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1 Fish remains (Elasmobranchii, Actinopterygii) from the Late Cretaceous of
2 the Benue Trough, Nigeria

3

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10

11 **Abstract**

12 Selachian and ray-finned fish remains from various Late Cretaceous localities of
13 Nigeria are described. Each locality has yielded only a very few specimens and the
14 diversity is therefore very low. However, some taxa are recorded for the first time in
15 Africa. The Ashaka locality in the Upper Benue Trough (northeastern Nigeria) has
16 yielded a small but interesting late Cenomanian assemblage of microremains, including
17 teeth of “*Carcharias*” *amonensis*, *Rhombopterygia zaborskii* sp. nov., *Hamrabatis* sp.,
18 “*Stephanodus*” sp., and a possible ionoscopiform. A large prearticular dentition coming
19 from the early Turonian beds of this locality is assigned to the large pycnodontiform
20 *Acrotemnus*, a poorly known genus here regarded as a senior synonym of
21 *Macropycnodon*. In the Lower Benue Trough (southeastern Nigeria), several localities
22 ranging in age from the late Cenomanian to the early Maastrichtian have yielded various
23 widespread taxa such as *Ptychodus*, *Scapanorhynchus*, *Squalicorax*, *Vidalamiinae*
24 indet., cf. *Protosphyraena*, and *Eodiaphyodus*. The seaway that occupied the Benue

25 Trough during transgressive episodes (late Cenomanian–early Turonian and
26 Maastrichtian) created opportunities for the dispersal of many marine fish taxa into new
27 areas, such as the proto-South Atlantic.

28

29 *Keywords:* Elasmobranchii; Actinopterygii; Late Cretaceous; Benue Trough; Nigeria.

30

31

32 **1. Introduction**

33

34 Late Cretaceous fish faunas from Africa are relatively well known (see López-
35 Arbarello, 2004 and Murray, 2000 for a review). In Nigeria, most of the works have
36 dealt with Paleogene material (Odunze et al., 2009, 2012; Stevens et al., 2011; White,
37 1926, 1934, 1955) whereas only a very few Cretaceous specimens have been reported.
38 Woods (1911) mentioned the presence of *Gigantichthys* (= *Onchosaurus*) sp. in the
39 Turonian of Kumberi (northern part of the Middle Benue Trough) on the basis of some
40 remains collected by J.D. Falconer and A. Longbottom and identified by A.S.
41 Woodward.

42 White (1934) described some fish remains coming from the southern part of the
43 Iullemmeden Basin (Gilbedi and Kaffe localities, Sokoto State, northwestern Nigeria).
44 On the basis of this material, all Maastrichtian in age, White (1934) identified the
45 following taxa: *Lamna appendiculata* var. *biauriculata* (= *Cretolamna biauriculata*),
46 *Lamna libyca* (= *Serratolamna serrata*), *Schizorhiza stromeri*, ?*Pristinae* indet.,
47 *Stephanodus libycus*, and Pycnodontidae indet., besides “selachian vertebrae and
48 remains of indeterminable bony fishes”. This assemblage was later assigned by Kogbe

49 (1974) to the Maastrichtian Dukamaje Formation.

50 Carter et al. (1963) provided two lists of fish taxa collected from two localities in
51 northeastern Nigeria and identified by E.I. White. The first list (i.e., *Onchosaurus*
52 *pharao*, *Schizorhiza stromeri*, *Enchodus* cf. *lamberti*, *Ceratodus* sp., *Lamna* sp.)
53 corresponds to a fish assemblage collected from a section in the Biriji River, near
54 Gombe, exposing the base of the Yolde Formation (Cenomanian in age). The second list
55 (i.e., *Schizorhiza stromeri*, ?*Stratodus apicalis*, *Lamna?* *serrata*, *Enchodus lamberti*)
56 indicates the fish taxa obtained from a well sunk into the Fika Shales Formation
57 (Turonian?–Coniacian to Santonian–Campanian? in age) at Damagum. The Fika Shales
58 are a clay sedimentary unit occurring in the most northwestern part of the Upper Benue
59 Trough, partly equivalent to the Pindiga Formation. It is worth noting that the known
60 stratigraphical range of some of these species is not consistent with the age of the
61 involved formations, thus suggesting possible misidentifications or sampling bias.
62 Unfortunately, the current whereabouts of the fish material reported by Carter et al.
63 (1963) is unknown and we were unable to re-examine these specimens. The section in
64 the Biriji River near Gombe was visited by one of us (P.C.) in 1990; the outcrops
65 occurring by that time were of variable quality, and it was not possible to obtain further
66 material. Similarly, no good outcrops or fossils were recently obtained from the Fika
67 Shales, despite numerous field observations by one of us (P.C.) in 1990.

68 Lastly, in a study on ammonites from the Ashaka quarry, Courville (1992: 314)
69 noted the presence of various, well-preserved remains of fishes (selachians, pycnodonts)
70 in three distinct stratigraphical levels; these specimens are described in the present work
71 (see below). In a paper dealing with foraminifera from the same quarry, Gebhardt
72 (1997) also mentioned the occurrence of fish remains in several beds of this section, late

73 Cenomanian to early Turonian in age.

74 The material studied in the present work represents the first marine fish remains
75 from the Benue Trough that are well constrained stratigraphically and geographically.
76 All of them were collected by one of us (P.C.) from 1989 to 1991 during field
77 prospections. This material was obtained by surface collecting, except microteeth from
78 one peculiar level of the Ashaka quarry, obtained by screen washing (see below).

79

80

81 **2. Geographical and geological settings**

82

83 In Nigeria, West Africa (Fig. 1A1), the Cretaceous marine formations mainly
84 extend in the eastern part of the country, alongside the Benue River and southern branch
85 of the Niger River. The Benue Trough corresponds to a multiple SW-NE strike-slip
86 basin, which origin is directly related to the Early Cretaceous South Atlantic opening
87 (Benkhelil, 1988, 1989; Guiraud, 1991). Its geographical location is particularly
88 interesting, as: 1) being opened to the Cretaceous oceanic domain (modern Calabar
89 flank; Fig. 1A2); 2) a link to the Saharan areas of northeastern Nigeria (Chad Basin;
90 Fig. 1A2), episodically opened to the Late Cretaceous trans-Saharan seaway related
91 itself to the southern margin of the Tethyan Ocean (Courville, 1993; Courville et al.,
92 1998; Reyment and Dingle, 1987).

93 The Nigerian Late Cretaceous formations and faunas (mainly ammonites and
94 other invertebrates) from the Benue Trough (northern part: Upper Benue Trough;
95 southern part: Lower Benue Trough) have been studied for long (e.g., Barber, 1958;
96 Carter et al., 1963; Reyment, 1955; Woods, 1911). More recently, the main marine

97 sedimentary units of the Benue Trough have been studied with a particular
98 biostratigraphical and palaeobiological consideration (e.g., Meister, 1989; Zaborski,
99 1983, 1987, 1990a). A synthesis of the historical and original data was realized by
100 Courville (1993).

101 In northeastern Nigeria, marine conditions partly occurred during the latest
102 Cenomanian–latest “Senonian” (Campanian–Maastrichtian?) interval; only one main
103 clay–shale-dominated sedimentary unit including basal limestone beds (Pindiga
104 Formation and equivalents; Fig. 1B2), occurs. Further south, marine conditions started
105 earlier and earlier (early Albian around the Niger Delta), and persisted continuously
106 during Late Cretaceous times; several local thick clay–shale formations are piling up
107 (Fig. 1B1).

108 From the Chad Basin part of the Upper Benue Trough (Fig. 1B2), quite
109 numerous fish remains were obtained from the Gongila Formation (partly equivalent to
110 the Pindiga Formation), at the classic section of the Ashaka quarry (levels 9>, 21> and
111 26 in Courville, 1992: fig. 3). The level 9> corresponds to a marly sediment including
112 an important sandy fraction and numerous phosphatized elements (mainly fish debris).
113 A few teeth were obtained by screen washing (using 0.5 and 1 mm mesh-sized sieves)
114 of a small amount (~500 g) of matrix from this level. It is considered as latest
115 Cenomanian in age (Saharan Gadeni Zone, partly equivalent to the standard Juddii
116 Zone; Courville, 1993). From the marly–nodular limestone level 21>, vertebrate
117 remains are far less common and include several shark and bony fish teeth and
118 vertebrae, plus several unidentified bone fragments; this level is regarded as the younger
119 local Cenomanian horizon (same biozone as level 9>). Lastly, the level 26 (lowermost
120 Turonian: Saharan Flexuosum Zone = Coloradoense Zone *pars.*) yielded only one large

121 pycnodont dentition.

122 From the central part of the Upper Benue trough (Fig. 1B2), only poorly-
123 preserved bones belonging to unidentifiable fishes or reptiles were collected from
124 various latest Cenomanian to middle Turonian limestone beds (for outcrop details, see
125 Zaborski, 1990a).

126 All other fish remains studied here were collected in southern Nigeria, from
127 various formations and palaeogeographic areas (Fig. 1B1):

- 128 - The latest Cenomanian to early middle Turonian clay–shale series with nodular
129 limestone beds of the Eze Aku Group was exposed with good conditions in
130 several outcrops along the expressway at Lokpanta, located at the Atlantic side
131 of the Lower Benue Trough (for detailed location and study, see Zaborski,
132 1987). These outcrops yielded quite common and diverse vertebrate remains,
133 often poorly preserved, including fish teeth, vertebrae, or partial skeletons, as
134 well as reptile bones.
- 135 - In the overlying clay–shale Awgu Formation of the same area, only poor
136 outcrops occurred by that time, closely located to the sites mentioned by
137 Reyment (1956); probably latest Coniacian to early Santonian in age (no recent
138 ammonite findings), this series yielded a few shark teeth and poorly-preserved
139 reptile bones. Further north, in the southern part of the Lower Benue Trough, the
140 Nkalagu Limestones [a northern equivalent to the basal Awgu Shales, which is
141 clearly early Coniacian in age (Courville, 1993; Offodile and Reyment, 1977;
142 Zaborski, 1990b)], yielded only one isolated fish tooth.
- 143 - In southern Nigeria, the younger Late Cretaceous series examined belong to the
144 fine–detritic Nkporo Shales Formation. Various but very poorly preserved,

145 mostly unidentifiable vertebrate remains occur in its lower part nearly in each
146 outcrop (P.C. pers. obs.). It is only in the most southern area that good outcrops
147 still existed, studied in details by Zaborski (1983, 1985). Rich ammonite faunas
148 clearly indicate that these fossil assemblages occur below and above the
149 Campanian–Maastrichtian boundary; amongst quite diverse and well-preserved
150 fossil assemblages including bivalves, gastropods and crustaceans, one shark
151 tooth and one fish tooth plate were collected in the early Maastrichtian beds of
152 the “fauna 13” fossil site, 42 km from Calabar (Zaborski, 1985: fig. 1).

153

154

155 **3. Systematic palaeontology**

156

157 *Specimen repository.* All the material studied in the present work is deposited in the
158 collections of Géosciences Rennes (GR), Université de Rennes 1, France.

159

160 Class CHONDRICHTHYES Huxley, 1880

161 Incerti ordinis (?HYBODONTIFORMES Patterson, 1966)

162 Family PTYCHODONTIDAE Jaekel, 1898

163 Genus *Ptychodus* Agassiz, 1838

164

165 *Ptychodus decurrens* Agassiz, 1838

166 (Fig. 2A)

167

168 *Material examined.* One tooth (GR/PC.1773).

169 *Age and locality.* Early Turonian (Nodosoides Zone), Lokpanta (level 31), southeastern
170 Nigeria.

171

172 *Description.* The specimen corresponds to a perfectly preserved tooth. It is wider (12.5
173 mm) than long (10 mm). The crown is not very high and bears eight transverse, curved
174 ridges that are concave labially. These ridges nearly reach the lateral margins of the
175 crown, where they can bifurcate. The narrow, rectangular marginal area of the crown
176 shows a granular surface, with short, irregular, anastomosed folds. The anaulacorhizous
177 root is relatively low and shows a weak basal concavity. A series of foramina is present
178 all around the specimen, just below the crown–root boundary. The root base is also
179 pierced by a few foramina.

180

181 *Remarks.* The morphology and features (e.g., small size, low crown, high number of
182 ridges) of this tooth allows its assignment to the globally widespread species *Ptychodus*
183 *decurrens* (see Verma et al., 2012). In Africa, this species was only reported from the
184 Cenomanian of Tunisia (Pervinquière, 1903) and late Turonian of Angola (Antunes and
185 Cappetta, 2002). Some teeth tentatively referred to *P. decurrens* were also reported
186 from the late Cenomanian–early Turonian black shales of Jbel Tselfat in Morocco
187 (Khalloufi et al., 2010).

188

189

190 Order LAMNIFORMES Berg, 1958

191 Family PSEUDOSCAPANORHYNCHIDAE Herman, 1979

192 Genus *Protolamna* Cappetta, 1980a

193

194 cf. *Protolamna* sp.

195 (Fig. 2B)

196

197 *Material examined.* Three incomplete teeth (including GR/PC.1774).

198 *Age and locality.* Latest Cenomanian (Gadeni Zone), Ashaka quarry (level 21>),

199 northeastern Nigeria.

200

201 *Description.* The best preserved tooth shows an erect, narrow cusp bearing a few slight
202 lingual folds. The labial face is nearly flat whereas the lingual face is strongly convex in
203 apical view. The lingual protuberance of the root is well developed. Lateral cusplets and
204 root lobes are not preserved.

205

206 *Remarks.* Although these teeth are incomplete, the shape and ornamentation of the main
207 cusp combined to root morphology indicate that these specimens can be tentatively
208 assigned to the widespread Cretaceous genus *Protolamna* (Cappetta, 2012). In the other
209 two pseudoscapanorhynchid genera *Leptostyrax* and *Pseudoscapanorhynchus*, the
210 mesiodistal compression at the base of the labial face of the main cusp is stronger
211 (Cappetta, 2012). In Africa, teeth of *Protolamna* and *Leptostyrax* were reported from
212 the Albian of Angola and Tunisia (Antunes and Cappetta, 2002; Cuny et al., 2004).

213

214

215 Family OTODONTIDAE Glikman, 1964

216

217 Genus *Cretolamna* Glikman, 1958

218

219 *Cretolamna* sp.

220 (Fig. 2C)

221

222 *Material examined.* One incomplete tooth (GR/PC.1775).

223 *Age and locality.* Coniacian?–Santonian, Awgu, southeastern Nigeria.

224

225 *Description.* The unique specimen corresponds to a large upper lateral tooth. The main
226 cusp bends distally and shows a convex mesial cutting edge. The distal cutting edge is
227 more rectilinear. Only the distal lateral cusplet is preserved. It is triangular, wider than
228 high, and relatively large. The root has a poorly marked lingual protuberance. The root
229 lobes are short and separated by a broad, rounded mediobasal notch.

230

231 *Remarks.* This tooth is very characteristic of this widespread genus. In Africa, teeth of
232 *Cretolamna* are common in Late Cretaceous marine deposits (e.g., Antunes and
233 Cappetta, 2002; Arambourg, 1952; Cuny et al., 2012; Darteville and Casier, 1949;
234 White, 1934). A lateral tooth with a similar morphology has been described as
235 *Cretolamna appendiculata* by Antunes and Cappetta (2002: pl. 10, fig. 12) from the late
236 Turonian of Iembe (Angola). Most of *Cretolamna* teeth found in Late Cretaceous
237 deposits have been commonly assigned to the type species *C. appendiculata*, but a
238 recent revision of this genus based on an abundant material from the Cenomanian–
239 Campanian interval shows that several species can be recognized among the *C.*
240 *appendiculata* group (Siverson et al., in press).

241

242

243 Family ANACORACIDAE Casier, 1947

244 Genus *Squalicorax* Whitley, 1939

245

246 *Squalicorax pristodontus* (Agassiz, 1843)

247 (Fig. 2D)

248

249 *Material examined.* One incomplete tooth (GR/PC.1776).

250 *Age and locality.* Early Maastrichtian (Neubergicus Zone), Calabar, southeastern

251 Nigeria.

252

253 *Description.* This wide (29 mm), large tooth shows a rather gibbous mesial edge and an
254 attenuated distal heel. Serrations of the cutting edges are well developed. The basal part
255 of the root is not preserved.

256

257 *Remarks.* This widespread species is well known in the latest Cretaceous marine
258 deposits of Africa, especially in the Democratic Republic of the Congo (Darteville and
259 Casier, 1943), Morocco (Arambourg, 1952), Egypt (Cappetta, 1991; Gemmellaro,
260 1920), Angola (Antunes and Cappetta, 2002) and Senegal (Cuny et al., 2012).

261

262

263 Family MITSUKURINIDAE Jordan, 1898

264 Genus *Scapanorhynchus* Woodward, 1889

265

266 *Scapanorhynchus* cf. *texanus* (Roemer, 1849)

267 (Fig. 2E, F)

268

269 *Material examined.* Three incomplete teeth (including GR/PC.1777, GR/PC.1778).

270 *Age and locality.* Coniacian?–Santonian, Awgu, southeastern Nigeria.

271

272 *Description.* These teeth are large (up to 41 mm in length) and relatively robust. The
273 crown consist of only one main cusp, without lateral cusplets. It is clearly sigmoid in
274 profile view. The lingual face is slightly convex and smooth whereas the labial face is
275 strongly convex and bears up to 25 well marked longitudinal folds. The root has a very
276 pronounced lingual protuberance marked by a short and deep groove. Only the distal
277 lobe of the root is preserved on the best preserved tooth (GR/PC.1777: Fig. 2E). It is
278 relatively robust and has a rounded extremity.

279

280 *Remarks.* The Nigerian specimens studied here are very similar to those figured by
281 Antunes and Cappetta (2002: pl. 9, fig. 4-7) from the late Turonian of Iembe (Angola).
282 However, the root lobes seem more robust in the Nigerian material. These teeth from
283 Awgu would confirm the occurrence of this species in the Late Cretaceous of Africa.

284

285

286 Incertae familiae

287 Incertae genus

288

289 “*Carcharias*” *amonensis* (Cappetta and Case, 1975a)

290 (Fig. 3A)

291

292 *Material examined.* One tooth (GR/PC.1779).

293 *Age and locality.* Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>),

294 northeastern Nigeria.

295

296 *Description.* The specimen corresponds to an upper lateral tooth. The main cusp is
297 labiolingually compressed and strongly bent distally. There is one pair of triangular
298 lateral cusplets, plus one additional incipient mesial cusplet. The root is damaged and no
299 lingual protuberance, median furrow or lobes can be observed.

300

301 *Remarks.* This small tooth is clearly referable to “*Carcharias*” *amonensis*, a
302 geographically widespread Cenomanian lamniform shark. This taxon corresponds to a
303 good biostratigraphical marker for this stage. It is mainly known from North American
304 and European localities where it can be abundant, while it seems to be slightly less
305 common in Africa. In this continent, it has been found in Morocco (Cavin et al., 2010),
306 Libya (Rage and Cappetta 2002), Egypt (Slaughter and Thurmond, 1974; Werner,
307 1989), and Angola (Antunes and Cappetta, 2002). It is also present in Lebanon, where a
308 few complete skeletons have been collected (Cappetta, 2012: 208). This species is
309 clearly not an odontaspimid s.l. (e.g., *Odontaspis*, *Carcharias*, and their fossil relatives)
310 and is only assigned to the genus *Carcharias* pending further study on its relationships
311 to other lamniform sharks.

312

313

314 Order RAJIFORMES Berg, 1940

315 Incertae familiae

316 Genus *Rhombopterygia* Cappetta, 1980b

317

318 *Rhombopterygia zaborskii* sp. nov.

319 (Fig. 3B–E)

320

321 *Holotype*. One anterior tooth (GR/PC.1780) (Fig. 3B).

322 *Paratypes*. Three anterolateral to lateral teeth (GR/PC.1781, GR/PC.1782,

323 GR/PC.1783) (Fig. 3C–E).

324 *Additional material*. Two incomplete teeth.

325 *Age and type locality*. Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>),

326 northeastern Nigeria.

327 *Etymology*. Species named in honour to Peter M. P. Zaborski, who led one of the author

328 (P.C.) to the Ashaka quarry.

329

330 *Diagnosis*. New species of *Rhombopterygia* with very small (about 0.5 to 0.8 mm wide)

331 teeth characterized by the following features: 1) cusped crown at least as wide as root,

332 2) lingual face with concave lateral margins in occlusal view, 3) well-developed median

333 uvula, 4) lateral uvulae reduced but always present.

334

335 *Differential diagnosis*. New species of *Rhombopterygia* with teeth differing from those

336 of *R. rajoides*, the type and only species of the genus, by the following features: 1)

337 anterior teeth narrower with crown as wide as root, 2) lateral margins of lingual face
338 concave in anterior teeth, 3) median uvula narrower and less rounded, 4) more marked
339 lateral uvulae, 5) cusp more developed in anterior teeth and present in lateralmost teeth,
340 6) smaller size.

341

342 *Description.* Anterior teeth (including the holotype GR/PC.1780: Fig. 3B) have a
343 subrectangular crown in occlusal view. The labial edge of the crown is convex. The
344 lingual face shows a well-developed, subtriangular median uvula that projects lingually,
345 whereas lateral uvulae are much more reduced. Both faces are separated by a transverse
346 crest that rises up into an obtuse central cusp. The root, not very high, is as wide as the
347 crown and shows in lingual view a pair of marginolingual foramina located below the
348 junction of the median and lateral uvulae. In basal view, the root is marked by a deep
349 median furrow that separates two subtriangular lobes. The furrow displays a foramen in
350 central position. Lateral teeth (including the paratype GR/PC.1783: Fig. 3E) have a
351 crown which is more expanded laterally and marked by a transverse crest bearing a
352 lower central cusp. The lingual edge shows a broad, triangular central uvula which is
353 flanked by one pair of smaller, poorly salient lateral uvulae. The root is narrower than
354 the crown.

355

356 *Remarks.* Two “rhinobatoid” taxa have been described from the early Late Cretaceous
357 of Africa. *Isidobatus* is a genus based on isolated “rhinobatoid”-like teeth from the late
358 Cenomanian of Egypt (Werner, 1989). The Ashaka teeth do not display the transverse
359 keels and crest present in those of *Isidobatus* and have less-developed median and
360 lateral uvulae. They can thus be easily distinguished from this peculiar genus. The

361 platyrrhinid genus *Tingitanius*, recently described on the basis of a nearly complete
362 specimen from the early Turonian of Morocco (Claeson et al., 2013), has teeth which
363 are rather similar to those found at Ashaka. However, the teeth of *Tingitanius* mainly
364 differ by the lack of a cusp and their higher root.

365 The teeth from Ashaka are here assigned to the genus *Rhombopterygia* on the
366 basis of its broad crown, the shape of the transverse crest, the presence of a small cusp,
367 and the morphology of the lingual uvulae. This genus has been originally described on
368 the basis of complete skeletons from the Cenomanian of Lebanon representing a single
369 species, *R. rajoides* (Cappetta, 1980b). In addition, isolated teeth assigned to
370 *Rhombopterygia* have been reported from the Cenomanian and Coniacian of Spain
371 (Bernárdez, 2002; Vullo et al., 2009), while there is a doubtful occurrence from the
372 Campanian of Germany (Müller, 1989). The teeth described by Bernárdez (2002: pl. 54,
373 figs. 1-4) as “*R. villae*” (*nomen nudum*) strikingly resembles those of *R. zaboriskii* sp.
374 nov. and are also late Cenomanian in age. Therefore, they might represent the same
375 species or closely related forms. Lastly, it can be noted that “*Rhinobatos*” *whitfieldi*
376 from the Cenomanian of Lebanon has similar teeth in overall morphology, but these are
377 smaller and more cuspidate (Cappetta, 1980b). *Rhombopterygia* was placed among the
378 Rhinobatidae by Cappetta (1980b, 2012), but the phylogenetic analysis performed by
379 Claeson et al. (2013) would not support this interpretation. This analysis found
380 “*Rhinobatos*” *whitfieldi* and *Rhombopterygia rajoides* as successive sister taxa to
381 *Zanobatos* and Myliobatiformes. However, it is worth noting that this result was
382 recovered by the 50% majority rule tree but not in the strict consensus.

383

384

385 Genus *Hamrabatis* Cappetta, 1991

386

387 *Hamrabatis* sp.

388 (Fig. 3F, G)

389

390 *Material examined.* Two teeth (GR/PC.1784, GR/PC.1785).

391 *Age and locality.* Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>),

392 northeastern Nigeria.

393

394 *Description.* The best preserved specimen (GR/PC.1784: Fig. 3F) is a small
395 anterolateral tooth. In occlusal view, it displays a rhombic crown as wide as long and
396 marked by a blunt transverse keel. The lingual area of the occlusal face shows an
397 irregular, alveolate surface whereas the labial area is almost smooth. The lingual face is
398 strongly concave in profile view. The basal part of the lingual face is subhorizontal, flat
399 and falciform in occlusal view. The root is not preserved. A poorly preserved lateral
400 tooth (GR/PC.1785: Fig. 3G) shows a crown more expanded laterally. It is apparently
401 devoid of transverse keel and ornamentation. The basal part of the lingual face is
402 damaged.

403

404 *Remarks.* *Hamrabatis* is known from the Late Cretaceous of Europe, Northern Africa,
405 Near East and North America (see Cappetta, 2012). Thus, the presence of *Hamrabatis*
406 in the Cenomanian of Nigeria represents the southernmost occurrence of this
407 widespread rajiform genus. So far, *H. bernardezi* from France and Spain is the only
408 known Cenomanian species of the genus (Bernárdez, 2002; Vullo et al., 2007, 2009).

409 The teeth from Ashaka differ from *H. bernardezi* by their crown almost devoid of
410 ornamentation, but this may be due to abrasion. Because of the scarcity and poor
411 preservation of the Ashaka material, these teeth are here referred to *Hamrabatis* sp.

412

413

414 Class OSTEICHTHYES Huxley, 1880

415 Order PYCNODONTIFORMES Berg, 1937

416 Family PYCNODONTIDAE Agassiz, 1833

417 Genus *Acrotemnus* Agassiz, 1836

418

419 *Acrotemnus* sp.

420 (Fig. 4A)

421

422 *Material examined.* One prearticular dentition (GR/PC.1786).

423 *Age and locality.* Early Turonian (Coloradoense Zone), Ashaka quarry (level 26),

424 northeastern Nigeria.

425

426 *Description.* The unique specimen corresponds to a large (92 mm long), complete right

427 prearticular dentition bearing 34 robust teeth. The symphysis is long (52 mm) but not

428 very thick. There are three rows of teeth. The ten teeth of the inner row are large, up to

429 18 mm wide. They are bean-shaped or oblong and marked medially by a narrow

430 transverse groove. The twelve teeth of the middle row are less transversally extended

431 and are marked by a granular central depression. Lastly, the twelve teeth of the outer

432 row are oval to subcircular, with an unornamented, rounded central depression.

433

434 *Remarks.* *Macropycnodon* is a large genus of pycnodont fish recently erected on the
435 basis of a single vomerine dentition (*M. streckeri*) and isolated teeth (*M.*
436 *megafrendodon*) from the Turonian of U.S.A. (Kansas and New Mexico, respectively)
437 (Shimada et al., 2010). Therefore, the prearticular dentition of *Macropycnodon* is
438 unknown and no direct comparisons can be made between the North American and the
439 Nigerian material. However, the dental features observed on the large prearticular jaw
440 from the Ashaka quarry are very similar to those present in *Macropycnodon*, especially
441 in the type species *M. streckeri* (specimen KUVF 946; Shimada et al., 2010: fig. 2). In
442 addition, the Nigerian specimen also shares with *Macropycnodon* the Turonian age and
443 the unusual large size. It can be distinguished from the prearticulars of the *Coelodus*
444 species, which bear teeth that are generally smooth and more elongated transversally
445 (Schultz and Paunović, 1997; Poyato-Ariza and Wenz, 2002: fig. 22a).

446 It is worth noting that some large pycnodont teeth and jaw fragments from the
447 Late Cretaceous (Turonian?) of the Damergou area in Niger (eastern Iullemeden
448 Basin) have been referred by Arambourg and Joleaud (1943) to the poorly known taxon
449 *Acrotemnus faba*, originally described on the basis of a few associated teeth from the
450 Late Cretaceous (Turonian) of England (Agassiz, 1833–1843; Woodward, 1909). Like
451 *Macropycnodon*, this genus has robust teeth characterized by a sharp transverse apical
452 ridge (Arambourg and Joleaud, 1943: pl. II, figs. 14-17). Furthermore, some teeth from
453 Damergou show a ring-like ridge and a central depression (Arambourg and Joleaud,
454 1943: pl. II, figs. 11, 13), indicating that the variation in tooth morphology is similar to
455 that observed in *Macropycnodon* and the prearticular dentition from Ashaka. Since
456 *Macropycnodon* and *Acrotemnus* share the same diagnostic features, the former appears

457 to be a junior synonym of the latter. Thus, *Acrotemnus streckeri* may be a subjective
458 junior synonym of *A. faba*, whereas *A. megafrendodon* is clearly a distinct species. The
459 Nigerian specimen here described is assigned to *Acrotemnus* sp. It must be noted that
460 two other Late Cretaceous species were referred to *Acrotemnus*: *A. splendens* from
461 Belgium (Leriche, 1911) and *A. yangaensis* from Angola (Darteville and Casier, 1949).
462 While the holotypic material of the former belongs in fact to the enigmatic, purported
463 pycnodontiform genus *Hadrodus*, the holotypic material (a single tooth) of the latter
464 must be regarded as Pycnodontidae indet.

465

466 Incerti ordinis (?PYCNODONTIFORMES Berg, 1937)

467 Incertae familiae

468 Genus “*Stephanodus*” Zittel, 1888

469

470 “*Stephanodus*” sp.

471 (Fig. 5A)

472

473 *Material examined.* Two teeth (including GR/PC.1787).

474 *Age and locality.* Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>),

475 northeastern Nigeria.

476

477 *Description.* This small hook-shaped branchial tooth shows a strong lateral

478 compression. A flattened discoid extension develops between the base and the hook.

479

480 *Remarks.* This dental morphotype is usually referred to the genus “*Stephanodus*”, which

481 may represent a parataxon (see discussion in Berreteaga et al., 2011). Such branchial
482 teeth are mainly present in pycnodontiforms (Kriwet, 1999), but can also be found in
483 other Mesozoic and Cenozoic fish groups. Thus, several authors considered
484 “*Stephanodus*” as a non-pycnodontid fish and referred it to the Eotrigonodontidae
485 within the Tetraodontiformes (e.g., Arambourg, 1952; Bardet et al., 2000; Darteville
486 and Casier, 1949; White, 1934).

487

488 Order AMIIFORMES Hay, 1929

489 Family AMIIDAE Bonaparte, 1837

490 Subfamily VIDALAMIINAE Grande and Bemis, 1998

491

492 Genus indet. A

493 (Fig. 4B, C)

494

495 *Material examined.* Two vertebrae (GR/PC.1788-1789).

496 *Age and locality.* Latest Cenomanian (Gadeni Zone), Ashaka quarry (level 21>),
497 northeastern Nigeria.

498

499 *Description.* The larger specimen (GR/PC.1788: Fig. 4B) corresponds to an abdominal
500 vertebral centrum, slightly broader than high and weakly compressed anteroposteriorly.
501 It shows insubstantial parapophyses. The neural and aortal facets are visible dorsally
502 and ventrally, respectively. In dorsoventral view, the smooth lateral surfaces appear
503 markedly concave. The second, smaller specimen (GR/PC.1789: Fig. 4C) is a posterior
504 caudal (ural) centrum, higher than wide.

505

506 *Remarks.* The shape of these vertebral centra is characteristic of those found in the trunk
507 (= abdominal) and caudal region of amiid fishes (Grande and Bemis, 1998). The fact
508 that no well-developed parapophyses are fused to the centrum indicates that these
509 specimens do not belong to the subfamily Amiinae (Grande and Bemis, 1998). Based on
510 their general morphology, these two centra can be assigned to the subfamily
511 Vidalamiinae (Grande and Bemis, 1998). The dorsal vertebral centrum closely
512 resembles that of an indeterminate vidalamiine described from the Late Cretaceous
513 (Maastrichtian) of Brazil (Martinelli et al., 2013). However, the latter does not display
514 the concavity of the lateral surface observed in dorsoventral view in GR/PC.1788.
515 Among other mid-Cretaceous amiids, similar large centra characterized by a weak
516 anteroposterior compression are also observed in the *Pachyamia* from the late Albian of
517 Mexico (Grande and Bemis, 1998) and the early Cenomanian of the Near East (Chalifa
518 and Tchernov, 1982), as well as in a partial vertebral column of a possible indeterminate
519 vidalamiine from the middle Turonian of Brazil (Gallo et al., 2007b).

520

521 Genus indet. B

522 (Fig. 4D)

523

524 *Material examined.* One vertebra (GR/PC.1790).525 *Age and locality.* Coniacian?–Santonian, Awgu, southeastern Nigeria.

526

527 *Description.* This specimen corresponds to a laterally extended vertebral centrum,
528 broader than high and anteroposteriorly compressed. No parapophyses are fused to the

529 centrum. In anteroposterior view, it shows a subrhombic shape, with dorsolateral (i.e.,
530 between the neural facets and parapophyses) and ventrolateral (i.e., between the aortal
531 facets and parapophyses) surfaces appearing slightly convex and concave, respectively.
532 This shape indicates a central trunk position.

533

534 *Remarks.* Like the amiid centra from the Ashaka quarry, this centrum shows anatomical
535 features that permit to assign it to the Vidalamiinae. However, it can be distinguished
536 from the Cenomanian abdominal vertebral centrum described above by a stronger
537 anteroposterior compression, a more rhombic outline, and the presence of slight
538 ventrolateral concavities. Thus, the material from Ashaka and Awgu may represent two
539 distinct vidalamiine taxa. Such ventrolateral concavities are an autapomorphic feature of
540 the non-marine (possibly marine?) genus *Melvius* from the Late Cretaceous
541 (Campanian–Maastrichtian) of North America (Bryant, 1987; Grande and Bemis,
542 1998), in which this character can be much more marked than in the centrum from
543 Ashaka. Unfortunately, the intracolumnar shape variation of the centra remains
544 unknown for the Ashaka vidalamiine, and a deeper comparison with *Melvius* is not
545 possible. Interestingly, the “early Senonian” (Coniacian–Santonian) locality of In
546 Beceten in southern Niger yielded an indeterminate amiid taxon (Broin et al., 1974). An
547 examination of the material (including isolated centra) housed at the Muséum national
548 d’Histoire naturelle of Paris indicates that the amiids from Awgu and In Beceten are at
549 least closely related (R.V. pers. observ.). It is worth noting that this specimen was
550 collected in the Awgu area beside a few teeth of the marine sharks *Cretolamna* and
551 *Scapanorhynchus*. However, all these fossils were found naturally cleaned on an
552 inclined outcrop surface, probably not exactly *in situ*. Furthermore, a different colouring

553 also suggests that the amiid and shark specimens originally came from two distinct
554 beds.

555

556 Order IONOSCOPIFORMES Grande and Bemis, 1998

557 Family and genus indet.

558 (Fig. 5B)

559

560 *Material examined.* One tooth (GR/PC.1791).

561 *Age and locality.* Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>),

562 northeastern Nigeria.

563

564 *Description.* This small tooth shows a subcircular base, slight longitudinal folds, and an
565 apex bearing a transverse, curved carina.

566

567 *Remarks.* This tooth resembles that described from the middle–late Cenomanian of
568 northern Spain (La Cabaña Formation) (Vullo et al., 2009), showing the typical

569 ionoscopiform dental features described by Mudroch and Thies (1996) and Thies and

570 Mudroch (1996). To date, ionoscopiform fishes are known from complete skeletons

571 from Middle Triassic to Early Cretaceous in Europe, Africa, and North and South

572 America (Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Brito and Alvarado-

573 Ortega, 2008). However, *Neorhombolepis*, known from a single incomplete skeleton

574 from the Lower Chalk (Cenomanian) of England (Woodward, 1888), has been

575 considered by some authors as a ionoscopiform genus, closely related or even

576 synonymous to the ophiopsid genus *Macrepistius* from the Albian of Texas (Grande and

577 Bemis, 1998; Patterson, 1973). In addition, it is noteworthy that the poorly known,
578 monospecific genus *Petalopteryx* from the Cenomanian of Lebanon (Pictet, 1850)
579 closely resembles the ophiopsid genera *Teoichthys* and *Placidichthys* (both from the
580 Early Cretaceous of America), and therefore may belong to this group of
581 ionoscopiforms. Lastly, the presence of some ionoscopiforms in the Cenomanian of
582 Komen (Slovenia) and the Island of Hvar (Croatia) was noted by Wenz and Kellner
583 (1986). All these data and observations would indicate that the temporal range of
584 ionoscopiforms fishes extends into the early Late Cretaceous, and thus would support
585 the assignment of the isolated teeth from the Cenomanian of Spain and Nigeria to this
586 primitive order of marine halecomorph fishes.

587

588

589 Order PACHYCORMIFORMES Berg, 1937

590 Family PACHYCORMIDAE Woodward, 1895

591 Genus *Protosphyraena* Leidy, 1860

592

593 cf. *Protosphyraena* sp.

594 (Fig. 4E)

595

596 *Material examined.* One incomplete tooth (GR/PC.1792).

597 *Age and locality.* Early Coniacian, Nkalagu, southeastern Nigeria.

598

599 *Description.* The crown is laterally compressed, not very elongated and triangular in
600 lateral view. The apex is broken, showing the very thin layer of enamel in cross-section.

601 One of the two face displays a single, short enamel fold near the apex. There are two
602 sharp carinae. These anterior and posterior cutting edges are slightly concave and
603 convex, respectively.

604

605 *Remarks.* In Africa, the only report of this genus is a single tooth from the Maastrichtian
606 of Egypt (Gemmellaro, 1920), whereas it is widespread in the Cretaceous of North
607 America and Europe. More recently, a few isolated teeth from the Campanian–
608 Maastrichtian of Saudi Arabia were tentatively assigned to *Protosphyraena* sp. (Kear et
609 al., 2009).

610

611

612 Order CROSSOGNATHIFORMES Taverne, 1987

613 Suborder PACHYRHIZODONTOIDEI Forey, 1977

614 Family and genus indet.

615 (Fig. 6)

616

617 *Material examined.* One caudal skeleton (GR/PC.1793).

618 *Age and locality.* Late Cenomanian (Juddii Zone), Lokpanta (level 33), southeastern

619 Nigeria.

620

621 *Description.* The caudal skeleton is embedded at the surface of a flattened, laminated
622 calcareous nodule. About ten preural vertebrae are preserved. Most of the bones of the
623 caudal fin have been removed by weathering and are now preserved as external moulds.

624 There are two well-developed dorsal and ventral caudal scutes. These bones are curved,

625 broaden medially and become thinner, needle-like at their extremities. Posteriormost
626 centra of the preural vertebrae are hardly visible, as well as the ural centra. The basal
627 (proximal) part of an element identified as the parhypural would indicate the position of
628 the first preural centrum (Pu1). Hypural elements seems to be largely fused (Hy1+Hy2
629 and Hy3+Hy4 condition?). Uroneural elements are damaged, possibly displaced, but
630 rather large and broad element (Un1?) with a pointed distal extremity can be observed.
631 Imprints of lepidotrichs, of which the bases partly overlap the hypurals, indicate a
632 significant degree of hypurostegy. Although distal parts of the caudal fin lobes are not
633 preserved, the symmetry of the tail suggests that it may have been forked and
634 homocercal. The upper and lower lobes show eleven and nine principal rays,
635 respectively. Outermost rays are well segmented. Between these two lobes, the tail
636 displays numerous thin and densely segmented lepidotrichs.

637

638 *Remarks.* Despite its state of preservation, this specimen shows some anatomical
639 features (i.e., well-developed caudal scutes and uroneurals, partly fused hypurals) that
640 are present in most of pachyrhizodontoid fishes, such as *Elopopsis*, *Goulminichthys* and
641 *Pachyrhizodus* (Cavin, 2001: fig. 13). This group of primitive teleosts are well
642 represented in the early Late Cretaceous of Northern Africa, with *Elopopsis* and
643 *Goulminichthys* from the Cenomanian and Turonian of Morocco, respectively (Cavin,
644 1995, 2001; Taverne, 1976).

645

646

647 Order AULOPIFORMES Rosen, 1973

648 Family ENCHODONTIDAE Woodward, 1901

649 Genus *Enchodus* Agassiz, 1835

650

651 *Enchodus* cf. *gladiolus* (Cope, 1872)

652 (Fig. 5C)

653

654 *Material examined.* Two teeth (including GR/PC.1794).

655 *Age and locality.* Late Cenomanian (Gadeni Zone), Ashaka quarry (level 9>),

656 northeastern Nigeria.

657

658 *Description.* The larger and best preserved tooth is sigmoid in lateral view and shows a

659 weak barb in the apical region of the posterior carina. In the posterior part of the crown,

660 there are a few longitudinal folds between the base and the barb.

661

662 *Remarks.* This tooth from Ashaka is very similar to those from the middle–late

663 Cenomanian of North America that are referred to *Enchodus* cf. *gladiolus* (Cumbaa et

664 al., 2010; Nagrodski et al., 2012; Shimada et al., 2006). As mentioned above, *Enchodus*

665 (*E. lamberti*) was reported in Nigeria from the Yolde and Fika Shales formations by

666 Carter et al. (1963).

667

668

669 Order ALBULIFORMES Nelson, 1973

670 Family PHYLLODONTIDAE Sauvage, 1875

671 Genus *Eodiaphyodus* Darteville and Casier, 1949

672

673 *Eodiaphyodus* cf. *granulosus* Arambourg, 1952

674 (Fig. 4F)

675

676 *Material examined.* One nearly complete tooth plate (GR/PC.1795).

677 *Age and locality.* Early Maastrichtian (Neubergicus Zone), Calabar, southeastern

678 Nigeria.

679

680 *Description.* This oval-shaped tooth plate (47 mm long and 37 mm wide) displays an
681 aggregation of numerous small subcircular teeth (between 2 and 4 mm in diameter). The
682 basal face of the plate shows the tooth bases which are thick, irregular and marked by a
683 central depression. The occlusal face of the plate is more convex and has a smooth
684 surface.

685

686 *Remarks.* This genus was originally described on the basis of complete and fragmentary
687 tooth plates from the Maastrichtian of the Democratic Republic of the Congo and
688 assigned to a new species, *Eodiaphyodus lerichei* (Darteville and Casier, 1949).

689 Arambourg (1952) described a second species (i.e., *E. granulosus*) from the

690 Maastrichtian (and Paleocene?) of Morocco. In addition, Arambourg (1952) recognized

691 a third species (i.e., *E. bebianoi*) that had been previously referred to the genus

692 *Pseudoegertonia* by Darteville and Casier (1949). This species was described on the

693 basis of a few isolated teeth and tooth plate fragments from the Paleocene of the

694 Democratic Republic of the Congo (Darteville and Casier, 1949). *E. bebianoi* might

695 represent a senior synonym of *E. granulosus*, but it is better to consider it as a *nomen*

696 *dubium* due to the incompleteness of the type material. Estes (1969) tentatively referred

697 the Moroccan species to the genus *Pseudoegertonia* and restricted the genus
698 *Eodiaphyodus* to the species *E. lerichei* alone, but this interpretation is not followed
699 here. As noted by Arambourg (1952), tooth plates of *E. lerichei* differ from those of *E.*
700 *granulosus* (and *E. bebianoi*) by their teeth that are relatively smaller, more numerous
701 and more slender. In *E. lerichei*, tooth bases are thinner, more regular and more circular,
702 showing a well-developed central depression (Dartevelle and Casier, 1949: pl. 18, fig.
703 1d). The tooth plate from Calabar described here is morphologically very close to *E.*
704 *granulosus*, although about twice smaller, and is tentatively referred to this species. In
705 Africa, *Eodiaphyodus* also occurs in the late Campanian–Maastrichtian of Angola
706 (Antunes and Cappetta, 2002) and thus seems to have been a common component of
707 latest Cretaceous to earliest Paleogene ichthyofaunas present along the Atlantic margin.

708

709

710 **4. Concluding remarks**

711

712 In all studied localities, the fish material is generally scarce and poorly diverse,
713 mainly due to sampling bias. Nevertheless, most of these sites have yielded one or
714 several taxa that are recorded for the first time in this part of Africa. Thus, these new
715 occurrences have significant palaeobiogeographical implications. The seaway that
716 occupied intermittently the Benue Trough during transgressive episodes is known to
717 have played a key role in the dispersal of many fish groups (Cavin, 2008; Cavin et al.,
718 2012; Gallo et al., 2007a; Maisey, 2000; Martín-Abad and Poyato-Ariza, 2013) and
719 marine invertebrates (e.g., Courville et al., 1998; Gebhardt, 1999; Néraudeau and
720 Courville, 1997; Néraudeau and Mathey, 2000), especially because it provided a

721 connection between the proto-South Atlantic and the Mediterranean Tethys (via the
722 trans-Saharan seaway) during both the early Late Cretaceous and late Late Cretaceous
723 intervals (e.g., Benkhelil, 1989; Néraudeau and Mathey, 2000; Reyment, 1980a, b;
724 Reyment and Dingle, 1987). The late Cenomanian fish material from Nigeria includes
725 taxa which probably dispersed from the southwestern Europe (Iberian Peninsula) and/or
726 southern Tethyan platforms (Morocco to Lebanon), such as “*Carcharias*” *amonensis*,
727 *Rhombopterygia* and *Hamrabatis*. Thus, “*C.*” *amonensis* was able to reach the South
728 Atlantic (Angola), corresponding to its southernmost and only Southern Hemisphere
729 occurrence (see Kitamura, 2013: fig. 3). As underlined by Cavin (2008), the
730 biogeographical history of pachyrhizodontoid fishes is not well understood. The
731 Nigerian occurrence could have resulted from either a vicariant or dispersal event. The
732 similarity between the vidalamiine from the late Cenomanian of northeastern Nigeria
733 (as well as both closely related forms from the younger beds of southern Nigeria and
734 Niger) and members of this clade from the Late Cretaceous of North and South America
735 may be indicative of an Early Cretaceous vicariant event, like for the genera
736 *Calamopleurus* and *Pachyamia* (Cavin, 2008). However, although most of Late
737 Cretaceous amiid fishes are regarded as non-marine forms, some of these fossils can be
738 recovered from marine deposits, such as the material studied here and the possible
739 vidalamiine specimen described from the Turonian of the Sergipe Basin in northeastern
740 Brazil (Gallo et al., 2007b). If these fragmentary specimens were not washed into the
741 sea and actually correspond to marine forms, a trans-Atlantic dispersal during the early
742 Late Cretaceous cannot therefore be rejected.

743 The origin and dispersal history of *Ptychodus decurrens* remains unclear. Verma
744 et al. (2012) have suggested that it could have dispersed from Western Australia to

745 Europe and North America via India or the South Atlantic. This species had a mid to
746 high-palaeolatitudinal distribution (Hoch, 1992; Verma et al., 2012) and its equatorial
747 occurrence in the early Turonian of southern Nigeria may have been due to episodically
748 colder sea water temperatures in this part of the Benue Trough directly connected to the
749 South Atlantic (Néraudeau and Mathey, 2000). Occurrences of this species in the
750 Cenomanian–earliest Turonian of North Africa (e.g., Tunisia, Morocco) would suggest
751 that it migrated southwards during the Turonian to reach the Lower Benue Trough
752 (Nigeria) and Benguela Basin (Angola) in the early and late Turonian, respectively.
753 Interestingly, *P. decurrens* was also reported in the early Turonian of the Sergipe Basin
754 (northeastern Brazil), then located in the northwestern margin of the proto-South
755 Atlantic, roughly at the same palaeolatitude as the Lower Benue Trough (Andrade,
756 2005; Carvalho and Gallo, 2002). Concerning the genus *Acrotemnus*, it might have
757 dispersed from European seas to the trans-Saharan seaway (Niger) and Benue Trough
758 (Nigeria), and also to the Western Interior Seaway (U.S.A.). A similar pattern of
759 dispersal has been recently proposed by Martín-Abad and Poyato-Ariza (2013) for
760 various Cenomanian–Turonian pycnodontid genera.

761 *Scapanorhynchus texanus* might have originated during the Turonian–Santonian
762 interval in the Afro–Arabian plate where it is relatively rare, known only by a few teeth
763 from Angola, Nigeria, and Jordan (Antunes and Cappetta, 2002; Mustafa, 2000;
764 Zalmout and Mustafa, 2001). During the Campanian–Maastrichtian interval, this
765 species seems to have been restricted to North America (Cappetta and Case, 1975b;
766 Case and Schwimmer, 1988; Welton and Farish, 1993) while it was apparently replaced
767 in Africa and Near East by *S. rapax* (Antunes and Cappetta, 2002; Bardet et al., 2000;
768 Quaas, 1902; Retzler et al., 2013). As discussed above, the presence of a vidalamiine

769 fish in the Coniacian?–Santonian beds of Awgu can be the result of either vicariant or
770 dispersal events.

771 The few Campanian–Maastrichtian occurrences of *Eodiaphyodus* along the
772 South Atlantic coast (Angola, Nigeria) are the oldest ones known for the genus. This
773 suggests that *Eodiaphyodus* originated in this part of Africa and dispersed northwards
774 (via the Atlantic coast of Western Africa or via the trans-Saharan seaway) to reach
775 northwestern Africa, where it is especially common in the late Maastrichtian of
776 Morocco (Arambourg, 1952).

777

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779

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789

790

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1166 Figure captions:

1167

1168 **Fig. 1.** Geographical and stratigraphical position of the fish remains studied here. A,
1169 Nigerian geographical framework (A1) and main Nigerian structural and sedimentary
1170 units (A2). B, synthetic stratigraphical successions of the Lower Benue Trough,
1171 southern Nigeria (B1) and Upper Benue Trough, northeastern Nigeria (B2). Map,
1172 stratigraphical successions and other data modified from Courville (1993) and Courville
1173 et al. (1998).

1174

1175 **Fig. 2.** A, *Ptychodus decurrens*, tooth (GR/PC.1773) in occlusal (A1), lingual (A2) and
1176 lateral (A3) views. B, cf. *Protolamna* sp., tooth (GR/PC.1774) in lingual (B1) and
1177 mesiodistal (B2) views. C, *Cretolamna appendiculata*, tooth (GR/PC.1775) in lingual
1178 (C1) and labial (C2) views. D, *Squalicorax pristodontus*, tooth (GR/PC.1776) in lingual
1179 (D1) and labial (D2) views. E, F, *Scapanorhynchus* cf. *texanus*, GR/PC.1777 (E) and
1180 GR/PC.1778 (F), teeth in lingual (E1, F), labial (E2) and distal (E3) views. Scale bars
1181 equal 5 mm (B) and 10 mm (A, C–F).

1182

1183 **Fig. 3.** A, “*Carcharias*” *amonensis*, tooth (GR/PC.1779) in lingual view. B–E,
1184 *Rhombopterygia zaborskii* sp. nov., holotype GR/PC.1780 (B), paratypes GR/PC.1781
1185 (C), GR/PC.1782 (D) and GR/PC.1783 (E), teeth in occlusal (B1, C, D1, E), lingual
1186 (B2, D2) and mesiodistal (B3) views. F, G, *Hamrabatis* sp., GR/PC.1784 (F) and
1187 GR/PC.1785 (G), teeth in occlusal (F1, G), lingual (F2) and mesiodistal (F3) views.
1188 Scale bars equal 500 μ m (B–G) and 1 mm (A).

1189

1190 **Fig. 4.** A, *Acrotemnus* sp., right prearticular dentition (GR/PC.1786) in occlusal view.
1191 B, C, Vidalamiinae indet. A, GR/PC.1788 (B) and GR/PC.1789 (C), abdominal and ural
1192 centra (respectively) in anterior (B1, C), posterior (B2), dorsal (B3), ventral (B4) and
1193 left lateral (B5) views. D, Vidalamiinae indet. B, abdominal centrum (GR/PC.1790) in
1194 anterior (D1), posterior (D2), dorsal (D3), ventral (D4) and left lateral (D5) views. E, cf.
1195 *Protosphyraena* sp., tooth (GR/PC.1792) in labiolingual views. F, *Eodiaphyodus* cf.
1196 *granulosus*, tooth plate (GR/PC.1795) in occlusal (F1), basal (F2) and lateral (F3)
1197 views. Scale bars equal 5mm (C, E) and 10 mm (A, B, D, F).

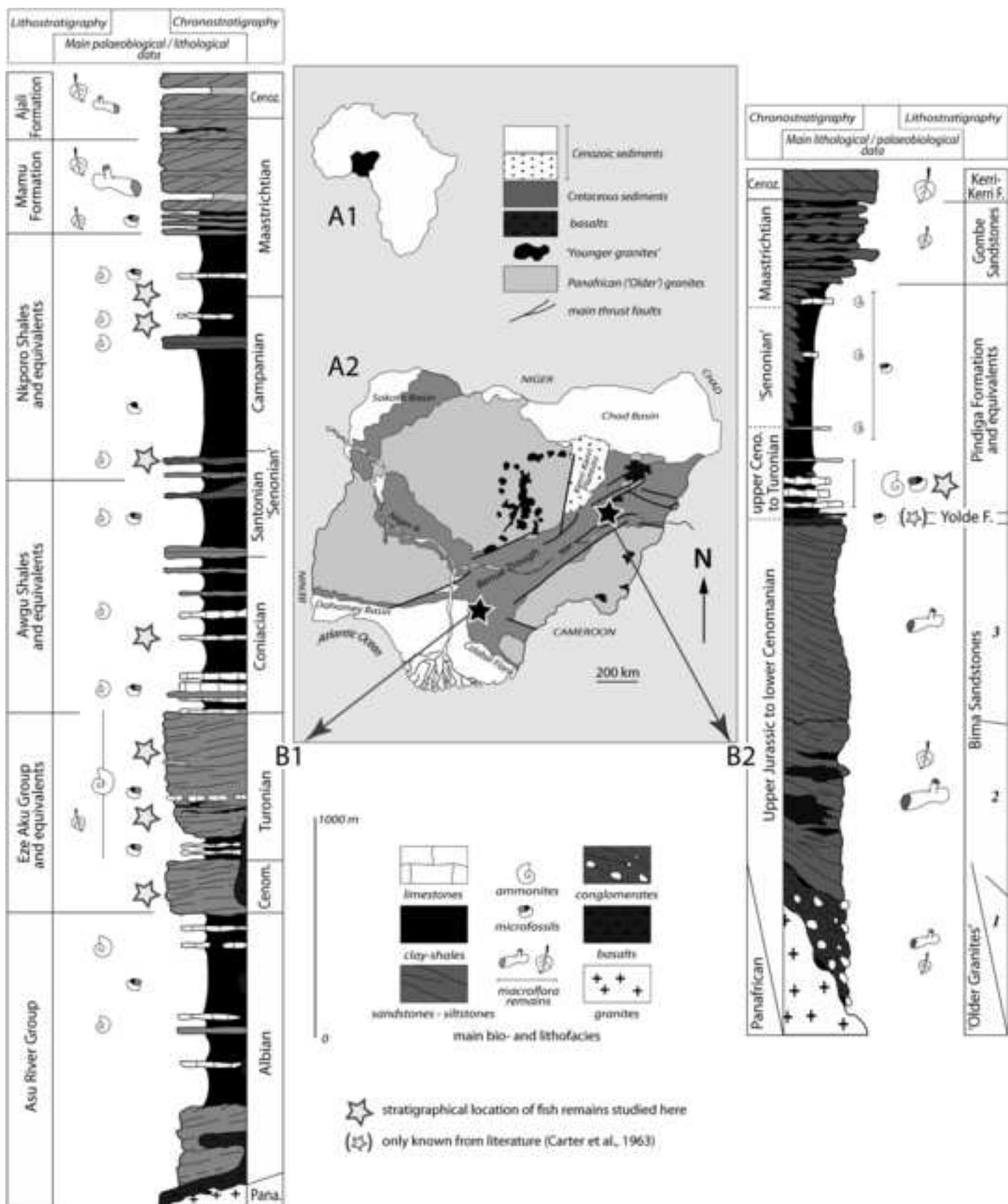
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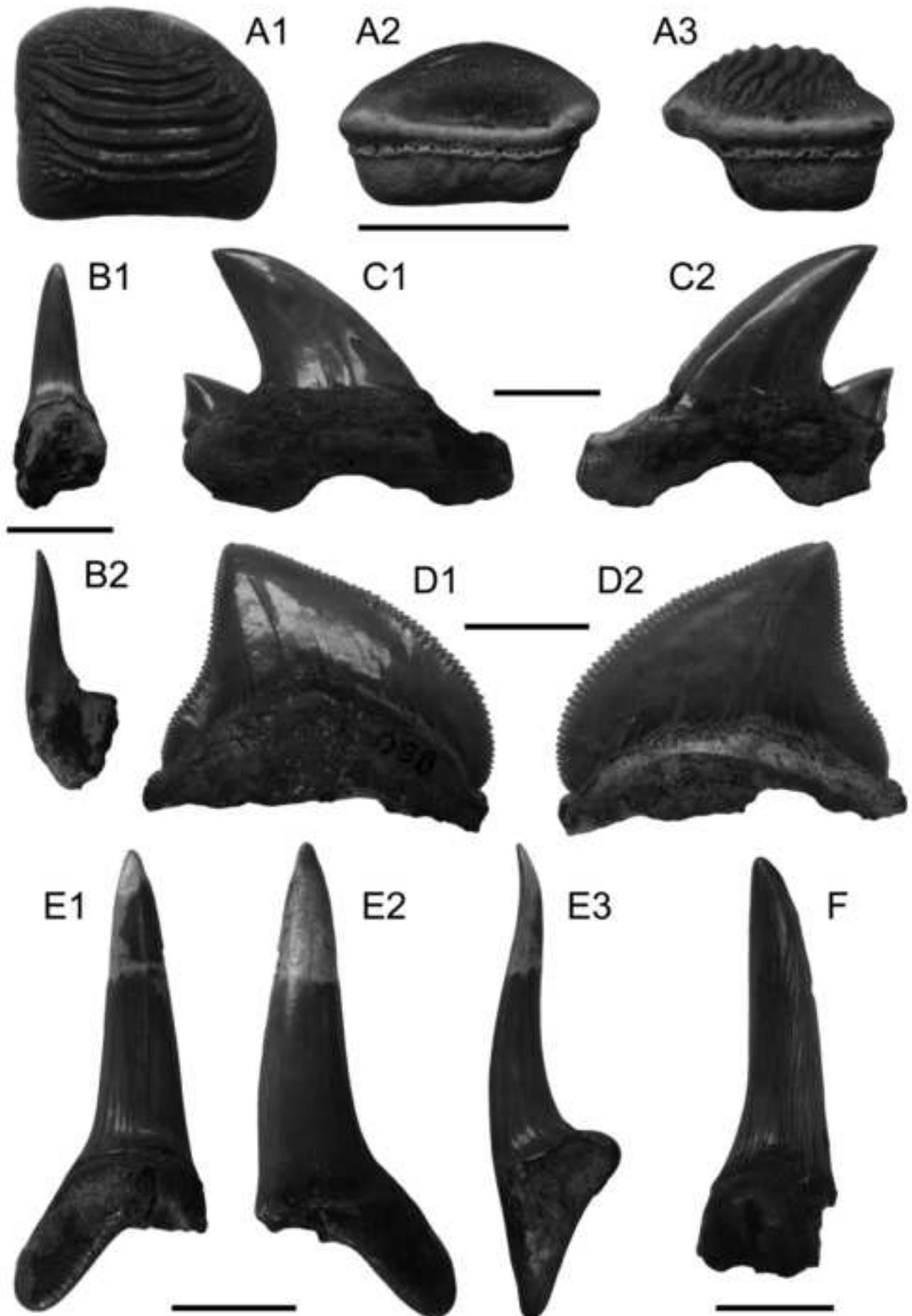
1199 **Fig. 5.** A, “*Stephanodus*” sp. (?Pycnodontiformes), branchial tooth (GR/PC.1787) in
1200 lateral view. B, Ionoscopiformes indet., tooth (GR/PC.1791) in mesiodistal? (B1),
1201 labial? (B2) and apical (B3) views. C, *Enchodus* cf. *gladiolus*, tooth (GR/PC.1794) in
1202 lateral view. Scale bars equal 500 μ m.

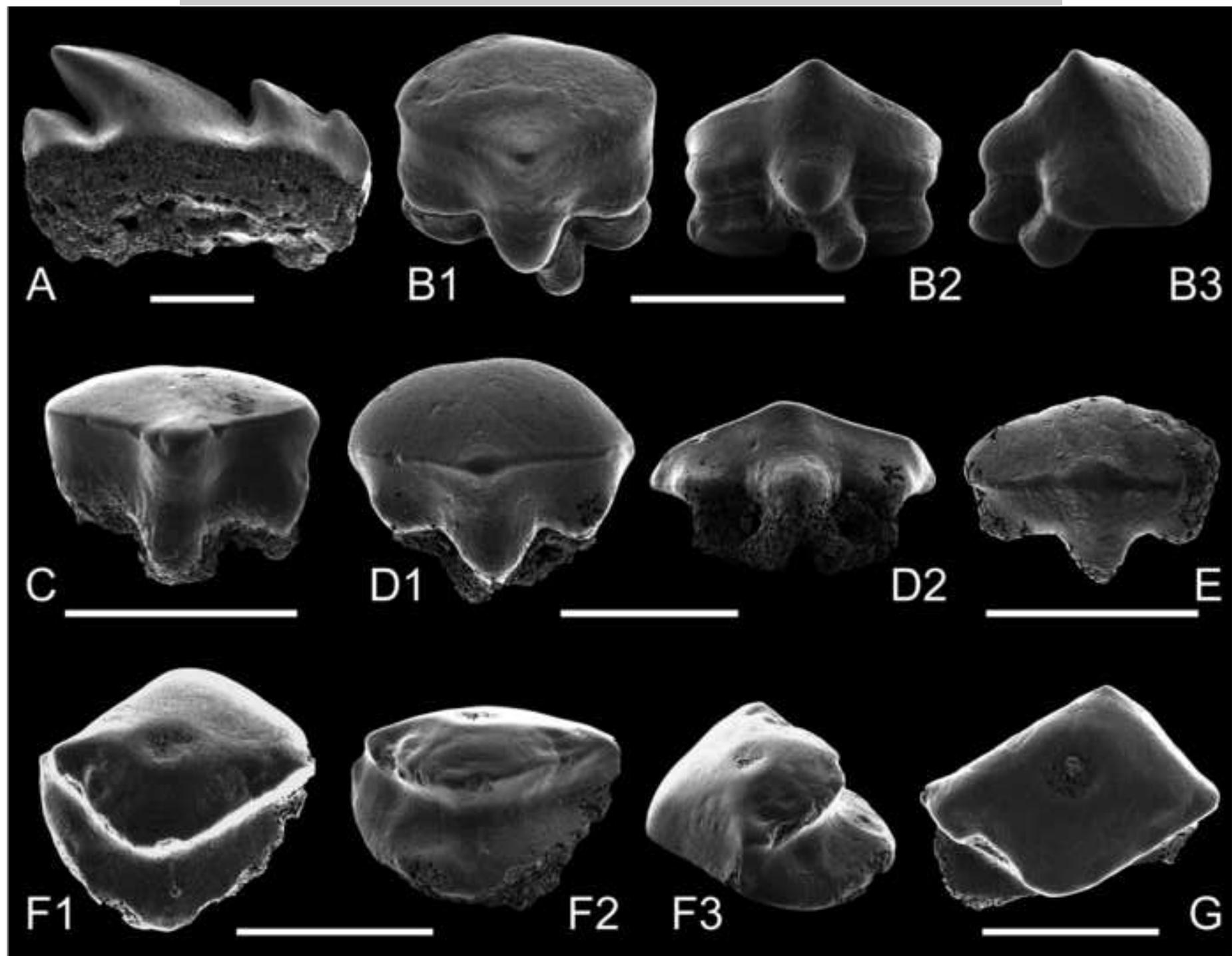
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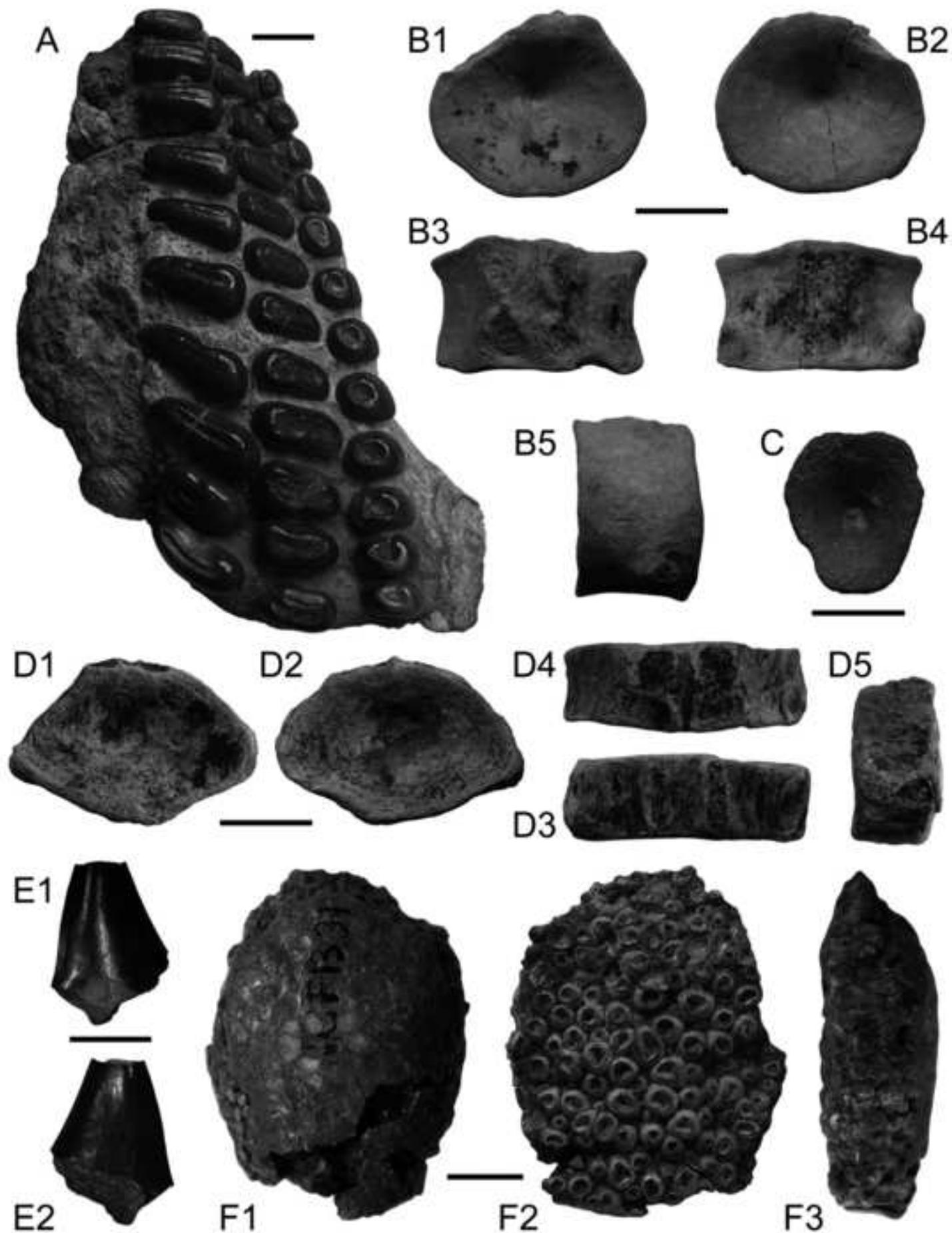
1204 **Fig. 6.** Pachyrhizodontoidei indet., caudal skeleton (GR/PC.1793) in right lateral view.
1205 Abbreviations: DCS, dorsal caudal spine; HS, hemal spine; Hy, hypural; Le,
1206 lepidotrichs; NS, neural spine; Ph, parhypural, Pu, preural vertebra; U, ural centrum;
1207 Un, uroneural; VCS, ventral caudal spine. Scale bar equals 50 mm.

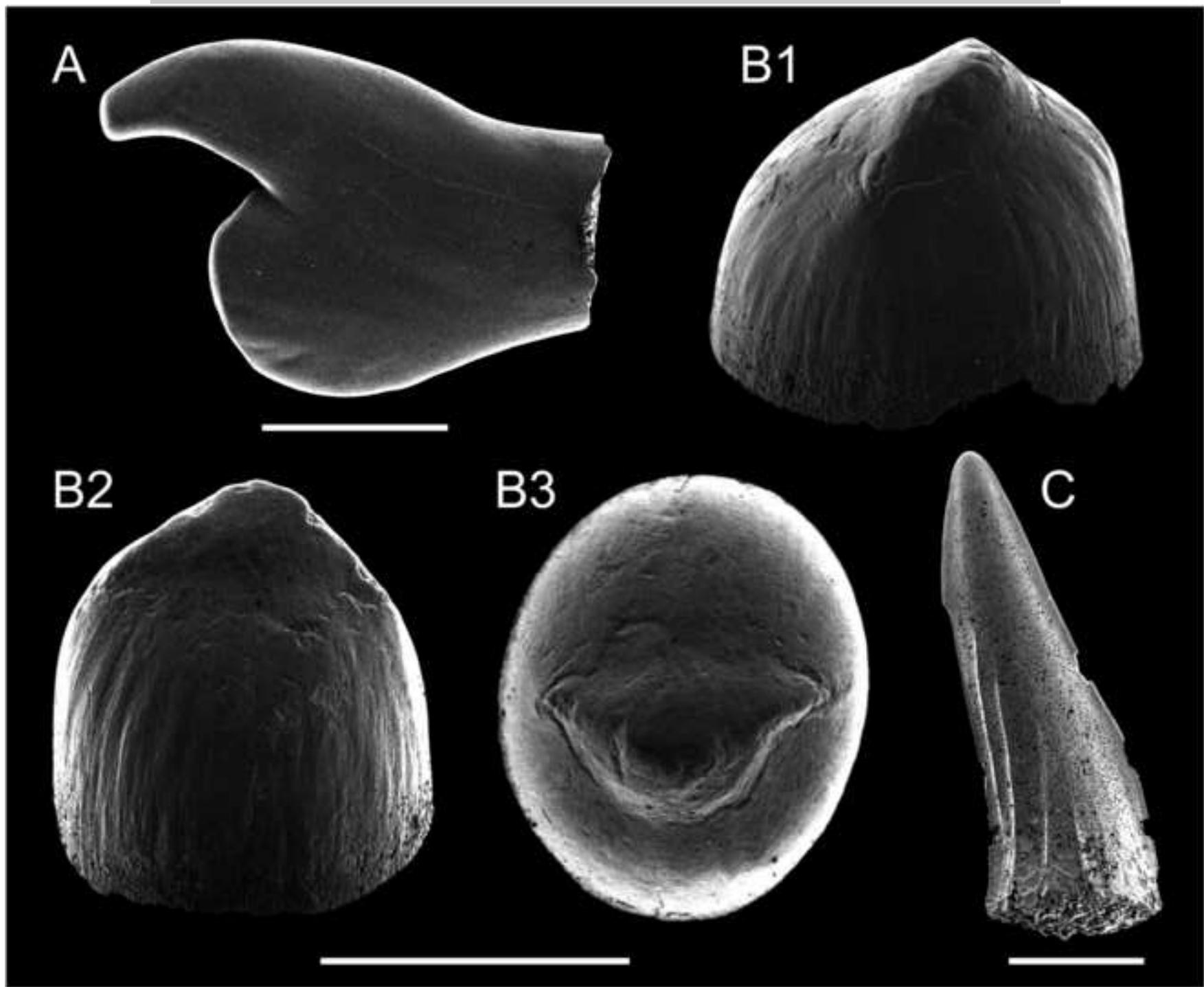
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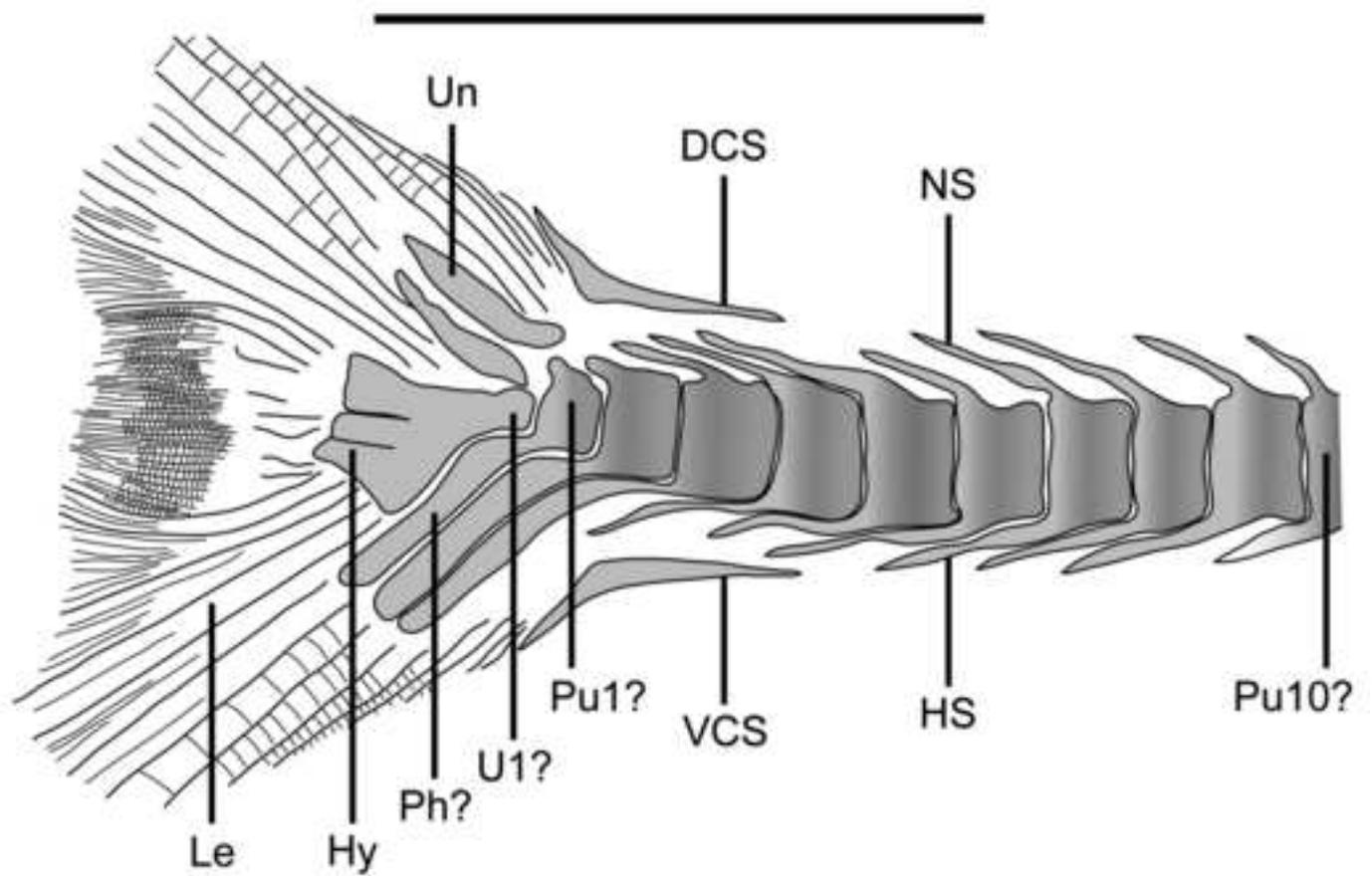












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1210 Highlights:

1211 - Selachian and ray-finned fishes are described from the Late Cretaceous of Nigeria.

1212 - Some fish taxa are recorded for the first time in Africa.

1213 - *Rhombopterygia zaborskii* sp. nov. is described from the Cenomanian of Ashaka.

1214 - The Benue Trough created opportunities for the dispersal of many marine fishes.

1215

ACCEPTED MANUSCRIPT