1 **The first fossil skull of an anteater (Vermilingua, Myrmecophagidae) from**

2 **northern South America, a taxonomic reassessment of *Neotamandua* and a**

3 **discussion of the myrmecophagid diversification**

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13 **Abstract.**—The evolutionary history of the South American anteaters, Vermilingua, is

14 incompletely known as consequence of the fragmentary and geographically biased nature of

15 the fossil record of this group. *Neotamandua borealis* is the only recorded extinct species from

16 northern South America, specifically from the Middle Miocene of La Venta area,

17 southwestern Colombia. A new genus and species of myrmecophagid for La Venta, Gen. et

18 sp. nov., is here described based on a new partial skull. Additionally, given that the co-

19 occurrent species of Gen. et sp. nov., *N. borealis*, was originally referred to as *Neotamandua*,

20 the taxonomic status of this genus is revised. The morphological and taxonomic analyses of

21 these taxa indicate that Gen. et sp. nov. may be related to *Tamandua* and that the justification

22   of the generic assignments of the species referred to as *Neotamandua* is weak or insufficient.

23   Two species previously referred to as *Neotamandua* (*N. magna* and *N.? australis*) were

24   designated as *species inquirendae* and new diagnostic information for the redefined genus and

25   its type species, *N. conspicua*, is provided. Together, these results suggest that the

26   diversification of Myrmecophagidae was taxonomically and biogeographically more complex

27   than what has been proposed so far. Considering the new evidence, it is proposed a synthetic

28   model on the diversification of these xenartrans during the late Cenozoic based on the

29   probable relationships between their intrinsic ecological constraints and some major abiotic

30   changes in the Americas.

31

Introduction

33   The anteaters of the suborder Vermilingua are part of Xenarthra, one of the more inclusive

34   clades in the evolutionary tree of the placental mammals (Eutheria) and a characteristic group

35   in the land mammal assemblages of the middle-late Cenozoic of the Americas (McDonald et

36   al., 2008; Foley et al., 2016; Halliday et al., 2016; Feijoo and Parada, 2017). Within

37   Xenarthra, Vermilingua belongs to Pilosa, a clade that also includes the sloths, i.e.,

38   Tardigrada. Today, Vemilingua comprises the genera *Cyclopes* (pygmy anteaters), *Tamandua*

39   (collared anteaters) and *Myrmecophaga* (giant anteaters). These genera groups ten extant

40   species, most of which (seven) belong to *Cyclopes*, according to the most recent exhaustive

41   taxonomic revision (Miranda et al., 2017). The classic phylogenetic hypothesis reunites

42   *Tamandua* and *Myrmecophaga* in the family Myrmecophagidae, while *Cyclopes* is located in

43   a basal position with respect to Myrmecophagidae as the only recent form of the family

44 Cyclopedidae (Engelmann, 1985). With the connotation of a superior taxonomic hierarchy

45 (i.e., at the family level; Barros et al., 2008; Gibb et al., 2015), according to an early

46 evolutionary divergence (Hirschfeld, 1976; Delsuc et al., 2001; Gibb et al., 2016) and in

47 recognition of a more extended use in the scientific literature, the names Myrmecophagidae

48 and Cyclopedidae are used here, instead of Myrmecophaginae and Cyclopinae *sensu* Gaudin

49 and Branham (1998), respectively. However, the taxonomic content of Myrmecophaginae and

50 Cyclopinae, including extinct forms, is considered as transferable to their counterparties

51 (McDonald et al., 2008).

52   The living anteaters, whose mean body mass ranges from ~0.4 to 30 kilograms (Gaudin

53 et al., 2018), are highly, morphologically specialized mammals due to their remarkable

54 skeleton and soft-anatomy modifications, which are closely related to their myrmecophagous

55 diets, i.e., diets consisting of at least 90% of ants/termites (Redford, 1987; McDonald et al.,

56 2008). Many of these adaptations, anatomically located in the skull and jaws, are associated

57 between themselves in several ways, being part of the architecture of an integrated functional

58 system of food apprehension and ingestion. Among these features, the following are some of

59 the most noteworthy: rostral elongation and narrowing, basicranial-basifacial axis curvature,

60 complete loss of teeth, gracile jaw, reduction of the adductor jaw muscles, unfused jaw

61 symphysis and protrusible long tongue (Reiss, 2001; Gaudin and McDonald, 2008; McDonald

62 et al., 2008). Several of these morphological specializations are convergent with those

63 described for other myrmecophagous mammals such as the pangolins (Pholidota) and the

64 aardvarks (Tubulidentata), so it is not surprising that early systematic researchers erroneously

65 proposed close common ancestry of Vermilingua with these Old world groups based on their

66 superficial similarities (e.g., Engelmann, 1978; Norman and Ashley, 1994).

67   In spite of their unique biology and ecology, at least in the context of the land mammals

68 of the Americas, the evolutionary history of the anteaters is largely obscured by their poor,

69 fragmentary and geographically biased fossil record (Hirschfeld, 1976; Gaudin and Branham,

70 1998; McDonald et al., 2008). Generally, five valid genera and nine species are recognized in

71 the fossil record of Vermilingua, two genera and two species of which have extant

72 representatives, i.e., *Myrmecophaga tridactyla* and *Tamandua tetradactyla*.

73 Myrmecophagidae groups nearly all of these fossil taxa (only one genus and one species for

74 Cyclopedidae) in a general biochron that begin ca. 18 million years ago (Mya), most of them

75 distributed throughout the Neogene (McDonald et al., 2008). But while the record of this

76 family for the latter period is taxonomically more diverse than that for the Quaternary, it also

77 poses more difficulties in the systematic framework of the implicated taxa. The oldest member

78 of Myrmecophagidae is *Protamandua rothi*, from the late Early Miocene of the Province of

79 Santa Cruz, southern Argentina (Ameghino, 1904). This species has been well validated from

80 a pair of incomplete skulls and several postcranial bones, but the validity of other co-occurrent

81 putative vermilinguan (myrmecophagid?) taxa is, at least, questionable (Hirschfeld, 1976;

82 McDonald et al., 2008). For the early Middle Miocene has been reported a myrmecophagid

83 doubtfully assigned to *Neotamandua*, and yet used to create a new species from isolated

84 humeral remains (*N.? australis*; Scillato-Yané and Carlini, 1998). In the latter genus,

85 postcranial material of a medium-to-large sized anteater from La Venta area, southwestern

86 Colombia, was also allocated with some uncertainty (Hirschfeld, 1985). The description of

87 this material represents the only nominal extinct species from northern South America.

88 *Neotamandua* chronologically extends to the Late Miocene and Early Pliocene with the

89 species *N. magna* (Ameghino, 1919), *N. greslebini* (Kraglievich, 1940) and *N. conspicua*

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90   (type species; Rovereto, 1914), all of which come from northwestern Argentina (Provinces of

91   Catamarca and Tucumán). This genus is typically recognized as morphologically similar

92   (even directly ancestral) to *Myrmecophaga*, although the latter is smaller in body size

93   (Hirschfeld, 1976; Gaudin and Branham, 1998). Considering the very few anatomically

94   correlatable elements on which the different species referred to as *Neotamandua* are based,

95   Hirschfeld (1976) and Scillato-Yané and Carlini (1998) suggested that this genus could be

96   paraphyletic. Furthermore, the latter authors proposed the hypothesis that *Neotamandua* is

97   composed by two distinct evolutionary lineages: the one more closely related to

98   *Myrmecophaga* and other to *Tamandua*. In turn, these two lineages would have diverged in

99   allopatry in South America, in such a way that the geographic origin of *Myrmecophaga* is

100   located in northern South America, while that of *Tamandua* is in southern South America.

101   In this article, we describe the first fossil skull of a myrmecophagid (and vermilinguan)

102   from northern South America. This specimen was collected in the Middle Miocene of La

103   Victoria Formation of La Venta area, Colombia. This allowed us to revise the taxonomic

104   status of *Neotamandua*, as it is the only nominal taxon previously reported for the same region

105   and geological unit in Colombia. The results prompt the development of a discussion on a

106   model of diversification for Myrmecophagidae in which new and previous hypothesis about

107   this evolutionary event are synthesized. This contribution is intended to revaluate, expand and

108   integrate biotic and abiotic evidence related to the diversification of this fascinating mammal

109   group, emphasizing on the biogeographic role of tropical, low latitude regions of the

110   Americas.

111

112   **Material and methods**

113   The cranial specimen described for the first time here for Colombia (VPPLT 975) comes from

114   a light-brown mudstone layer in the Llano Largo field, around 2 Km northeast of La Victoria

115   town, Municipality of Villavieja, Department of Huila (Fig. 1). Strata of the La Victoria

116   Formation outcrop there, within the paleontologically relevant area of La Venta. La Victoria

117   Formation is a geological unit of ~500 m in thickness which is mainly composed by

118   bioturbated mudstones (Anderson et al., 2016). These sedimentites are interrupted by very

119   continuous, coarse-to-fine grained sandstones with crossbedding and erosive bases. According

120   to the lithostratigraphic scheme of Guerrero (1997; Fig. 1), the new skull was found at a level

121   stratigraphically close (<20 m) and below the Chunchullo sandstone beds, i.e., the lower part

122   of the La Victoria Formation. This corresponds to the unit referred to as "Unit between the

123   Cerro Gordo and Chunchullo sandstone beds". As described by the same author, this unit,

124   whose thickness ranges from ~80 to 160 m, is predominantly composed of mudstones and

125   some interlayers of sandstones. This sedimentary body bears abundant plutonic and volcanic

126   fragments from the lower Jurassic basement of the Honda Group (Saldaña Formation), as well

127   as clasts of volcanic rocks formed in the magmatic arc of the Cordillera Central of Colombia

128   during the Middle Miocene (Anderson et al., 2016).

129   The general paleoenvironment inferred for the La Victoria Formation is a meandering

130   fluvial system (except for the Cerbatana conglomerate, associated to an anastomosed system)

131   with significant soil development in flood plain zones (Guerrero, 1997). The ages calculated

132   by Guerrero (1997) and Flynn et al. (1997) using magnetic polarity stratigraphy and

133   geochronology, indicate sedimentary deposition took place in an interval of 13.8☐12.5 Mya.

134   These results have recently been reinforced by the U-Pb geochronology of detrital zircons

135   recovered in this formation (Anderson et al., 2016), showing an age range of 14.4 ± 1.9 ☐

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136   13.2 ± 1.3 Mya. This interval coincides approximately with the early Serravalian, sub-stage of

137   the Middle Miocene.

138   With some nomenclatural modifications, cranial measurements are based on those of

139   Hossotani et al. (2017) (Fig. 2; see Anatomical Abbreviations). All these measurements are in

140   millimetres (mm). The description of the new skull of La Venta includes a rough body mass

141   estimation of the respective individual from a traditional allometric approach. All these data

142   and analyses are compiled in the Supplementary material (Appendices S1 and S3). For the

143   taxonomic analysis of the genus *Neotamandua*, the justifications of the generic allocations for

144   the referred species (at least doubtfully) were revised in all the relevant scientific literature.

145   These species are: *Neotamandua conspicua* Rovereto, 1914 (type species); *Neotamandua*

146   *magna* Ameghino, 1919; *Neotamandua greslebini* Kraglievich, 1940; *Neotamandua borealis*

147   Hirschfeld, 1976; *Neotamandua*? *australis* Scillato-Yané and Carlini, 1998. Additionally,

148   some observations were made on the holotypes of *N. conspicua* (MACN 8097) and *N.*

149   *borealis* (UCMP 39847) to reexamine the described characteristics for these species in the

150   original publications (Rovereto [1914] and Hirschfeld [1976], respectively). The conceptual

151   model of Plotcnick and Warner (2006) for the identification of taxonomic wastebaskets was

152   applied to *Neotamandua*. From the foregoing and the designation of the specimen FMNH

153   P14419 as epitype of *N. conspicua*, a diagnosis for *Neotamandua* was proposed. See a list of

154   all the studied fossil specimens in the Appendix S1 of the Supplementary material.

155   On the other hand, considering that Hirschfeld (1976), in her description of *N. borealis*,

156   did not include morphological comparisons based on postcranial bones of this species and

157   homologous elements of species referred to as *Neotamandua* from southern South America,

158   we performed this task and a preliminary character distribution analysis from postcrania of

159   these taxa to explore the hypothesis that they are closely related. Forcibly, *N. magna* and *N.?*

160   *australis* are excluded from the comparisons since they do not have osteological elements

161   correlated with those of *N. borealis* (or any other species referred to as *Neotamandua*).

162   Additionally, as a result of the loss of its holotype (McDonald et al., 2008), comparisons with

163   *N. greslebini* are based exclusively on the non-illustrated description by Kraglievich (1940).

164   Other comparisons include postcranium collected by Juan Méndez in 1911 in the upper

165   Miocene of the Andalhuala locality, Province of Catamarca, Argentina. This material was

166   assigned to *Neotamandua* (*Neotamandua* sp.) without a reference publication. McDonald et

167   al. (2008) manifested doubt about this taxonomic assignment (*Neotamandua*?), but these

168   authors simultaneously speculated that it might be the lost holotype of *N. greslebini*.

169   Following McKenna and Bell (1997), the genus *Nunezia* is considered a junior synonym

170   of *Myrmecophaga*. Myological inferences are based on Hirschfeld (1976) and Gambaryan et

171   al. (2009).

172   *Repositories and institutional abbreviations*.—CAC: Cátedra de Anatomía Comparada,

173   Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata; FMNH: Field

174   Museum, Chicago, IL., USA; ICN: Instituto de Ciencias Naturales, Facultad de Ciencias,

175   Universidad Nacional, Bogotá, Colombia; MACN: Museo Argentino de Ciencias Naturales

176   'Bernardino Rivadavia', Buenos Aires, Argentina; MLP: Museo de La Plata, Facultad de

177   Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; MPT:

178   Museo Provincial de Tucumán, Tucumán, Argentina; UCMP: University of California

179   Museum of Paleontology, Berkeley, CA., USA; VPPLT: Museo de Historia Natural La

180   Tatacoa, La Victoria, Huila, Colombia; YPM: Peabody Museum, Yale University, New

181   Haven, CT, USA.

182   *Anatomical abbreviations*.—Abbreviations of equivalent measurements by Hossotani et al.,

183   (2017) in parenthesis. FL, frontal length; GSL (SL), greatest skull length; MBW (NC),

184   maximum braincase width; ML, maxilla length; NL, nasal length; NW (NB), nasal width; PL,

185   parietal length.

186

187   **Systematic paleontology**

188   Superorder Xenarthra Cope, 1889

189   Order Pilosa Flower, 1883

190   Suborder Vermilingua Illiger, 1811

191   Family Myrmecophagidae Gray, 1825

192   New genus

193   *Type species*.—Gen. et sp. nov. (see below).

194   *Diagnosis*.—As for the type species by monotypy.

195   *Etymology*.—[this space is left in blank intentionally]

196   *Remarks*.—We propose the creation of Gen. nov. partly based on direct or indirect

197   comparison between the holotypic skull of the only known and type species, Gen. et sp. nov.,

198   and cranial/postcranial material assigned to the species *Neotamandua borealis* and *N.*

199   *conspicua* (see below the sections "Revised taxonomy of the genus *Neotamandua*" and

200   "Systematic account for *Neotamandua*").

201

202   Gen. et sp. nov.

203   *Holotype*.—VPPLT 975, anterior portion of a skull, without jugals nor premaxillae.

204   *Diagnosis*.—Middle sized myrmecophagid, slightly smaller than *Tamandua* and even more

205   than *Neotamandua*. It can be differentiated from other genera/species of anteaters by the

206   following combination of cranial features: relatively width rostrum, similar to *Tamandua*;

207   narrow and strongly tapered nasals toward their anterior end; anteroposterior length of the pre-

208   orbital section of frontals equal to more than two thirds of the anteroposterior length of nasals;

209   jugals inserted from the same level of the most anterior border of the lacrimal; anterior portion

210   of the orbit more laterally extended in the superior wall in the inferior one, without forming a

211   conspicuous dome as in *Neotamandua conspicua*.

212   *Description*.— The rostrum is proportionally shorter and more robust than those in

213   *Myrmecophaga* and *N. conspicua* (see below), but less than in *Tamandua*. In dorsal view, it is

214   very similar to the skull of *Tamandua*, with at least four characteristics remarkably different

215   with respect this extant genus: (1) lower rostrum; (2) rostrum more regularly tapered; (3)

216   narrower and more anteriorly tapered nasals; (4) pre-orbital section of the frontals more

217   anteroposteriorly elongated. In dorsal view, the rostrum shows a slight bulge in its middle

218   part, similar to that in *Tamandua* and *Myrmecophaga*. However, in VPPLT 975 this bulge is

219   even subtler than in the living myrmecophagids. Apparently, the nasals are shorter than

220   frontals and are poorly exposed in lateral view. The jugals are absent by preservation, but it is

221   possible to recognize their insertion location, which is more anterior than in *Myrmecophaga*,

222   but more posterior than in *Tamandua*. Associated to the insertion of the jugal, there is a

223   reduced posterolateral process of the maxilla in comparison with that of *Myrmecophaga*,

224   similar in *Tamandua*. The right side of the skull preserves better the lacrimal zone, but it is

225   simultaneously more deformed around the fronto-maxillary suture than in the left side. The

226   lacrimal is longer in its anteroposterior axis than in that dorsoventral. The same bone is

227   proportionally smaller than in *Tamandua* and even more than in *N. conspicua*. It has a

228   triangular outline (at least anteriorly), similar to *Myrmecophaga* and unlike *Tamandua*

229   (irregularly rounded, ovated, or, infrequently, sub-triangular lacrimal). The maxilla is not part

230   of the orbit. The superior wall of the orbit is more laterally expanded than the inferior wall,

231   without forming a conspicuous dome as in *N. conspicua*. This is similar to the condition

232   observed in *Myrmecophaga* and differs from that in *Tamandua*, in which the inferior wall is

233   prominent given that it is more laterally expanded. It is not possible to recognize lacrimal nor

234   orbital foramina. In ventral view, the dorsal border of the orbit is regularly concave. The

235   palatines are less laterally extended than in *Tamandua* and apparently there are no palatine

236   "wings" (noticeable lateral expansions of the palatines), unlike *N. conspicua*.

237   *Etymology*.—[this space is left in blank intentionally]

238   *Remarks*.—See cranial measurements taken for this new species and other myrmecophagids in

239   the Table 1. The estimated body mass for this individual is ca. 3.9 Kg (Appendix S3 of the

240   Supplementary material). As consequence of the preservation, some sutures in VPPLT 975 are

241   distinguishable in dorsal and lateral views, but virtually no suture is clearly detectable in

242   ventral view.

243

244   Revised taxonomy of the genus *Neotamandua*

245   *Taxonomic history and discussion on the taxonomic status of Neotamandua*.—The genus

246   *Neotamandua* was proposed by Rovereto (1914) based on a posterior portion of a skull

247   (MACN 8097), which was collected from upper Miocene-to-Pliocene strata of the Province of

248   Catamarca, Argentina. The name *Neotamandua*, literally meaning 'new tamandua', was

249   coined by Rovereto in allusion to the cranial similarity of the type species, *N. conspicua*, with

250   the extant genus *Tamandua*, rather than with *Myrmecophaga*. This detail would be historically

251   paradoxical, as will be shown below. It is important to note that Rovereto (1914) did not

252   provide a diagnosis for *Neotamandua*, but he just briefly described the holotype of *N.*

253   *conspicua*, emphasizing its elongated parietals. However, this feature, more comparable with

254   that in *Myrmecophaga* than that in any other myrmecophagid, was correlated with the

255   anteroposterior length of the parietals in *Tamandua*. A few years after Rovereto's work,

256   Carlos Ameghino (Ameghino, 1919) used a pelvis (MPT 58) recovered in contemporary strata

257   from the Province of Tucuman, Argentina, to create a new species, *N. magna*. Despite the

258   taxonomic assignment of this pelvis to *Neotamandua*, Ameghino discussed that, alternatively,

259   this species could belong to other genus of larger body size, as Kraglievich (1940) also held.

260   Formally, *N. magna* has not been reevaluated, but McDonald et al. (2008) suggested that,

261   given that this species was transferred to *Nunezia* by Kraglievich (1934), and *Nunezia* is

262   considered a junior synonym of *Myrmecophaga* (Hirschfeld, 1976; McKenna and Bell, 1997),

263   then *N. magna* should be included in the latter genus, i.e., *Myrmecophaga magna* comb. nov.

264   (unpublished). Indeed, the morphological differences cited by Ameghino (1919) and

265   Kraglievich (1940) between the pelvis of *N. magna* and that of *M. tridactyla* (e.g., greater

266   width and ventral flattening of the intermediate sacral vertebrae) do not seem sufficient to

267   consider a generic distinction between these species.

268   Two decades later, Kraglievich (1940) proposed a new species based on postcranium

269   collected in the upper Miocene of the Province of Catamarca. This was initially assigned to *N.*

270   *conspicua*. According to Kraglievich, the then new species, *N. greslebini*, is easily identifiable

271   by its large size, intermediate between those of *N. conspicua* and *N. magna*. Similar to

272   Rovereto (1914), this author correlated with *Tamandua* his generic assignment of *N.*

273   *greslebini* to *Neotamandua*, considering the similarity between the fossil specimens of this

274   species and homologous elements of the living collared anteater (Kraglievich, p. 633). The

275   holotype of *N. greslebini* is missing or mixed up with material labelled with generic names of

276   extinct anteaters (i.e., *Neotamandua* and *Palaeomyrmidon*) in the Museo Argentino de

277   Ciencias Naturales (MACN), in Buenos Aires, Argentina (McDonald et al., 2008).

278   Already in the second half of the 20th century, a controversy about a possible

279   synonymy between *Neotamandua* and *Myrmecophaga* arose. This means that there was a

280   radical paradigmatic shift in myrmecophagid systematics from the early 20th-century

281   perspectives which considered that *Neotamandua* is closely related to *Tamandua*, to the late

282   20th century ones which considered that *Neotamandua* was even a serious candidate to be a

283   junior synonym of *Myrmecophaga*. This historical change began with the non-cladistic

284   systematic analysis of Hirschfeld (1976), in which *Neotamandua* was originally proposed as

285   the direct ancestor (anagenetic form) of *Myrmecophaga*. In the same work, Hirschfeld created

286   the first and, until now, only nominal extinct species of Vermilingua and Myrmecophagidae

287   for northern South America, *N. borealis* (Middle Miocene of Colombia). Given the scarcity

288   and fragmentation of the specimens referred to as *Neotamandua*, Hirschfeld (1976)

289   recognized the need to revise the taxonomic validity of *N. conspicua*, *N. magna* and *N.*

290   *greslebini*. Indeed, she went beyond and stated that *Neotamandua* species could be

291   representatives of more than one single genus. However, her assignment of *N. borealis* to

292   *Neotamandua* was based primarily on the idea that the fossils she studied are "considerably

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293   more advanced than those known from the Santacruzian [late Early Miocene], closer to the

294   Araucanian [Late Miocene-Pliocene] species and…to the line leading to *Myrmecophaga* than

295   *Tamandua*" (Hirschfeld, p. 421). For this author, many postcranial traits of *N. borealis* are

296   intermediate between *Tamandua* and *Myrmecophaga*. As a questionable methodological

297   aspect, it is important to note that Hirschfeld (1976) did not make osteological comparisons

298   with the southern species of *Neotamandua*, only with postcrania of *Protamandua*, *Tamandua*

299   and *Myrmecophaga* (extant species of the two latter genera).

300   In implicit reply to Hirschfeld (1976), Patterson et al. (1992) highlighted the

301   morphological similarities between the unpublished skull FMNH P14419, catalogued as *N.*

302   *conspicua* in the Field Museum, and the modern skulls of *Myrmecophaga*. For these authors,

303   FMNH P14419 only differs from skulls of the living giant anteater in its smaller size.

304   Consequently, Patterson et al. (1992) suggested to synonymize *Neotamandua* and

305   *Myrmecophaga*, with nomenclatural priority for the latter. Nevertheless, Gaudin and Branham

306   (1998) provided (weak) support for the validity of *Neotamandua* through a comprehensive

307   phylogenetic analysis of Vermilingua. Their results indicate that *Neotamandua* is an

308   independent taxon based on two autapomorphies, being one of them ambiguous and the other

309   one unambiguous. The latter is the horizontal inclination of the glenoid. In the only most

310   parsimonious tree recovered by Gaudin and Branham (1998), *Neotamandua* is closely related

311   to *Myrmecophaga*, not *Tamandua*, as opposed to Rovereto (1914) and Kraglievich (1940).

312   Finally, the last species referred, with doubt, to the genus was *N.? australis* (Scillato-

313   Yané and Carlini, 1998). The holotype of this species consists only of a humerus (MLP 91-IX-

314   6-5) collected in the lower Middle Miocene of the Province of Río Negro, Argentina. Scillato-

315   Yané and Carlini (1998) highlighted some similarities of this material with the humerus of

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316   *Tamandua*. They also expressed considerably uncertainty in assigning it to *Neotamandua*, not

317   only by its fragmentary nature, but from the idea of Hirschfeld about the non-natural (i.e.,

318   non-monophyletic) status of this genus. Without performing a phylogenetic analysis, these

319   authors proposed a hypothesis that *N. borealis* is closely related to *Myrmecophaga*, while *N.*

320   *conspicua* and *N.? australis* are closer to *Tamandua*. If this hypothesis is correct, *N. borealis*

321   does not belong to *Neotamandua* as consequence of the application of the nomenclatural

322   priority principle.

323   In summary, multiple historical factors, including the lack of a diagnosis, insufficient

324   number of anatomically correlatable/highly diagnostic postcranial elements and, especially,

325   absence of cranial-postcranial associations, aroused the relatively arbitrary use of

326   *Neotamandua* as a wastebasket taxon, i.e., a residual genus deriving from weak and/or

327   inadequate systematic analysis. According to the conceptual model of Plotnick and Warner

328   (2006), *Neotamandua* has five (from a total of seven) properties of a genus potentially

329   classifiable as wastebasket: (1) it is an old name (i.e., more than one century to the present);

330   (2) it is [relatively] rich in species (five species, i.e., the most speciose extinct genus of

331   Vermilingua); (3) it has a [relatively] high number of occurrences; (4) it has wide temporal

332   and geographic distributions; (5) it [primarily] groups together specimens poorly preserved

333   and/or difficult to identify. To these five properties we may add the lack of a diagnosis, which

334   is related in some way to the property number two of the Plotnick-Warner model, i.e., genera

335   diagnosed from generalized characters, probably plesiomophies or easily recognizable

336   characters.

337   As it was shown, *Neotamandua* has been invoked as a directly ancestral form of

338   *Tamandua*, or, more recently, of *Myrmecophaga*, from its morphological characteristics in

15

339   common with these two extant genera. But precisely because of this character mosaic, the

340   generic allocation of isolated postcranial remains of myrmecophagids potentially referable to

341   *Neotamandua* should not be reduced or exclusively focused on their comparison with the

342   crown-group, but should also consider the effect of possible homoplasies (e.g., those related to

343   ecological convergences), plesiomorphies and limitations of the fossil record (Plotnick and

344   Warner, 2006). In other words, the apparent affinity between isolated postcranial elements of

345   any Neogene anteater and their homologous in *Myrmecophaga* is not enough to make a

346   reliable generic allocation in *Neotamandua*; diagnostic information of the latter genus is

347   needed, preferably autapomorphies, which enable it to be individually identified and not

348   simply as a set of forms similar to *Myrmecophaga*.

349

350   *Comparisons between northern and southern species referred to as Neotamandua*.— See the

351   Table 2 and 3 for comparisons of postcranial measurements between these species.

352   *N. borealis* and *N. greslebini*.—Both *N. borealis* and *N. greslebini* show two

353   longitudinal, parallel radial ridges, of which the lateral ridge is higher and reaches a more

354   distal level than the cranial one. This is similar to the condition observed in *Myrmecophaga*

355   and differs from the distally convergent radial ridges of *Tamandua*. In *N. borealis*, the lateral

356   ridge is even more distally extended than in *N. greslebini,* in such a way that the flanks of this

357   structure contact the lateral border of the styloid process. According to Kraglievich (1940), in

358   the Argentinean species this ridge ends at an intermediate level between the distal end of the

359   cranial ridge and the styloid process.

16

360   The type material of *N. borealis* includes a proximal epiphysis and part of the diaphysis of a

361   right tibia. According to Kraglievich (1940), the holotype of *N. greslebini* includes two

362   fragments of a tibia, one of them proximal and the other one distal. Both Hirschfeld and

363   Kraglievich claimed greater overall similarity between the tibial fragments of these species

364   and the homologous parts of *Tamandua*, rather than *Myrmecophaga*. This way, the mid-

365   section of the tibias both of *N. borealis* and *N. greslebini* is not as strongly triangular as in

366   *Myrmecophaga*. Rather, this bone segment may vary from gently triangular to sub-rounded in

367   these two species referred to as *Neotamandua*, not as rounded as in *Tamandua*.

368   Hirschfeld (1976) described the astragalus of *N. borealis* (Fig. 4) as intermediate in

369   morphology and size between those in *Tamandua* and *Myrmecophaga*. In contrast,

370   Kraglievich (1940) stated that the astragalus of *N. greslebini* closely resembles that of

371   *Tamandua*. New observations enable us to determine that, in dorsal view, the astragalus of *N.*

372   *borealis* is more similar to that in *Tamandua* than *Myrmecophaga* as consequence of a lateral

373   side of the trochlea larger than the medial one (trochlear asymmetry). As *N. greslebini*, the

374   regular concavity in which is inserted the *flexor digitorum fibularis* tendon extends

375   posteroventrally like a well-defined wedge ("pointed shape" in Kraglievich's words) and it

376   contacts the calcaneal facets across the entire width of the latter. In ventral view, the

377   arrangement of the calcaneal facets in *N. borealis* is a kind of "transition" between that in

378   *Myrmecophaga* and *Tamandua*. In *N. borealis*, the ectal and sustentacular are largely

379   separated by a wide and deep sulcus, but there is an incipient connection. This condition is

380   approximately comparable to that described by Kraglievich (1940) for *N. greslebini* and

381   differs from the fully separated calcaneal facets in *Protamandua* and *Tamandua*. In this sense,

382   Kraglievich was not very explicit in pointing out the degree of development of the connection

383   between these facets, but it is inferred that it is not exactly wide as in *Myrmecophaga* when he

384   wrote that "…these calcaneal articulations are, *apparently*, posteriorly fused…" (italics are

385   ours; Kraglievich, p. 635).

386   Similar to *N. greslebini*, *N. borealis* has a narrow fibular calcaneal facet, which is located

387   laterally and in a slightly different plane with respect to that of the ectal facet (Fig. 4). In both

388   of the former species, the *sustentaculum* is less medially projected than in *Myrmecophaga*.

389   They also show an accessory facet in the anterior end of the calcaneum that articulates with

390   the astragalar head, similarly to *Tamandua*. In all the aforementioned taxa, this facet is closer

391   (even in contact) to the cuboid facet. In *N. borealis* and *N. greslebini*, the cuboid facet is

392   transversely ovate and concave. A unique feature in common for them is the presence of a

393   short tendinous groove (shorter than in *Myrmecophaga*) and strongly concave (Fig. 4). It is the

394   continuation of the longitudinal and conspicuous ridge that runs the calcaneum in its lateral

395   side. The latter separates tendons of the *fibularis longus* and *accesorius* muscles (Hirschfeld,

396   1976; Gambaryan et al., 2009). In *N. borealis*, this ridge is more conspicuous than in

397   *Tamandua* and less than in *Myrmecophaga*.

398   *N. borealis* and *Neotamandua* sp.—See the Table 3 for comparison of postcranial

399   measurements between these species. The distal epiphysis of the radius in *Neotamandua* sp.

400   (MACN 2408) is more massive than that in *N. borealis*. In the latter species, the distal end of

401   the radius is relatively stylized, similar to *Tamandua*. However, the morphologies of *N.*

402   *borealis* and *Neotamandua* sp. are more comparable between them. In distal view, the styloid

403   process of these species is more elongated and posteriorly oriented than in *Tamandua*. In the

404   latter extant genus, the transverse axis (longer axis) of the facet for distal articulation is

405   forming an angle close to 45° with respect to the plane of the anterior side of the radius, while

18

406   this axis is nearly parallel with respect that plane in *N. borealis* and *Neotamandua* sp. This

407   difference gives a non-rotated appearance to the distal radius of the compared *Neotamandua*

408   species, unlike the same epiphysis in *Tamandua*. In anterior view, the distal articulation facet

409   of *N. borealis* and *Neotamandua* sp. is visible in wedge shape pointing towards the medial

410   border. Additionally, in the same view, this facet exhibits comparable exposures in both of the

411   latter species, considerably more than in *Tamandua*. The posterior side of the distal epiphysis

412   is from flat to slightly concave in *N. borealis* and *Neotamandua* sp., unlike the convex

413   posterior side in *N. greslebini* (this observation could suggest that the material of

414   *Neotamandua* sp. is not the holotype of *N. greslebini*, as speculated by McDonald et al., 2008)

415   and *Tamandua*. The distal extension of the lateral ridge in *N. borealis* and *Neotamandua* sp. is

416   similar.

417   The astragalus of *Neotamandua* sp. (MACN 2406) is only represented by the astragalar body.

418   The medial trochlea is smaller than the lateral trochlea, but this asymmetry is lower than in *N.*

419   *borealis*. In addition, these sections of the trochlea are proportionally less separated in the

420   latter species than in *Neotamandua* sp. On the other hand, the calcaneum is fragmentary in

421   *Neotamandua* sp. (MACN 2411). As in the case of the astragalus, the preserved portion is the

422   bone body. The ectal facet is sub-triangular in shape in *Neotamandua* sp., while it is

423   approximately sub-oval in *N. borealis*. The sustentacular facet is more medially extended in

424   the latter species than in *Neotamandua* sp. In both species, the cuboid facet is partially visible

425   in dorsal view, particularly in *Neotamandua* sp. In the same view, the lateral ridge is slightly

426   exposed in *N. borealis*, not so much as in *Neotamandua* sp.

427   *Discussion.*—The former comparisons allow for recognizing a few morphological

428   similarities and differences between homologous postcranial elements of *N. borealis*, *N.*

19

429   *greslebini* and *Neotamandua* sp. It is considered that some similarities in these species are

430   potentially diagnostic at the genus level, namely the sub-rounded to gently triangular shape of

431   the tibial mid-section; ectal and sustentacular facets incipiently connected in the astragalus;

432   and a short tendinous groove in the lateral side of the calcaneum (Table 4). These similarities

433   seem to support the hypothesis that these northern and southern South American species

434   referred to as *Neotamandua* are closely related and, consequently, that they are correctly

435   included in the same genus. Alternatively, these common features could be

436   symplesiomorphies of a hypothetical lineage of myrmecophagids more late diverging than

437   *Protamandua* and apparently closer to *Myrmecophaga* than *Tamandua*. Provisionally, from

438   the analysis presented, it is proposed to circumscribe the genus *Neotamandua* to the nominal

439   species *N. conspicua* (type species), *N. greslebini* and *N. borealis*. Since *N. magna* and *N.*?

440   *australis* are doubtfully assigned to *Neotamandua* or its allocation in this genus has been

441   seriously questioned (McDonald et al., 2008; this work), they are considered *species*

442   *inquirendae*, following the International Code of Zoological Nomenclature (Ride et al., 1999).

443   To denote the questionable generic allocation of *N. magna* is suggested the use of inverted

444   commas, i.e., '*N.*' *magna*. The material referred to as *Neotamandua* sp. seems correctly

445   referred to this genus, but it should be further tested. It is possible that these specimens

446   correspond to a new species.

447   The diagnosis for *Neotamandua* proposed below is largely based on the designation of the

448   specimen FMNH P14419 as epitype for the type species (see below), *N. conspicua*, after

449   considering the fragmentary nature of the holotype of this taxon (MACN 8097; Rovereto,

450   1914), and, consequently, its ambiguity or lack of some taxonomically relevant features,

451   particularly in the rostrum. In addition, the potentially diagnostic postcranial features for

452   *Neotamandua* that has been identified above are also incorporated in the new diagnosis until

453   cranial-postcranial associations are found and studied.

454

Systematic account for *Neotamandua*

456   Suborder Vermilingua Illiger, 1811

457   Family Myrmecophagidae Gray, 1825

458   Genus *Neotamandua* Rovereto, 1914

459   *Type species.—N. conspicua* Rovereto, 1914.

460   *Other species.—'N.' magna* Ameghino, 1919; *N. greslebini* Kraglievich, 1940; *N. borealis*

461   Hirschfeld, 1976; *N.? australis* Scillato-Yané and Carlini, 1998.

462   *Diagnosis.*—Middle-to-large sized myrmecophagid, larger than *Tamandua* but smaller than

463   *Myrmecophaga*. It can be differentiated from other vermilinguans by the following

464   combination of characteristics: in dorsal view, rostrum strongly tapered towards its anterior

465   end (more than in any other myrmecophagid), with a regular transition in width from the

466   anterior portion of the frontals to the anterior end of the nasals; reduced lacrimal which is not

467   part of the orbit; jugal inserted in posteroventral position with respect to the lacrimal and

468   slightly projected in posterodorsal direction; frontal forming a dorsal dome at the orbit level;

469   hard palate well extended towards the posterior end of the skull, close to the ventral border of

470   the occipital condyles; squamosal (= posterior) zygomatic process dorsally inclined; presence

471   of palatine "wings"; horizontal inclination of the glenoid (Gaudin and Branham, 1998); sub-

472   oval to gently triangular shape of the tibial mid-section; ectal and sustentacular facets

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473   incipiently connected in the astragalus; short tendinous groove in the lateral side of the

474   calcaneum.

475   *LSID*.—urn:lsid:zoobank.org:act:4EC0ABE1-C013-4113-9956-5DBD6E79FCEA

476

477   *Neotamandua conspicua* Rovereto, 1914

478   *Holotype*.—MACN 8097, posterior portion of a skull.

479   *Epitype*.—FMNH P14419, nearly complete skull but with fractured rostrum and partially

480   eroded frontals and parietals.

481   *Diagnosis*.—See the diagnosis for *Neotamandua* above. The postcranial diagnostic features

482   included there do not belong to material known for this species.

483   *Occurrence*.—MACN 8097 is from an indeterminate locality in the Santa María Valley,

484   Province of Catamarca, Argentina (Rovereto, 1914). Probably from the Andalhuala

485   Formation. Upper Miocene (McDonald et al., 2008; Bonini, 2014; Esteban et al., 2014).

486   FMNH P 14419 is from the Corral Quemado area, Province of Catamarca, Argentina. Corral

487   Quemado Formation. Lower Pliocene (Bonini, 2014; Esteban et al., 2014). This specimen was

488   collected by Robert Thorne and Felipe Méndez during the Second Captain Marshall Field

489   Paleontological Expedition, which was led by Elmer S. Riggs and developed in Argentina and

490   Bolivia in 1926□1927 (Simpson, pers. comm.; Riggs, 1928). In the Field Museum, where it is

491   deposited, has been catalogued as *N. conspicua*. There are no known referencial publications

492   that support the taxonomic assignation to this species, except in Gaudin and Branham (1998)

493   and, now, in this work from direct comparison with its holotype.

494   *Description.*—The skull FMNH P14419 is anteroposteriorly elongated, with a general

495   architecture which is more similar to that in *Myrmecophaga* than *Tamandua*. In dorsal view,

496   both the rostrum, in general, as well as the nasals, in particular, are anteriorly tapered. The

497   pre-orbital section of the frontals is proportionally less elongated than in *Myrmecophaga*. The

498   lacrimal has a sub-triangular outline and its anteroposterior and dorsoventral lengths are

499   similar, unlike *Myrmecophaga*, whose lacrimal is triangular and more anteroposteriorly

500   elongated. The insertion of the jugals is more ventral and posterior than in *Myrmecophaga* and

501   even more than *Tamandua*. Each jugal is slightly tapered by mediolateral compression in its

502   posterior end and it is posterodorsally projected, instead of posteroventrally as in

503   *Myrmecophaga*. The posterolateral process of the maxilla contacts the entire anterior and

504   ventral borders of the lacrimal. The orbital ridge is less prominent than in *Myrmecophaga*.

505   The superior orbital wall is laterally expanded, forming a roof more developed than in

506   *Myrmecophaga*. At the orbit level, the palatines are also laterally expanded, forming palatine

507   "wings". These structures make the anterior hard palate look wider than the posterior palate.

508   The posterior end of the hard palate is less ventrally projected, as opposed to *Tamandua* and

509   *Myrmecophaga*. In lateral view, the squamosal zygomatic processes are dorsally inclined,

510   contrary to the ventral inclination of the same bone projection in *Tamandua* and

511   *Myrmecophaga*. This feature would be a convergence with *Cyclopes*. The braincase is

512   proportionally larger than in *Myrmecophaga*, but smaller than in *Tamandua*. The tympanic

513   bulla is less developed than in *Tamandua*. The external auditory meatus has subcircular to

514   circular shape, similar to *Myrmecophaga* (ovated in *Tamandua*). In *N. conspicua* the same

515   opening is located in a posterodorsal position, as *Myrmecophaga* and in contrast with

516   *Tamandua*, in which it has an anterodorsal position. Despite the palatopterygoid suture is not

23

517   well preserved, it appears to be more similar to the irregular suture in *Myrmecophaga*, with a

518   posteriorly opened, asymmetrical "V" shape, than the regular suture in *Tamandua*, with an

519   anteriorly opened, symmetrical "V" shape. There is no interpterygoid vacuity where a soft

520   palate could be established, similar to *Myrmecophaga*. The occipital condyles are

521   proportionally larger than in *Myrmecophaga*.

522   *LSID*.—urn:lsid:zoobank.org:act:C4DC62D5-6470-4A04-B152-D42ED3BA332C

523   *Remarks*.—The cranial measurements taken for FMNH P14419 are shown in the Table 1.

524

Discussion

526   *Systematic implications*.—This works includes the first description of a new, valid extinct

527   genus for Myrmecophagidae in the last century, i.e., Gen. nov. Likewise, it constitutes a novel

528   taxonomic comprehensive reassessment for *Neotamandua* since the work by Hirschfeld

529   (1976). The results suggest that there are still critical gaps in our knowledge on the

530   composition and diversity of the Neogene assemblages of these xenartrans, particularly in the

531   tropical region of South America. With the inclusion of Gen. et sp. nov. (Fig. 6),

532   Myrmecophagidae now comprises at least five genera (three of them fully extinct) and 11

533   nominal species (eight extinct species), namely [the dagger means extinct species]:

534   *Protamandua rothi*[†]; *Neotamandua? australis*[†]; *Neotamandua borealis*[†]; Gen. et sp. nov. [†];

535   '*Neotamandua*' *magna*[†]; *Neotamandua greslebini*[†]; *Neotamandua conspicua*[†]; *Myrmecophaga*

536   *caroloameghinoi*[†]; *Myrmecophaga tridactyla*; *Tamandua tetradactyla*; and *Tamandua*

537   *Mexicana* (McDonald et al., 2008; this work). Of these taxa, only two genera and two species

538   have fossil occurrence in northern South America: *N. borealis* (Middle Miocene of Colombia;

539   Hirschfeld, 1976) and Gen. et sp. nov. (Middle Miocene of Colombia; this work) (Fig. 7). The

540   latter taxon is a small-to-middle sized myrmecophagid, comparable but slightly smaller than

541   *Tamandua*. The general morphology of the skull of this new anteater resembles more to that

542   of *Tamandua* than any other known taxon. It shows remarkable features such as: (1) strongly

543   tapered nasals toward its anterior rostrum; (2) relatively low rostrum and anterior section of

544   frontals; (3) large pre-orbital section of frontals; and (4) strongly triangulated (anterior)

545   lacrimal. The tapering of nasals is a characteristic in common with *N. conspicua*, but in the

546   latter species the entire rostrum is tapered, not only the nasals, as Gen. et sp. nov. The

547   relatively low rostrum and anterior section of frontals seems to indicate a plesiomorphy, given

548   that this feature is apparently present in *P. rothi*. A large pre-orbital section of frontals is

549   shared, in (nearly) extreme condition, by *N. conspicua* and, especially, *Myrmecophaga*, but it

550   should be noted that in Gen. et sp. nov. there is no such as elongated skull. And, finally, the

551   strongly triangulated (anterior) lacrimal in the latter species is superficially similar to that in

552   *Myrmecophaga*. Estimates of cranial measurements and features (rostrum length, exposure of

553   the maxilla in the orbit and curvature of the basicranial-basifacial axis) used for coding the

554   characters with numbers 4, 8, 9 and 42 of the character list by Gaudin and Branham (1998),

555   enable us to tentatively infer the phylogenetic position of Gen. et sp. nov. as a taxon included

556   within the clade *Tamandua + Neotamandua + Myrmecophaga* and located in a polytomy with

557   *Tamandua*. Under this preliminary phylogenetic analysis, which is not presented in the results

558   section because there is no enough information for coding the new taxon, *Protamandua* is

559   well supported as the most basal myrmecophagid as consequence of sharing several character

560   states with non-Myrmecophagidae Vermilingua (i.e., *Cyclopes* and *Palaeomyrmidon*; for

561   more details, see Gaudin and Branham, 1998). For future studies, the subfamilial name

25

562   "Myrmecophaginae" is tentatively suggested for all the Myrmecophagidae more late

563   diverging than *Protamandua*, including possibly Gen. et sp. nov. In this sense, new and more

564   complete material referable to the latter taxon is required to shed light on its phylogenetic

565   position.

566   On other hand, the taxonomic analysis of *Neotamandua* and its referred species

567   indicates that these taxa were based on a poorly supported taxonomy. Other case of extinct

568   vermilinguans with flawed systematics in low levels of the taxonomic hierarchy was noted by

569   McDonald et al. (2008) with regard to genera and species proposed from isolated postcranial

570   elements of putative myrmecophagids or even members of new, distinct families from the

571   Early Miocene of Santa Cruz, southern Argentina. These authors, partially based on

572   comparisons by Hirschfeld (1976), argued that the number of taxa claimed for that area and

573   interval (seven genera and nine species; e.g., *Promyrmephagus*, *Adiastaltus*; Ameghino, 1894)

574   has been artificially inflated, even though it is still possible to revalidate taxa other than the

575   well validated species *P. rothi* (McDonald et al., 2008). All these research problems in

576   systematics imply the need to regularly reevaluate the taxonomy of extinct anteaters through

577   reexamination, when possible, of previously described material and the study of new

578   specimens. While it is true that the fossil record of Vermilingua is poor and fragmentary in

579   comparison, for instance, with that of other xenartrans such as the Tardigrada, the sampling

580   effort should be increased in order to have greater recovery of fossil material for this group,

581   especially in areas known for their preservation potential (e.g., southern and northwestern

582   Argentina, southwestern Colombia).

583   Even though, no diagnosis for this genus was found through the reevaluation of the

584   taxonomic status of *Neotamandua*. The newly proposed diagnosis includes multiple cranial

585 and potential postcranial characteristics, which uphold that *Neotamandua*, whether it is a

586 natural group or not, certainly contains species that do not belong to *Myrmecophaga*, despite

587 their great resemblance with the latter. This outcome is congruent with the taxonomic opinion

588 of Gaudin and Branham (1998) and is at odds with Patterson et al. (1992). Now, can we

589 confidently say that *Neotamandua* is monophyletic from current evidence? As previously

590 defined by other workers, *Neotamandua* may be composed of successive basal species or

591 genera in relation to the hypothetical clade of *Myrmecophaga* (i.e., *My. tridactyla + My.*

592 *caroloameghinoi*). If that is correct, *Neotamandua* would be paraphyletic by definition, since

593 it excludes some of its descendants (Sereno et al., 1991). This possible pattern of basal

594 paraphyly is consequence of a taxonomy that is not defined by clades, but grades (Huxley,

595 1958; Wood and Lonergan, 2008). The monophyly of *Neotamandua*, as was redefined here

596 (i.e., *N. conspicua + N. greslebini + N. borealis*), is tentatively supported by three potential

597 synapomorphies shared by two of its species whose postcranium is known (*N. greslebini* and

598 *N. borealis*): (1) sub-oval to gently triangular mid-section of the tibia; (2) ectal and

599 sustentacular facets incipiently connected in the astragalus; (3) short tendinous groove in the

600 lateral side of the calcaneum. However, the synapomorphic conditions of these features for

601 *Neotamandua* need to be further tested from systematic analysis of new, more complete

602 and/or associated material of Gen. et sp. nov. and species referred to as *Neotamandua*. That

603 would enable us to assess more adequately the global morphological variability and character

604 distribution in Miocene myrmecophagids more late diverging than *Protamandua*. In turn,

605 when there is a better knowledge of such distribution, it is more likely to disentangle the

606 taxonomic identities and affinities of the *Neotamandua* species in order to corroborate the

607 monophyly of this genus. For the moment, the hypothesis of Hirschfeld (1976) that

608   *Neotamandua* is not monophyletic is, in principle, less probable if the *species inquirendae*

609   '*N.*' *magna* and *N.*? *australis* are excluded from the genus, as it was decided here, than if they

610   are retained within it. The exclusion of the *species inquirendae* does not affect the hypothesis

611   that *Neotamandua* is closer to *Myrmecophaga* than any other known nominal genus.

612   Consequently, the type species of *Neotamandua*, *N. conspicua*, is reiterated as closer to

613   *Myrmecophaga* than *Tamandua*, in line with the phylogeny of Gaudin and Branham (1998)

614   and unlike the hypothesis of Scillato-Yané and Carlini (1998).

615   Finally, the material referred to as *Neotamandua* sp. that was used in this study to make

616   comparisons with *N. borealis*, seems correctly allocated in that genus, but it might eventually

617   be assigned to a new species with very large body size, larger than *N. greslebini*. This is

618   partially conditioned to the clarification of the taxonomic status of '*N.*' *magna*, which is a

619   species comparable in body size to *Neotamandua* sp., so they could be (or not) the same

620   taxon.

621

622   *The diversification of Myrmecophagidae*.—McDonald et al. (2008) pointed out that since the

623   highly incomplete fossil record of Vermilingua, several fundamental questions on the

624   evolution of this group, including morphological trends and the acquisition of ecological

625   preferences in its distinct taxa, are largely unknown. Likewise, they highlighted some

626   uncertainty related to the divergence times of possible sub-clades. However, several

627   inferences and hypotheses about the evolutionary history of anteaters and, particularly, the

628   myrmecophagids, can be outlined from the current evidence, including that presented in this

629   work. Following Pascual and Ortiz-Jaureguizar (1990), McDonald et al. (2008) and Toledo et

630   al. (2017), the next discussion is based on multiple paleobiological, ecological and

28

631   biogeographic aspects as major constraints and/or consequences of the myrmecophagid

632   evolution.

633   The diversification of Myrmecophagidae was a macroevolutionary event that occurred

634   through the Neogene, at least as early as the Burdigalian (Early Miocene), according to the

635   minimal age estimated for the most basal genus, i.e., *Protamandua*. The beginning of this

636   diversification is approximately overlapped in time with the onset or development of similar

637   events in other higher taxa in South America, such as the xenartrans Megatherioidea,

638   Mylodontidae, Glyptodontidae and Dasypodini (Croft et al., 2007; McDonald and De Iuliis

639   2008; Bargo et al., 2012; Carlini et al., 2014; Boscaini et al., 2019), or the South American

640   native ungulates Pachyrukhinae, Mesotheriinae and Toxodontidae related to *Pericotoxodon*

641   and *Mixotoxodon* (Seoane et al., 2017; Armella et al., 2018a; Armella et al., 2018b). This

642   pattern shows the importance of the Early Miocene, particularly the Burdigalian, as a critical

643   interval for the diversification of multiple South American land mammal lineages. In light of

644   the geographic provenance of *Protamandua*, the most probable ancestral area for

645   Myrmecophagidae is southern South America (Fig. 7). The paleonvironmental conditions

646   inferred for the Early Miocene of this area are considerably warmer and more humid

647   (1000□1500 mm/year) than today, with presence of a subtropical dry forest (Iglesias et al.,

648   2011; Quattrocchio et al., 2011; Kay et al., 2012; Brea et al., 2017; Raigenborm et al., 2018).

649   In line with this reconstruction, Palazzesi et al. (2014) reported that southern Argentina

650   harboured in the Early Miocene a plant richness comparable to that documented today for the

651   Brazilian Atlantic Forest, in southeastern Brazil. Similar to *Tamandua*, *Protamandua* would

652   have preferred forested habitats and would have had semiarboreal habits (Gaudin and

653   Branham, 1998; McDonald et al., 2008; Kay et al., 2012). Whether the ancestral condition of

29

654 substrate use in Myrmecophagidae is arboreal, as held by Gaudin and Branham (1998), the

655 preference for open biomes (e.g., savannah) and terrestriality in *Myrmecophaga* (and possibly

656 in *Neotamandua*) is a derived condition (McDonald et al., 2008; Toledo et al., 2017). The

657 semiarboreal habits of *Tamandua* are explained from niche conservatism or, alternatively,

658 from convergence with *Protamandua* if the ancestor of *Tamandua* was hypothetically

659 terrestrial.

660   Since their particular, low basal metabolic rates and myrmecophagous diets (McNab,

661 1984, 1985), it is likely that the global warm recovery during the early Neogene (Early

662 Miocene to early Middle Miocene; including the Middle Miocene Climatic Optimum or

663 MMCO; Fig. 8), linked to a latitudinal temperature gradient reduction and an expansion of the

664 tropical (warm) forest belt towards higher latitudes in the continents (including South

665 America; see Anderson, 2009; Herold et al., 2011; Morley, 2011; Palazzesi et al., 2014), has

666 influenced the evolutionary differentiation of the myrmecophagids, maybe predominantly *in*

667 *situ* as in the climatically-induced evolution of other small Cenozoic mammals (Fortelius et

668 al., 2014), such as *Protamandua*. This differentiation would have been triggered by an

669 increase in the suitable area in terms of preferred biomes (warm forests in this case) and,

670 especially, temporarily sustained availability of social insects for their feeding (McDonald et

671 al., 2008; Kay et al., 2012; Toledo et al., 2017). Indeed, extant termites and ants (Termitidae

672 and Formicidae, respectively) concentrate the vast majority of their biomass (and species

673 richness) in the tropics and warm subtropical regions (Hölldobler and Wilson, 1990; Tobin,

674 1995; Davidson and Patrell-Kim, 1996; Eggleton et al., 1996; Davidson et al., 2003; Ellwood

675 and Foster, 2004; Keller and Gordon, 2009). This ecogeographic pattern is consistent with the

676 fossil record of the former higher taxa, which shows a strong tropical niche conservatism from

677   their respective evolutionary origins in the Late Cretaceous/Early Paleogene (see below;

678   Archibald et al., 2011; LaPolla et al., 2013; Guénard et al., 2015; Bourguignon et al., 2017).

679   According to Blois and Hadly (2009), the responses of mammalian taxa to climate

680   change throughout the Cenozoic are causally interconnected. These responses at the level of

681   individual taxa may include changes in abundance, genetics, morphology and/or distributional

682   range, and they may instigate multitaxa responses such as diversification events comparable to

683   that placed on the root of the evolutionary tree of Myrmecophagidae. This case of a

684   cladogenetic event possibly induced by climate contrasts in kind of biome with those that have

685   been repeatedly documented for intervals of grassland expansion (e.g., Equidae, Bovidae,

686   Cervidae, Ochotonidae, Hippopotaminae; MacFadden, 2000; Bouchenak-Khelladi et al., 2009;

687   Boisserie and Merceron, 2011; Ge et al., 2013).

688   In the Middle Miocene, *N.? australis*, *N. borealis* and Gen. et sp. nov. exhibit a mosaic

689   of morphological features in common with *Tamandua* and/or *Myrmecophaga*, as well as some

690   exclusive characteristics, which suggest an early, important increase in morphological

691   disparity in Myrmecophagidae and possibly the evolutionary divergence of those lineages

692   comprising its crown-group. This coincides with the interpretation of Hirschfeld (1976),

693   according to which the lineages that included the extant genera of Myrmecophagidae

694   differentiated morphologically at least from the Friasian (Middle Miocene). Likewise, it is

695   compatible with the results of the molecular phylogenies by Delsuc et al. (2001, 2012) and

696   Gibb et al. (2016), which estimated that the evolutionary divergence of *Tamandua* and

697   *Myrmecophaga* occurred in the late Middle Miocene, ca. 13 Mya. On the other hand, relative

698   body sizes inferred for the Middle Miocene taxa show an apparent trend towards body size

699   increase in comparison with the basal taxon *Protamandua*. During this interval, the

31

700   myrmecophagids have a wide geographic distribution in South America (Fig. 7), from low to

701   medium-high latitudes. This is in line with the evolution of larger body sizes since the

702   increase in this attribute occurs, the foraging area also increases and, with it, the distributional

703   range, according the general foraging strategy of the extant myrmecophagids (Naples, 1999;

704   Toledo et al., 2017; Gaudin et al., 2018). The co-occurrence pattern of *N. borealis* and Gen. et

705   sp. nov. in La Venta area in Colombia constitutes the earliest pattern of this kind for

706   Myrmecophagidae until pending systematic revisions for putative taxa from the Early

707   Miocene of Santa Cruz, Argentina, are carried out. These revisions would make it possible to

708   determine whether there are two or more co-occurrent myrmecophagid taxa in the latter area.

709   The fact that *N. borealis* and Gen. et sp. nov. are probably not sister taxa would imply a non-

710   sympatric diversification followed by a dispersal of at least one of the involved taxa. The

711   habitat preference of Gen. et sp. nov. in the paleoenvironmental mosaic of La Venta area (Kay

712   and Madden, 1997; Spradley et al., 2019) is thought to be a tropical forest (semiarboreal?) by

713   analogy with *Protamandua*, while it is proposed a more generalized habitat selection for *N.*

714   *borealis* in line with the paleobiological inference of predominantly terrestrial locomotion for

715   the latter taxon by Hirschfeld (1976). If this held true, it would open the possibility that *N.*

716   *borealis* was the oldest myrmecophagid inhabiting zones with semi-open or even open

717   vegetation (see below).

718   The morphological and probably taxonomic diversification of Myrmecophagidae

719   continued in the Late Miocene. Inferred body sizes range from larger than *Tamandua* and

720   nearly comparable to *Myrmecophaga*. Considering the wide geographic distribution during the

721   Middle Miocene, there is probably a geographic bias in the fossil record of the

722   myrmecophagids during the Late Miocene as the only known occurrences are *Myrmecophaga-*

723   like forms from northwestern Argentina (Fig. 7). If *N. borealis* and *N. greslebini* are sister

724   taxa, as it seems, that would mean that there was a biogeographic connection for

725   Myrmecophagidae between northern and southern South America in the late Middle/early

726   Late Miocene. This inference is congruent with the paleobiogeographic analyses of Cozzuol

727   (2006) and Carrillo et al. (2015), according to which the affinities between several Late

728   Miocene, northern and southern South American land mammal assemblages are strong or, at

729   least, not so distant as those between Middle Miocene assemblages from the same regions.

730   This pattern might be explained from the geographic shrinks of the Pebas Mega-Wetland

731   System and the Paranean Sea in the Middle-Late Miocene transition (Aceñolaza and

732   Sprechmann, 2002; Cozzuol, 2006; Salas-Gismondi et al., 2015). It is also possible that the

733   expansion of open biomes in South America during the Late Miocene has facilitated this

734   biotic connection, as it has been acknowledged in the case of other mammal taxa (e.g.,

735   Glyptodontinae, a xenartran group as Myrmecophagidae; Ortiz-Jaureguizar and Cladera,

736   2008; Oliva et al., 2010). Indeed, from a paleoenvironmental viewpoint, the (partial?) co-

737   occurrence of '*N.*' *magna*, *N. greslebini* and *N. conspicua* in northwestern Argentina is

738   important inasmuch as this pattern is related, for the first time in the evolutionary history of

739   Myrmecophagidae, to savannahs that were well developed with respect to other kinds of

740   vegetation cover (Latorre et al., 1997; Brandoni et al., 2012; Cotton et al., 2014; Amidon et

741   al., 2017; Zimicz et al., 2018). On the basis of the foregoing and by generalization of

742   morphological and ecological features of the living vermilinguans, e.g., less dependence on

743   trees related to greater taxonomic and/or ecological diversity of consumed insects (Hirschfeld,

744   1976; Montgomery, 1985a; Rodrigues et al., 2008; Toledo et al., 2017; Table 5), it is

745   hypothesized that, as early as the late Middle Miocene, with the triggering of a global cooling

746   (Fig. 8), *Neotamandua* was involved in a niche evolution process within Myrmecophagidae

747   which implied a significative increase in dietary diversity as myrmecophagous and expansion

748   of substrate use and biome selection. Probably the species of this genus preferred the frequent

749   use of the ground by biomechanical constraints and made inroads into largely open

750   environments as humid savannahs, without excluding the use of forested environments, as

751   *Myrmecophaga* usually does (Fuster et al., 2018; Gaudin et al., 2018). The former model is

752   further supported according to the evolutionary response pattern to major climatic-

753   vegetational changes documented by Badgley et al. (2008) in a faunal sequence of land

754   mammals from the Late Miocene of southern Asia, according to which the trophic niche

755   evolution and, particularly the expansion of this attribute, in conjunction with habitat changes,

756   are related to an increase in the probabilities of local and regional survivorship in the studied

757   lineages.

758   On the other hand, the fossil record of the crown-group genera, *Tamandua* and

759   *Myrmecophaga*, is confined to the Pliocene-Pleistocene, but the evolutionary (morphological)

760   divergence of *Myrmecophaga* would date back at least to the late Middle Miocene according

761   the first appearance of *Neotamandua*, i.e., *N. borealis*. Under this assumption, the hypothesis

762   of '*N.*' *magna* as a species of *Myrmecophaga* is perfectly feasible. In any case, the

763   biogeographic dynamics of the two extant myrmecophagid genera may have been constrained

764   by their respective ecological tolerances and, these in turn, by the rapidly changing habitat and

765   biome distribution in the Americas during at least the last five or six million years (de Vivo

766   and Carmignotto, 2004; Salzmann et al., 2011; Sniderman et al., 2016; Amidon et al., 2017;

767   Roberts et al., 2018; Grimmer et al., 2018). This applies especially to the case of *Tamandua*

768   since this taxon is less generalist in relation to habitat selection than *Myrmecophaga*

34

769   (McDonald, 2005). Considering the hypothesis of niche expansion for *Neotamandua*, the

770   differentiation of *Myrmecophaga* would have accentuated this putative evolutionary trend

771   through stronger preference for open environments, which is consistent with the general

772   paleoenvironment of savannah in the Early Pliocene of the area where occurs the oldest

773   species of the latter genus, i.e., *My. caroloameghinoi* (Zavala and Navarro, 1993; McDonald

774   et al., 2008).

775   The myrmecophagid evolution has a late episode with the complete formation of the

776   Panama Land Bridge (PLB) in the terminal Neogene (Coates and Stallard, 2013; O'dea et al.,

777   2016; Jaramillo, 2018). *Myrmecophaga tridactyla* invaded and colonized Central- and

778   southern North America (northern Mexico) at least as early as the Early Pleistocene (Shaw

779   and McDonald, 1987; Fig. 7). This dispersal event is part of the Great American Biotic

780   Interchange (GABI), specifically the episode referred as GABI 2 (Woodburne, 2010). Today,

781   the northern boundary of this species is located in northern Central America, over 3000 Km to

782   the south of the northernmost fossil record (Gaudin et al., 2018). This distributional difference

783   was interpreted by Shaw and McDonald (1987) in the light of the occurrence of warmer and

784   more humid conditions in the Early Pleistocene of southern North America (southern United

785   States-northern Mexico) than today in the same area. These conditions would have enabled

786   *Myrmecophaga* to colonize subtropical savannahs with permanent availability of insects

787   included in its diet (Croxen III et al., 2007; McDonald, 2005). However, due extirpation,

788   subsequent climatic-vegetational shifts (desertification) during the Late Pleistocene would

789   have forced a range shrinkage of this taxon towards lower latitudes (McDonald, 2005;

790   Ferrusquía-Villafranca et al., 2017). The distributional range pattern of tropical taxa expanded

791   towards southern North America during some intervals of the Pleistocene has been well

792   supported from the records of multiple taxa other than *Myrmecophaga*, including mammals

793   and sauropsids (Shaw and McDonald, 1987; Moscato and Jasinski, 2016; Ferrusquía-

794   Villafranca et al., 2017).

795   As *Myrmecophaga* did, *Tamandua* also colonized (or evolved in) northern continental

796   territories outside South America. This is supported from the occurrence of *Tamandua* sp. in

797   the terminal Pleistocene of Central Mexico (Arroyo-Cabrales et al., 2004; Ferrusquía-

798   Villafranca et al., 2010; Fig. 7). In its northern zone, the current distributional area of *T.*

799   *mexicana* includes latitudes comparable with that of the referred fossil record for this species

800   (Navarrete and Ortega, 2011). Central Mexico is part of the transitional area between the

801   current Neotropical and Neartic regions, called Mexican Transition Zone (MTZ; Halffter and

802   Morrone, 2017). All these observations, in conjunction with the above interpretation of the

803   Neogene biogeographic and environmental patterns, suggest that Myrmecophagidae kept

804   throughout its evolutionary history a niche conservatism associated with tropical (warm)

805   habitats (a case of phylogenetic niche conservatism or PNC; see Cooper et al., 2011; Fig. 8),

806   possibly in parallel with the same pattern in species groups of its prey insects (Thompson,

807   1994). Even more, the fact that Myrmecophagidae currently accumulates its highest species

808   richness in the warmest and wettest belt of the Americas (Hayssen, 2011; Navarrete and

809   Ortega, 2011; Miranda et al., 2017; Gaudin et al., 2018) is further interpreted as evidence that

810   this higher taxon represents support for the tropical niche conservatism hypothesis (TCH;

811   Wiens and Donoghue, 2004; Wiens and Graham, 2005). However, in line with the discussion

812   above, this major ecological constraint in Myrmecophagidae is not only related to

813   environmental thermal tolerance (see McNab [1985] for an analysis on the

814   thermophysiological constraints of the Xenarthra; McNab [1984] also discussed the same

36

815   issue for myrmecophagous mammals), as emphasized by TCH, but it is also driven by food

816   availability, at least by limiting or preventing historical colonization of low-productivity

817   regions far from the tropics (Shaw and McDonald, 1987; McDonald, 2005; Šímová and

818   Storch, 2017; Fig. 8).

819

Conclusion

821   The systematic evidence presented here suggests that probably the diversification of

822   Myrmecophagidae is taxonomically and biogeographically more complex than previously

823   thought. This insight is based on the description of the new taxon Gen. et sp. nov. for the

824   Middle Miocene of Colombia (co-occurrent species of *N. borealis*) and the determination of

825   *Neotamandua*, as previously defined, as a wastebasket taxon which is probably formed by

826   species belonging to more than one single genus. While Gen. et sp. nov. possibly has affinities

827   with *Tamandua*, more information is needed to test its phylogenetic position within

828   Myrmecophagidae. On the other hand, *N. borealis*, *N. greslebini* and *Neotamandua* sp. share

829   postcranial features (potential synapomorphies) that imply some grade of kinship between

830   them. Therefore, the two nominal species among the former ones are provisionally kept within

831   *Neotamandua*. Alternatively, these features may also constitute symplesiomorphies of a

832   hypothetical lineage which is apparently close to *Myrmecophaga*. The remaining nominal

833   species referred to as *Neotamandua*, i.e., '*N.*' *magna* and *N.? australis* were designated as

834   *species inquirendae*. Overall, it is necessary to develop new systematic revisions, including

835   new phylogenetic analyses similar to that by Gaudin and Branham (1998), using new material

836   referable to Gen. et sp. nov. and the referred species to *Neotamandua*, so as to obtain enough

837   evidence to solidly determine the phylogenetic position of the new species from La Venta and

838   corroborate the putative monophyletic status of *Neotamandua*. In line with the foregoing

839   considerations, the paleontological exploration of Neogene sedimentary units in northern

840   South America and northern Argentina is crucial to improve our understanding of the

841   diversification of Myrmecophagidae.

842

Disclosure statement

843

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845

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846

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867

868   Statement of data archiving

869   The nomenclatural acts contained in this work are registered in Zoobank:

870   [identifier Gen. et sp. nov.]

871   *LSID.* urn:lsid:zoobank.org:act:4EC0ABE1-C013-4113-9956-5DBD6E79FCEA

872   *LSID.* urn:lsid:zoobank.org:act:C4DC62D5-6470-4A04-B152-D42ED3BA332C

873

874   Accesibility of supplemental data

875   Data available from the Dryad Digital Repository: [intentional blank space]

876

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Figure captions

Figure 1. Geographic and stratigraphic provenance of the skull VPPLT 975 of the new taxon described here and the holotype of *Neotamandua borealis* (Hirschfeld, 1976). (**1**), location of the Department of Huila in Colombia; (**2**), location of the fossil area of interest, i.e., northern of La Venta area, in the Department of Huila (small rectangle); (**3**), location of the fossil site (black star), near the La Victoria town; (**4**), stratigraphic scheme of Guerrero (1997) for La Venta area, with approximate stratigraphic provenance of VPPLT 975 and the holotype of *N. borealis*.

Figure 2. Cranial measurements used in this work. All of them are based on Hossotani et al. (2017). Nomenclatural modifications from these measurements are shown in the section of Anatomical Abbreviations. (**1**), skull of *Tamandua* in dorsal view; (**2**), the same skull in ventral view. *Abbreviations*. FL, frontal length; GSL, greatest skull length; MBW, maximum braincase width; ML, maxilla length; NL, nasal length; NW, nasal width; PL, parietal length.

Figure 3. Holotypic skull (VPPLT 975) of Gen. et sp. nov. (**1**), dorsal view; (**2**), right lateral view; (**3**), ventral view; (**4**), left lateral view; (**5**), anatomical drawing in dorsal view; (**6**), anatomical drawing in right lateral view. *Abbreviations*. fr, frontal; ji, jugal insertion; la, lacrimal; mx, maxilla; na, nasal; or, orbit. Scale bar equal to 30 mm.

Figure 4. Two very informative postcranial bones of the holotype (UCMP 39847) of *Neotamandua borealis* (Hirschfeld 1976). (**1**), right astragalus, dorsal view; (**2**), right astragalus, ventral view; (**3**), left calcaneum, dorsal view; (**4**), left calcaneum, lateral view; (**5**), anatomical drawing of the astragalus in dorsal view; (**6**), anatomical drawing of the astragalus in ventral view; (**7**), anatomical drawing of the calcaneum in dorsal view; (**8**), anatomical drawing of the calcaneum in lateral view. *Abbreviations*. af, calcaneal accessory facet; cf, cuboid facet; ct, calcaneal tuber; ef, ectal facet; ff, fibular facet; h, astragalar head; lr, lateral ridge; lt, lateral trochlea; mt, medial trochlea; sf, sustentacular facet. Scale bar equal to 20 mm.

Figure 5. Epitype (FMNH P14419) of *Neotamandua conspicua*. (**1**), dorsal view; (**2**), right lateral view; (**3**), ventral view; (**4**), left lateral view; (**5**), right hemimandible; (**6**), left hemimandible; (**7**), anatomical drawing in dorsal view; (**8**), anatomical drawing in ventral view; (**9**), anatomical drawing in left lateral view. *Abbreviations*. ab, auditory bulla; fr, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; oc, occipital condyles; pal, palatine; par, parietal; ptb, pterygoid bulla; pte, pterygoid; sq, squamosal; szp, squamosal zygomatic process. Scale bar equal to 80 mm.

Figure 6. Reconstruction of the external appearance in life of Gen. et sp. nov. (close-up view). In the background, individuals of the macraucheniid *Theosodon* (left) and the alouattine *Stirtonia* (upper right corner) in the tropical forest of La Venta, late Middle Miocene of Colombia.

Figure 7. Geographic and chronological distribution of the myrmecophagid fossil records during the Late Cenozoic. Note the only two fossil records of these xenartrans outside South America in the Pleistocene of southern and northern Mexico (*Tamandua* sp. and

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Myrmecophaga tridactyla, respectively). Based on information compiled by McDonald et al. (2008). Original references in the same work and, largely, in the main text here.

Figure 8. Chronological collation of data on: (**1**), biochrons of the myrmecophagid genera or questionable grouping (horizontal solid bars and dashed line, respectively); (**2**), distribution of the highest latitudinal fossil records (northern and/or southern) of myrmecophagids (horizontal solid bars) and approximate, chronologically discrete latitudinal ranges of tropical rainforest plus tropical and subtropical dry broadleaf forest (i.e., frost-free areas [mean annual temperatures higher than 15°C] with significant rainfall, at least seasonally; large vertical rectangles); (**3**), general trend curve of global temperature and climatic episodes during the Late Cenozoic: [a] early Neogene warm recovery, including the thermal peak in the late Early-early Middle Miocene known as Middle Miocene Climatic Optimum or MMCO; [b] Middle Miocene climatic transition; [c] late Middle-Late Miocene cooling; [d] Early Pliocene warming; [e] Late Pliocene-Pleistocene cooling and glaciations. The vertical dashed line indicates the time of complete formation of the Panama Land Bridge, which represented thereafter a fundamentally continuous physical connection between South- and North America. Paleocological data used for the plot in "B" is from the following references: Huntley and Webb III (1988); Toby Pennington et al. (2000); Williams et al. (2004); Williams (2009); Chan et al. (2011); Morley (2011); Kay et al. (2012); Pound (2012); Pound et al. (2012); Forrest et al. (2015); Lohmann et al. (2015); Dowsett et al. (2016); Sniderman et al. (2016); Henrot et al. (2017); Frigola et al. (2018). The temperature curve in "C" is based on Zachos et al. (2001, 2008) and it is reproduced with permission.

Table captions

Table 1. Cranial measurements (in mm) for the holotype of Gen. et sp. nov. and other myrmecophagid species.

Table 2. Comparison of some postcranial measurements (in mm) between *N. borealis* and *N. greslebini*. Data for the latter species after Kraglievich (1940).

Table 3. Comparison of some postcranial measurements (in mm) between *N. borealis* and *Neotamandua* sp.

Table 4. Distribution of some postcranial characters of species referred to as *Neotamandua* and other myrmecophagid taxa. The characters marked with asterisk contain potentially diagnostic character states (synapomorphies?) for *Neotamandua*.

Table 5. Taxonomic breadth in diet (genus level) of extant genera of Vermilingua and habitat preference of their MDCs (genera or species groups considered main dietary components). Key for the references: (1) Best and Harada (1985); (2) Fuster et al. (2018); (3) Gallo et al. (2017); (4) Gaudin et al. (2018); (5) Gómez et al. (2012); (6) Hayssen (2011); (7) Hayssen et al. (2012); (8) Jiménez et al. (2018); (9) Lubin and Montgomery (1981); (10) Medri et al. (2003); (11) Miranda et al. (2009); (12) Montgomery (1981); (13) Montgomery (1985a); (14) Montgomery (1985b); (15) Morales-Sandoval (2010); (16) Navarrete and Ortega (2011); (17) Redford (1985); (18) Rodrigues et al. (2008); (19) Sandoval-Gómez et al. (2012).

Measurement	Gen. et sp. nov.[a]	*P. rothi* [b]	*N. conspicua* [c]	*T. tetradactyla* [d]	*M. tridactyla* [e]

Table 1. Cranial measurements (in mm) for the holotype of Gen. et sp. nov. and other myrmecophagid species

Measurement		N. borealis	N. greslebini		
GSL	80.7*	77*	210**	125.7	327.5
NL	30.9	□	~110	38.2	127.5
NW	4.8	□	11.1	7.7	14.2
FL	□	~27	□	53.1	143.9
MBW	□	36	~51	42.2	60.4
PL	□	~20	□	20.1	26

a. VPPLT 975 (holotype)
b. YPM-15267
c. FMNH P14419
d. Mean of a sample of (sub) adults, n = 8 (Appendix 2, Supplementary material)
e. Mean of a sample of (sub) adults, n = 10 (Appendix 2, Supplementary material)

*Incomplete skull. Rough estimate of GSL for Gen. et sp. nov. from a simple linear model based on some skull measurements for *Tamandua* (see Supplementary Material) is equal to 118.6 mm.

**Fractured rostrum

Table 2. Comparison of some postcranial measurements (in mm) between *N. borealis* and *N. greslebini*. Data for the latter species after Kraglievich (1940).

Measurement	N. borealis	Neotamandua sp.
Maximum distal width of the radius	16.5	29
Maximum proximal width of the tibia	29.5	46
Proximo-distal length of the astragalus	41.5	55
Maximum width of the astragalus	16.4	20.5

Table 3. Comparison of some postcranial measurements (in mm) between *N. borealis* and

Neotamandua sp.

Maximum distal width of the radius	16.5	35
Maximum width of the tibial articulation of the astragalus	20	24
Maximum width of the calcaneum	20	~21

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Table 4. Distribution of some postcranial characters of species referred to *Neotamandua* and other myrmecophagid taxa. The characters marked with asterisk contain potentially diagnostic character states (synapomorphies?) for *Neotamandua*.

	N. borealis	*N. greslebini*	*Neotamandua* sp.	*Protamandua*	*Tamandua*	*Myrmecophaga*
Relative body size	Medium to large	Large	Very large	Small	Medium	Very large
Character						
1. Arrangement of the radial ridges	Parallel ridges	Parallel ridges	Parallel ridges	NA	Distally convergent ridges	Parallel ridges
2. Rotated appearance of the distal radius	Absent	Absent	Absent	Absent	Present	Absent
3. Tibial mid-section*	Sub-rounded to gently triangular	Sub-rounded to gently triangular	NA	NA	Rounded	Strongly triangular
4. Arrangement of the ectal and sustentacular facets in the astragalus*	Largely separated, but with an incipient connection	Largely separated, but with an incipient connection	NA	Fully separated	Fully separated	Widely connected
5. Tendinous groove in the lateral side of the calcaneum*	Short	Short	NA	Absent	Absent	Long

Table 5. Taxonomic breadth in diet (genus level) of extant genera of Vermilingua and habitat preference of their MDCs (genera or species groups considered main dietary components). Key for the references: (1) Best and Harada (1985); (2) Fuster et al. (2018); (3) Gallo et al. (2017); (4) Gaudin et al. (2018); (5) Gómez et al. (2012); (6) Hayssen (2011); (7) Hayssen et al. (2012); (8) Jiménez et al. (2018); (9) Lubin and Montgomery (1981); (10) Medri et al. (2003); (11) Miranda et al. (2009); (12) Montgomery (1981); (13) Montgomery (1985a); (14) Montgomery (1985b); (15) Morales-Sandoval (2010); (16) Navarrete and Ortega (2011); (17) Redford (1985); (18) Rodrigues et al. (2008); (19) Sandoval-Gómez et al. (2012).

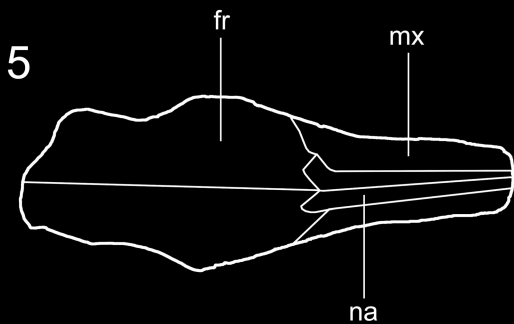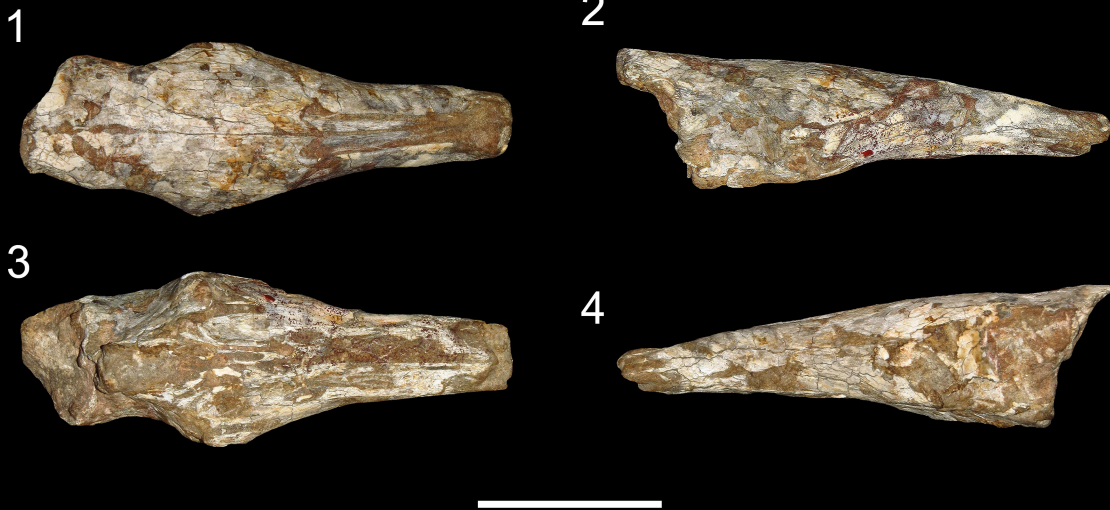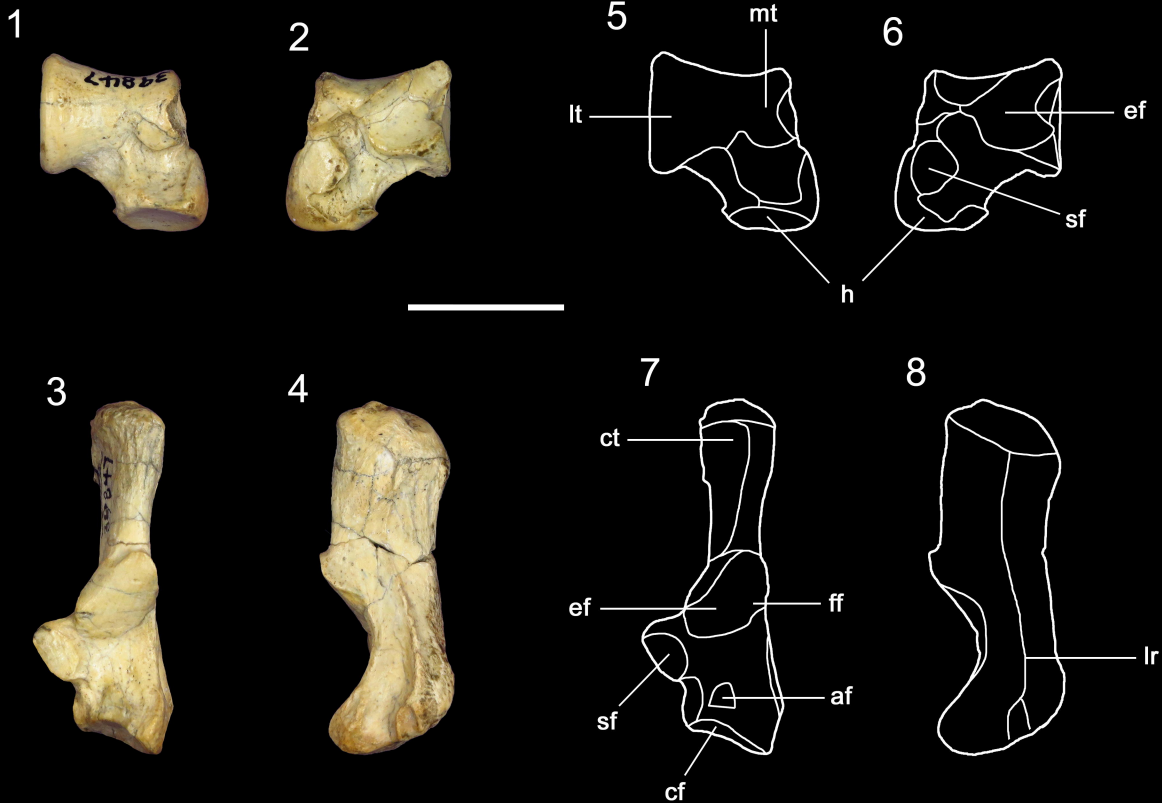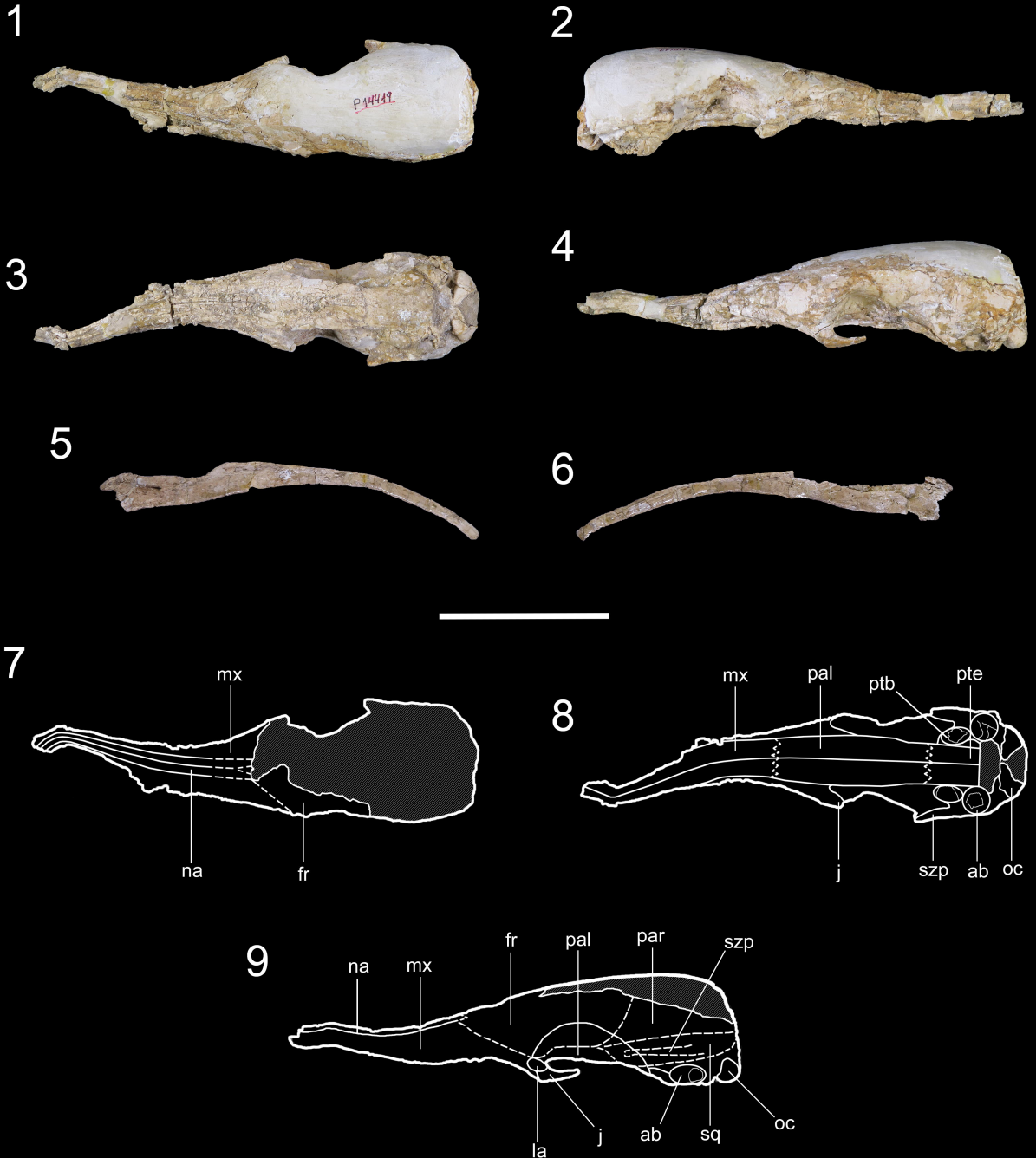| Extant anteater genera	Termite genera	Ant genera	Some MDCs	Habitat preference of MDCs	References
Cyclopes	0	8	*Camponotus* *Dolichoderus* *Solenopsis*	Rainforest, seasonally dry tropical forest; trees	1, 7, 11, 13, 19
Tamandua	7	17	*Nasutitermes* *Camponotus* *Crematogaster* *Solenopsis*	Seasonally dry tropical forest, rainforest; trees and ground	3, 6, 9, 12, 14, 15, 16
Myrmecophaga	8	31	*Cornitermes* *Syntermes* *Atta* *Solenopsis* *Camponotus* *Acromyrmex* *Pheidole*	savannah, grassland; ground	2, 3, 4, 5, 8, 10, 14, 17, 18, 19

Figure 1
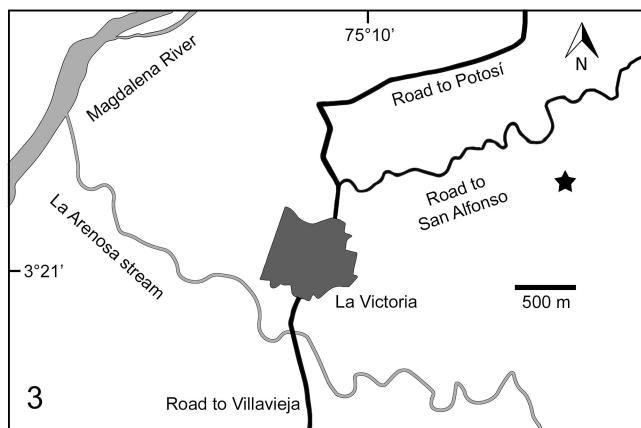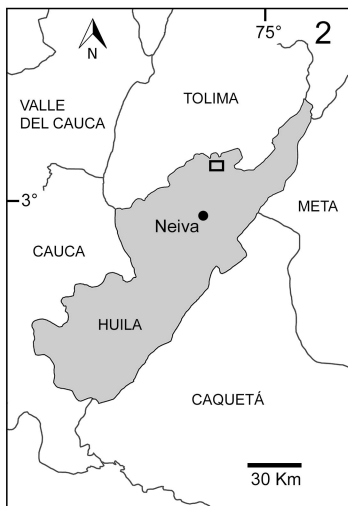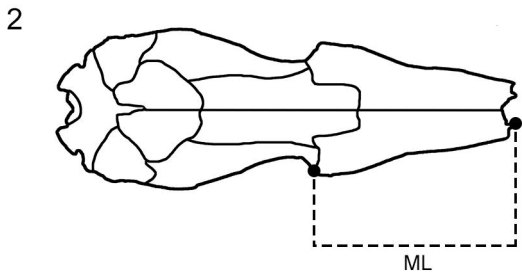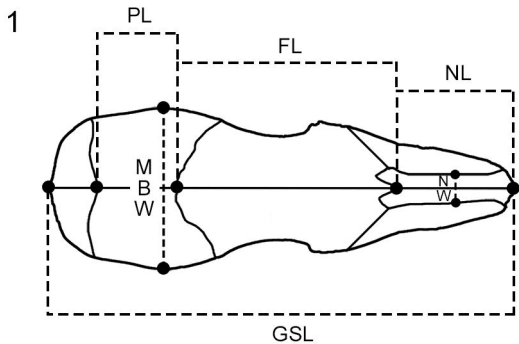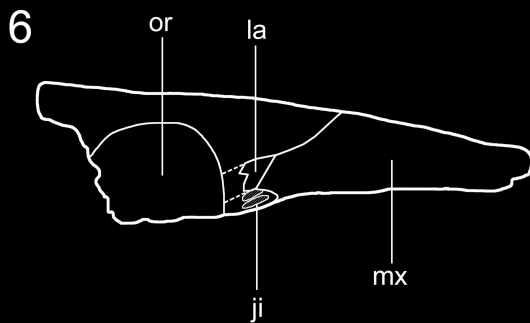
Figure 2

Figure 3

Figure 4

Figure 5

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Figure 7

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