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1 **A reassessment of the Oligocene hyracoid mammals from Malembo, Cabinda,**
2 **Angola**

3

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17

18

19 **Abstract**

20 The Oligocene Malembo locality, Cabinda exclave, Angola has yielded a rich vertebrate fauna
21 represented by fragmentary remains. This fossiliferous locality is the only definite
22 occurrence of Oligocene terrestrial mammals in sub-Saharan West Africa. The hyracoids
23 from Malembo have only been very succinctly described and compared thus far, so that
24 their systematic attribution is not consensual among specialists. A revision now allows the
25 identification of three (or four) medium to large-sized species represented by *Geniohyus*
26 *dartevellei*, *Pachyhyrax* cf. *crassidentatus*, and two undetermined taxa. The species *G.*
27 *dartevellei* is revived for the holotype of *Palaeochoerus dartevellei* Hooijer, 1963; this species
28 is unique to Malembo but appears close to *Geniohyus mirus*, a species only known from the
29 early Oligocene of the Fayum, Egypt. Other species of *Geniohyus* and *Pachyhyrax*
30 *crassidentatus* are also only known from the early Oligocene of the Fayum. The presence of
31 *Geniohyus* and *Pachyhyrax* cf. *crassidentatus* at Malembo supports thus an early Oligocene
32 age for the fauna.

33

34 **Keywords:** Hyracoidea, *Geniohyus*, *Pachyhyrax*, Paleogene, Africa

35

36

37 1. Introduction

38 Living representatives of the mammalian order Hyracoidea comprise only five small-
39 sized species within three closely related genera (*Dendrohyrax*, *Heterohyrax*, and *Procavia*)
40 placed in the Procaviidae, this family being restricted to Africa and the Middle East (Shoshani
41 et al., 2013). By contrast, hyracoids were highly diversified during the Paleogene when they
42 represented the dominant ‘ungulate’ group of the Afro-Arabian continent (Rasmussen and
43 Gutiérrez 2010). Late Eocene to early Oligocene sites of the Fayum in Egypt are particularly
44 famous for their rich hyracoid fossil record illustrating the families Geniohyidae,
45 “Saghatheriidae”, and Titanohyracidae (Barrow et al., 2010; Rasmussen and Gutiérrez, 2010;
46 Tabuce, 2016). In addition to the Fayum area, several other Oligocene localities in Africa
47 have yielded hyracoids, namely localities in Libya (Jebel al Hasawnah and Zallah; Gheerbrant
48 et al., 2007; Coster et al., 2015), Saudi Arabia (Harrat al Ujayfa area; Zalmout et al., 2010),
49 Oman (Thaytiniti and Taqah; Pickford et al., 1994; Al-Kindi et al., 2017), Ethiopia (Chilga;
50 Kappelman et al., 2003; Sanders et al., 2004; Rasmussen and Gutiérrez, 2010), Kenya
51 (Losodok and Lokone; Rasmussen et al., 2009; Ducrocq et al., 2010; Hammond, Foecke and
52 Kelley, 2019), Tanzania (Rukwa Rift Basin; Stevens et al., 2009), and Angola (Malembo;
53 Pickford, 1986; Rasmussen, 1989). As a result, hyracoids are known to have been widespread
54 during the Oligocene in the Afro-Arabian continent and at least locally abundant. Despite
55 this important diversity, numerous questions persist concerning their systematics and
56 phylogeny. Problematic hyracoids include those belonging to the family Geniohyidae.

57 Geniohyids embrace the genera *Geniohyus*, *Bunohyrax*, *Pachyhyrax*, and *Brachyhyrax*
58 which are essentially Oligocene in age, and possibly the Eocene genera *Namahyrax* and
59 *Seggeurius* (Rasmussen and Gutiérrez, 2010; Pickford, 2019). The latter two are instead
60 considered as ‘basal’ hyracoids along with *Microhyrax* and *Dimaitherium* by some authors
61 (Cooper et al., 2014; Tabuce et al., 2017). There are two main reasons why the view of
62 geniohyids is not consensual. First, most species remain poorly documented and
63 represented by scarce partially preserved specimens, particularly *Geniohyus*, the type genus
64 of the family. Second, their bunodont molars and simple premolars give them a
65 plesiomorphic and conservative morphology. As pointed out by Rasmussen and Simons
66 (1988), geniohyid molars were characterized by lingual cusps that stand alone, not
67 connected by cristids or lophs to the buccal cusps. Rasmussen and Gutiérrez (2010)
68 suggested that this peculiar morphology parallels that of some lineages of artiodactyls.

69 The dental similarities between geniohyids and some artiodactyls were consequently
70 a source of confusion in the past. For instance, when Andrews (1904) originally described the
71 genus *Geniohyus* based on a lower mandible bearing p1-m3 discovered from the Fayum, he
72 placed it in the suoids but later recognized it as a hyracoid (Andrews 1907). Similarly,
73 Darteville (1935) and Hooijer (1965) attributed the two geniohyids from Malembo, Angola,
74 to artiodactyls (suoids and anthracotheriids); their hyracoid nature was recognized only in
75 the 1980's by Pickford (1986) and Rasmussen (1989) but these authors disagreed about their
76 generic affinities. In the most recent overview of Paleogene hyracoids (Rasmussen and
77 Gutiérrez, 2010), only one of the two species from Malembo is mentioned and a third
78 systematic attribution, distinct from that of Pickford (1986) and Rasmussen (1989), was
79 proposed for this hyracoid species. Despite these disagreements, the specimens from
80 Malembo have only been very succinctly described and compared so far. Given the
81 uncertainty about the generic assignment of the hyracoids from this locality, a detailed
82 revision appeared necessary, especially because they are the best preserved specimens of
83 the locality, which is the only definite occurrence of Oligocene terrestrial mammals in sub-
84 Saharan West Africa.

85

86 **2. Geological and paleontological context**

87 Malembo (Cabinda enclave, Angola), also called Malembe in older literature, is a
88 geological cliff section and fossil site located along the west coast of Africa within the Lower
89 Congo Basin, 10 km south of the city of Landana (Fig. 1). The fossiliferous locality of
90 Malembo was first mentioned by Cornet (1906) and then by Vincent et al. (1913) who
91 described the lamellibranch *?Plicatula malembeensis*. In 1933, during an expedition funded
92 by the *Fonds Jacques Cassel* of the *Université Libre de Bruxelles*, the zoologist and
93 paleontologist Edmond Darteville discovered a rich assemblage of vertebrates composed of
94 fragmentary bony fish, elasmobranch, crocodylian, turtle, and mammal remains; the fauna
95 was considered Miocene in age (Darteville 1934). In April 1935, at a scientific congress
96 organized as part of the Brussels International Exposition, Darteville (1935) succinctly
97 discussed this new fauna. He identified, but did not figure, remains of a cetacean, a
98 perissodactyl (a probable Chalicotheriidae), an artiodactyl (*Palaeochoerus* sp.), a
99 proboscidean (*Mastodon* sp.), and a sirenian (*?Halitherium* sp.). Based on the associated
100 shark and ray fauna, which was compared to that of Chandane in Mozambique, Darteville

101 (1935) maintained a Miocene age for the Malembo fauna. This age was confirmed by
102 Darteville and Casier (1943, 1959) in their monograph of the fossil elasmobranch faunas
103 from Lower Congo and adjacent areas, based in part on material collected during a second
104 research expedition to the region (1937-1938). Darteville and Casier (1943 p. 63-64) also
105 detailed and figured the stratigraphic succession exposed at Malembo. According to these
106 authors, the fossiliferous sequence constitutes the central portion of a shallow syncline
107 overlying Lutetian deposits that outcrop near Landana to the North and Cabinda to the
108 South. Two recent analyses by Solé et al. (2019) and Steeman et al. (2020) have revised
109 Paleogene deposits of Landana and also concluded that part of them are Lutetian in age.
110 Steeman et al. (2020) also concluded that the uppermost part of the Landana section is no
111 younger than early Oligocene.

112 Almost thirty years after Darteville's first study, Hooijer (1963) reassessed the
113 mammalian fauna from Malembo. He identified five taxa: a carnivoran attributed to cf.
114 *Amphicyon* (I³ RMCA-RGPP6419), a proboscidean attributed to *Trilophodon angustidens*
115 (several molar fragments numbered RMCA-RGP6413, RMCA-RGP6414, RMCA-RGP6420,
116 RMCA-RGP6421), a chalicotheriid attributed to ? *Macrotherium* (I^{sup} RMCA-RGP6411; an
117 enamel fragment RMCA-RGP6422), undetermined anthracotheriids (left m3 in a mandible
118 fragment RMCA-RGP6423, a phalanx RMCA-RGP6425), and a new suoid species named
119 *Palaeochoerus dartevillei* based on the holotype RMCA-RGP6412, an isolated right m3.
120 Hooijer (1963) also attributed to this new species a fragment of a possible m1 (RMCA-
121 RGP6416), a fragmentary lower incisor (RMCA-RGP6415), and with caution a sesamoid
122 (RMCA-RGP6419). He also mentioned that the latter specimen number referred to a sample
123 that also includes a small fragment of a suoid molar. In this study, Hooijer (1963) did not
124 revise the two marine mammals mentioned by Darteville (1935). Based on the terrestrial
125 fauna he identified, Hooijer (1963) proposed a Miocene age for the Malembo fauna as
126 initially suggested (Darteville, 1934, 1935; Darteville and Casier, 1943, 1959).

127 Pickford (1986) proposed a radical new and interesting interpretation of the same
128 fauna. After a re-examination of the specimens, he identified an anthropoid primate (for the
129 'canid' incisor), the embrithopod *Arsinoitherium* (for the 'chalicotheriid' fragments), two
130 hyracoids namely *Bunohyrax* aff. *fajumensis* and *Geniohyus* cf. *mirus* (for the
131 'anthracotheriid' and '*Palaeochoerus dartevillei*' molars, respectively). He also attributed
132 the proboscidean fragments to *Phiomia* sp.? or *Hemimastodon* sp. Referring to these new

133 identifications, Pickford (1986) concluded that the locality is early Oligocene in age, but
134 possibly younger than the Fayum due to the possible occurrence of *Hemimastodon*, a genus
135 which is documented from the late Oligocene of Pakistan (Gheerbrant and Tassy 2009). The
136 presence of the characteristic Fayum genera *Arsinoitherium*, *Bunohyrax*, *Geniohyus*, and
137 possibly *Phiomia* also led Pickford (1986) to propose a widespread geographic uniformity of
138 the African Oligocene mammalian fauna; Malembo was at that time the unique evidence —
139 South of the Equator— of this hypothesis. Since then, Malembo is regularly cited in research
140 papers and review articles among the few known African Paleogene mammalian faunas.

141 Recent fieldwork at Malembo (called Malembo Point by Jacobs et al., 2016) by
142 Projecto PaleoAngola allowed the discovery of two new mammal specimens, unfortunately
143 poorly preserved and unfigured (Jacobs et al. 2016, Mateus et al. 2019). According to Jacobs
144 et al. (2016:351), “The first is a ptolemaiidan molar more similar to *Kelba* from Songhor,
145 Kenya (19.5 Ma) than to Fayum *Ptolemaia*...” and “The second specimen from Malembo is
146 the P4 of a large primate unlike any described taxon, ...”. Considering these findings, a late
147 Oligocene age was advocated for Malembo.

148 Darteville (1934) and Jacobs et al. (2016) have insisted on the difficulty to access the
149 fossiliferous deposits, only accessible along sea cliffs; moreover, according to Darteville and
150 Casier (1943 p.63-64) the stratigraphic section is limited to a few meters in the lower part of
151 the cliff. Instead, the West African margin and the Congo deep-sea fan display a major
152 regional unconformity in the basal Oligocene (the “Oligocene unconformity”) overlain by the
153 Oligo-Miocene Malembo Formation, comprised of predominant terrigenous sediments and
154 thinning northwards, from Angola to Congo (Broucke et al., 2004; Anka et al., 2009 and
155 2010). The Malembo Formation corresponds to deltaic sediments prograding westwards, as
156 a response to massive sediment discharge from the inland Congo Basin, in turn due to a
157 gradual tectonic uplift of Africa and to a synchronous global fall in sea-level during the
158 Oligocene ice age (Lavier et al., 2001; Anka et al., 2009 and 2010; De Putter and Ruffet,
159 2020). The Malembo Formation unconformably overlies the Paleocene-Eocene Landana
160 Formation. In this way, the offshore succession is overall similar to that on the littoral at
161 Malembo, and both point to a relative westward migration of deltaic environments in the
162 Oligocene. The dinoflagellate cyst assemblage studied from the Oligocene deposits for the
163 Malembo Formation indicates a late Oligocene age (Willumsen et al., 2004). This result is
164 however insufficient to support a late Oligocene age for the Malembo mammalian fauna

165 because further fieldwork is required to stratigraphically locate the mammalian-bearing bed
166 relative to the offshore borehole stratigraphy. A revision of the rich elasmobranch fauna
167 found at Malembo (Darteville and Casier, 1943) is also required in this regard. Absolute age
168 determination also still needs to be performed for these deposits (contra the *lapsus* in
169 Seiffert, 2010 p.21, where the crossmark in the table is for Rukwa, Tanzania).

170

171 **3. Material and methods**

172 *3.1. Abbreviations*

173 AMNH: American Museum of Natural History, New York, USA

174 CGM: Egyptian Geological Museum, Cairo, Egypt

175 DPC: Duke Lemur Center Division of Fossil Primates, Durham, North Carolina, USA

176 GSP: Geological Survey of Pakistan

177 NHMUK: Natural History Museum, Department of Palaeontology, London, UK

178 RMCA-RGP: Royal Museum for Central Africa, Tervuren, Belgium – Registre Général

179 Paléontologie

180 SMNS: Staatliches Museum für Naturkunde Stuttgart, Germany

181 UM-PFY: Université Montpellier, France – Pech du Fraysse collection

182 YPM: Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

183

184 *3.2. Revised material*

185 RMCA-RGP6423: left m3 in a mandible fragment (Figs. 2-4)

186 RMCA-RGP6425: a phalanx (Fig. 2)

187 RMCA-RGP6412: isolated right m3 (Figs. 2-4)

188 RMCA-RGP6416: fragment of m1 (Figs. 2-3)

189 N.B. the specimens RMCA-RGP6415 (fragments of a possible lower incisor) and RMCA-

190 RGP6419 (a sesamoid and a tiny fragment of a molar) originally described by Hooijer (1963)

191 are too badly preserved to be discussed.

192

193 *3.3. Dental terminology*

194 Based on an exhaustive examination of the complex hyracoid dentition, it appeared that

195 traditional hyracoid dental terminology (e.g., Rasmussen and Simons, 1988; Tabuce et al.,

196 2001; Barrow et al., 2010) does not allow a precise description of all observed structures. We

197 thus complete the classic nomenclature in adding several new terms (Fig. 4(A)), inspired by
198 those that have been used in artiodactyls (Boisserie et al., 2010. Boivin et al., 2018) and
199 perissodactyls (Vautrin et al., 2019, in press). For instance, we propose that the classic term
200 protocristid (the cristid between the protoconid and the metaconid, sensu Szalay 1969,
201 which is homologous of the protolophid, sensu Van Valen 1966) should no longer be used in
202 hyracoids as this structure is clearly formed by two distinct cristids arising from two distinct
203 cuspids: a first cristid (here named postprotocristid) rises from the distal side of the
204 protoconid and a second cristid (here named postmetacristid) rises from the distal side of
205 the metaconid. These two cristids may (in lophodont taxa) or may not (in bunodont taxa)
206 join together. The co-occurrence and the orientation of these two cristids are variable
207 among stem hyracoids but also among other early paenungulates (e.g., the postmetacristid
208 is absent and the postprotocristid joins the cristid obliqua in *Seggeurius* and *Eritherium*, the
209 basalmost hyracoid and proboscidean respectively). Interestingly, the identification and
210 naming of homologous cristids among stem paenungulates evidence that the incipient
211 “protolophid” of stem hyracoids (*Microhyrax*, *Dimaitherium*, Geniohyidae –this study-) and
212 *Eritherium* is not homologous: it is composed by a connection between the postprotocristid
213 and the postmetacristid in the hyracoids whereas it is composed by a connection between
214 the preprotocristid and the postmetacristid in *Eritherium*. Regarding the hypocristid (the
215 cristid between the hypoconid and the entoconid, sensu Rasmussen and Simons 1988), we
216 also propose to abandon the use of this structure as it is also composed by two distinct
217 cristids arising from two distinct cuspids: a first cristid (here named endohypocristid) rises
218 from the hypoconid and a second cristid (here named endoentocristid) rises from the
219 entoconid. Because these cristids are variable in length (e.g., very short in *Seggeurius*),
220 direction (e.g., mesially directed in *Bunohyrax*), and elevation (e.g., high in *Megalohyrax*),
221 they have a significant systematic value (see Rasmussen and Simons 1988, fig.4 p.72); we
222 therefore prefer to adopt a precise terminology. Importantly, vast majority of the cristids we
223 name present no intraspecific variation regarding their presence, length, and course (Fig. 4).
224 Consequently, the detailed dental nomenclature here proposed is a key issue for dental
225 homology within hyracoids (and other paenungulates) and future phylogenetic analyses.

226 **4. Systematic paleontology**

227 Class Mammalia Linnaeus, 1758

228 Order Hyracoidea Huxley, 1869

229 Family Geniohyidae Andrews, 1906

230 Genus **Geniohyus**, Andrews, 1904

231 **Type species:** *Geniohyus mirus* Andrews, 1904.

232 **Included species:** *G. mirus*, *G. diphyicus*, *G. magnus*, *G. dartevellei*.

233 **Diagnosis:** see Rasmussen and Gutiérrez (2010).

234

235 *Geniohyus dartevellei* (Hooijer 1963)

236 Figs. 2(A-C), 3(B), 4(B)

237 vp 1963. *Palaeochoerus dartevellei* – Hooijer, p.50, pl. 9, fig. 3

238 v 1986. *Bunohyrax* aff. *fajumensis* – Pickford, p. 1206, pl. 1, fig. 4

239 v 1989. *Bunohyrax* sp. or *Geniohyus* sp. – Rasmussen, p. 67

240 v 2010. *Bunohyrax* ?*fajumensis* – Rasmussen and Gutiérrez, p. 129

241 **Holotype:** RMCA-RGP6412, right m3

242 **Measurements:** length = 26.3 mm; width = 16.1 mm

243 **Emended diagnosis:** Differs from all other geniohyids except *Geniohyus* by centrally
244 positioned cuspids and symmetrical in shape and size lingual-labial cuspid pairs. *Geniohyus*
245 *dartevellei* is significantly larger than *G. diphyicus* and *G. major*. *Geniohyus dartevellei* is
246 slightly larger than *G. mirus* and differs in lacking a mesoconid, in having a posthypocristulid
247 which connects the entoconulid, and in having a posthypocristid which connects the
248 prehyoconulid.

249 **Description:** The m3 has a robust morphology with centrally positioned cuspids and a similar
250 inflated development of both labial and lingual cuspids, giving a symmetrical aspect of the
251 tooth in occlusal view. The trigonid is barely wider and higher than the talonid. Due to wear,
252 the postprotocristid and postmetacristid appear connected but —considering the presence
253 of a gutter mesially to these cristids— the protoconid and the metaconid were originally
254 certainly separated. The metaconid bears, in addition to the postmetacristid, a short
255 endometacristid, a postectometacristid, and a premetacristid which connects a large wear
256 facet (this facet certainly corresponds to the premetastylid). Symmetrically, the protoconid
257 bears a short endoprotocristid and a preprotocristid which connects the paraconid. The
258 labial cingulid is only present below the paraconid, the ectoflexid, and below the
259 prehypocristulid on the talonid. The hypoconid and entoconid are equally developed. The

260 hypoconid bears a long cristid obliqua which connects the postmetacristid; there is no trace
261 of mesoconid. The hypoconid also bears a low endohypocristid oriented to the
262 endoentocristid; these two cristids are worn, so that the hypoconid and the entoconid were
263 originally certainly separated by a large furrow. The entoconid bears, in addition to the
264 endoentocristid, a long preentocristid, and short postendo- and postectocristid. The
265 hypoconulid lobe is bulbous and presents a complex morphology. The hypoconulid is labially
266 displaced; it connects the entoconulid and prehypoconulid by the posthypocristulid and
267 prehypocristulid, respectively. The hypoconulid also presents an ectohypocristulid directed
268 to the labial cingulid. The entoconulid bears two mesial cristids, the labial one is parallel to a
269 very short portion of lingual cingulid.

270 **Remarks:** RMCA-RGP6412 was the holotype of *Palaeochoerus dartevellei* Hooijer, 1963. In
271 addition to the holotype, the hypodigm of this species was composed, as mentioned above,
272 of a fragmentary possible m1 RMCA-RGP6416 (see below) and a fragmentary lower incisor
273 RMCA-RGP6415. The proximal sesamoid RMCA-RGP6419 was also putatively attributed to *P.*
274 *dartevellei*. The attribution of this material to the suoids by Hooijer (1963) was not discussed
275 and argued; this author may have been influenced by Dartevelle (1935) who has erroneously
276 identified *Palaeochoerus* in the fauna. In their defense, Oligocene hyracoids were very
277 poorly known at that time (see Tabuce 2016 for an historical review). Today, as a result of
278 modern progress that had been made on African faunas, we conclude that RMCA-RGP6412
279 documents a hyracoid. It clearly differs from *Palaeochoerus* (Fig. 4(I)) by the following
280 features: the size is larger, the talonid is wider, the trigonid cristids do not have the same
281 length and orientation, the cristid obliqua is longer, the very large mesoconid which is
282 typically a suoid trait is absent, and the hypoconulid lobe is more complex with the presence
283 of accessory conids and cristids. Recognizing the hyracoid affinity of RMCA-RGP6412,
284 Pickford (1986) attributed this specimen to *Bunohyrax* aff. *fajumensis*, unfortunately without
285 justification. Likewise, Rasmussen (1989) considered without discussion that it undoubtedly
286 belongs to *Bunohyrax* or *Geniohyus*. Finally, Rasmussen and Gutiérrez (2010) indicated that
287 it could represent *Bunohyrax fajumensis*, a species which only occurs in the early Oligocene
288 of the lower and upper sequences of the Fayum.

289 *Bunohyrax fajumensis* is the best-known species of the genus (Fig. 4(D)). Its m3 has a
290 similar size as RMCA-RGP6412 but differs by the occurrence of a postendometacristid and
291 the combined absence of a postendoentocristid, a prehypoconulid, and an entoconulid.

292 Conversely, the m3 of *B. major* (Fig. 4(E)), a species also known from the early Oligocene of
293 the Fayum, is similar to RMCA-RGP6412 in having a prehypocostid and in lacking the
294 postendometacristid. However, the m3 of this species is significantly larger than RMCA-
295 RGP6412 and differs from the latter by the morphology of the trigonid which is very distinct
296 and bears no paraconid but a very long preprotocristid joining a huge premetastylid.
297 Moreover, *Bunohyrax major* and *B. fajumensis* differ from the Malembo species in
298 consistently displaying a long marked endohypocostid. We consider this latter dental
299 feature as diagnostic of *Bunohyrax* (note that it also occurs on the tiny *B. matsumotoi* from
300 the late Eocene of Algeria, Tabuce et al., 2000). Finally, m3s of *Bunohyrax* differ from RMCA-
301 RGP6412 by further apart and less symmetrical cuspids (the protoconid and hypoconid are
302 broader than the metaconid and entoconid). These dental traits are regularly cited to
303 distinguish *Bunohyrax* from *Geniohyus* (Rasmussen and Gutiérrez 2010). Lower molars of
304 *Geniohyus* are indeed characterized by centrally positioned cuspids and symmetrical lingual-
305 labial cuspid pairs. These characters, which are also present on RMCA-RGP6412, strongly
306 support its attribution to *Geniohyus*.

307 *Geniohyus* is a poorly known and problematic genus only documented from the early
308 Oligocene of the Fayum. The definition of this genus relies essentially on what is known of
309 the large type species *G. mirus*. The allocation of the two other species (the small-sized *G.*
310 *magnus* and the medium-sized *G. diphycus*) to this genus, rather than *Bunohyrax* or a new
311 genus, is discussed (Rasmussen and Gutiérrez, 2010). The m3 of *G. diphycus* is unknown,
312 which precludes comparisons with RMCA-RGP6412. As for *G. magnus*, a unique lower jaw
313 was attributed to this species by Rasmussen and Simons (1988); however, in being quite
314 high-crowned and in having narrow talonid, sharp cristids and acute cuspids, its lower
315 molars are so distinct from those of *G. diphycus*, and *G. mirus* that the genus allocation
316 remains doubtful. Anyway, the m3 RMCA-RGP6412 is very distinct to the putative m3 of *G.*
317 *magnus* and is more similar to *Geniohyus mirus*.

318 *Geniohyus mirus* is known by a few historical specimens (Andrews, 1904, 1906, 1907);
319 only two m3s are observable on the specimens NHMUK 9485 (right p4-m3) and CGM 8634
320 (right p1-m3). These two m3s are identical (note however that the hypoconulid lobe of the
321 m3 on CGM 8634 is broken); they only differ from each other by a short labial cristid on the
322 premetastylid (only present in NHMUK 9485; Fig. 4(C)). All other dental traits are constant
323 and the similarities with RMCA-RGP6412 are striking. In addition to the centrally positioned

324 cuspids, which are inflated at their base and symmetrical lingual-labial cuspid pairs, the
325 cristids of the trigonid present the same length and orientation (the occurrence of a long
326 premetacristid is particularly significant). On the talonid, there are also numerous similarities
327 such as the combined presence of a postendoentocristid, an entoconulid (bearing two small
328 cristids), a prehyoconulid, and an ectohypocristulid directed to a portion of the labial
329 cingulid below the prehyoconulid. The m3 of *Geniohyus mirus* and RMCA-RGP6412 also
330 share the presence of the two other portions of the labial cingulid (below the paraconid and
331 ectoflexid). RMCA-RGP6412 differs however from the m3s of *Geniohyus mirus* in being
332 longer and slightly wider (m3 NHMUK 9485 = 23.4 mm x 15.2 mm), in lacking a mesoconid,
333 in having a posthypocristulid which connects the entoconulid, and in having a
334 posthypocristid which connects the prehyoconulid. Considering these characters, RMCA-
335 RGP6412 documents a species distinct from *Geniohyus mirus*, and we propose therefore to
336 keep the species name *G. dartevellei*. This hypothesis could appear tenuous considering a
337 unique molar and the unknown variability of the m3 of *Geniohyus mirus*; but it is supported
338 by the very weak variability of the m3s of the other, well-documented, geniohyids from the
339 Fayum (*Bunohyrax fajumensis* and *Pachyhyrax crassidentatus*) (Fig. 4).

340

341 Genus ***Pachyhyrax*** Schlosser, 1910

342 **Type and unique species:** *Pachyhyrax crassidentatus* Schlosser, 1910.

343 **Diagnosis:** see Rasmussen and Gutiérrez (2010).

344

345 *Pachyhyrax* cf. *crassidentatus*

346 Figs. 2(D-F), 3(A), 4(F)

347 vp 1963. Anthracotheriidae gen. et sp. indet. – Hooijer, p.56, pl. 9, fig. 1-2

348 v 1986. *Geniohyus* aff. *mirus* – Pickford, p. 1209, pl. 1, fig. 3

349 v 1989. *Pachyhyrax* cf. *crassidentatus* – Rasmussen, p. 67

350 **Material:** RMCA-RGP6423, left m3 on a mandible fragment

351 **Measurements:** length = 26.4 mm; width = 14.6 mm

352 **Description:** The mandible fragment retains on its lingual side a small part of a deep and
353 broad mandibular depression, the superior border of this structure is rather curved. The m3
354 has bunoselenodont labial cusps (protoconid, hypoconid, and hypoconulid) and a rather
355 rectangular occlusal outline with the trigonid slightly wider than the talonid. The

356 hypoconulid lobe is large and has angular borders. The labial base of the tooth bears a
357 strong and continuous cingulid. On the trigonid, the preprotocristid and the premetacristid
358 have a quite mesial direction without any trace of a paraconid and premetastylid. On the
359 protoconid, the existence of a short endoprotocristid is uncertain due to wear. The
360 metaconid bears a short endometracristid and a long and labially curved
361 postectometacristid. There is a short lingual cingulid mesial to the metaconid. The
362 postmetacristid and the (worn) postprotocristid form a low continuous cristid connected to
363 an elongated cristid obliqua. On the talonid, a furrow separates the endohypocristid and
364 endoentocristid. The posthypocristid is connected to the prehypocristulid, accentuating the
365 incipient selenodonty. The preentocristid is labially oriented whereas the postentocristid is
366 lingually oriented and longer, directed towards a huge isolated entoconulid. The strong and
367 long endohypocristulid stops in the middle of the hypoconulid basin. The hypoconulid also
368 bears an ectohypocristulid and a high posthypocristulid, which is disconnected from the
369 entoconulid by a shallow groove.

370 **Remarks:** RMCA-RGP6423 was identified by Hooijer (1963) as an anthracotheriid, possibly a
371 new species close to a specimen attributed to '*Anthracotherium punjabiense*' sensu Colbert,
372 1935 (= *Microbunodon silistrensis* sensu Lihoreau et al., 2004). However, although RMCA-
373 RGP6423 and the m3 of *M. silistrensis* have basic similarities on the trigonid and talonid
374 cristids (e.g., presence of endometracristid, postendometracristid, preentocristid,
375 postectoentocristid, and ectohypocristulid) (Fig. 4(H)), there are notable differences. RMCA-
376 RGP6423 is indeed clearly apart anthracotheriids by the occurrences of a strong and
377 continuous labio-distal cingulid, a labial orientation of the preprotocristid, a large
378 hypoconulid lobe, and above all the presence of an internal mandibular depression, which is
379 found in many fossil hyracoids (Andrews, 1906; Meyer, 1973; De Blieux et al., 2006). This
380 typical hyracoid feature found in RMCA-RGP6423 was first mentioned by Pickford (1986).
381 Among hyracoids having developed this structure, we observe intrageneric variability and
382 different patterns of sexual variation. Basically, the internal depression presents two
383 morphologies: (i) a deep opened fossa that extends bellow the premolars and molars
384 (species among *Geniohyus*, *Pliohyrax*, and *Meroehyrax*) or (ii) a large round to subround
385 fenestra situated bellow m2-m3 that opens into a chamber within the corpus of the
386 mandible (species among *Pachyhyrax*, *Thyrohyrax*, *Bunohyrax*, and *Megalohyrax*). In RMCA-
387 RGP6423, the depression of the mandible is too fragmentary to recognize a fossa or a

388 fenestra with certitude. However, as already mentioned by Rasmussen (1989), the superior
389 border of the depression is curved as in the genera having developed a fenestra. This
390 condition contrasts with the flat superior border of the fossa observed in *Pliohyrax* and
391 *Geniohyus*; such a character challenges the attribution of RMCA-RGP6423 to *Geniohyus*
392 proposed by Pickford (1986). The unique genus having developed a fossa with a curved
393 superior border is *Meroehyrax*, but the depression ends below m2 instead of m3 as in
394 RMCA-RGP6423.

395 Dental morphology also supports that RMCA-RGP6423 is significantly different from
396 *Geniohyus*, *Pliohyrax*, and *Meroehyrax*. The pliohyracids *Pliohyrax* and *Meroehyrax* have
397 indeed very high-crowned and buccolingually narrow lower molars with high crescentic
398 lophs; such a morphology differs from the brachyodont and wide lower molar with incipient
399 selenodontology of RMCA-RGP6423. Regarding *Geniohyus*, RMCA-RGP6423 differs in having a
400 strong continuous labio-distal cingulid, the cuspids that are placed near the periphery of the
401 crown, and the labial cuspids (protoconid, hypoconid, and hypoconulid) that have developed
402 an incipient selenodontology. As stated by Rasmussen (1989), these dental features are
403 diagnostic of *Pachyhyrax*. The attribution of RMCA-RGP6423 to *Pachyhyrax* is also supported
404 by the furrow that separates the endohypocristid to the endoentocristid (=“hypocristid
405 interrupted by a deep furrow” sensu Rasmussen and Simons, 1988); this trait constitutes a
406 diagnostic feature of *Pachyhyrax* (Rasmussen and Gutiérrez, 2010).

407 *Pachyhyrax* is known by *P. crassidentatus* from the early Oligocene of the Fayum
408 (Schlosser, 1911; Meyer, 1978; Rasmussen and Simons, 1988) and by a yet undescribed new
409 species from the late Oligocene of Chilga, Ethiopia (Kappelman et al., 2003; Rasmussen and
410 Gutiérrez, 2010). Since the revision of Rasmussen and Simons (1988), *Pachyhyrax*
411 *crassidentatus* is a morphologically distinctive species; it is common but restricted to the
412 upper sequence of the Fayum. The m3 of *P. crassidentatus* (e.g., YPM 31191, YPM 29166,
413 and DPC 18670) (Fig. 4(G)) share with RMCA-RGP6423 many similarities. Cuspids (position
414 and development) and cristids (length and orientation) of the trigonid and talonid are quite
415 identical. The measurements of RMCA-RGP6423 (26.4 x 14.6 mm) are also near the means of
416 *P. crassidentatus* (28.8 x 15.1 mm, N=4) which presents a sexual dimorphism of molar
417 dimensions (males can be 15–20% larger than the females, and both sexes have a
418 mandibular chamber, De Blieux et al., 2006). To that respect, the small females YPM 31191
419 (25.9 x 14.1 mm) and DPC 7514 (28.5 x 13.8 mm) have similar measurements with RMCA-

420 RGP6423 (note here that we performed a 3D reconstruction of the lower jaw DPC 7514 to
421 measure the unerupted m3 preserved on this specimen). The unique disparities between
422 RMCA-RGP6423 and m3 of *P. crassidentatus* concern the hypoconulid lobe. RMCA-RGP6423
423 has a wider hypoconulid lobe with larger and isolated entoconulid, longer and stronger
424 endohypocristulid, longer ectohypocristulid (note that the presence of this cristid is variable
425 in *P. crassidentatus*), and presents a connection between the posthypocristid and
426 prehypocristulid accentuating the incipient selenodonty. These characters could indicate
427 that RMCA-RGP6423 represents a new species, very close to *P. crassidentatus*. However,
428 because they concern only the hypoconulid lobe, we refrain from naming a new species. As
429 for the undescribed and unfigured new species from Chilga, direct comparisons with RMCA-
430 RGP6423 are impossible. However, according to Kappelman et al. (2003) and Rasmussen and
431 Gutiérrez (2010), this species differs from *P. crassidentatus* in being more gracile and in
432 having higher, sharper and more delicate cristids. These few characters also indicate that the
433 Malembo species is distinctive.

434

435 Hyracoidea

436 Family, genus and species indet.

437 Figs. 2(G-I), 3(C)

438 **Material:** RMCA-RGP6416, fragment of right m1 or m2

439 **Description:** This molar fragment was part of the hypodigm of *Palaeochoerus dartevellei*
440 Hooijer, 1963. It preserves the entoconid and the lingual part of the hypoconid, a short
441 postentocristid, the endoentocristid, a part of the endohypocristid, and a small hypoconulid
442 on the distal cingulid. Although the occlusal surface is heavily worn that the area of the
443 entoconid and hypoconid is abraded flat to the dentin, the absence of a posthypocristid
444 indicates that it does not belong to the geniohyids. Members of this family have a long
445 posthypocristid directed towards the cingular hypoconulid (e.g., *Bunohyrax fajumensis*
446 AMNH 14460, AMNH 14469); with wear the hypoconid connects the hypoconulid. In RMCA-
447 RGP6416, the hypoconulid is instead separate from the hypoconid as in titanohyracids and
448 saghatheriids (e.g., *Megalohyrax eoceanus* SMNS 43933, AMNH 13341). The specimen is
449 unfortunately too fragmentary for any further identification. Interestingly however, it
450 documents the existence of a third medium to large-sized species at Malembo, similar in size
451 with the two previous ones.

452

453 Hyracoidea

454 Family, genus and species indet.

455 Fig. 2(J-O)

456 **Material:** RMCA-RGP6425, proximal phalanx

457 **Measurements:** length = 28 mm; width = 16.5 mm

458 **Description:** This phalanx is characterized by a robust aspect. The proximal facet is concave
459 and oval in outline with a very tiny median indentation on the plantar border but no median
460 keel. The distal facet is convex, rounded in lateral view and dorso-plantarly extended.

461 Hooijer (1963) attributed this phalanx to an anthracotheriid. However, phalanges of
462 anthracotheriids, notably those of the Oligocene species *Bothriogenys gorrigei*, *B. andrewsi*,
463 *B. fraasi*, and *B. rugulosus* from the Fayum (SMNS collection; Schmidt, 1913), differ by the
464 presence of a well-marked median keel on the proximal facet and a less extended distal
465 facet (in dorsal and plantar views), which forms a relatively deep symmetric trochlea.

466 Anthracotheriids also differ by the occurrence of plantar tuberosities proximo-lateral to the
467 two condyles of the distal trochlea. Instead, the morphology of RMCA-RGP6423 is identical
468 to that is observed in living and extinct hyracoids for which proximal phalanges are known
469 (the saghatheriids *Thyrohyrax* and *Saghatherium*, the titanohyracid *Afrohyrax*, and the
470 pliohyracid *Prohyrax*) (Meyer, 1973; Fischer, 1986; Pickford, 1994; Gheerbrant et al., 2007).

471 The unique significant difference between all these taxa concerns the general outline of the
472 phalanges in dorsal view: whereas RMCA-RGP6423 and *Prohyrax* have a moderate median
473 constriction, *Afrohyrax* and living procaviids have a more marked constriction, and
474 *Thyrohyrax* and *Saghatherium* have quite rectilinear lateral and medial margins. The
475 systematic importance of this character remains to be determined. Pending a better
476 knowledge of the postcranial anatomy of the medium to large-sized hyracoids from the
477 Fayum, RMCA-RGP6423 is attributed to Hyracoidea *incertae sedis*. It documents a species
478 compatible in size with one of the three previously described species.

479

480 5. Conclusion

481 The small set of hyracoid specimens from Malembo remarkably documents three (or
482 four) medium to large-sized species. This hyracoid assemblage is consistent with faunas
483 recovered elsewhere in Africa during the Oligocene. For instance, the early Oligocene Quarry

484 A-B from the Fayum yielded nine species and the latest Oligocene locality Losodok in Kenya
485 yielded four species. Some of them are medium to large-sized species as at Malembo. Pan-
486 African Oligocene hyracoids demonstrated however a large range of body mass, from 3 kg to
487 2000 kg (Schwartz et al. 1995); small-sized species (e.g., *Saghattherium* spp. and *Thyrohyrax*
488 ssp.) are particularly abundant in most Oligocene localities. Regarding Malembo, the
489 absence of such small-sized species is probably a sampling or taphonomic bias, due to size-
490 sorting by marine depositional process. Despite an apparently biased fossil record at
491 Malembo, the identification of *Pachyhyrax* cf. *crassidentatus* and *Geniohyus dartevellei*, a
492 species very close to *G. mirus*, helps to refine the age of the locality. To our current
493 knowledge, the genus *Pachyhyrax* is distributed from the early Oligocene (Fayum) to the late
494 Oligocene (Chilga) and *Geniohyus* is restricted to the early Oligocene of the Fayum. The
495 species *G. mirus* is only documented by a few specimens without precisely known
496 stratigraphic position, but certainly from the lower sequence of the Jebel Qatrani Formation,
497 possibly near the Quarry A-B (Barrow et al., 2010), which is dated at ~33-31 Ma (Seiffert
498 2010). As a result, pending the revision of the rich elasmobranch fauna and the description
499 of the ?primate and ptolemaiid recently discovered at Malembo (Jacobs et al., 2016; Mateus
500 et al., 2019), our data supports an early Oligocene age for the Malembo fauna and series.
501 This age fits well within the evolution of the local paleo-environment in the Oligocene, with
502 terrigenous deltaic deposits prograding westwards as a response to a tectonic uplift of the
503 continent and a synchronous sea-level decrease in the early Oligocene glaciation. The minor
504 morphological differences in the hyracoid species between Malembo and the Fayum could
505 indicate a geographical variation or a small age difference, especially if the species
506 *Pachyhyrax* cf. *crassidentatus* is new.

507

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518

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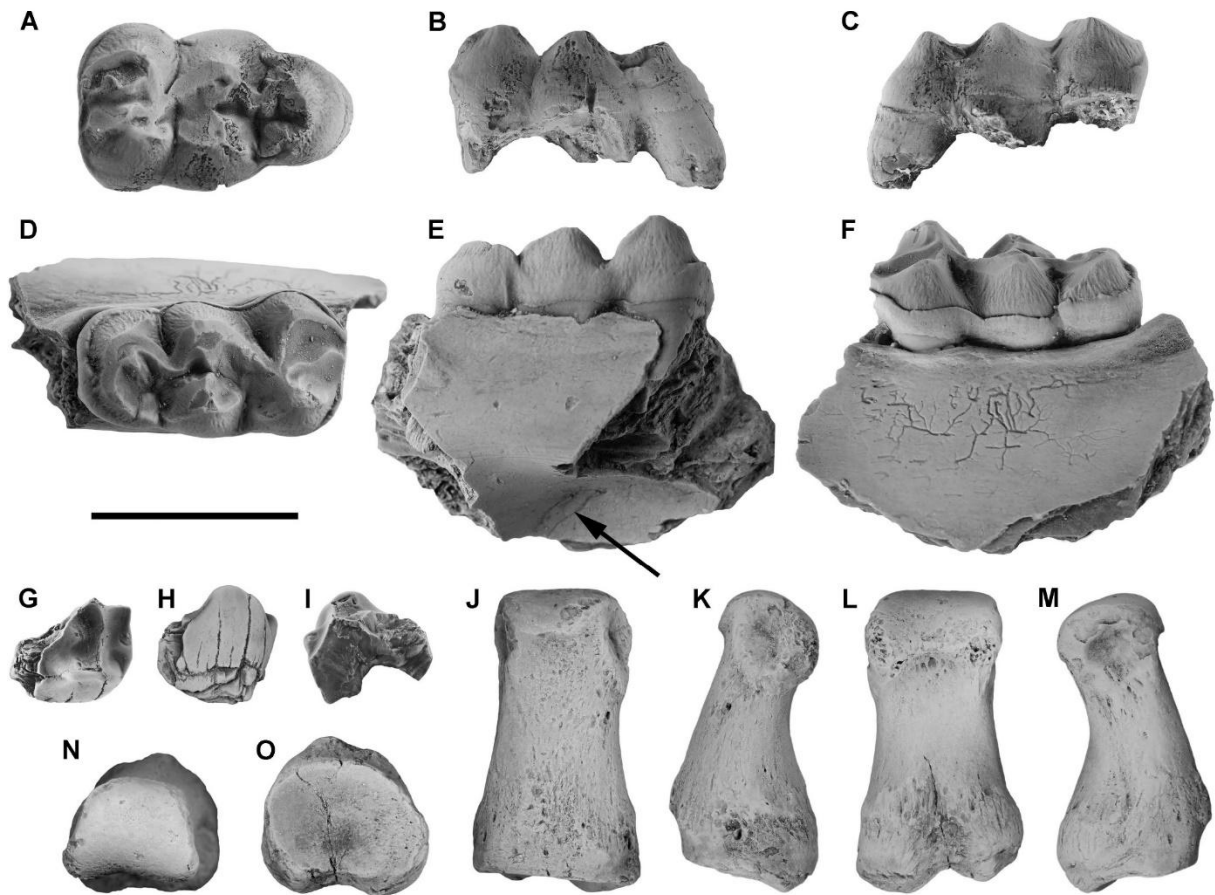


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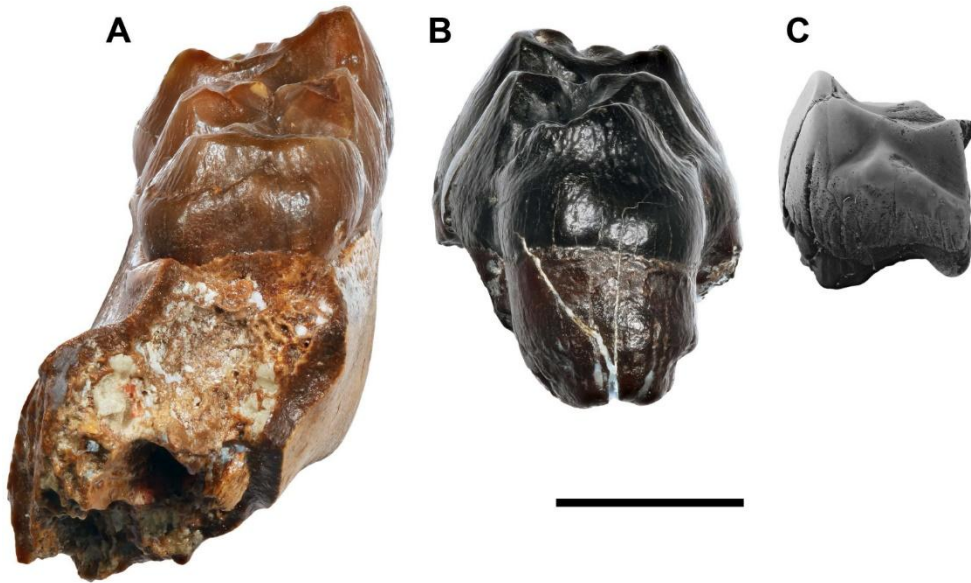
698 **Figure 1.** Map of Congo Basin margin Basin showing the fossiliferous Malembo locality in

699 western Central Africa.



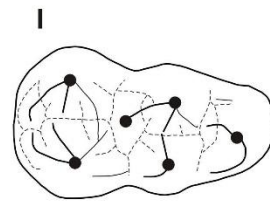
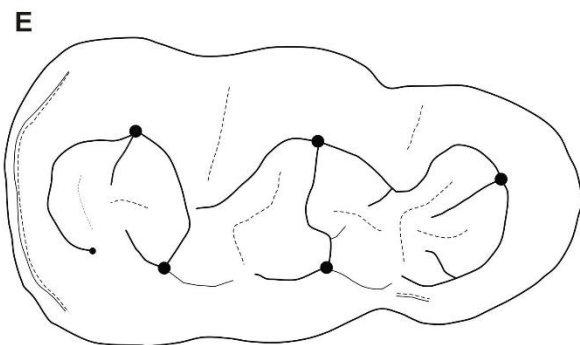
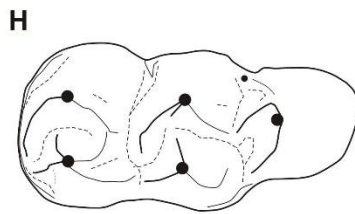
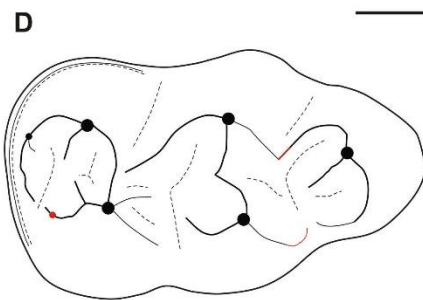
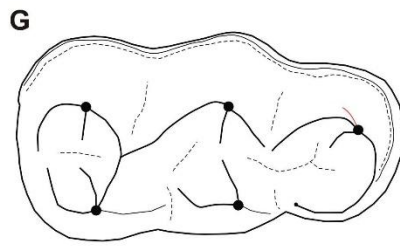
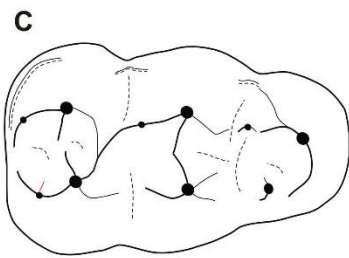
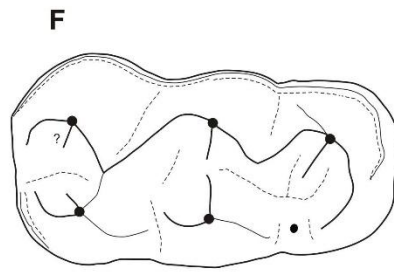
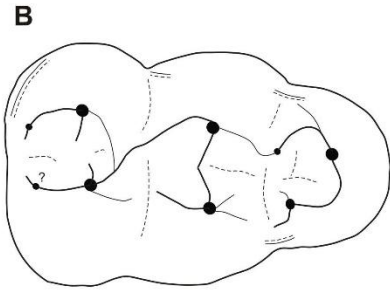
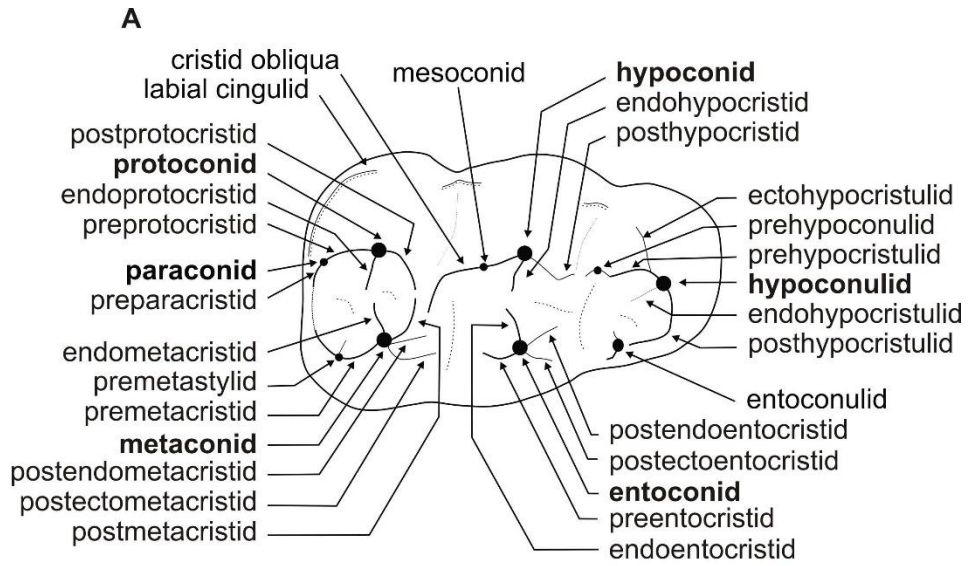
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Figure 2. Hyracoids from Malembo, Angola: *Geniohyus dartevellii*, RMCA-RG6412, right m3 in occlusal (A), lingual (B), and labial (C) views; *Pachyhyrax* cf. *crassidentatus*, RMCA-RG6423, left m3 on a mandible fragment in occlusal (D), lingual (E), and labial (F) views (the arrow indicates the mandibular depression, see text for details); Hyracoidea, genus and species indet., RMCA-RG6416, fragment of a right m1 or m2 in occlusal (G), lingual (H), and labial (I) views; Hyracoidea, genus and species indet., RMCA-RG6425, a proximal phalanx in dorsal (J), plantar (K), and lateral (L, M), distal (N), and proximal (O) views. Scale bar = 1cm.



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712 **Figure 3.** Hyracoids from Malembo, Angola: *Pachyhyrax* cf. *crassidentatus*, RMCA-RGP6423,
713 left m3 on a mandible fragment in posterior view (A); *Geniohyus dartevellei*, RMCA-
714 RGP6412, right m3 in posterior view (B); RMCA-RGP6416, fragment of a right m1 or m2 in
715 posterior view (C). Scale bar = 1cm.



717 **Figure 4.** Dental terminology (A) and comparison of m3 tooth structure of some hyracoids
718 (B-G) and artiodactyls (H-I): *Geniohyus dartevellei*, RMCA-RGP6412 (B); *Geniohyus mirus*,
719 based on NHMUK 9485 and CGM 8634 (C), *Bunohyrax fajumensis*, based on NHMUK 10187,
720 AMNHN 14460, AMNHN 13335, AMNHN 13347, SMNS 43930, SMNS 43939, SMNS 43951,
721 and SMNS 47765 (D); *Bunohyrax major*, AMNH 13346 (E); *Pachyhyrax* cf. *crassidentatus*,
722 RMCA-RGP6423 (F); *Pachyhyrax crassidentatus*, based on YPM 31191, YPM 29166, and DPC
723 7514 (G); *Microbunodon silistrensis* GSP Y21063 (H); *Palaeochoerus* sp. UM-PFY 3267 (I).
724 Variable traits are indicated in red color; all other structures are observable in all mentioned
725 specimens. Scale bar = 1cm.
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