloum region during the Paleogene. The presence of *Odontorhynchus* cf. *pappenheimi* and absence of *O. priemi* in the top level of the Matam Fm. (Matam area) and in Lam Lam Fm. in Sine-Saloum regions also confirm that both deposits are penecontemporaneous (see Tabuce et al., 2019). A previous study confirmed that the coquina limestone of the Lam Lam Fm. in Sanghaye Bele is subcontemporaneous with

those of the clay-limestone unit ending the Matam Fm., and that it is indicative of a littoral environment (Sambou et al. 2017).

The Gorgol Fm. (Thanetian) in Matam area probably corresponds to neritic deposal as suggested by analysis of the elasmobranch fauna (Sambou et al., 2017) and lithology (Pascal, 1987). The presence of *Atlantitrygon sudrei* in Thanetian deposits of Senegal, Niger and Togo suggests the establishment of an extended marine realm with faunal connection along the past Guinea Gulf. During the lower Eocene period, the Senegal basins underwent a succession of transgressions and regressions that install the mesobathyal and neritic deposits in the southwestern region (Thiam, 2014; Thiam and Sarr, 2014). The Ypresian marine deposits in the Matam area (lower part of Matam Fm.) are mainly dominated by limestones, clays, and phosphates deposited during the transgression phases that largely extended the marine area to the eastern edge of the Senegal basin (Monciardini and Pascal, 1966). A preliminary study of the elasmobranch fauna (see Sambou et al., 2017) enabled to reconstruct a continuous sea water communication with the large and deeper southernmost gulf (Slansky, 1980) to the North Gambia (Miyouna et al., 2009). Ostracods also testify that this inner platform was flooded by relative warm to temperate sea waters (Thiam and Sarr, 2018). Presence of *Atlantitrygon senegalensis* nov. sp. and *Odontorhynchus priemi* nov. sp. in subcontemporaneous deposits of Mali and Morocco also suggests wider faunal connection along the Central Western Atlantic coasts during the Ypresian period. Coupled with some Ypresian tectonics (Miyouna et al 2009), the decrease of sea level began at the end of Ypresian as previously reported in Casamance area (Ly AND Anglada, 1991) and in the Mbour-Joal area (Western Senegal; Sarr 1999). The strong decrease in selachian diversity recovered in the higher clay-limestone unit (top of Matam Fm.) coupled with the persistence of only small coastal species are clearly indicative of a more littoral environment in Matam (Sambou et al., 2017) with contemporaneous development of anoxic conditions in southwestern platform (Thiam and

Sarr, 2018). However, the co-occurrence of *Atlantitrygon senegalensis* nov. sp. and *Odontorhynchus* cf. *pappenheimi* in the early Lutetian limestones of both localities also indicates the persistence of a relictual Est-West marine connection in central Senegal (between Matam and Sine-Saloum areas) during the early Lutetian regional regression (Thiam, 2014 ; Thiam and Sarr, 2014, 2018)

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References

622 Adnet, S., Cappetta, H., Elnahas, S., Strougo, A., 2011. A New Priabonian Chondrichthyans
 623 assemblage from the Western Desert, Egypt: Correlation with the Fayum Oasis. *Journal of*
 624 *African Earth Sciences* 61 (1), 27–37.
 625
 626 Adnet, S., Salas Gismondi, R., Antoine, P. O., 2014. Comparisons of Dental Morphology in
 627 River Stingrays (Chondrichthyes: Potamotrygonidae) with New Fossils from the Middle
 628 Eocene of Peruvian Amazonia Rekindle Debate on Their Evolution. *Naturwissenschaften* 101
 629 (1), 33–45.
 630
 631 Arambourg, C., 1952. Les Vertébrés Fossiles Des Gisements de Phosphates (Maroc-Algérie-
 632 Tunisie). *Notes et Mémoires du Service géologique du Maroc* 92, 1–372.
 633
 634 Beebe, W., Tee-Van, J., 1941. Eastern Pacific expeditions of the New York Zoological
 635 Society. XXVIII. Fishes from the tropical eastern Pacific. Part 3. Rays, Mantas and
 636 Chimaeras. *Zoologica, Scientific Contributions of the New York Zoological Society* 26 (3),
 637 245–280.
 638
 639 Bloom, D. D., Lovejo, N. R., 2017. On the Origins of Marine-Derived Freshwater Fishes in
 640 South America, *Journal of Biogeography* 44 (9), 1927–1938.
 641
 642 Böhm, J., 1926. Über tertiäre Versteinerungen von den Bogenfelsen diamantfeldern, In E.
 643 Kaiser (Edt.), *Die Diamantwüste Südwestafrikas*. Berlin. pp. 55–87.
 644
 645 Brito, P. M., Deynat, P. P., 2004. Freshwater Stingrays from the Miocene of South America
 646 with Comments on the Rise of Potamotrygonids (Batoids, Myliobatiformes), In *Recent*

647 *advances in the Origin and Early Radiation of Vertebrates*, verlag Dr. Friedrich Pfeil:
 648 München, Germany, pp 575–582.
 649
 650 Cappetta, H., 1972. Les Poissons Crétacés et Tertiaires Du Bassin Des Iullemmeden
 651 (République du Niger). *Palaeovertebrata* 5 (5), 179–251.
 652
 653 Cappetta, H., 1980. Modification Du Statut Générique de Quelques Espèces de Sélaciens
 654 Crétacés et Tertiaires. *Palaeovertebrata* 10 (1), 29–42.
 655
 656 Cappetta, H., 1981. Additions a La Faune de Sélaciens Fossiles Du Maroc. 1: Sur La Présence
 657 Des Genres *Hepranchias*, *Alopias* et *Odontorhynchus* Dans l'Yprésien Des Ouled Abdoun.
 658 *Géobios* 14 (5), 563–575.
 659
 660 Cappetta, H., 1987. Chondrichthyes II Mesozoic and Cenozoic Elasmobranchii. Schultze, H.-
 661 P. (Edt.) *Handbook of Paleoichthyology*, Gustav Fischer Verlag: Stuttgart-New York. 193 p.
 662
 663 Cappetta, H., 2012. Chondrichthyes II Mesozoic and Cenozoic Elasmobranchii: Teeth.
 664 Schultze, H.-P., (Edt.) *Handbook of Paleoichthyology*; verlag Dr. Friedrich Pfeil: Stuttgart-
 665 New York. 512 p.
 666
 667 Cappetta, H., Traverse, M., 1988. Une Riche Faune de Sélaciens Dans Le Bassin à Phosphate
 668 de Kpogamé-Hahotoé (Eocène Moyen Du Togo): Note Préliminaire et Précisions Sur la
 669 Structure et l'âge du Gisement. *Géobios* 21 (3), 359–365.
 670

671 Carrillo-Briceño, J. D., Aguilera, O. A., Rodriguez, F., 2014. Fossil Chondrichthyes from the
672 Central Eastern Pacific Ocean and Their Paleooceanographic Significance. *Journal of South*
673 *American Earth Sciences* 51, 76–90.

674

675 Carrillo-Briceño, J. D., Maxwell, E., Aguilera, O. A., Sánchez, R., Sánchez-Villagra, M. R.,
676 2015. Sawfishes and Other Elasmobranch Assemblages from the Mio-Pliocene of the South
677 Caribbean (Urumaco Sequence, Northwestern Venezuela). *Plos One* 10 (10), e0139230.

678

679 Carrillo-Briceño, J. D., Argyriou, T., Zapata, V., Kindlimann, R., Jaramillo, C. A., 2016. New
680 Early Miocene (Aquitania) Elasmobranchii Assemblage from the La Guajira Peninsula,
681 Colombia. *Ameghiniana* 53 (2), 77–99.

682

683 Carrillo-Briceño, J. D., Carrillo, J. D., Aguilera, O. A., Sanchez-Villagra, M. R., 2018. Shark
684 and Ray Diversity in the Tropical America (Neotropics)—an Examination of Environmental
685 and Historical Factors Affecting Diversity. *PeerJ* 6, e5313.

686

687 Carvalho, M. R. D., Loboda, T. S., Da Silva, J. P. C. B., 2016. New Subfamily, Styracurinae,
688 and New Genus, *Styracura*, for *Himantura Schmardae* (Werner, 1904) and *Himantura*
689 *Pacifica* (Beebe and Tee-Van, 1941) (Chondrichthyes: Myliobatiformes). *Zootaxa* 4175 (3),
690 201–221.

691

692 Case, G. R., 1994. Fossil Fish Remains from the Late Paleocene Tuscahoma and Early
693 Eocene Bashi Formations of Meridian, Lauderdale County, Mississippi. Part I. Selachians.
694 *Palaeontographica Abteilung serie A* 230 (4–6), 97–138.

695

696 Case, G. R., Cappetta, H., 1990. The Eocene Selachians Fauna from the Fayum Depression in
697 Egypt. *Palaeontographica Abteilung Serie A* 212, 1–30.
698

699 Case, G. R., West, R. M., 1991. Geology and Paleontology of the Eocene Drazinda Shale
700 Member of the Khirthar Formation, Central Western Pakistan, Part II Late Eocene Fishes.
701 *Tertiary Research* 12 (3–4), 105–120.
702

703 Chabain, J., Antoine, P.-O., Altamirano-Sierra, A. J., Marivaux, L., Pujos, F., Salas Gismondi,
704 R., Adnet, S., 2017. Cenozoic Batoids from Contamana (Peruvian Amazonia) with Focus on
705 Freshwater Potamotrygonins and Their Paleoenvironmental Significance. *Géobios* 50 (5),
706 389–400.
707

708 Claeson, K. M., Sarr, R., Hill, R. V., Sow, E. H., Malou, R., O’Leary, M. A., 2015. New
709 Fossil Scombrid (Pelagia: Scombridae) Fishes Preserved as Predator and Prey from the
710 Eocene of Senegal. *Proceedings of the Academy of Natural Sciences of Philadelphia* 164 (1),
711 133–147.
712

713 Darteville, E., Casier, E., 1943. Les Poissons Fossiles Du Bas-Congo et Des Région Voisines.
714 *Annales du Musée du Congo Belge, Série A (Minéralogie Géologie, Paléontologie)* 3- 2 (1),
715 1–200.
716

717 Darteville, E., Casier, E., 1959. Les Poissons Fossiles Du Bas Congo et Des Région Voisines.
718 *Annales du Musée du Congo Belge, Série A (Minéralogie Géologie, Paléontologie)* 3- 2 (3),
719 257–568.
720

721 Flicoteaux, R., 1974. Biozonation des formations paléogènes de la retombée orientale du
722 dôme de Ndias (Sénégal occidental). Vth African Colloquium on Micropalaeontology, Addis-
723 Abeba, Ethiopia, 1972, Madrid, Enadimsa p. 349-362.

724

725 Guinot, G., Adnet, S., Shimada, K., Underwood, C. J., Siversson, M., Ward, D. J., Kriwet, J.,
726 Cappetta, H., 2018. On the Need of Providing Tooth Morphology in Descriptions of Extant
727 Elasmobranch Species. *Zootaxa* 4461 (1), 118-126.

728

729 Guinot, G., Amoudji, Y.Z., Kassegne, K.E., Sarr, R., Johnson, A.K.C., Da Costa, P.Y.D.,
730 Hautier, L., 2020. Elasmobranchs from the upper Palaeocene of Togo. *Géobios*, in press.
731 <https://doi.org/10.1016/j.geobios.2019.12.003>.

732

733 Gheerbrant, E., Cappetta, H., Feist, M., Jaeger, J. J., Sudre, J., Vianey-Liaud, M., Sige, B.,
734 1993. La Succession Des Faunes de Vertébres d'âge Paléocène Supérieur et Éocène Inférieur
735 Dans Le Bassin d'Ouarzazate, Maroc. Contexte Géologique, Portée Biogéographique et
736 Paléogéographique. *Newsletters on Stratigraphy* 28 (1), 35–58.

737

738 Hautier, L., Sarr, R., Tabuce, R., Lihoreau, F., Adnet, S., Domning, D. P., Samb, M., Hameh,
739 P. M., 2012. First Prorastomid Sirenian from Senegal (Western Africa) and the Old World
740 Origin of Sea Cows. *Journal of Vertebrate Paleontology* 32 (5), 1218–1222.

741

742 Hautier, L., Sarr, R., Lihoreau, F., Tabuce, R., Marwan Hameh, P., 2014. First record of the
743 family Protocetidae in the Lutetian of Senegal (West Africa). *Palaeovertebrata* 1-7,
744 10.18563/pv.38.2.e2

745

746 Landini, W., Altamirano-Sierra, A., Collareta, A., Di Celma, C., Urbina, M., Bianucci, G.,
 747 2017. The Late Miocene Elasmobranch Assemblage from Cerro Colorado (Pisco Formation,
 748 Peru). *Journal of South American Earth Sciences* 73, 168–190.
 749
 750 Last, P. R., De Carvalho, M. R., Corrigan, S., Naylor, G. J., Séret, B., Yang, L., 2016. *The*
 751 *Rays of the World*, CSIRO Publishing, Melbourne. 40, 790 pp.
 752
 753 Ly, A., Anglada, R., 1991. Le bassin sénégal-mauritanien dans l'évolution des marges
 754 périalatiques au Tertiaire. *Cahier de Micropaléontologie. Nouvelle Série* 6 (2), 23-47.
 755
 756 Merzeraud, G., Essid, E. M., Marzougui, W., Ammar, H. K., Adnet, S., Marivaux, L., Tabuce,
 757 R., Vianey-Liaud, M., 2016. Stratigraphie et Sédimentologie Des Dépôts Marins et
 758 Continentaux d'âge Éocène Moyen à Miocène en Tunisie Centrale (Région Du Djebel El
 759 Kébar). *Bulletin de la Société Géologique de France* 187 (1), 11–25.
 760
 761 Miyouna, T., Sow, E.H., Diop, A., Ndiaye, P.M., Niang Diop, I., 2009. Evolution Morpho-
 762 structurale et bathymétrique de la partie Septentrionale du bassin Sénégalais au Paléogène.
 763 *Journal des Sciences* 9 (1), 1 –16.
 764
 765 Monciardini, C., Pascal, M., 1966. Recherche de phosphates. Rapport complémentaire. Le
 766 phosphate de chaux au Sénégal. Synthèse des résultats acquis, étude paléogéographique et
 767 essai prévisionnel. Rapport du BRGM, DAK 66 A8, 31p (1)
 768

769 Murray, A. M., Cook, T. D., Attia, Y. S., Chatrath, P., Simons, E. L., 2010. A Freshwater
 770 Ichthyofauna from the Late Eocene Birket Qarun Formation, Fayum, Egypt. *Journal of*
 771 *Vertebrate Paleontology* 30 (3), 665–680
 772
 773 Murray, A. M., Argyriou, T., Cook, T. D., Sues, H.-D., 2014. Palaeobiogeographic
 774 Relationships and Palaeoenvironmental Implications of an Earliest Oligocene Tethyan
 775 Ichthyofauna from Egypt. *Canadian Journal of Earth Sciences* 51 (10), 909–918.
 776
 777 Noubhani, A., Cappetta, H., 1995. Batoïdes Nouveaux Ou Peu Connus (Neoselachii:
 778 Rajiformes, Myliobatiformes) des Phosphates Maastrichtiens et Paléocènes du Maroc.
 779 *Belgian Geological Survey, Professional Paper* 278, 157–183.
 780
 781 Noubhani, A., Cappetta, H., 1997. Les Orectolobiformes, Carcharhiniformes et
 782 Myliobatiformes (Elasmobranchii, Neoselachii) Des Bassins à Phosphate Du Maroc
 783 (Maastrichtien-Lutétien Basal). *Systématique, Biostratigraphie, Évolution et Dynamique Des*
 784 *Faunes. Palaeo Ichthyologica* 8, 1–327.
 785
 786 O’Leary, M.A., Sarr, R., Malou, R., Sow, E.H., Lepre, C., Hill, R.V., 2012. A new fossil
 787 amiid from the Eocene of Senegal and the persistence of extinct marine amiids after the
 788 Cretaceous–Paleogene boundary. *Copeia* 4, 603–608.
 789
 790 Pascal, M. 1987. Nouvelles découvertes de minéralisations phosphatées au Sénégal : les
 791 gisements de N’Diendouri-Ouali Diala (Département de Matam, Région du Fleuve),
 792 *Chronique de la recherche minière* 486 : 3–24.
 793

794 Priam, J.P., 1986. Géologie de la bordure méridionale du golfe tertiaire de Casamance
795 (Sénégal, Guinée Bissau). Document du BRGM n°101, ISSN 0221-2536, 5-32.
796

797 Priam, J. P., 1987. The Farim-Saliquinhe Eocene phosphate deposits Guinea Bissau, West
798 Africa. In : *Phosphate deposits of the World* Vol. 2 Phosphate rock resources. Notholt, A.J.G,
799 Sheldon, R.P., Davidson, D.F. (Edt.), Cambridge University press, pp. 277-283.
800

801 Priem, M. F., 1905. Sur les poissons fossiles de l'Eocène moyen d'Egypte. Extrait du Bulletin
802 de la Société Géologique de France 4 V, 633–641.
803

804 Priem, M. F., 1909. Note Sur Les Poissons Fossiles Des Phosphates de Tunisie et d'Algérie.
805 Extrait du Bulletin de la Société Géologique de France 4 IX, 315–324.
806

807 Priem, M. F., 1915. Sur Les Vertébrés Du Crétacé et de l'Eocène d'Egypte. Extrait du
808 Bulletin de la Société Géologique de France 4 XIV, 366–382.
809

810 Roger, J., Noël, B.J., Barusseau, J. P., Serrano, O., Nehlig, P., Duvail, C., 2009. Notice
811 explicative de la carte géologique du Sénégal à 1/500 000, feuilles nord-ouest, nord-est et sud-
812 ouest. Ministère des Mines, de l'Industrie et des PME, Direction des Mines et de la Géologie,
813 Dakar, 61 p.
814

815 Salame, I., Asan, A., 2019. A new *Odontorhynchus* species (Chondrichthyes) from the middle
816 Eocene of Elgedida Mine, Bahariya Oasis, Egypt. *Egyptian Journal of Geology* 63, 407-415.
817

818 Sambou, B. S., 2018. Etudes sédimentologique, biostratigraphique et paléoenvironnementale
819 des séries phosphatées du gisement Paléogène de la région de Matam (Sénégal), Unpublished
820 thesis, Université Cheikh Anta Diop Dakar, 1-200
821

822 Sambou, B. S., Sarr, R., Hautier, L., Cappetta, H., Adnet, S., 2017. The Selachian Fauna
823 (Sharks and Rays) of the Phosphate Series of Ndendouri-Ouali Diala (Matam, Western
824 Senegal): Dating and Paleoenvironmental Interests. Neues Jahrbuch für Geologie und
825 Paläontologie Abtheilung 283 (2), 205–219.
826

827 Sarr, R., 1999. Le Paléogène de la région de Mbour-Joal (Sénégal occidental) :
828 biostratigraphie, étude systématique des ostracodes, paléoenvironnement. Revue de
829 Paléobiologie, Genève 18 (1), 1-29.
830

831 Solé, F., Noiret, C., Desmares, D., Adnet, S., Taverne, L., De Putter, T., Mees, F., Yans, J.,
832 Steeman, T., Louwye, S., Folie, A., Stevens, N.J, Gunnell, G.F., Baudet, D., Kitambala Yaya,
833 N., Smith, T., 2018. Reassessment of Historical Sections from the Paleogene Marine Margin
834 of the Congo Basin Reveals an Almost Complete Absence of Danian Deposits. Geoscience
835 Frontiers 10 (3), 1039-1063.
836

837 Stevens, N. J., Eastman, J. T., Odunze, S. O., Cooper, L. N., Obi, G. C., 2011. Paleocene
838 Ichthyofauna and Paleoenvironmental Setting, Imo Formation, Southeastern Nigeria. Neues
839 Jahrbuch für Geologie und Paläontologie Abtheilung 260 (3), 289–296.
840

841 Strömer, E., 1910. Reptilien-Und Fischreste Aus Dem Marinen Alttertiär von Südtogo
842 (Westafrika). Monatsbericht der deutschen geologischen Gesellschaft 62 (7), 478–505.

843

844 Strougo, A., Cappetta, H., Elnahas, S. A., 2007. Remarkable Eocene Ichthyofauna from the
845 ElGedidia Glauconitic Sandstone, Bahariya Oasis, Egypt, and Its Stratigraphic Implications,
846 MERC Ain Shams University, Earth Sciences Series 21, 81–98.

847

848 Tabuce, R., Adnet, S., Cappetta, H., Noubhani, A., Quillevéré, F., 2005. Aznag (Bassin
849 d'Ouarzazate, Maroc), Nouvelle Localité à Sélaciens et Mammifères de l'Eocène Moyen
850 (Lutétien) d'Afrique. Bulletin de la Société Géologique de France 176 (4), 381–400.

851

852 Tabuce, R., Sarr, R., Adnet, S., Lebrun, R., Lihoreau, F., Martin, J., Sambou, B., Thiam, M.,
853 Hautier, L., 2019. Filling a gap in the proboscidean fossil record: a new genus from the
854 Lutetian of Senegal. Journal of Paleontology, in press. doi.org/10.1017/jpa.2019.98

855

856 Thiam, M., 2014. Etudes biostratigraphiques et paleoenvironnementales du Cénozoïque de la
857 marge continentale ouest africaine en Casamance (Sénégal) d'après les ostracodes et les
858 foraminifères. Unpublished thesis, Université Cheikh Anta Diop Dakar, 1-208

859

860 Thiam, M., Sarr, R., 2014. Etude des paléoenvironnements du Paléocène au Miocène du
861 bassin sédimentaire sénégalais (Casamance, Afrique de l'Ouest) par analyse factorielle des
862 populations de foraminifères benthiques. Revue de Paléobiologie, Genève 33 (1), 143-157.

863

864 Thiam, M., Sarr, R., 2018. L'Eocène de la marge continentale Ouest Africaine en Casamance
865 (Sénégal) : Biostratigraphie et Paléoenvironnement à partir des ostracodes. Revue Ramres 06
866 (1), 68-72.

867

868 Underwood, C. J., Ward ,D. J., King, C., Antar, S. M., Zalmout, I. S., Gingerich, P. D., 2011.
869 Shark and Ray Faunas in the Middle and Late Eocene of the Fayum Area, Egypt. Proceedings
870 of the Geologists' Association 122 (1), 47–66.
871
872 Underwood, C. J., Johanson, Z., Welten, M., Metscher, B., Rasch, L. J., Fraser, G. J., Smith,
873 M. M., 2015. Development and Evolution of Dentition Pattern and Tooth Order in the Skates
874 And Rays (Batoidea; Chondrichthyes). Plos One 10 (4), e0122553.
875
876 Underwood, C. J., Kolmann, M. A., Ward, D. J., 2017. Paleogene Origin of Planktivory in the
877 Batoidea. Journal of Vertebrate Paleontology 37 (3), e1293068.
878
879 Vandenberghe, N., Hilgen, F.J.,Speijer, R.P., 2012. The Paleogene Period. In: Gradstein, F.
880 M., Ogg, J. G., Schmitz, M. D., and Ogg, G. M., (Edts.) *The Geological Time Scale* 2012,
881 Oxford, Elsevier Science, p. 855-921
882
883 Werner, F., 1904. Die Fische der zoologisch-vergleichend-anatomischen Sammlung der
884 Wiener Universität. I. Teil. Cyclostomen, Chondropterygier, Ganoiden, Dipnoer. Zoologische
885 Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere (Jena) 21 (3), 263–
886 302.
887
888 White, E. I., 1926. Eocene Fishes from Nigeria. Bulletin of the Geological Survey Nigeria 10,
889 1–82.
890
891 White, E. I., 1934. Fossil Fishes of Sokoto Province. Bulletin of the Geological Survey
892 Nigeria 14, 1–78.

893

894 White, E. I., 1955. Notes on African Tertiary Sharks. Bulletin of the Geological Society

895 Nigeria 5 (3), 319–325.

896

897

898

899

900

901

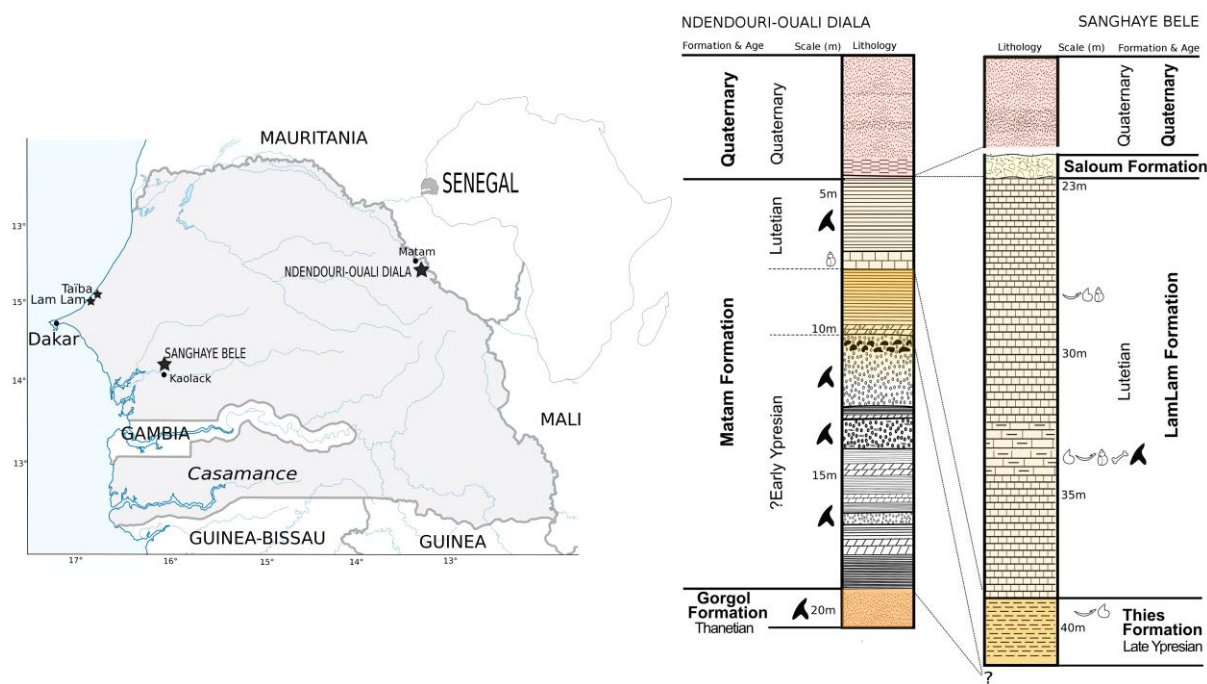


Fig. 1. Location and hypothetical stratigraphic correlation of Senegal Paleogene deposits between studied fossil localities of Sanghayé Bele and Ndendouri-Ouali Diala. Logs and details from Tabuce et al. (2019) and Sambou et al. (2017), respectively. Black teeth outline indicating levels with elasmobranch remains.

Fig. 1. Localisation et hypothèse de corrélation stratigraphique des gisements paléogènes du Sénégal entre les localités fossilifères étudiées de Sanghayé Bélé et Ndendouri-Ouali Diala. Logs et détails des coupes issus de Tabuce et al. 2019 et Sambou et al. 2017, respectivement. Les silhouettes des dents noires indiquent les niveaux avec les restes d'élasmobranches.

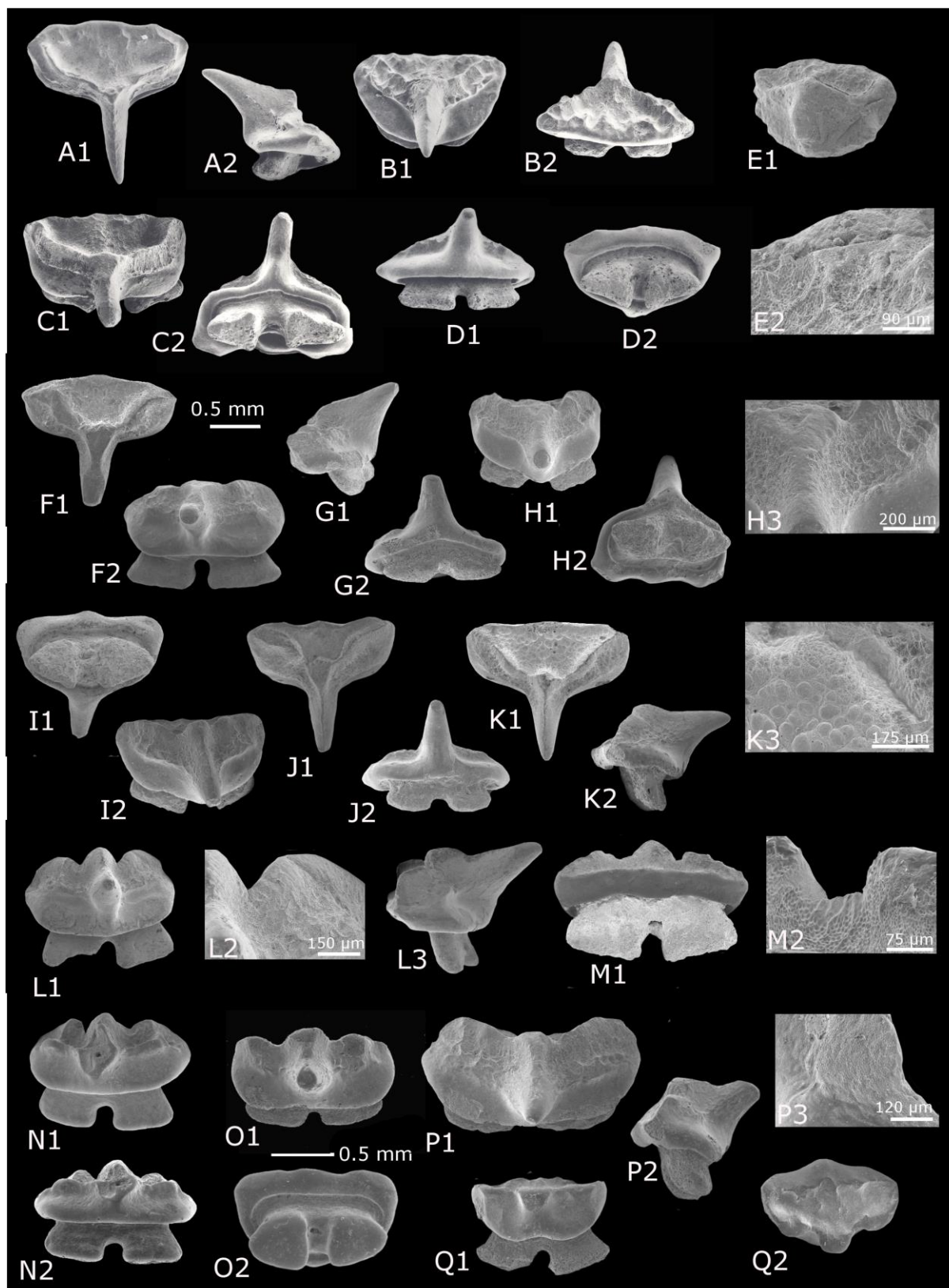


Fig. 2. *Atlantitrygon sudrei* nov. sp.: Thanetian of Sessao, Niger - Fig. A. SES64 (holotype);
 B. SES65; C. SES62; D. SES63; E. MAM-03 (well P53, Unit 0 in Sambou et al., 2017) ;

916 *Atlantitrygon senegalensis* nov. sp.: Fig F-J: MAM-04 to MAM-08; Fig. K: MAM-09
917 (holotype); Fig. L-M: MAM-10 to MAM-11 (well F0 9.18-9.3m, Unit 2 in Sambou et *al.*,
918 2017) ?Early Ypresian, Matam Fm. ; Fig. N-Q. SNSAN/2011/01 to SNSAN/2011/04 Lower
919 Lutetian, Lam Lam Fm.

920 **Fig. 2.** *Atlantitrygon sudrei* nov. sp.: Thanétien de Sessao, Niger - Fig. A. SES64 (holotype);
921 B. SES65; C. SES62; D. SES63; E. MAM-03 (puits P53, Unité 0 dans Sambou et *al.*, 2017) ;
922 *Atlantitrygon senegalensis* nov. sp.: Fig F-J: MAM-04 à MAM-08; Fig. K: MAM-09
923 (holotype); Fig. L-M: MAM-10 à MAM-11 (puits F0 9.18-9.3m, Unité 2 dans Sambou et *al.*,
924 2017) ?Yprésien inférieur, Formation de Matam; Fig. N-Q. SNSAN/2011/01 à
925 SNSAN/2011/04 Lutétien inférieur, Formation de Lam Lam.

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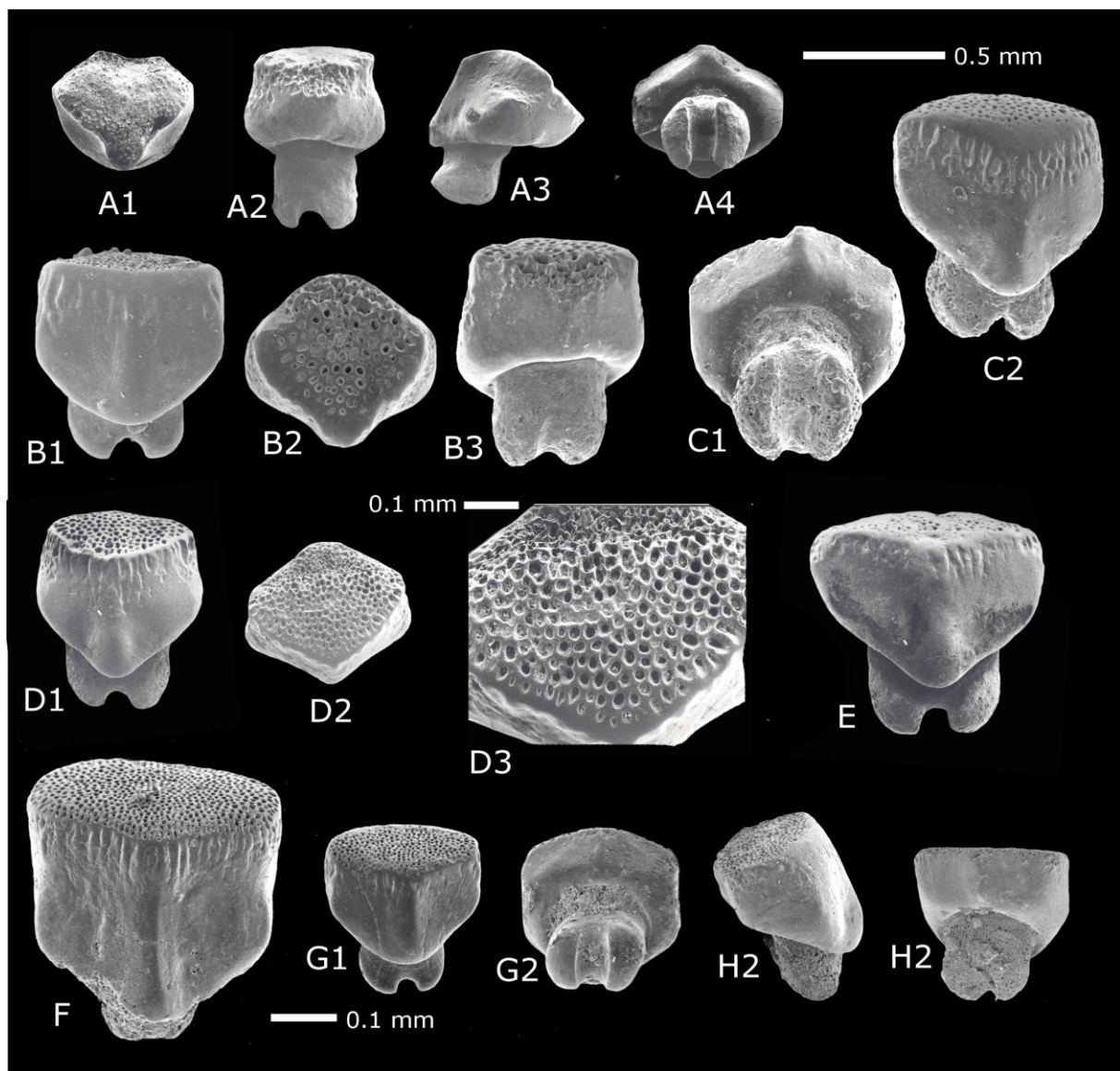


Fig. 3. *Microtriftis matami* nov. gen. nov. sp. A MAM-12 (well F0 9.18-9.3m, Unit 2 in Sambou et al., 2017) ?Early Ypresian, Matam Fm.; B-C MAM-13 and MAM-14 (well P1, Unit 2 in Sambou et al., 2017) ?Early Ypresian, Matam Fm.; D-E MAM-15 (holotype) and MAM-16 (well F0 9.18-9.3m, Unit 2 in Sambou et al., 2017) ?Early Ypresian, Matam Fm.; F-H SNSAN/2011/05 to SNSAN/2011/07 Lower Lutetian, Lam Lam Fm.

Fig. 3. *Microtriftis matami* nov. gen. nov. sp. A MAM-12 (puits F0 9.18-9.3m, Unité 2 dans Sambou et al., 2017) ?Yprésien inférieur, Formation de Matam; B-C MAM-13 et MAM-14 (puits P1, Unité 2 dans Sambou et al., 2017) ?Yprésien inférieur, Formation de Matam; D-E MAM-15 (holotype) et MAM-16 (puits F0 9.18-9.3m, Unité 2 dans Sambou et al., 2017)

937 ?Yprésien inférieur, Formation de Matam ; F-H SNSAN/2011/04 à SNSAN/2011/07 Lutétien

938 inférieur, Formation de Lam Lam.

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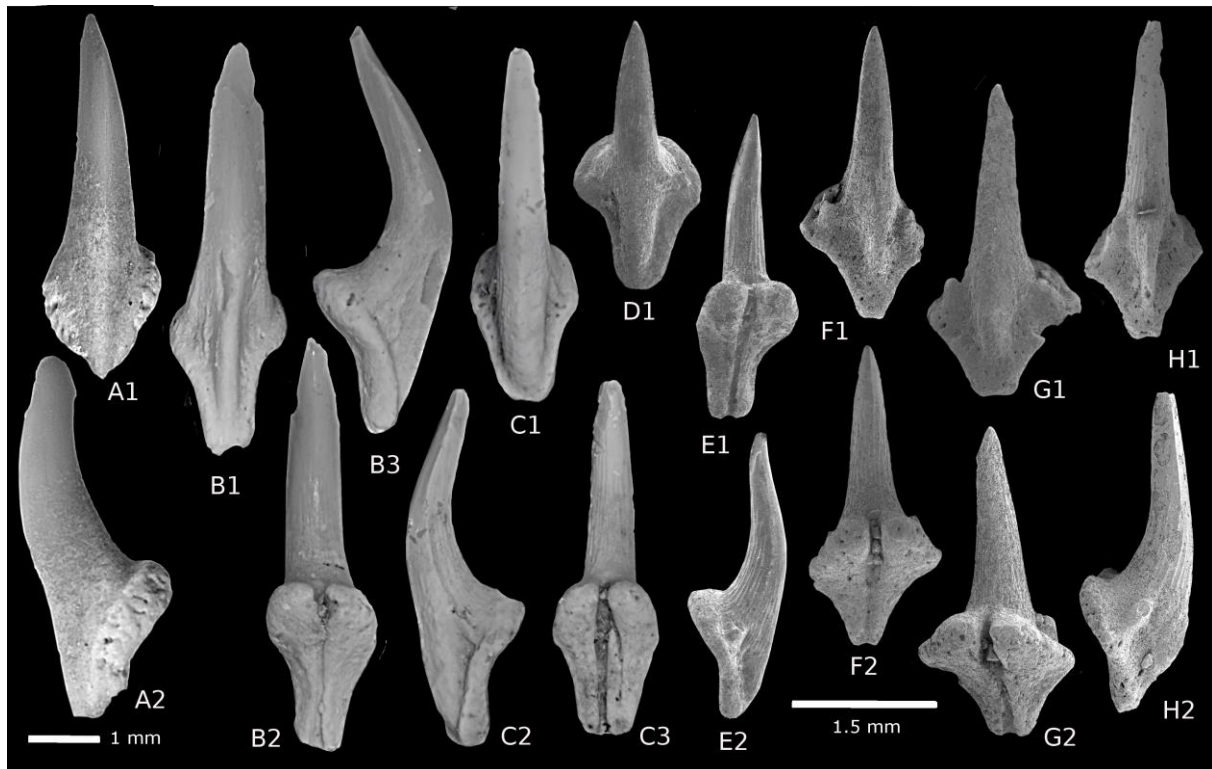


Fig. 4. A. *O. cf. pappenheimi*: Lower Lutetian, Lam Lam. Fm., SNSAN/2011/08; B-F. *Odontorhytis priemi* nov.sp., : B: MAM-18 from (well F3, Unit 2 in Sambou et al., 2017) ?Early Ypresian, Matam Fm., C: MAM-19 (well F0 9.18-9.3m, Unit 2 in Sambou et al., 2017) (holotype) ?Early Ypresian, Matam Fm, D: MAM-20 (well F3, Unit 2 in Sambou et al., 2017) ?Early Ypresian, Matam Fm; E: MAM-21 (well P1A, Unit 2 in Sambou et al., 2017) ?Early Ypresian, Matam Fm ; F-H MAM-22 to MAM-24 (well P53, Unit 0 in Sambou et al., 2017); Thanetian, Gorgol Fm.

Fig. 4. A. *O. cf. pappenheimi*: Lutétien inférieur, Formation de Lam Lam, SNSAN/2011/08; B-F. *Odontorhytis priemi* nov.sp., : B: MAM-18 de (puits F3, Unité 2 dans Sambou et al., 2017) ?Yprésien inférieur, Formation de Matam, C: MAM-19 (puits F0 9.18-9.3m, Unité 2 dans Sambou et al., 2017) (holotype) ?Yprésien inférieur, Formation de Matam, D: MAM-20 (puits F3, Unité 2 dans Sambou et al., 2017) ?Yprésien inférieur, Formation de Matam; E: MAM-21 (puits P1A, Unité 2 dans Sambou et al., 2017) ?Yprésien inférieur, Formation de

954 Matam; F-H MAM-22 à MAM-24 (puits P53, Unité 0 dans Sambou et *al.*, 2017); Thanétien,
955 Formation de Gorgol.

956