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# 1 **A dyrosaurid from the Paleocene of Senegal**

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3 Jeremy E. Martin<sup>1</sup>, Raphaël Sarr<sup>2</sup>, Lionel Hautier<sup>3</sup>

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5 <sup>1</sup>Univ. Lyon, ENS de Lyon, Université Claude Bernard Lyon 1, CNRS, UMR 5276

6 Laboratoire de Géologie de Lyon: Terre, Planètes, Environnement, F-69342 46 Allée d'Italie,

7 Lyon, France.

8 <sup>2</sup>Laboratoire de Sédimentologie et Biostratigraphie, Département de Géologie, Université

9 Cheikh Anta Diop de Dakar, Sénégal

10 <sup>3</sup>Institut des Sciences de l'Evolution, UMR5554, CNRS, IRD, EPHE, Université de

11 Montpellier, Montpellier, France.

12

13 **Running Header:** Paleocene dyrosaurid from Senegal

14

15 **Abstract.**—We describe a partial dyrosaurid skeleton recently prepared out of a limestone

16 block discovered in the 1930s from Danian strata along the Atlantic coast of Senegal. The

17 specimen, from a single individual, comprises nicely preserved elements of the appendicular

18 and axial skeleton from the abdominal and sacral region, which enables us to refine our

19 knowledge on some postcranial characteristics of the Dyrosauridae. Although Dyrosauridae

20 are abundant in early Eocene deposits of North Africa, the present discovery in the Danian of

21 Senegal fills a patchier record early after the K/Pg boundary and provides an important

22 comparative datapoint with the few other Danian dyrosaurid records such as *Atlantosuchus*

23 from nearby Morocco or *Guarinisuchus* and *Hyposaurus* from Brazil and the USA,

24 respectively.

25

26

27

## 28 **Introduction**

29

30 The Dyrosauridae represent a monophyletic group of crocodylomorphs that radiated in the  
31 marine environment during the Cretaceous. Their earliest record dates from the Late  
32 Cretaceous with mentions from the Campanian (Churcher and Russel, 1992; Lamanna et al.  
33 2004; Kear et al. 2008; Salih et al. 2015) or from undetermined Late Cretaceous levels  
34 (Sertich et al. 2006) and perhaps from levels as old as the Cenomanian (Buffetaut and  
35 Lauerjat, 1978). The group survived through the end Cretaceous biological crisis and  
36 became extinct during the early Eocene, most probably during the Ypresian (Buffetaut,  
37 1978a; Buffetaut, 1982; Hill et al. 2008; Martin et al. 2014). Accounts of dyrosaurid remains  
38 in the Lutetian (Pilgrim, 1940; Tessier, 1952; Buffetaut, 1978a, b) should be re-evaluated in  
39 view of recent stratigraphic studies (e.g. O’Leary et al. 2006) before they can be validated or  
40 not. Although the fossil record of dyrosaurids is especially abundant with relatively complete  
41 specimens from the late Paleocene (Buffetaut, 1980; Jouve, 2007) and early Eocene  
42 (Bergounioux, 1956; Buffetaut, 1978a; Jouve, 2005), fewer representatives from the early  
43 Paleocene have been reported so far. They include genera such as *Hyposaurus* from the  
44 Danian of the USA (Troxell, 1925; Denton et al. 1997), *Atlantosuchus* from the Danian of  
45 Morocco (Buffetaut, 1979; Jouve et al. 2008) and *Guarinisuchus* from the Danian of Brazil  
46 (Barbosa et al. 2008). The genus *Phosphatosaurus* has been reported from Mali and Niger  
47 and may also be Danian in age according to Buffetaut (1978a). Other fragmentary finds from  
48 Bolivia (Buffetaut, 1991), Brazil (Cope, 1886), Pakistan (Buffetaut, 1977) and Senegal  
49 (Tessier, 1952) have been attributed a Danian or early Paleocene age. Current data indicate  
50 that dyrosaurid diversity was lower during the Late Cretaceous than during the Paleocene (6

51 genera versus 11, respectively). On the other hand, the diversity of dyrosaurids during the  
52 Cretaceous may parallel that of the Paleocene depending on phylogenetic resolution within  
53 Dyrosauridae (Hill et al. 2008). Some authors have proposed that this could be explained by a  
54 shift with the extinction of Cretaceous predators such as mosasaurs freeing space for  
55 dyrosaurids (Jouve et al., 2008; Barbosa et al. 2008). Nevertheless, such diversity counts  
56 merge the dyrosaurid fossil record of the entire Paleocene, and dyrosaurid diversity  
57 immediately after the K/Pg crisis is poorly known and difficult to evaluate. Records of large  
58 vertebrate predators immediately after the K/Pg boundary are equally important as those from  
59 the Maastrichtian because they may provide insights into the reorganization of marine  
60 foodwebs following a major biotic disruption.

61 Here, we describe a dyrosaurid specimen collected in the 1930s by two French  
62 geologists, Fernand Jacquet and Maurice Nicklès, who both worked for the Service  
63 Géologique de l'Afrique Occidentale Française (AOF) in Dakar. Their survey of Paleogene  
64 outcrops along the Atlantic coast of Senegal led to the discovery, near the village of  
65 Poponguine (Fig. 1), of the presently described specimen, which has been briefly mentioned  
66 in several notes (Malavoy, 1934 p.7; 1935 p. 7; Jacquet, 1936). The specimen consists of  
67 articulated postcranial elements belonging to a single individual, the bones of which were  
68 deposited in a low energy marine environment of Danian age according to associated  
69 microfossils.

70

71 *History of the discovery.*—Before we borrowed the specimen for preparation and study, the  
72 following inscription was visible on the surface of the sediment: “Poponguine – Sénégal,  
73 Falaise du Bungalow” (Fig. 3). “La Falaise du Bungalow” is a small seaside cliff subjected to  
74 wave erosion and made of an alternating sequence of marls and limestones (see geological



75 section). Nowadays, the Presidential residence is sitting on top of it, having replaced the  
76 bungalow of the “Gouverneur général de l’Afrique Occidentale Française”.

77 A note from the head of the Service géologique de l’AOF indicates 1934 as the year of  
78 the discovery of the Poponguine specimen, originally identified as a fossil mammal with eight  
79 vertebrae, three elongate bones and six ribs (Malavoy, 1934). The following year, the same  
80 specimen was identified as a crocodile from Poponguine (Malavoy, 1935). Jacquet (1936),  
81 reporting on some debris of a marine crocodylian, provided a brief context for the specimen  
82 indicating a provenance from alternating levels of marls and limestones from Poponguine. He  
83 attributed the deposits to be early Eocene in age on the basis of their invertebrate content,  
84 although more recent studies consider the deposits to be Danian in age (see geological  
85 section). Following the tragic loss in 1937 of F. Jacquet during a field survey in Mauritania,  
86 M. Nicklès was put in charge of handling the works of his colleague (Legoux, 1937). A few  
87 years later, Arambourg and Joleaud (1943 p. 63) mentioned that M. Jacquet recovered  
88 vertebrae and limb bones belonging to *Dyrosaurus* in the area of Poponguine. Tessier (1952)  
89 mentions that this material has been observed by C. Arambourg, citing “1943 *Dyrosaurus* sp.  
90 Arambourg (6), p. 63” and referring to the collection Jacquet of the MNHN (Muséum  
91 National d’Histoire Naturelle, Paris). Therefore, the specimen must have been part of the  
92 MNHN collections at least until 1952 but it is unclear when the specimen was transferred  
93 from Dakar to Paris. From this date, the whereabouts of the specimen become unknown and  
94 no mention of it is made in the literature. The specimen re-surfaces much later in Toulouse.  
95 The dyrosaurid specimen was stored in the collections of the Institut Catholique de Toulouse  
96 from an unknown date until the mid 90s when it was donated to the Toulouse Museum  
97 (MHNT) on September 09 1996 (Y. Laurent, pers. comm.). Understanding how the specimen  
98 transited from MNHN Paris to Toulouse is unclear at this stage and we can only speculate on  
99 potential links between Camille Arambourg (1885–1969), then Professor at MNHN who

100 made the observations on the specimen (see above), and Frédéric-Marie Bergounioux (1900–  
101 1983), paleontologist and theologian at the Institut Catholique de Toulouse. Both researchers  
102 knew each other, with C. Arambourg having sent to F-M. Bergounioux several fossil turtle  
103 specimens for study (Bergounioux, 1952). It is therefore possible that the dyrosaurid  
104 specimen arrived at the collections of Toulouse in this way. However, no mention of the  
105 Poponguine specimen is made in Bergounioux' monograph, which extensively describes  
106 dyrosaurid material from Tunisia (Bergounioux, 1956).

107

### 108 **Geological setting**

109

110 Paleocene strata crop out on a narrow littoral stretch between Toubab Dialaw until the  
111 southern end of the horst of Diass (Fig. 1). Most of the outcrops are represented by alternating  
112 marls and limestones, which take part in the Ndayane Formation. This formation is overlain  
113 by discording shelly limestones of the Poponguine Formation, which crop out East of  
114 Poponguine. The Ndayane Formation is visible in a cliff, the altitude of which is less than 10  
115 m above sea level. The Ndayane Formation unconformably overlies the Maastrichtian gritty  
116 limestone containing ammonites with a conglomeratic level (Castelain et al. 1965). A  
117 lithological section along the stretch of coastline shows the following units totalling 27 m in  
118 thickness:

119       From the base, grey argillaceous limestone becomes replaced by lenticular limestone  
120 (2.5 m thick) with gypsum veins;

121       Most of the cliff (17.5 m thick) is made of limestone beds alternating with yellowish  
122 marly limestones with gypsum veins. The limestone beds become thicker in the median  
123 section of the cliff and the marly limestone beds become lenticular. Near the summit,  
124 limestone beds become thinner whereas marly-limestone beds become thicker.

125 Marls containing calcite rosettes show at their base thin lenticular levels of marly  
126 limestones (7m thick).

127 The microfauna of the Ndayane Formation is rich and diverse and includes planktonic  
128 and benthic foraminifers as well as ostracods. These microfaunas have been studied by  
129 several authors (Castelain et al., 1965; Faye, 1983; Sarr, 1995; Sarr and Ly, 1998; Sarr, 1998)  
130 who established a middle to upper Danian age for the formation on the basis of the following  
131 planctonic foraminifer species, also identified here in sediment associated with  
132 MHNT.PAL.2012.0.45: *Chiloguembelina morsei* (Kline), *Morozovella inconstans*, *M.*  
133 *pseudobulloides* (Plummer), *M. cf. trinidadensis* (Bolli), and *Planorotalites compressa*  
134 (Plummer) (Fig. 2). This age is in agreement with that established by Tessier (1952) on the  
135 basis of macrofaunas.

136 The depositional environment corresponds to a middle to external platform with a water depth  
137 comprised between 100 and 150 m) with a muddy bottom covered with algae, receiving  
138 episodically coarse material from the infralittoral environment (Sarr, 1998).

139

## 140 **Systematic Paleontology**

141

142 Crocodylomorpha Hay, 1930

143 Dyrosauridae De Stefano, 1903

144 Dyrosauridae indet.

145 Figures 3–10

146

147 *Description.*—The specimen was preserved as three blocks (Fig. 3.1), which underwent acid  
148 preparation (Fig. 3.2). The largest block was prepared so that most elements of the specimen  
149 preserve their articulation. Several elements were totally freed from the matrix and could be

150 described individually. The main block preserves the last five thoracal vertebrae (#11 to #15);  
151 thoracal vertebra #10 has been freed from the matrix as well as two other thoracal vertebrae  
152 (one being heavily weathered and the other only consisting of the centrum) thus totalizing  
153 eight thoracic vertebrae. The two sacral vertebrae are preserved on the main block. The  
154 second sacral vertebra is split in half and is loose from the main block (Fig. 4). Four caudal  
155 vertebrae are also available. The right ischium is firmly connected to a fragmentary ilium  
156 (Fig. 5). The right femur (Fig. 6) is preserved and is slightly displaced from the pelvic area.  
157 The articulated vertebrae are positioned within a mix of ribs, gastralia, and displaced dorsal  
158 and ventral osteoderms.

159

160 *Materials.*—MHNT.PAL.2012.0.45, postcranial elements of a single specimen from the  
161 abdominal and sacral region.

162

163 *Thoracal vertebrae.*—The anteriormost thoracal vertebra is complete (Fig. 4.1–5) and  
164 corresponds to thoracal vertebra #10. In anterior or posterior views, the amphicoelous  
165 centrum has a subquadrangular outline, being nearly higher than wide. The posterior margin  
166 of the centrum displays a pathological area near its anterolateral corner, which may  
167 correspond to an erosive lesion (arrow in Fig. 4.2). The centrum is slightly elongated, being  
168 longer than high. In lateral view, the ventral margin of the centrum is faintly concave. The  
169 main corpus of the centrum is slightly constricted laterally with thick anterior and posterior  
170 margins that define the limits of the anterior and posterior surfaces. The neurocentral suture is  
171 visible and runs transversally along the lateral margin of the centrum, in its dorsal half. A  
172 distinct and shallow circular pleurocoele spreads over the centrum and neural arch, below the  
173 posterior margin of the transverse process. The neural arch is robustly attached to the  
174 centrum. The neural spine is relatively short, being nearly as high as the centrum. Its dorsal

175 margin is straight and represents half the length of the centrum. The dorsal surface of the  
176 neural spine is vascularized. In anterior and posterior views, the neural arch shows an  
177 extensive medial sulcus. The neural canal is heart-shaped in cross-section with its dorsal  
178 margin receiving a ventrally projecting lamina at the level of the neural spine. The anterior  
179 extent of the prezygapophyses is almost in line with the anterior margin of the centrum,  
180 whereas the posterior extent of the postzygapophyses project far beyond the posterior margin  
181 of the centrum. The articular faces on the pre- and postzygapophyses are obliquely oriented  
182 with respect to the neural spine. The laminar transverse processes are short and comparable in  
183 dimensions to the centrum width, but their anteroposterior length is slightly shorter than the  
184 length of the centrum. In dorsal view, the distal margin of the transverse processes is unequal  
185 with a parapophysis shorter than the diapophysis.

186

187 *Sacrum*.—The anterior part of the first sacral vertebra is connected to the rest of the vertebral  
188 column and is partly embedded in the sediment. The second sacral vertebra detached during  
189 preparation, revealing a strong sutural surface. Much like *Hyposaurus* (Schwarz et al., 2006),  
190 the two sacral vertebrae appear to have not fused together, whereas these bones are fused in  
191 *Dyrosaurus* sp. (Schwarz et al., 2006). The anterior and posterior surfaces of the sacral centra  
192 are ovoid in outline, being wider than tall. The sutural surface of the anterior margin of the  
193 second sacral vertebra is complex and presents two parallel sulci along its midline (Fig. 4.6).  
194 Such similar sulci have previously been reported on the posterior, but not anterior, surface of  
195 the second sacral vertebra of *D. phosphaticus* and of *Hyposaurus* (YPM 753) by Schwarz et  
196 al. (2006). The second sacral vertebra can be observed in ventral aspect and no obvious  
197 shallow sulcus is observed here close to its anterior margin, contrary to the condition in  
198 *Dyrosaurus* sp. and cf. *Rhabdognathus* (Schwarz et al. 2006). As observed in dorsal view, the  
199 first and second sacral ribs are hourglass shaped. The sacral ribs of the first sacral vertebra are

200 about twice as long as the ribs of the second sacral vertebra (Figs. 3, 4.8), as is commonly  
201 observed among crocodylians. The first sacral rib occupies the anterior two thirds of the  
202 lateral surface of the centrum length, whereas the second sacral rib occupies the entire length  
203 of the centrum. On the first sacral vertebra, as observed in posterior view, a distinct circular  
204 fossa is visible at the sutural intersection of the neural arch, centrum and sacral rib. As in  
205 *Dyrosaurus* sp., the proximal insertion of the sacral rib for the second sacral vertebra is  
206 restricted to the corpus of the second sacral centrum (Schwarz et al. 2006) and unlike the  
207 condition in *Rhabdognathus* where the sacral rib overlaps on the centrum of the first caudal  
208 vertebra (Langston, 1995). The iliac symphyseal surface of the first rib does not exceed the  
209 anterior and posterior margins of the centrum. An anterolateral process is present as in  
210 *Dyrosaurus* sp. and cf. *Rhabdognathus* (Schwarz et al. 2006). In lateral view, the anterolateral  
211 process is thin and shows a concave articular surface; the posterior articular process of the rib  
212 is located more medially than the anterolateral process and is nearly as tall as the centrum  
213 height, being concave. The iliac symphyseal surface of the second sacral rib is slightly smaller  
214 and symmetrical to the first sacral rib, with a tall anterior surface and a thin posterior process.  
215 This iliac symphyseal surface exceeds slightly the posterior margin of the second sacral  
216 vertebra. The neural spines have weathered out in the described specimen.

217

218 *Caudal vertebrae*.—At least three caudal vertebrae were prepared out of the second block.  
219 Schwarz et al. (2006) described shallow bowl-shaped fossae on the anterior and posterior  
220 surfaces of the centrum of the caudal vertebrae. Here, such fossae are also observed on both  
221 thoracal and caudal vertebrae. The first caudal vertebra possesses no facets for the haemal  
222 arches (Figs. 4.14, 4.15). The second caudal vertebra possesses a facet for the haemal arches  
223 only on the posteroventral margin of its centrum (Figs. 4.19, 4.20). The third caudal vertebra  
224 possesses articular facets for the haemal arches both on the anteroventral and posteroventral

225 margins of its centrum (Fig. 4.21). This pattern of articulation between caudal centra and  
226 haemal arches differs from that described in *Dyrosaurus* sp. and cf. *Rhabdognathus* where the  
227 facet is present on the anteroventral surface from the second vertebra (Langston, 1995;  
228 Schwarz et al. 2006). It is, however, similar to *Congosaurus bequaerti* where this pattern of  
229 articulation starts from the third caudal vertebra (Schwarz et al. 2006). The first caudal  
230 vertebra has proportions of the centrum similar to the sacral vertebrae; from the second caudal  
231 vertebra, the centrum is longer than high with a quadrangular outline of the anterior and  
232 posterior margins; the posteroventral margin is also distinctly lowered than the anteroventral  
233 margin (compare Figs. 4.15, 4.20, 4.21).

234

235 *Ischium*.—The nearly complete right ischium is preserved in connection with the ilium in the  
236 main block (Figs. 3, 5, 5.7, 5.8, 5.9). The left ischium was isolated during preparation; it is  
237 eroded on its medial surface and misses its distal blade (Fig. 5.5, 5.6). The ischium measures  
238 about 100 mm in its maximum length, the blade representing about 70 percent of this length.  
239 The anterior and posterior margins of the blade are parallel and do not seem to expand  
240 significantly near the distal end of the blade, but this area is damaged. The medial surface of  
241 the right element is smooth and gently concave. The broken blade of the left element shows  
242 that the anterior margin is thinner than the posterior margin.

243         The proximal portion of the ischium shows the distinct acetabular foramen, which is  
244 bordered anteriorly by the forward-projecting anterior iliac process and posteriorly by the  
245 posterior iliac process. The anterior margin of the anterior iliac process is vertical and bears in  
246 its lower half an anteriorly oriented pubic process. The pubic process sends a short spiny  
247 ventral projection, resulting in a markedly concave margin. The facet for accommodating the  
248 ilium is flat and obliquely oriented. On the posterior iliac process, the dorsal facet for the  
249 ilium is concave, pierced by foramina and bordered by a thin bony rim; its lateral portion is

250 shorter than the medial portion, matching the triangular outline of the connecting ilium.  
251 Anterior to this facet, there is a flat surface that descends within the acetabulum and  
252 corresponds to the articular area for the femoral head (in lateral view, this gives to the  
253 posterior iliac process, a truncated outline). The anterior region of the acetabulum, at the level  
254 of the anterior iliac process, is anterolaterally depressed. In the same area but near the medial  
255 border, the margin is faintly crested. As seen in posterior view, the posterior iliac process  
256 possesses a short but distinct muscle scar near its proximal end (Fig. 5.9)

257

258 *Ilium*.—The right ilium measures 67 mm in its maximum height, is connected to the ischium  
259 in the main block (Fig. 3) but is heavily damaged. The left ilium is complete, although its  
260 internal surface is slightly eroded (Figs. 5.1, 5.2, 5.3, 5.4). The anterior process of the ilium is  
261 massive and projects dorsally whereas it projects anteriorly in *Congosaurus*. Just below it, the  
262 supraacetabular crest is well defined as a thin ridge delimiting the anterodorsal outer margin  
263 of the acetabulum. The anterior peduncle of the ilium is mediolaterally thin with the ischial  
264 facet, although eroded, facing ventromedially. The posterior peduncle is massive, D-shaped in  
265 ventral view and the ischial facet is here facing fully ventrally. The acetabulum occupies  
266 about one third of the lateral surface of the bone and nearly reaches the dorsal surface. The  
267 acetabular foramen is large and occupies more space than in *Congosaurus*. The posterior  
268 blade of the ilium is concave on its lateral surface, and in dorsal view, the ilium is sigmoidal.  
269 Except near the anterior spine, the dorsal margin of the blade is widely convex (not wasp-  
270 waisted), and is indented for muscle attachment. The posteroventral margin of the blade bears  
271 strong indentations, especially on the medial surface. The dorsal and ventral margins of the  
272 blade merges into a short peduncle projecting posteriorly. The ventral margin between the  
273 posterior peduncle and the strong indented area is smooth and concave on the lateral side.

274



275 *Femur*.—The right femur preserves much of the femoral head and a proximal portion of the  
276 shaft. The left femur is complete and partly connected to the block (Fig. 6). The femur has a  
277 general sigmoid curvature with a strongly medially bent femoral head, a thick shaft, ovoid in  
278 section and terminated distally with a pair of massive and ventrally directed condyles. In  
279 proximal view, the femoral head is ovoid being wider than high. On its dorsal surface, an  
280 anomalous depression filled with sediment is visible (star in Fig. 6.2). The medial most  
281 outline of the femoral head is distinctly set apart from the main shaft as originally observed in  
282 *Hyposaurus* (Troxell, 1925). The ventral margin close to the femoral head possesses a small  
283 but distinct knob, which sits on the proximal part of an acute ridge that marks the  
284 ventrolateral margin of the femoral head. This ridge merges with the lateral margin of the  
285 shaft, which is straight and also acute until the level of the fourth trochanter. Dorsal to this  
286 ridge, the lateral surface of the femur bears a large depressed zone (Figs. 6.2, 6.7) but is also  
287 heavily weathered. At this level, a process is visible on the dorsal surface (Fig. 6.2, 6.7). The  
288 fourth trochanter is prominent and is projecting ventrally. Dorsal to it, a shallow ovoid surface  
289 corresponds to the caudofemoral flange, which faces fully medially. From this level, and as  
290 seen in medial or lateral view, the shaft gently bends ventrally with two massive condyles that  
291 project strongly ventrally toward the distal extremity of the shaft. The distal portion of the  
292 shaft is largely hidden by an osteoderm. In ventral view, a wide intercondylar fossa is present  
293 (Fig. 6.4), which separates a narrow medial condyle from a more massive lateral condyle (Fig.  
294 6.5). The medial surface of the medial condyle is flat and the condyle expands as a narrow  
295 outgrowth dorsally, giving to the dorsal surface of the femur an uneven outline. The lateral  
296 condyle is sturdy and possesses a slight projection on its convex lateral margin.

297

298 *Tibia*.—The proximal epiphysis of a left tibia is preserved and is bent from the shaft in a  
299 posteromedial direction (Fig. 6). The proximal end is 45 mm mediolaterally by 41 mm

300 anteroposteriorly, and the oval shaft, as preserved is much thinner being 20 mm  
301 mediolaterally by 18 mm anteroposteriorly. It strongly resembles another indeterminate  
302 dyrosaurid tibia described from Pakistan (Fig. 9 in Storrs, 1986). Its proximal articular surface  
303 is deeply depressed in the middle as in *Congosaurus bequaerti* (Schwarz et al. 2006). This  
304 surface possesses two articular facets that are continuous on the medial and posterior margins.  
305 Both facets are separated by a marked posterior cleft (Figs. 6.9, 6.11). The medial articular  
306 facet is about twice larger and markedly concave in comparison to the posterior one. The  
307 anterior margin of the articular surface is straight and does not show an articular facet. In  
308 anterior view, the medial facet is angled relative to the rest of the proximal margin of the  
309 tibia, giving to the shaft a strongly concave medial margin. Conversely, the lateral margin is  
310 straight and nearly perpendicular with the articular surface (Fig. 6.10). Here, the cnemial crest  
311 is not particularly standing out, being distinct only in its most proximal portion where a step-  
312 like process accommodates the proximal margin of the fibula (Figs. 6.9, 6.11). A 9 mm long  
313 ovoid depression is observed on the anterolateral corner of the tibia (Fig. 6.8), as previously  
314 observed in the tibia of *Guarinisuchus munizi* (Sena et al. 2017, fig. 3M).

315

316 *Calcaneum*.—A complete left calcaneum is preserved (Fig. 7). The anterior ball is  
317 demarcated from the posterior tuber by an extensive medial channel that runs along most of  
318 the medial surface of the posterior tuber, just posterior to the medial flange. As observed in  
319 medial view, the calcaneal socket, which accommodates the astragalar peg, is deep. Posterior  
320 to it, the anterior face of the medial flange is vast and has a gently concave margin that may  
321 have limited rotation of the astragalar peg. The anterior ball is convex in its anterior and  
322 dorsal parts, and flat in its plantar margin as in extant crocodylians. From a lateral view, the  
323 anterior ball shows a vertical wall. Ventrally, it is well demarcated from the posterior tuber by

324 a deep lateroventral channel. The posterior tuber shows on its posterior margin a shallow and  
325 rugose groove.

326

327 *Radiale*.—The right radiale is preserved but misses most of its proximal portion (Figs. 8.1,  
328 8.2) and is heavily eroded on its posterior surface. A portion of the facet for the ulnare is  
329 preserved on the lateral margin and distinctly projects laterally from the proximal portion of  
330 the bone. The shaft is wasp-waisted. The distal articular surface is concave.

331

332 *Metacarpals*.—Three metacarpals are preserved. The right metacarpal I (Figs. 8.3–8.6) is 35  
333 mm long and possesses a straight shaft with proximal and distal portions being nearly as wide  
334 and in line with each other. On the proximoventral edge of the bone, a large and wider than  
335 long depression is observed on a lateral projection lateral (Figs. 8.3, 8.5) to the main shaft.  
336 The proximal articular surface is marked by a distinct dorsoventral sulcus (Fig. 8.3). The  
337 distal surface bears two condyles, each possessing deep pits on their medial and lateral  
338 surfaces. The right (Figs. 8.7, 8.10) and left metacarpals II or III are preserved. Each bone is  
339 41 mm long with a rod-like shaft and a flared and convex proximal margin. In dorsal view,  
340 the proximal epiphysis is rugose and projects briefly along the lateral half of the shaft (rp in  
341 Fig. 8.8). Immediately medial to it, an extensive flat facet is inclined toward the medial  
342 margin (Fig. 8.8). In palmar view (Fig. 8.9), a wide shallow depression is delimited by a  
343 proximomedial bony ridge. The shaft has a rotated axis with the distal condyles  
344 approximately 90° from the proximal portion (Fig. 8.10), as observed in *Congosaurus* and  
345 *Hyposaurus* (Schwarz et al. 2006). The distal condyles are well individualized and possess  
346 marked pits on their medial and lateral edges. The right or left metacarpal V (Fig. 8.11) is  
347 partly weathered at both extremities, has a rod-like shaft and is 38 mm long.

348

349 *Phalanx*.—A single carpal phalanx is preserved (Figs. 8.12–8.15). It is 18 mm long, wasp-  
350 waisted with a proximal portion nearly as wide as the distal portion. In palmar view, the distal  
351 condyles are well demarcated by a marked intercondylar groove.

352

353 *Osteoderms*.—Several osteoderms are associated with the skeleton (Figs. 3, 9). They are all  
354 displaced and therefore no clear configuration of the dorsal or ventral shield can be deduced.  
355 All dorsal osteoderms lack an external keel (Figs. 3, 9.1, 9.2) a condition identical to that of  
356 various hyposaurine dyrosaurids (Schwarz et al. 2006). The dorsal osteoderms attributed to  
357 the paravertebral shield are square to trapezoidal in outline being slightly wider than long.  
358 Their anterior and posterior margins are slightly vaulted and thin in comparison to the thick  
359 median body. As observed in dorsal view, the anterior margin is concave in its median portion  
360 and its dorsal surface shows a smooth facet covering the entire width of the osteoderm. A  
361 short anterolateral process emerges from this smooth facet. Just posterior to the anterior facet,  
362 a row of nearly circular and well-aligned cupules is present. This row is distinct from the rest  
363 of the dorsal surface, which is slightly raised and ornamented with slightly larger and  
364 randomly distributed cupules. The posterior margin is gently convex. The median and lateral  
365 margins are nearly straight. As for the lateral margin, some incipient indentations are  
366 sometime visible and may have contacted a more lateral osteoderm. The ventral surface is  
367 perfectly smooth and sometime exhibits a few foramina.

368         Isolated ventral osteoderms were also identified and present a wide V-shaped margin  
369 and a peg on the opposite margin (Fig. 9.3). Part of the ventral shield is still articulated but  
370 sediment hides much of the organization. A suite of four articulated osteoderms is visible on  
371 one side of the specimen and is positioned ventral to the gastralium (Figs. 9.4, 9.5). Ventral  
372 osteoderms are smaller than dorsal osteoderms and are distinctly wider than long. Their  
373 margins possess interdigitations for suturing to other osteoderms. The medial margin is

374 strongly concave whereas the lateral margin possesses a pointed process that strongly projects  
375 laterally (Fig. 9.3). The external surface is ornamented with a few barely visible shallow  
376 circular pits, which do not spread near the margins of the osteoderm. Those ventral  
377 osteoderms are gently vaulted, being nearly flat.

378

379 *Ribs, gastralialia and other structures.*—Several elongated elements are preserved in the main  
380 block and are intertwined with the locally disarticulated skeletal parts. Their encasing in the  
381 sediment and the hiding of articular portions render their identification tentative. Thin,  
382 straight rod-like structures with a perfectly circular cross section spread to the left of the  
383 thoracic region from the eleventh to thirteenth thoracal vertebrae (Fig. 3). They are less than 5  
384 mm in diameter. Thicker elements, about 10 mm in diameter, correspond to ribs that are also  
385 scattered in this area and offer sigmoid outlines. Another type of morphology is represented  
386 by two nearly complete structures observed in this same area (Fig. 3) as well as by some  
387 fragments recovered during acid preparation (Fig. 10). These are wide, flat on one side,  
388 convex on the other, and gently curved rib-like structures with an articular facet on one end.  
389 Remarkably, they display numerous ovoid pits on both sides that range in diameter from 1 to  
390 3 mm. These pits are similar to those observed on the external surface of osteoderms.

391

392 *Gastroliths.*—At least five pebbles (1 to 3 cm large) are scattered adjacent to the thirteenth  
393 thoracal vertebra (Fig. 3). Another one is observed near the eleventh vertebra. Another one  
394 was freed from the block. The nature of these stones is pure quartz and therefore different to  
395 the embedding carbonate matrix. The pebbles are not perfectly rounded and possess smooth  
396 angular edges.

397

398 **Discussion**

400 *Taxonomic identification and comparison.*—The material was initially identified as a suite of  
401 vertebrae and limb bones belonging to the genus *Dyrosaurus* in Arambourg and Joleaud  
402 (1943). The unprepared block permitted observations of weathered bone surface only (Fig. 3),  
403 and although no details are given in Arambourg and Joleaud (1943), some osteoderms were  
404 obviously identifiable. Since Thevenin (1911a,b), dyrosaurids were recognized as part of the  
405 Crocodylia with ample descriptions available, for example *Hyposaurus* (Troxell, 1925) or  
406 *Congosaurus* (Swinton, 1950). As noted by Brochu et al. (2002), dyrosaurid taxonomy has  
407 been largely established on characters of the rostrum and lower jaw. Most recently erected  
408 dyrosaurid species have also been established on the basis of complete skulls (Barbosa et al.  
409 2008; Hastings et al. 2010; 2011; 2015). Isolated skull remains or partially articulated  
410 postcranial elements are difficult to assign to a given genus or species, despite extensive  
411 description of the postcranial anatomy for Hyposaurinae (e.g. Schwarz et al. 2006). Although  
412 the presently described skeleton from Senegal, MHNT.PAL.2012.0.45, lacks those diagnostic  
413 characters established on cranial morphology, it is assigned to the Dyrosauridae on the basis  
414 of the following postcranial characters in association: (1) amphiplatyan vertebral centra; (2)  
415 femoral head being twisted along the shaft by about 30° from the distal condyles; (3) femur  
416 with strong beak-like projection of the proximal head (Troxell, 1925); (4) strong posterior  
417 cleft on the proximal surface of the tibia; (5) ischium with forward-projecting anterior iliac  
418 process; (6) elongated anterior ball and narrow posterior tuber of the calcaneum; (7) absence  
419 of external keel on dorsal osteoderms; (8) presence of ventral osteoderms being twice as wide  
420 as long. A last character, (9) deeply pitted rib-like structures, may not be used in the diagnosis  
421 of Dyrosauridae, but is discussed herein due to a single previous report in a dyrosaurid  
422 specimen. These characters are detailed below and anatomical comparisons are made with  
423 *Alligator mississippiensis*, which represents an extant eusuchian.

424           Amphiplatyan vertebrae widely occur in non-eusuchian crocodylomorphs. In the post-  
425 Cretaceous fossil record, only two groups of crocodylomorphs possess such a type of  
426 vertebrae: Sebecosuchia represented by taxa living exclusively in the continental  
427 environment, and Dyrosauridae sharing the marine habitat with longirostrine eusuchians, for  
428 which vertebral centra cannot be confounded due to their procoelous intervertebral  
429 articulation.

430           The femur from Poponguine is identical to that of any dyrosaurid in possessing a  
431 beak-like projecting head. As such, a right femur with a “strong beak-like curve of the head  
432 and the weak fourth trochanter” was described in *Hyposaurus* (Troxell, 1925). The right  
433 femur of *Congosaurus bequaerti* was described by Jouve and Schwarz (2004) and by  
434 Schwarz et al. (2006). A flattened femur is known for *Acherontisuchus guajiraensis*, for  
435 which “the fourth trochanter is large for the family and the paratrochanteric fossa is deeper  
436 than the shallow pit seen in *C. bequaerti*” (Hastings et al. 2011). Sena et al. (2017) described  
437 the proximal portion of a right femur for *Guarinisuchus munizi*. A right dyrosaurid femur was  
438 described by Arambourg (1952), who noticed that the proximal head is in line with the distal  
439 condyles (Arambourg, 1952, fig. 62), a condition also identified in the specimen from  
440 Poponguine (measuring about 30°). On the other hand, the proximal head is arranged  
441 perpendicular to the distal condyles in *Congosaurus bequaerti* and modern crocodylians  
442 (Arambourg, 1952; Schwarz et al. 2006 report 140° in *Congosaurus bequaerti*). According to  
443 previous works, the morphology of the femur is variable within the family and the specimen  
444 from Poponguine most resembles *Hyposaurus* in sharing with it a weakly developed fourth  
445 trochanter and with the dyrosaurid femur described by Arambourg (1952) in sharing with it a  
446 femoral head in line with the distal condyles.

447           The tibia of dyrosaurids is distinctive in possessing a marked posterior cleft as well as  
448 a strong embayment underlining the cnemial crest, both features being well expressed at the

449 proximal extremity of the bone. Although these features are present in *Alligator* too, they are  
450 not as marked. Overall, the tibia of MHNT.PAL.2012.0.45 is similar to other tibia described  
451 for dyrosaurids (Langston, 1995; Schwarz et al. 2006; Sena et al., 2017).

452 The acetabular foramen is completely enclosed by both the ischium and the ilium,  
453 which contribute to two-third and one third of it, respectively. No clear difference is  
454 noticeable between the Senegalese ilium and that of extant eusuchians. The ischium of  
455 MHNT.PAL.2012.0.45 is comparable to other dyrosaurid ischia as described for *Hyposaurus*  
456 (Troxell, 1925, fig. 13), for an indeterminate Pakistanese dyrosaurid (Storrs, 1986), for  
457 *Dyrosaurus* sp. (Schwarz et al. 2006), for *Dyrosaurus maghribensis* (Jouve et al. 2006) and  
458 for *Acherontisuchus guajiraensis* (Hastings et al. 2011), which all display a strongly  
459 projecting anterior ischium process, an overhanging projection of the ischium process that  
460 holds the dorsoventrally elongate facet for the pubis, a narrow to blade-like shaft with nearly  
461 parallel edges and a distal process that does not particularly widen distally. These characters  
462 are also visible in some notosuchians such as *Yacarerani boliviensis* (Leardi et al., 2015, fig.  
463 13) or *Stratiotosuchus maxhechti* (Riff and Kellner, 2011, fig. 12). This is contrary to the  
464 situation observed in thalattosuchians (e.g. Herrera et al. 2013, fig. 5), in extant eusuchians  
465 (e.g. Mook, 1921, fig. 17) or in coelognathosuchians such as the pholidosaurids *Terminonaris*  
466 *robusta* (Fig.7 in Wu et al. 2001), *Oceanosuchus boecensis* (Hua et al. 2007, fig. 4) or the  
467 goniopholidid *Anteophthalmosuchus* (Martin et al. 2016, fig. 15). The shaft in the continuity  
468 of the ischiac blade of MHNT.PAL.2012.0.45 is wide but not as wide as that of *Dyrosaurus*  
469 sp. (Schwarz et al. 2006) and the overhanging anterior ischiac process is not as much  
470 constricted against the shaft as that seen in *Dyrosaurus* sp. (compare with Schwarz et al.  
471 2006, fig. 10C).

472 The only other described calcaneum for a dyrosaurid belongs to *Rhabdognathus* sp.  
473 from the Paleocene of Saudi Arabia (Storrs, 1995), which is preserved in connection with an



474 astragalus and is similar in its proportions to MHNT.PAL.2012.0.45. The calcaneum of  
475 MHNT.PAL.2012.0.45 differs from that of the extant *Alligator* in possessing a longer than  
476 wide anterior ball and a taller than wide posterior tuber. The calcaneum of *Alligator* possesses  
477 a lateral projection arising from the lateral surface of the posterior tuber; in the dyrosaurid  
478 MHNT.PAL.2012.0.45, this process is absent. All other characters described in  
479 MHNT.PAL.2012.0.45 are similar to that of *Alligator*.

480         The dermal armor of dyrosaurids is composed of both a dorsal and a ventral shield  
481 (e.g. Schwarz et al. 2006), and the specimen from Poponguine preserves disarticulated dorsal  
482 elements as well as some ventral elements in articulation (Fig. 9). The dorsal elements of  
483 MHNT.PAL.2012.0.45 are quadrangular and lack a median keel, a condition seemingly  
484 unique to Dyrosauridae (Schwarz et al. 2006; Martin, 2015). Among Dyrosauridae, the  
485 osteoderms of *Anthracosuchus balrogus* are different from those described here or from any  
486 other dyrosaurids in being thick, unpitted and devoid of an imbricating surface (Hastings et  
487 al., 2015). Thick osteoderms have also been described in *Congosaurus bequaerti* (Jouve and  
488 Schwarz, 2004; Schwarz et al., 2006) but these are not as thick as in *A. balrogus*. The dorsal  
489 osteoderms of the median series in *D. maghribiensis* exhibit a laterally projecting peg on their  
490 anterolateral margin (Jouve et al., 2006). None of these characters are seen in the Poponguine  
491 specimen, which osteoderms morphology is typical of hyposaurine taxa (Schwarz et al.,  
492 2006). As stated previously and contrary to Dyrosauridae, the osteoderms of Goniopholididae  
493 and Pholidosauridae share a wider than long morphology and the possession of an  
494 anterolateral keel (Martin, 2015). In MHNT.PAL.2012.0.45, a series of four elements of the  
495 ventral shield are preserved in articulation (Figs. 9.4, 9.5). These wider than long elements are  
496 not comparable to the hexagonal ventral elements described in goniopholidids (Martin et al.  
497 2016) or in the pholidosaurid *Terminonaris robusta* (Wu et al. 2001).

498 Massive, flat and deeply pitted rib-like structures are present in the Poponguine  
499 specimen (Fig. 10). Similar bony structures were briefly described and figured for  
500 *Rhabdognathus* sp. by Langston (1995) and identified as costal cartilages. At present, these  
501 elements cannot be identified with certainty. Their morphology is intriguing and attention  
502 should be kept in the future on such elements, whether they could be pathological or more  
503 widespread among dyrosaurids.

504 The present description of dyrosaurid postcranial elements, although not permitting an  
505 identification beyond Dyrosauridae indet., brings some additional knowledge on the  
506 morphology of this particular group with details often obscured by compression or  
507 articulation when relatively complete specimens are available. A close relationship between  
508 dyrosaurids and outgroup taxa such as the Pholidosauridae, Thalattosuchia or Gavialoidea has  
509 often been proposed in phylogenetic works and problems related to branch attraction in  
510 phylogenies have been discussed (Pol and Gasparini, 2009; Martin et al. 2016). Updating  
511 phylogenetic codings with new morphological details as those presented here, may help tease  
512 apart such problems. For example, the morphology of osteoderms, both dorsal and ventral,  
513 differs between these groups of longirostrine forms. Current efforts of describing the  
514 postcranial anatomy of various crocodylomorph lineages (e.g. Pol et al. 2011; Herrera et al.  
515 2013; Leardi et al. 2015; Martin et al. 2016) will, among other phylogenetic problems, permit  
516 to identify what characters are independent of longirostry.

517

518 *Presence of gastroliths.*—The presence and significance of gastroliths or stomach stones in  
519 marine reptiles (Taylor, 1993) and more generally among vertebrates (Wings, 2007) has been  
520 discussed at length. Denton et al. (1997) interpreted the presence of gastroliths in the  
521 stomachal area of the dyrosaurid *Hyposaurus* to serve as ballasts, both for diving or to prevent  
522 rolling in the waves. Our observations on the Senegalese specimen does not support this view

523 because despite their sizeable dimensions, the total mass of the gastroliths is estimated at  
524 about 100 grams and is insufficient to account for a role as ballast in comparison to the total  
525 weight of the animal. Indeed, the animal total weight cannot be precisely reconstructed here  
526 but may have certainly surpassed 50 kg, which is a highly imprecise estimation. It is  
527 nevertheless highly unlikely that 0.2% of this weight would have a ballast effect.  
528 Furthermore, previous studies including crocodiles fed experimentally with stones and  
529 experimental models revealed that gastrolith masses accounting for less than 2% of body  
530 mass do not play a role in buoyancy or stability because the studied crocodiles compensate for  
531 added weight by augmenting lung volume (Kirshner, 1985; Henderson, 2003; Grigg and  
532 Kirshner, 2015).

533         One hypothesis that requires further attention invokes an improvement of dive time  
534 thanks to gastrolith weight due to the indirect consequence of increasing lung volume  
535 (Seymour, 1982 and discussion in Gregg and Kirshner 2015). Observations on extant  
536 crocodiles have shown that pebbles are deliberately swallowed with some animals going into  
537 specific areas to collect gastroliths (Cott, 1961). The gastroliths preserved in the stomachal  
538 cavity of MHNT.PAL.2012.0.45 are clearly allochthonous, the depositional environment  
539 where the specimen was recovered consisting exclusively of fine-grained limestone.  
540 Dyrosaurids had enhanced capacities for swimming (Schwarz et al. 2006) and may have  
541 travelled long oceanic distances. Therefore, the origin of the gastroliths is unknown and their  
542 precise function, if any, remain unknown.

543

544 *Fossil record of Danian dyrosaurids.*—The Senegalese dyrosaurid described in the present  
545 work adds to the limited record of Danian dyrosaurids from Africa. Originally presented as  
546 Montian (an equivalent to the Selandian) by Buffetaut (1979), the taxon *Atlantosuchus*  
547 *coupatezi* from Sidi Chenane in the Oulad Abdoun Basin of Morocco has been attributed a

548 Danian age based on the selachian assemblage recovered in the sedimentary matrix (Jouve et  
549 al. 2008). *Atlantosuchus coupatezi* is known from a mandibular symphysis (Buffetaut, 1979)  
550 and from skull elements including a nearly complete skull as well as some cervical vertebrae  
551 (Jouve et al. 2008). There is no anatomical overlap with the material from Poponguine so no  
552 comparison can be made. Another African dyrosaurid of possible Danian age is  
553 *Phosphatosaurus* sp. reported on the basis of a portion of symphysis from Gadamata in the  
554 Adar Douthi of Niger as well as from fragmentary remains collected by René Lavocat in  
555 Mali (Buffetaut, 1978a). Again, no anatomical overlap exists with the Senegalese specimen.

556 At about the same latitude as Senegal, dyrosaurids are also known from Danian  
557 deposits in Brazil (Cope, 1886) and from the early Paleocene of Bolivia (Buffetaut, 1991).  
558 Given the proximity of coastlines during the Eocene of the recently opened North Atlantic  
559 Ocean, faunal exchanges between these two provinces may have been easily covered by  
560 marine dwelling organisms such as dyrosaurids. Reports from the Danian of Brazil including  
561 *Hyposaurus derbianus* (Cope, 1886) concerned fragmentary specimens from the Maria  
562 Farinha Formation (see review in Hastings et al. 2010). *Guarinisuchus munizi* is known from  
563 a complete skull and few postcranial elements, also from the Maria Farinha Formation of  
564 Brazil (Barbosa et al. 2008) and recently, other mandibular and cranial remains have been  
565 assigned to this species (Sena et al. 2017).

566 Finally, Danian material from Alabama, USA has been revised and assigned to  
567 *Hyposaurus rogersii* by Denton et al. (1997). The material includes various vertebrae,  
568 osteoderms, an ischium, part of a femur and other postcranial fragments (see list in Denton et  
569 al. 1997). Although anatomical overlap with the Poponguine material exists, the Alabama  
570 specimens have not been described in detail. Moreover, their attribution to *Hyposaurus*  
571 *rogersii* needs to be re-evaluated by emending the diagnosis of the species with postcranial

572 material. Presently, the most diagnostic specimen of the species comprises one complete skull  
573 from the Maastrichtian of New Jersey (Buffetaut, 1976; Denton et al. 1997).

574 A revision of *H. rogersii* is potentially important to better understand dyrosaurid  
575 survival across the K/Pg boundary. As presently understood, four species of dyrosaurids  
576 (perhaps five if *Phosphatosaurus* is included) are known from Danian deposits worldwide  
577 and include *Atlantosuchus coupatezi*, *Guarinisuchus munizi*, *Hyposaurus derbianus* and  
578 *Hyposaurus rogersii*. Previous studies have merged post-K/Pg dyrosaurid diversity (i.e.  
579 Danian, Selandian, Thanetian) in a whole Paleocene time bin (e.g. Jouve et al. 2008), which  
580 may overestimate diversity counts and not reflect the effects of the K/Pg mass extinction on  
581 dyrosaurid survival directly after the event. Therefore, focusing on the Danian diversity  
582 through collecting efforts will certainly improve this aspect. Jouve et al. (2008) and Barbosa  
583 et al. (2008) concurred with the idea that dyrosaurids may have been under competition with  
584 the diverse mosasaurs of the Maastrichtian. Whether the extinction of mosasaurs at the K/Pg  
585 boundary freed some ecological space for dyrosaurids during the Paleocene is possible but  
586 still untested (Martin et al. 2017). It is equally possible that dyrosaurid diversity only started  
587 to increase later in the Paleocene but admittedly, the dating constraints on the Paleocene  
588 dyrosaurid record remains imprecise, despite the availability of some stratigraphic studies,  
589 notably from Mali (Hill et al. 2008).

590

## 591 **Conclusions**

592

593 Although the early Paleocene marine deposits of Senegal are less fossiliferous with respect to  
594 vertebrate remains than other terrains in northern Africa such as the phosphate deposits of  
595 Morocco, they are potentially important for the fossil record of the Dyrosauridae and other  
596 marine reptiles that survived the end Cretaceous mass extinction events. The present

597 description of a partial dyrosaurid skeleton from Danian deposits adds to the limited record of  
598 dyrosaurids of that age worldwide. Thanks to its state of preservation, the specimen also  
599 provides an update on the postcranial morphology of the Dyrosauridae and therefore adds  
600 new insights into potential characters to consider in future phylogenies.

601

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603

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610

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799

800 FIGURE CAPTIONS

801

802 FIGURE 1—Location of the dyrosaurid specimen presented in this work. **(1)** Map of Senegal  
803 indicating the locality of Poponguine; **(2)** the Danian succession at Poponguine where the  
804 specimen was discovered as photographed by G. Labitte in the 1920s from Tessier (1952).

805

806 FIGURE 2—Planktonic foraminifers recovered from the sediment of MHNT.PAL.2012.0.45,  
807 except in **(2)**, which is from Toubab Dialaw. *Chiloguembelina morsei* (Kline, 1941) in **(1)**  
808 lateral view (PV4); **(2)** lateral view for comparison (TD90/4); **(3)** Apertural view (P88/34).  
809 *Morozovella cf. trinidadensis* (Bolli, 1957) in **(4)** umbilical (P88/23); **(5)** apertural (P88/23)  
810 and **(6)** spiral (P88/33) views. *Planorotalites compressa* (Plummer, 1926) in **(7)** spiral  
811 (P88/14), **(8)** umbilical (P88/14). *Morozovella inconstans* (Subbotina, 1953) in **(9)** spiral  
812 (P88/38) and **(10)** umbilical (P88/38) views. *Morozovella pseudobulloides* (Plummer, 1928)  
813 in **(11)** spiral (P88/10) and **(12)** spiral (P88/40) views.

814

815 FIGURE 3—Main block containing the partially articulated dyrosaurid skeleton  
816 MHNT.PAL.2012.0.45 from the Danian of Poponguine, Senegal, **(1)** before as indicated with  
817 the stipple area and **(2)** following preparation. Abbreviations: g=gastrolith; lf=left femur;  
818 lil=left ilium; lis=left ischium; ost=osteoderm; rf=right femur; ril=right ilium; ris=right  
819 ischium; rls=rib-like structures; c1–c4=caudal vertebrae; s1–s2=sacral vertebrae; t11–  
820 t15=thoracic vertebrae.

821

822 FIGURE 4—Selected vertebrae of MHNT.PAL.2012.0.45 from the Danian of Poponguine,  
823 Senegal. Thoracic vertebra #10 in **(1)** anterior; **(2)** posterior; **(3)** dorsal; **(4)** ventral and **(5)** left  
824 lateral views; sacral vertebra #2 in **(6)** anterior; **(7)** posterior; **(8)** dorsal; **(9)** ventral and **(10)**  
825 right lateral views; caudal vertebra #1 in **(11)** anterior; **(12)** posterior; **(13)** dorsal; **(14)** ventral  
826 and **(15)** left lateral views; caudal vertebra #2 in **(16)** anterior; **(17)** posterior; **(18)** dorsal; **(19)**  
827 ventral and **(20)** left lateral views; caudal vertebra #3 in **(21)** right lateral view. The black  
828 arrows indicate the position of haemal facets; the white arrow indicates the erosive lesion.

829

830 FIGURE 5—Elements of the sacrum of MHNT.PAL.2012.0.45 from the Danian of  
831 Poponguine, Senegal. Left ilium in **(1)** dorsal; **(2)** ventral; **(3)** lateral; **(4)** medial views. Left  
832 ischium in **(5)** dorsal and **(6)** lateral views. Right ischium and fragmentary right ilium in  
833 lateral view with **(7)** line drawing and **(8)** associated photograph; **(9)** posterior view.  
834 Abbreviations: af=acetabular foramen; afi=anterior facet for ilium; afis=anterior facet for  
835 ischium; afp=anterior facet for pubis; aip=anterior iliac process; ap=anterior process;  
836 fe=femur; ff=facet for femur; ib=ischiac blade; il=ilium; ost=osteoderm; pfi=posterior facet  
837 for ilium; pfis=posterior facet for ischium; pip=posterior iliac process; pp=posterior process;  
838 ps=posterior scar; sac=supraacetabular crest; s1=sacral vertebra 1.

839

840 FIGURE 6—The hind limb of MHNT.PAL.2012.0.45 from the Danian of Poponguine,  
841 Senegal. Left femur in **(1)** proximal view; **(2)** dorsal view of the proximal third portion; **(3)**  
842 ventral view of the proximal third portion; **(4)** ventral view of the distal end; **(5)** distal view;  
843 **(6)** medial and **(7)** lateral views. Left tibia in **(8)** lateral; **(9)** proximal; **(10)** anterior and **(11)**  
844 posterior views. Abbreviations: cff=caudofemoralis flange; cn=enemial crest; dep=depressed  
845 zone; lc=lateral condyle; k=knob; mc=medial condyle; ost=osteoderm; pcl=posterior cleft;  
846 proc=process; 4t=fourth trochanter.

847

848 FIGURE 7—The left calcaneum of MHNT.PAL.2012.0.45 from the Danian of Poponguine,  
849 Senegal in **(1)** medial; **(2)** anterior; **(3)** lateral; **(4)** posterior; **(5)** dorsal and **(6)** ventral views.  
850 Abbreviations: ab=anterior ball; cs=calcaneal socket; lvc=lateroventral channel; mc=medial  
851 channel; mf=medial flange; ptu=posterior tuber.

852

853 FIGURE 8—Elements of the manus of MHNT.PAL.2012.0.45 from the Danian of Poponguine,  
854 Senegal. Right radiale in *1*, anterior and *2*, distal views. Right metacarpal I in **(3)** proximal;  
855 **(4)** dorsal; **(5)** palmar and **(6)** distal views. Right metacarpal II or III in **(7)** proximal; **(8)**  
856 dorsal; **(9)** palmar and **(10)** distal views. **(11)** Metacarpal V in lateral or medial view. Phalanx  
857 in **(12)** proximal; **(13)** dorsal; **(14)** palmar and **(15)** distal views. Abbreviations: mf=medial  
858 facet; plf=proximolateral flange; uf=ulnare facet of radiale; vlp=ventrolateral projection;  
859 rp=rugose projection; sd=shallow depression. For proximal and distal views, the dorsal aspect  
860 is up.

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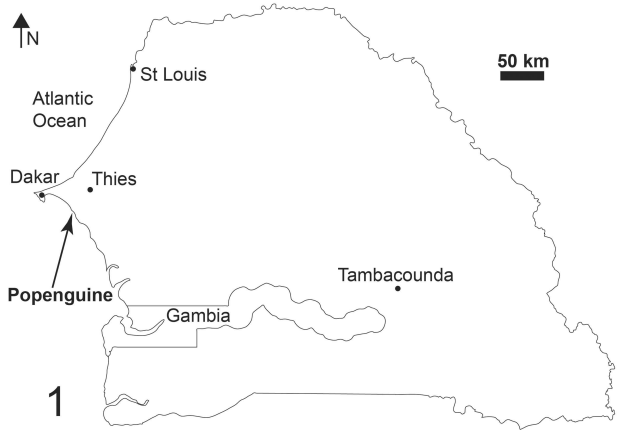
862 FIGURE 9—The osteoderms of MHNT.PAL.2012.0.45 from the Danian of Poponguine,  
863 Senegal. **(1, 2)** examples of dorsal elements and of a **(3)** ventral element with an arrow

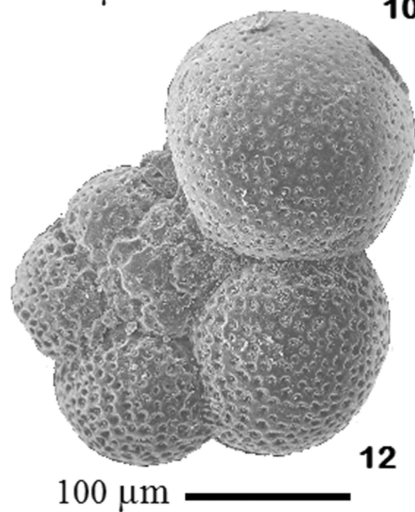
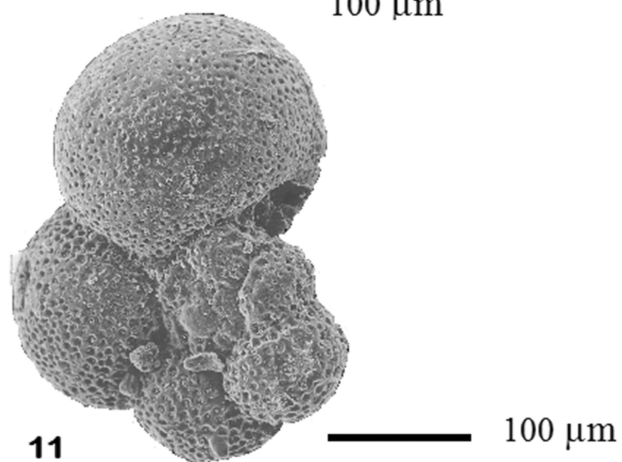
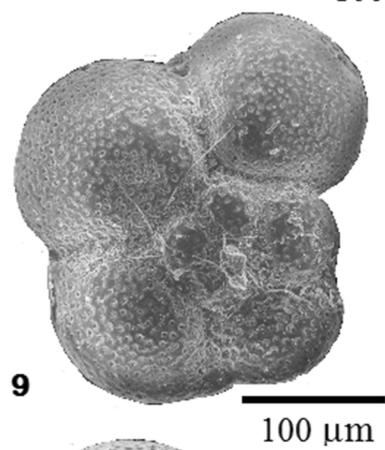
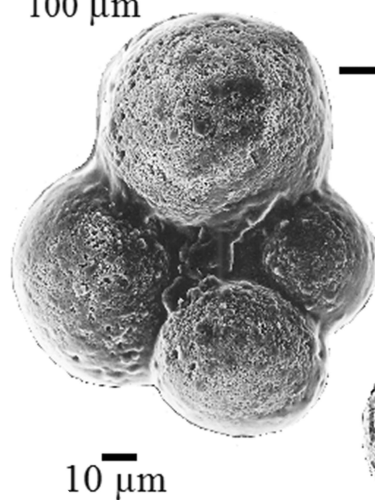
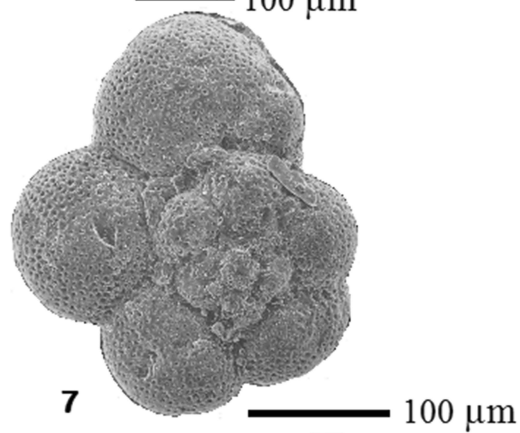
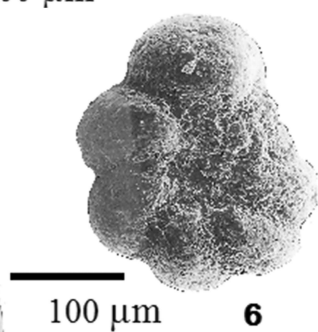
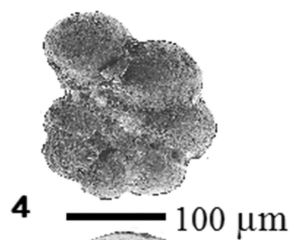
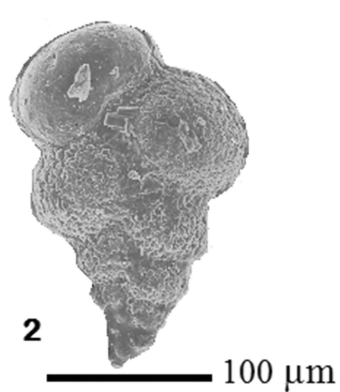


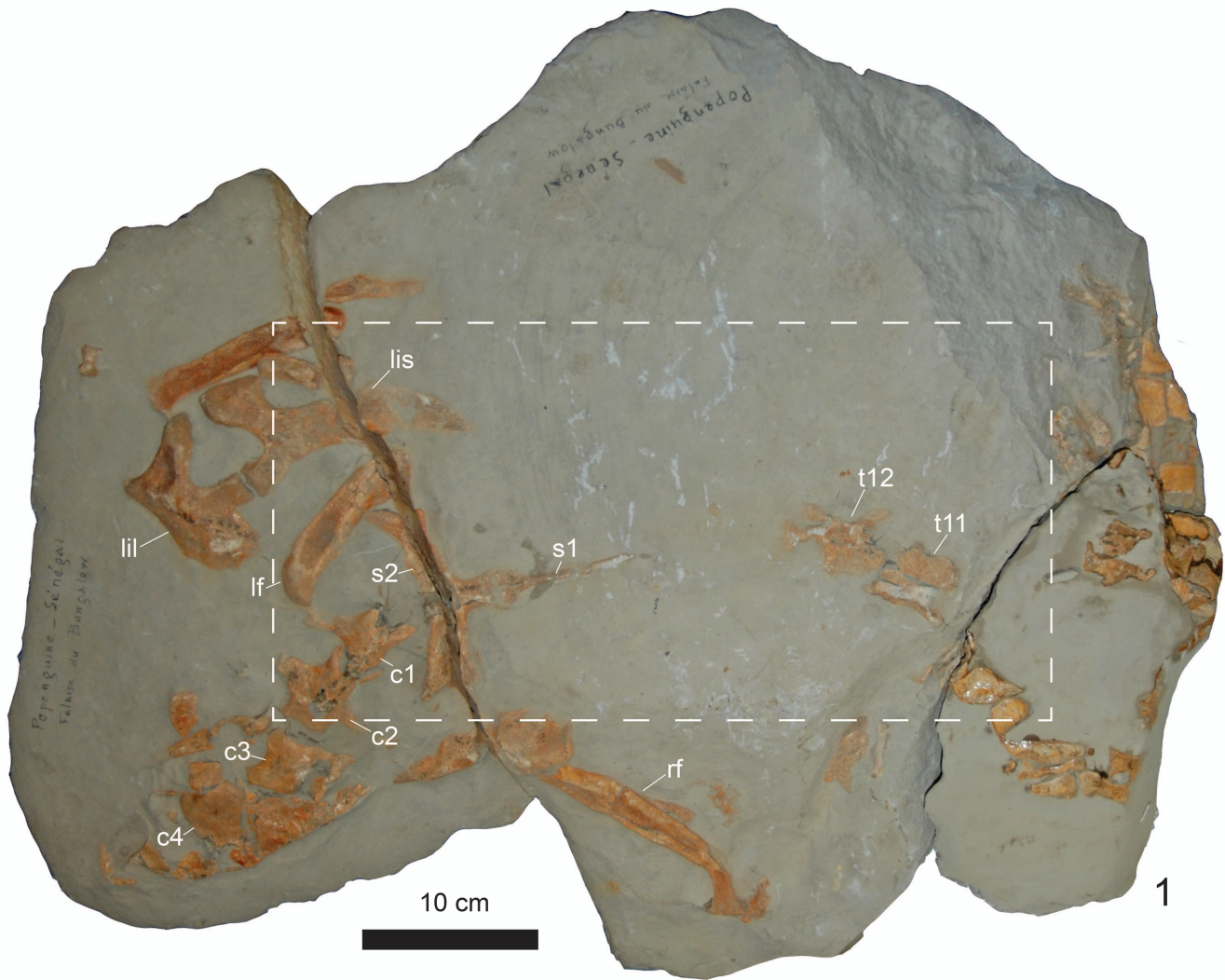
864 indicating the lateral expansion. Series of four osteoderms from the ventral shield preserving  
865 their original organization in **(4)** ventral and **(5)** lateral views.

866

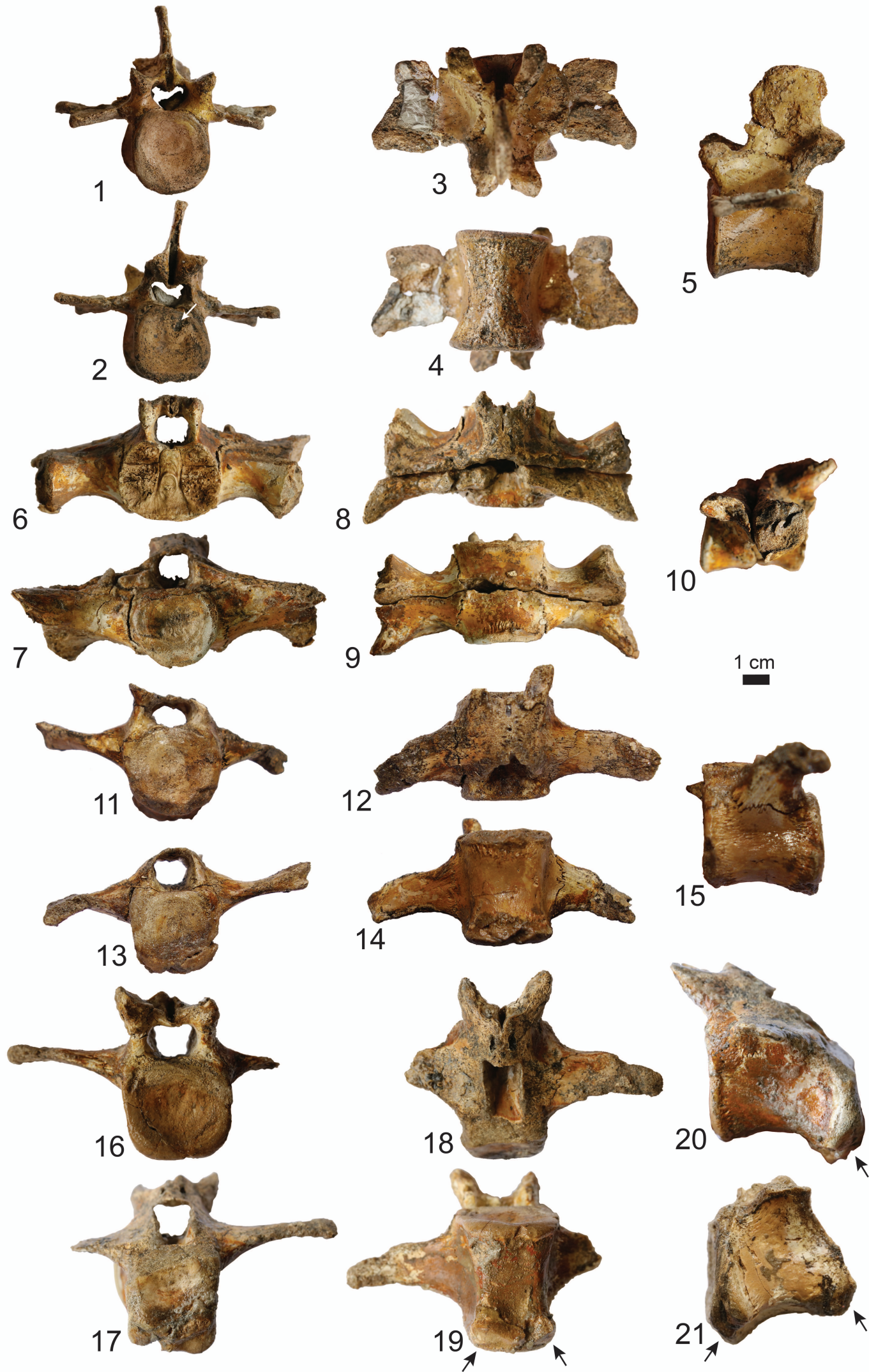
867 FIGURE 10—Rib-like element of MHNT.PAL.2012.0.45 from the Danian of Poponguine,  
868 Senegal presenting numerous ovoid pits on its surface. Abbreviation: af=articular facet.

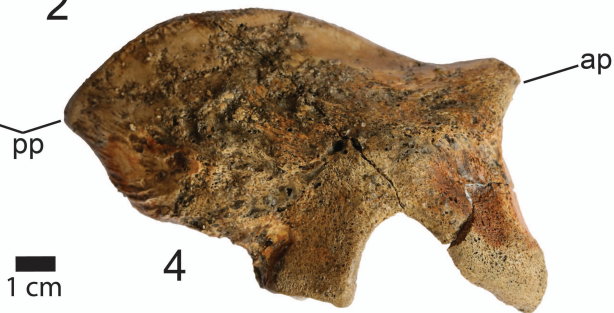




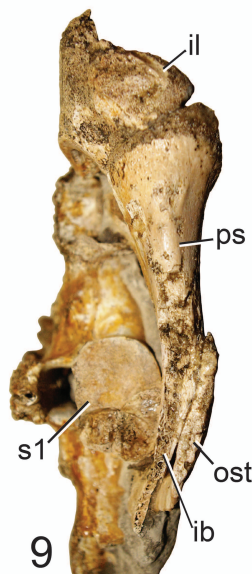
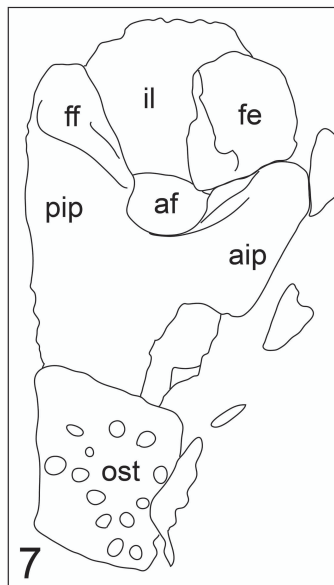
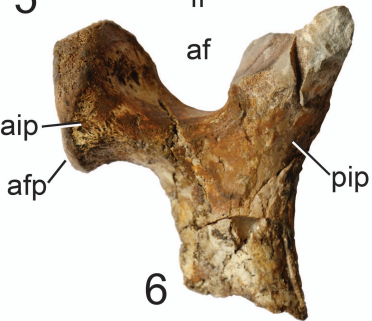




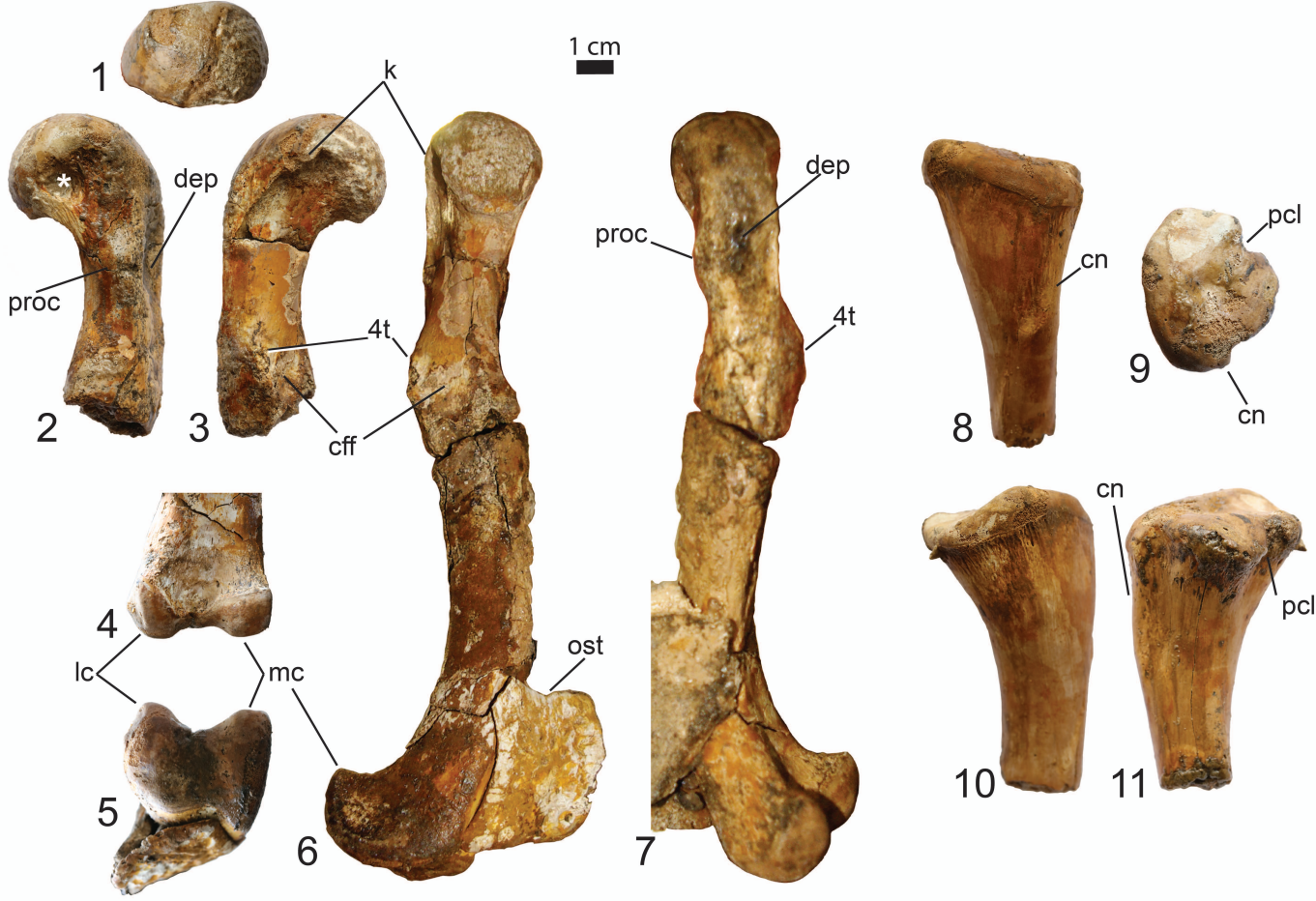


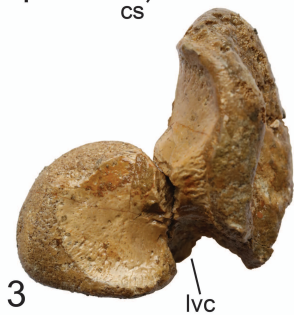
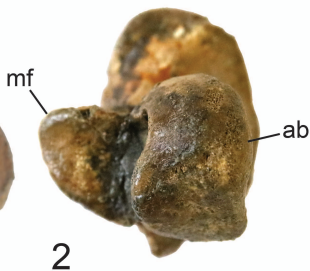
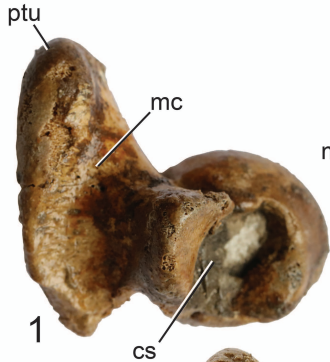


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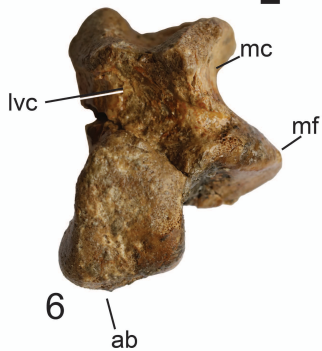
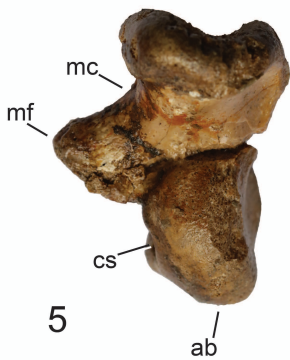




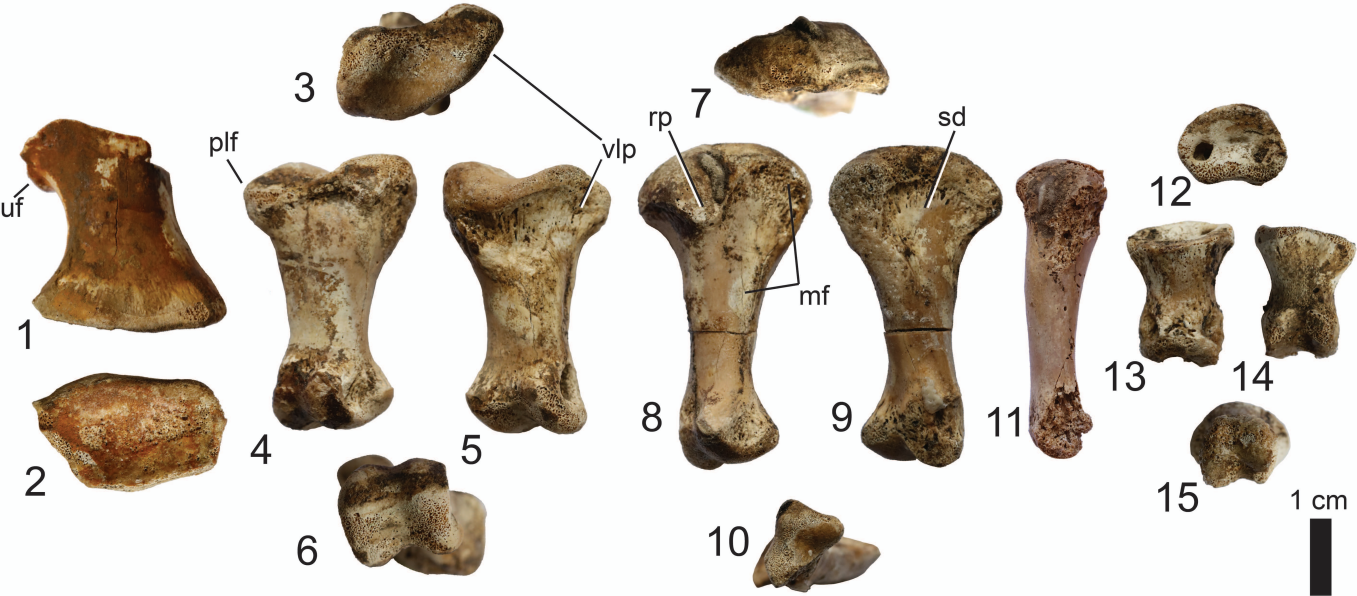


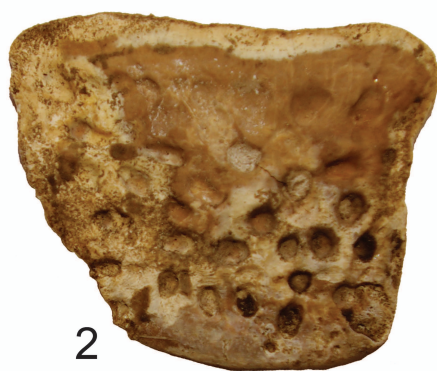


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