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

2

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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 gastralia (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 thoracic 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 thoracic 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.

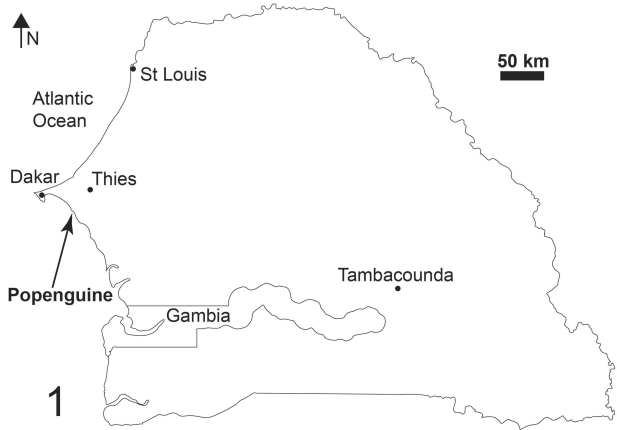
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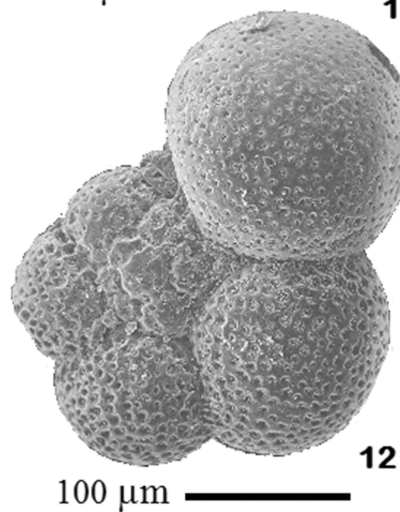
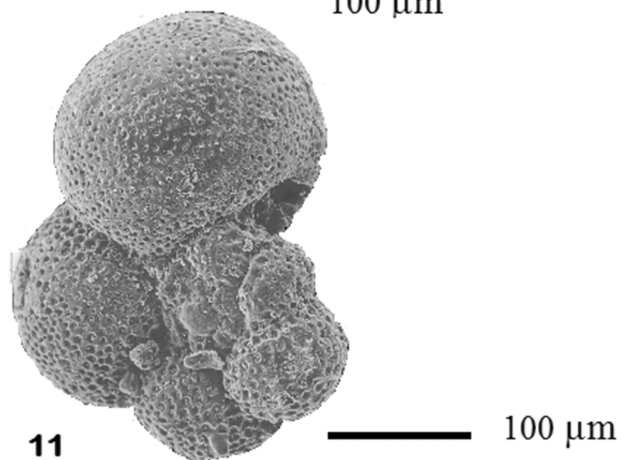
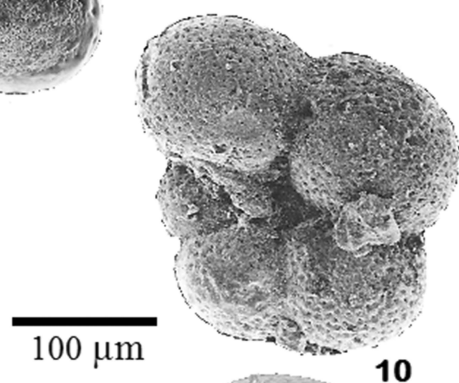
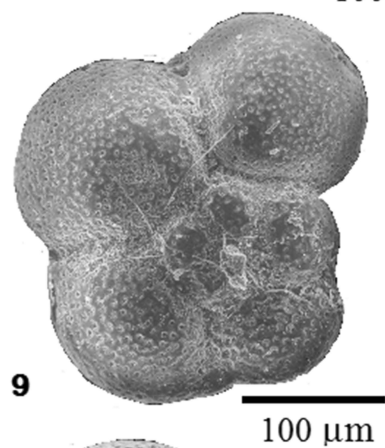
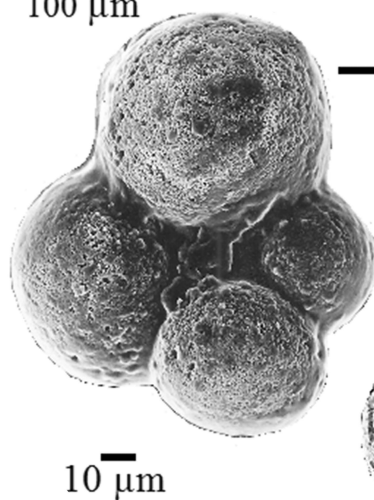
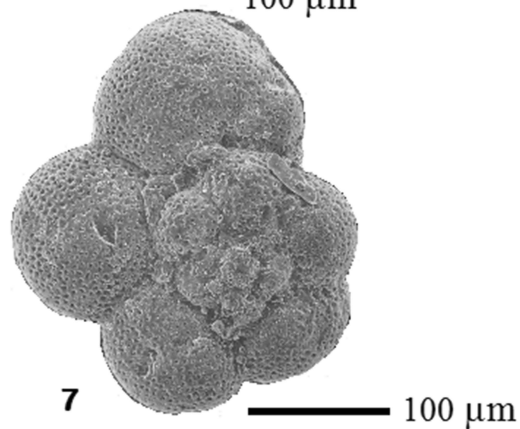
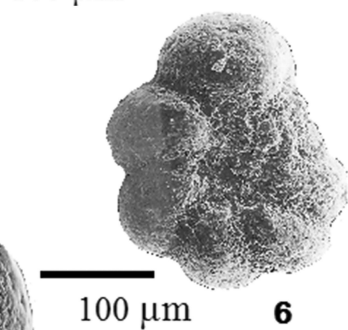
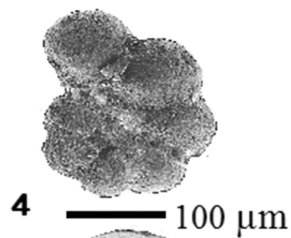
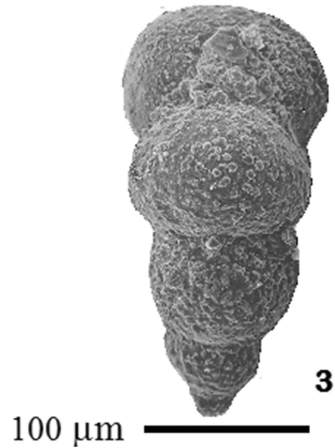
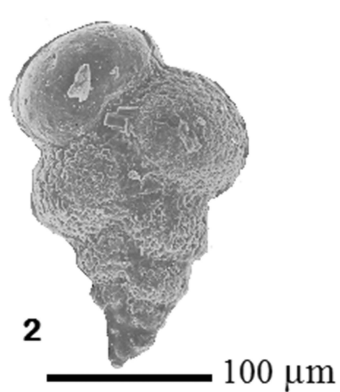
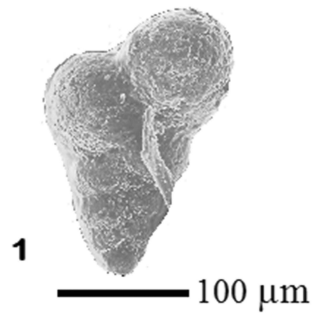
862 FIGURE 9—The osteoderms of MHNT.PAL.2012.0.45 from the Danian of Poponguine,
863 Senegal. **(1, 2)** examples of dorsal elements and of a **(3)** ventral element with an arrow

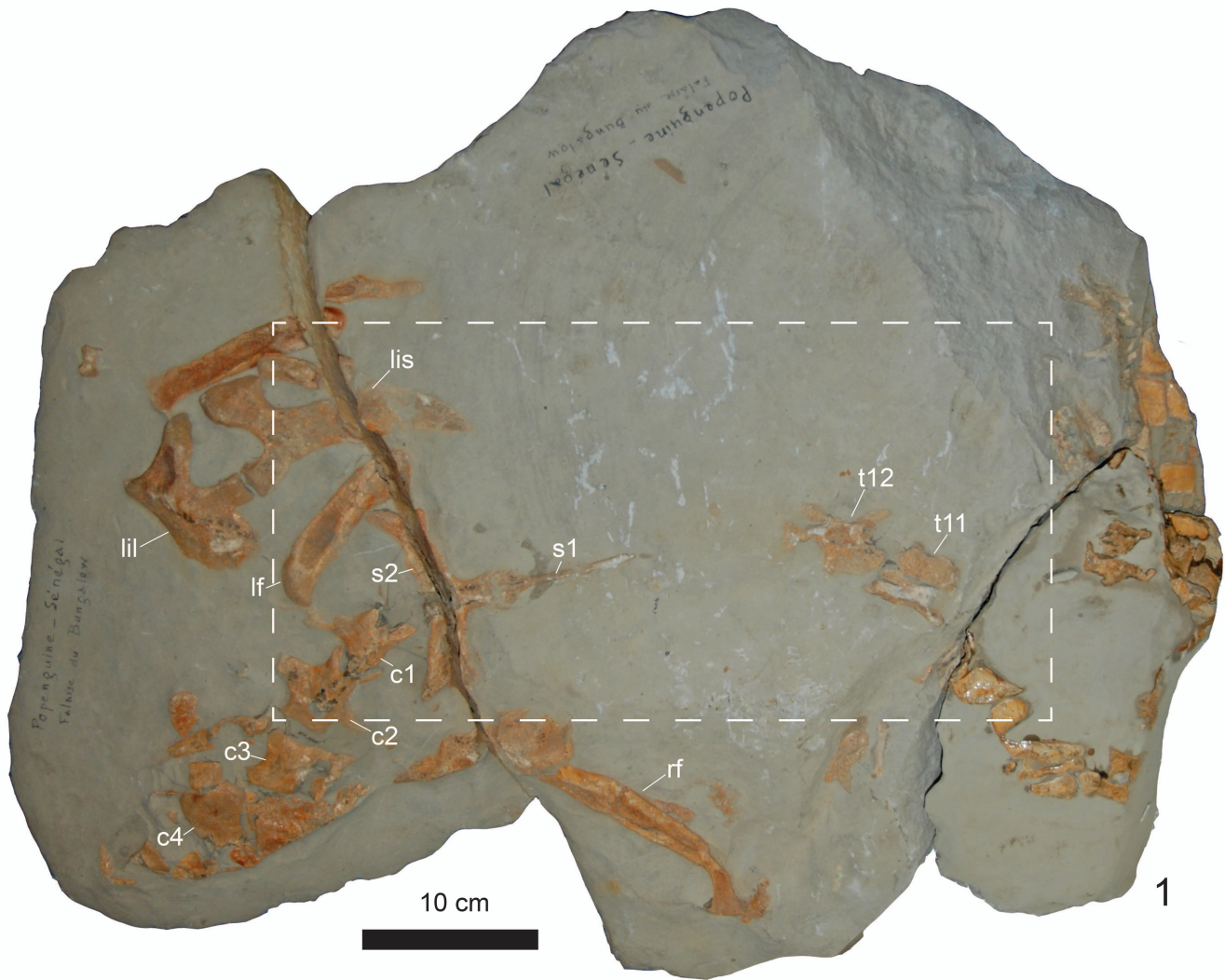
864 indicating the lateral expansion. Series of four osteoderms from the ventral shield preserving
865 their original organization in **(4)** ventral and **(5)** lateral views.

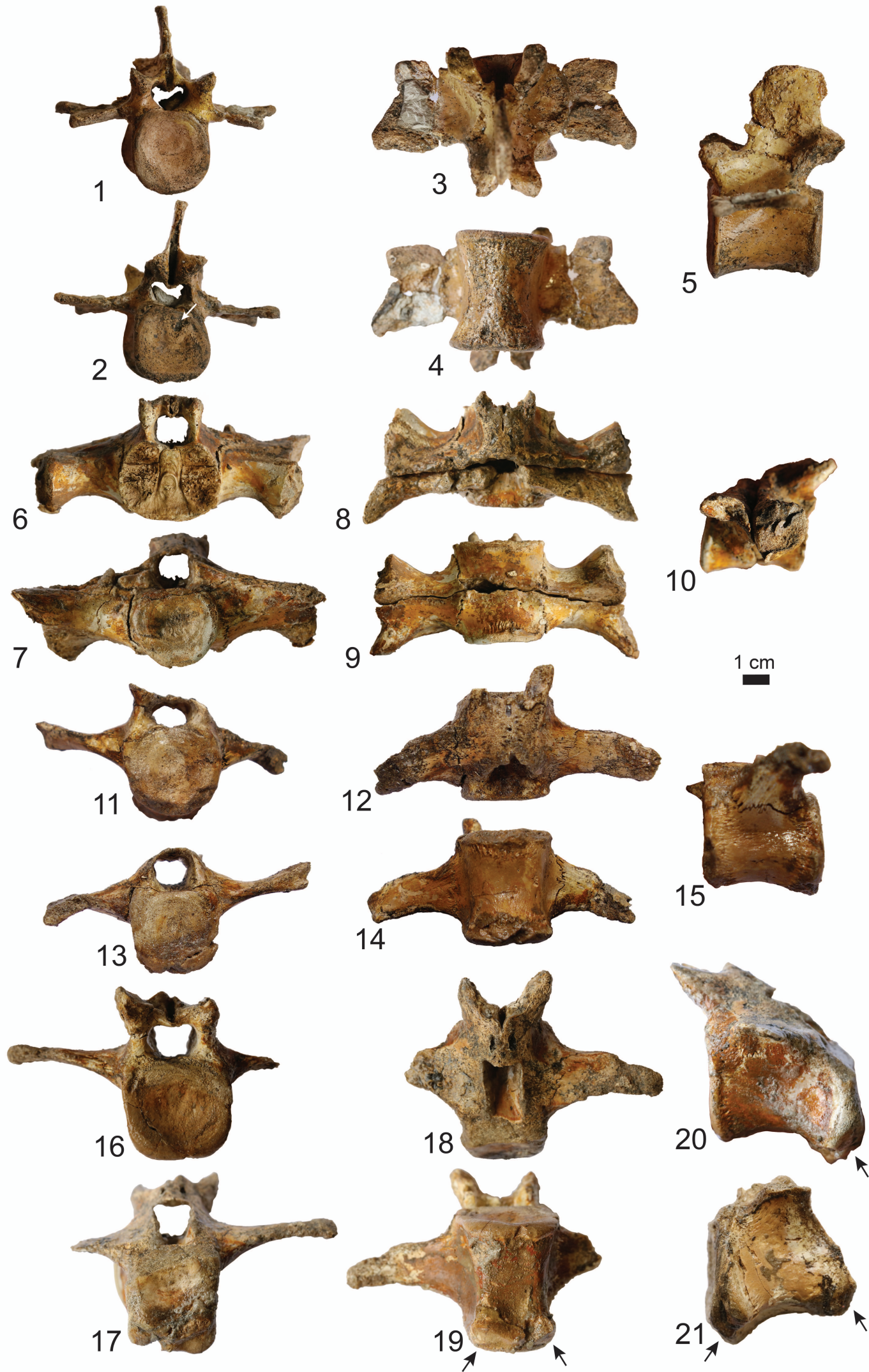
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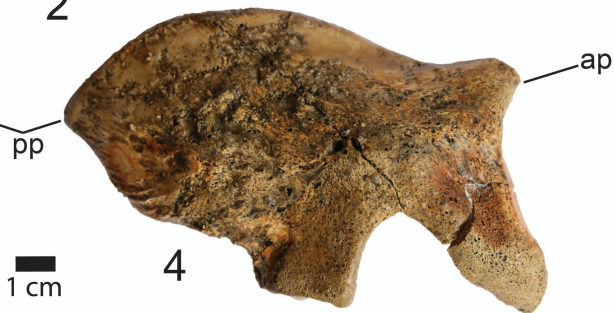
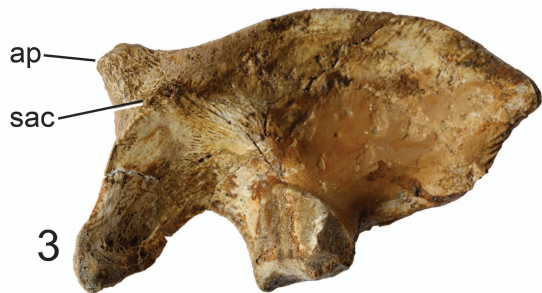
867 FIGURE 10—Rib-like element of MHNT.PAL.2012.0.45 from the Danian of Poponguine,
868 Senegal presenting numerous ovoid pits on its surface. Abbreviation: af=articular facet.



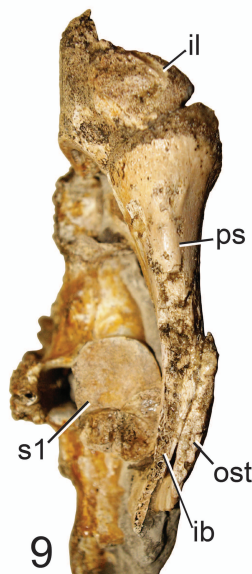
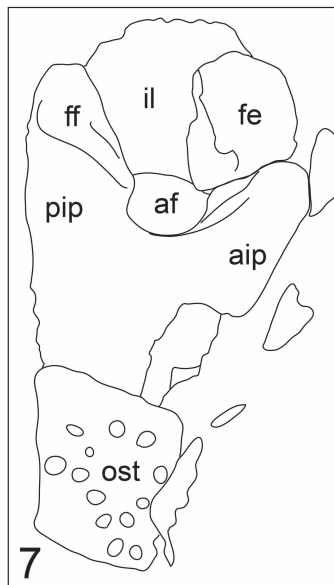
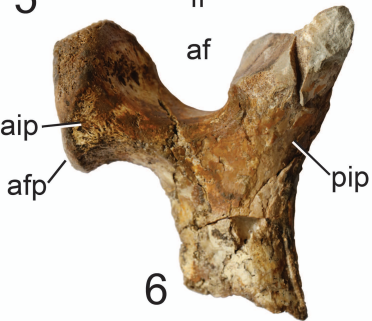


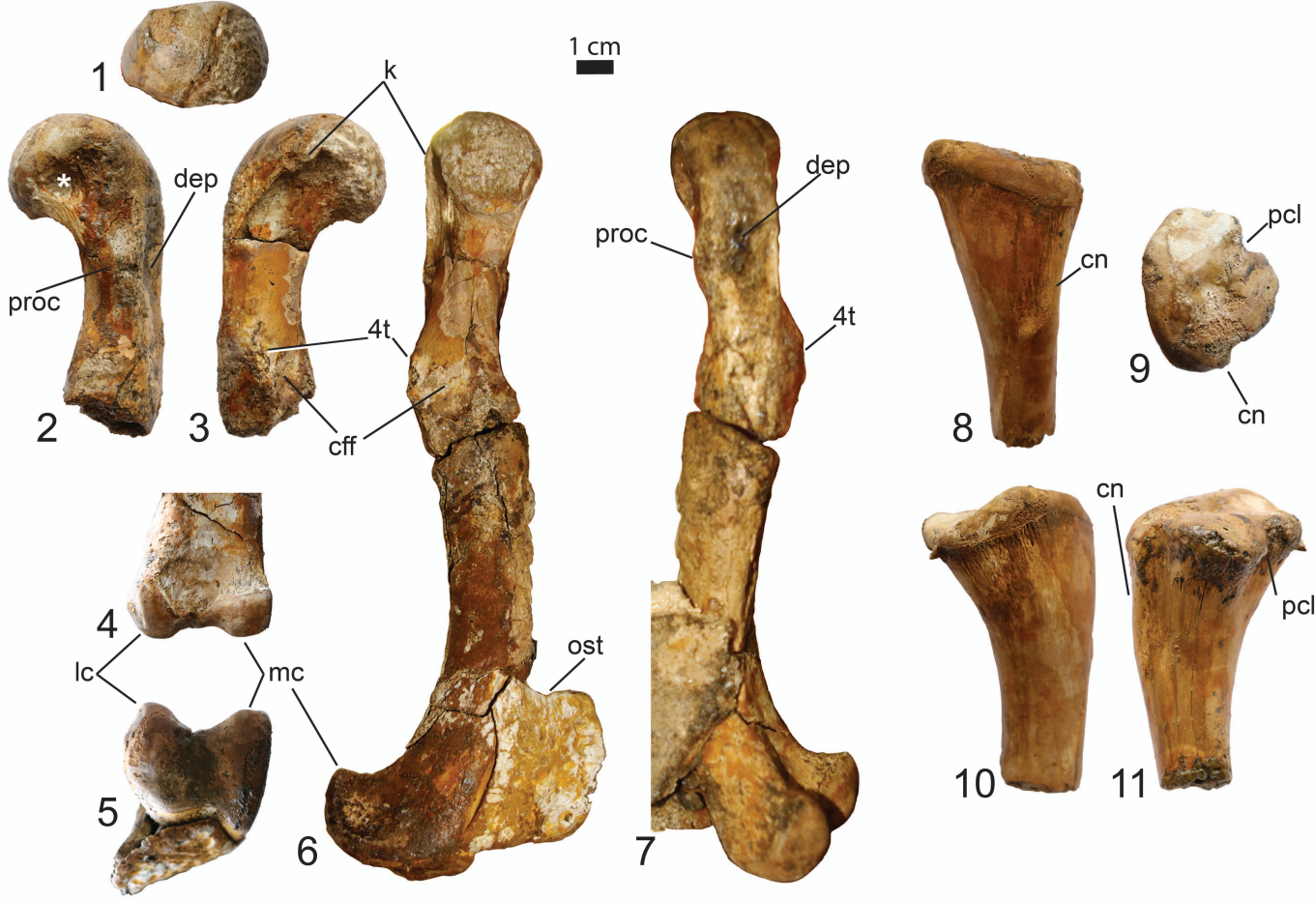


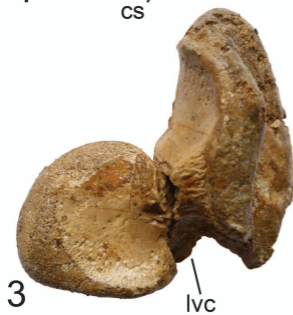
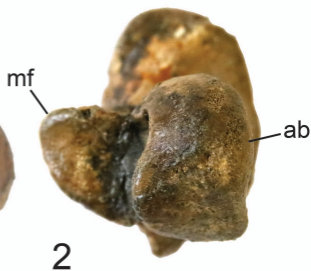
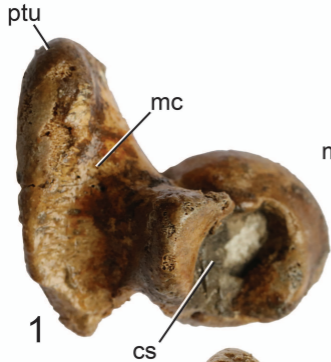




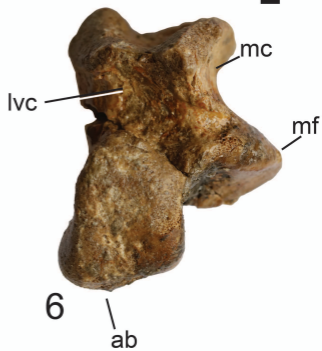
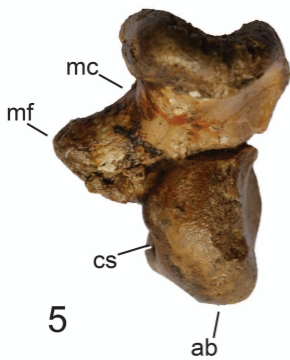
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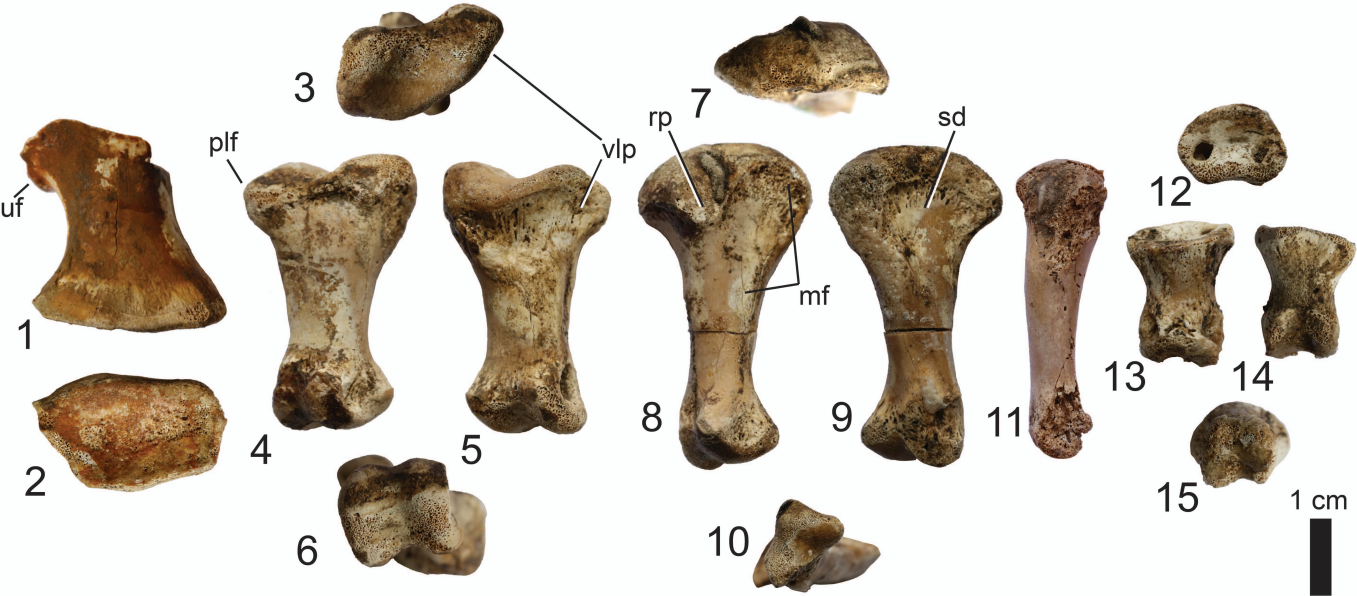


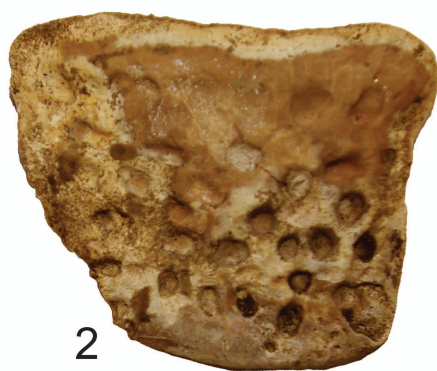




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