First fossil skull of an anteater (Vermilingua, Myrmecophagidae) from northern South America, a taxonomic reassessment of *Neotamandua* and a discussion of the myrmecophagid diversification

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The evolutionary history of the South American anteaters, Vermilingua, is incompletely known as consequence of the fragmentary and geographically biased nature of the fossil record of this group. The only record of a nominal extinct species for northern South America is *Neotamandua borealis*, from the Middle Miocene of La Venta area, southwestern Colombia (Hirschfeld 1976). A new genus and species of myrmecophagid for La Venta is described here from a new partial skull. Additionally, the taxonomic status of the genus to which was referred the co-occurrent species of Gen. et sp. nov., i.e. *Neotamandua*, is revised. The morphological and taxonomic analyses of these taxa indicate that Gen. et sp. nov. may be related to *Tamandua* and that the justification of the generic assignments of the referred species to *Neotamandua* is weak, with high probability of reassigning some of them to a new genus. Two species previously referred to *Neotamandua* (*N. magna* and *N.*? *australis*) were designated as *species inquirendae* and new diagnostic information for the redefined genus and its type species, *N. conspicua*, is provided. Together, these results suggest that the diversification of Myrmecophagidae was taxonomically and biogeographically more complex than that what has been proposed so far. Considering the new evidence, it is proposed a synthetic model on the diversification of these xenartrans during the late Cenozoic based on the probable relationship between their intrinsic ecological constraints and some major abiotic changes in the Americas.

Key words: Vermilingua, Myrmecophagidae, diversification, *Neotamandua*, La Venta area, Neogene.

Introduction

The anteaters of the suborder Vermilingua are part of Xenarthra, one of the more inclusive clades in the evolutionary tree of the placental mammals (Eutheria) and a characteristic group in the land mammal assemblages of the middle-late Cenozoic of the Americas (McDonald et al. 2008; Foley et al. 2016; Halliday et al. 2016; Feijoo & Parada 2017). Within Xenarthra, Vermilingua belongs to Pilosa, a clade that also includes the sloths, i.e. Tardigrada. Today, Vemilingua comprises the genera *Cyclopes* (pygmy anteaters), *Tamandua* (collared anteaters) and *Myrmecophaga* (giant anteaters). These genera groups ten extant species, the most of them (seven) belonging to *Cyclopes*, according to the most recent exhaustive taxonomic revision (Miranda et al. 2017). The classic phylogenetic hypothesis reunites *Tamandua* and *Myrmecophaga* in the family Myrmecophagidae, while

Cyclopes is located in a basal position with respect to Myrmecophagidae as the only recent form of the family Cyclopedidae (Engelmann 1985). With the connotation of a superior taxonomic hierarchy (i.e. at the family level; Barros et al. 2008; Gibb et al. 2015) by an early evolutionary divergence (Hirschfeld 1976; Delsuc et al. 2001; Gibb et al. 2016) and in acknowledgment of a more extended use in the scientific literature, the names Myrmecophagidae and Cyclopedidae are used here, instead of Myrmecophaginae and Cyclopinae *sensu* Gaudin & Branham (1998), respectively. However, the taxonomic content of Myrmecophaginae and Cyclopinae, including extinct forms, is considered as transferable to their counterparties (McDonald et al. 2008).

The living anteaters, whose mean body mass ranges from ~0.4 and 30 kilograms (Gaudin et al. 2018), are highly, morphologically specialized mammals by exhibiting remarkable skeleton and soft-anatomy modifications, which are closely linked to their myrmecophagous diets, i.e. diets consisting of at least 90% of ants/termites (Redford 1987; McDonald et al. 2008). Many of these adaptations, anatomically located in the skull and jaws, are associated between them in several ways by being part of the architecture of an integrated functional system of food apprehension and ingestion. Among these features, the following are some of the most noteworthy: rostral elongation and narrowing, basicranial-basifacial axis curvature, complete loss of teeth, gracile jaw, reduction of the adductor jaw muscles, unfused jaw symphysis and protrusible long tongue (Reiss 2001; Gaudin & McDonald 2008; McDonald et al. 2008). Several of these morphological specializations are convergent with those described for other myrmecophagous mammals such as the pangolins (Pholidota) and the aardvarks (Tubulidentata), so it is not surprising that early systematic researchers erroneously proposed close common ancestry of Vermilingua with these Old world groups from their superficial similarities (e.g. Engelmann 1978; Norman & Ashley 1994).

Despite their unique biology and ecology, at least in the context of the land mammals of the Americas, the evolutionary history of the anteaters is largely obscured by their poor, fragmentary and geographically biased fossil record (Hirschfeld 1976; Gaudin & Branham 1998; McDonald et al. 2008). Generally, five valid genera and nine species are recognized in the fossil record of Vermilingua, of which two genera and two species have extant representatives, i.e. *Myrmecophaga tridactyla* and *Tamandua tetradactyla*. Myrmecophagidae groups nearly all these fossil taxa (only one genus and one species for Cyclopedidae) in a general biochron beginning c. 18 million years before present, most of them distributed throughout the Neogene (McDonald et al. 2008). But while the record of this family for the latter period is taxonomically more diverse than that for the Quaternary, it also poses more difficulties in the systematic framework of the implicated taxa. The oldest member of Myrmecophagidae is *Protamandua rothi*, from the late Early Miocene of the Santa Cruz Province, southern Argentina (Ameghino 1904). This species has been well validated from a pair of incomplete skulls and several postcranial bones, but the validity of other co-occurrent putative vermilinguan (myrmecophagid?) taxa is, at least, questionable (Hirschfeld 1976; McDonald et al. 2008). For the early Middle Miocene has been reported a myrmecophagid doubtfully assigned to *Neotamandua*, and yet used to create a new species from isolated humeral remains (*N.*? *australis*; Scillato-Yané & Carlini 1998). In the latter genus was also allocated, with some uncertainty, postcranial material of a middle-to-large sized anteater recorded in the late Middle Miocene of La Venta area, southwestern Colombia, whose description includes the only nominal extinct species for northern South

America, i.e. *N. borealis* (Hirschfeld 1976). *Neotamandua* chronologically extends to the Late Miocene and Early Pliocene with the species *N. magna* (Ameghino 1919), *N. greslebini* (Kraglievich 1940) and *N. conspicua* (type species; Rovereto 1914), all of them from northwestern Argentina (provinces of Catamarca and Tucumán). This genus is typically recognized as morphologically similar (even directly ancestral) to *Myrmecophaga*, although smaller in body size (Hirschfeld 1976; Gaudin & Branham 1998). Considering the very few anatomically correlatable elements in which are based the different species referred to *Neotamandua*, Hirschfeld (1976) and Scillato-Yané & Carlini (1998) have suggested that this genus could be paraphyletic. Furthermore, the latter authors proposed the hypothesis that *Neotamandua* is composed by two distinct evolutionary lineages: one more closely related to *Myrmecophaga* and other one to *Tamandua*. In turn, these two lineages would have diverged in allopatry in South America, in such a way that the geographical origin of *Myrmecophaga* is located in northern South America, while that of *Tamandua* is in southern South America.

In this article, we describe the first fossil skull of a myrmecophagid (and vermilinguan) from northern South America. This specimen was collected in the Middle Miocene La Victoria Formation of La Venta area, Colombia. Additionally, in coming to analysis because it is the only nominal taxon reported for the same region and geological unit, the taxonomic status of *Neotamandua* is revised. The results prompt the development of a discussion on a model of diversification for Myrmecophagidae in which new and previous hypothesis about this evolutionary event are synthesized. This contribution is intended to revaluate, expand and integrate biotic and abiotic evidence related to the diversification of this fascinating mammal group, with emphasis on the biogeographic role of tropical, low latitude regions of the Americas.

Material and methods

The cranial specimen described for the first time here for Colombia (VPPLT 975) comes from a light-brown mudstone layer in the Llano Largo field, around 2 Km northeast of La Victoria town, Municipality of Villavieja, Department of Huila (Fig. 1A-C). Strata of the La Victoria Formation outcrop there, within the palaeontologically relevant area of La Venta. The La Victoria Formation is a geological unit of ~500 meters in thickness which is mainly composed by bioturbated mudstones (Anderson et al. 2016). These sedimentites are interrupted by very continuous, coarse-to-fine grained sandstones with crossbedding and erosive bases. According to the lithostratigraphic scheme of Guerrero (1997; Fig. 1D), the new skull is from a level stratigraphically close (<20 m) and below the Chunchullo sandstone beds, i.e. the lower part of the La Victoria Formation. This corresponds to the unit referred as “Unit between the Cerro Gordo and Chunchullo sandstone beds”. As described by the same author, this unit, whose thickness ranges from ~80 to 160 m, is predominantly composed of mudstones and some interlayers of sandstones. This sedimentary body bears abundant plutonic and volcanic fragments from the lower Jurassic basement of the Honda Group (Saldaña Formation), as well as clasts of volcanic rocks formed in the magmatic arc of the Cordillera Central of Colombia during the Middle Miocene (Anderson et al. 2016).

The general palaeoenvironment inferred for the La Victoria Formation is a meandering fluvial system (except for the Cerbatana conglomerate, associated to an anastomosed system) with significant soil development in flood plain zones (Guerrero 1997). The ages calculated by Guerrero (1997) and Flynn et al. (1997) using magnetic polarity stratigraphy and geochronology indicate sedimentary deposition during the interval 13.8□12.5 million years ago (mya). These results have recently been reinforced by the U-Pb geochronology of detrital zircons recovered in this formation (Anderson et al. 2016). The age range obtained is 14.4 ± 1.9 □ 13.2 ± 1.3 mya. This interval coincides approximately with the early Serravalian, sub-stage of the Middle Miocene [Insert Fig. 1 here].

Cranial measurements, with some nomenclatural modifications, are based on those of Hossotani et al. (2017) (Fig. 2; see Anatomical Abbreviations). All these measurements are in millimetres (mm). The description of the new skull of La Venta includes a rough body mass estimation of the respective individual from a traditional allometric approach. All these data and analyses are compiled in the Supplementary material (Appendices S1 and S3). For the taxonomic analysis of the genus *Neotamandua* were revised the justifications of generic allocations for the referred species (at least doubtfully) in all the relevant scientific literature. These species are: *Neotamandua conspicua* Rovereto 1914 (type species); *Neotamandua magna* Ameghino 1919; *Neotamandua greslebini* Kraglievich 1940; *Neotamandua borealis* Hirschfeld 1976; *Neotamandua*? *australis* Scillato-Yané & Carlini 1998. Additionally, some observations were made on the holotypes of *N. conspicua* (MACN 8097) and *N. borealis* (UCMP 39847) to reexamine the described characteristics for these species in the original publications (Rovereto 1914 and Hirschfeld 1976, respectively). The conceptual model of Plotcnick & Warner (2006) to recognize taxonomic wastebaskets was applied to *Neotamandua*. From the foregoing and the designation of the specimen FMNH P14419 as epitype of *N. conspicua*, it was proposed a diagnosis for *Neotamandua*. See a list of all the studied fossil specimens in the Appendix S1 of the Supplementary material [Insert Fig. 2 here].

On other hand, considering that Hirschfeld (1976), in her description of *N. borealis*, did not include morphological comparisons from postcranial bones of this species and homologous elements of the species referred to *Neotamandua* for southern South America, we performed this task and a preliminary character distribution analysis from postcrania of these taxa to explore the hypothesis that they are closely related. Forcibly, *N. magna* and *N.*? *australis* are excluded from the comparisons since they do not have osteological elements correlated with those of *N. borealis* (or any other species referred to *Neotamandua*). Additionally, as a result of loss of its holotype (McDonald et al. 2008), comparisons with *N. greslebini* are based exclusively on the non-illustrated description by Kraglievich (1940). Other comparisons include postcranium collected by Juan Méndez in 1911 in the upper Miocene of the Andalhuala locality, Catamarca Province, Argentina. This material was assigned to *Neotamandua* (*Neotamandua* sp.) without a reference publication. McDonald et al. (2008) manifested doubt about this taxonomic assignment (*Neotamandua*?), but these authors simultaneously speculated that it might be the lost holotype of *N. greslebini*.

Following to McKenna & Bell (1997), the genus *Nunezia* is considered a junior synonym of *Myrmecophaga*. Myological inferences are based on Hirschfeld (1976) and Gambaryan et al. (2009).

Institutional abbreviations

CAC: Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata; **FMNH:** Field Museum, Chicago, IL., USA; **ICN:** Instituto de Ciencias Naturales, Facultad de Ciencias, Universidad Nacional, Bogotá, Colombia; **MACN:** Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; **MLP:** Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MPT:** Museo Provincial de Tucumán, Tucumán, Argentina; **UCMP:** University of California Museum of Paleontology, Berkeley, CA., USA; **VPPLT:** Museo de Historia Natural La Tatacoa, La Victoria, Huila, Colombia; **YPM:** Peabody Museum, Yale University, New Haven, CT, USA.

Anatomical abbreviations

Abbreviations of equivalent measurements by Hossotani et al. (2017) in parenthesis. **FL**, frontal length; **GSL (SL)**, greatest skull length; **MBW (NC)**, maximum braincase width; **ML**, maxilla length; **NL**, nasal length; **NW (NB)**, nasal width; **PL**, parietal length.

SYSTEMATIC PALAEONTOLOGY

Xenarthra Cope, 1889

Pilosa Flower, 1883

Vermilingua Illiger, 1811

Myrmecophagidae Gray, 1825

Gen. nov.

Etymology. [intentionally in blank].

Diagnosis. Same as that of the type and only known species.

Gen. et sp. nov.

(Fig. 3)

Etymology. [intentionally in blank]

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

Diagnosis. Middle sized myrmecophagid, slightly smaller than *Tamandua* and even more than *Neotamandua*. It can be differentiated from other genera/species of anteaters by the following combination of cranial features: relatively width rostrum, similar to *Tamandua*; narrow and strongly tapered nasals toward their anterior end; anteroposterior length of the pre-orbital section of frontals equal to more than two thirds of the anteroposterior length of nasals; jugals inserted from the same level of the most anterior border of the lacrimal; anterior portion of the orbit more laterally extended in the superior wall in the inferior one, without forming a conspicuous dome as in *Neotamandua conspicua*.

Comparative description of the holotype of Gen. et sp. nov. The specimen VPPLT 975 consists of a partial skull that preserves nearly all the anatomical elements from the anterior section of the frontals (at the mid anteroposterior level of the orbit) to the anterior end of the rostrum. See cranial measurements taken for this new taxon and other myrmecophagids in the Table 1. The estimated body mass for this individual is around 3.9 Kg (Appendix S3 of the Supplementary material). As consequence of the preservation, some sutures are distinguishable in dorsal and lateral views, but virtually no suture is clearly detectable in ventral view. The rostrum is proportionally shorter and more robust than those in *Myrmecophaga* and *N. conspicua* (see below), but less than in *Tamandua*. In dorsal view, it is very similar to the skull of *Tamandua*, with at least four characteristics remarkably different with respect this extant genus: (1) lower rostrum; (2) rostrum more regularly tapered; (3) narrower and more anteriorly tapered nasals; (4) pre-orbital section of the frontals more anteroposteriorly elongated. In dorsal view, the rostrum shows a slight bulge in its middle part, similar to that in *Tamandua* and *Myrmecophaga*. However, in VPPLT 975 this bulge is even subtler than in the living myrmecophagids. Apparently, the nasals are shorter than frontals and are poorly exposed in lateral view. The jugals are absent by preservation, but it is possible to recognize their insertion location. This is more anterior than in *Myrmecophaga*, but more posterior than in *Tamandua*. Associated to the insertion of the jugal, there is a reduced posterolateral process of the maxilla in comparison with that of *Myrmecophaga*, similar in *Tamandua*. The right side of the skull preserves better the lacrimal zone, but it is simultaneously more deformed around the fronto-maxillary suture than in the left side. The lacrimal is longer in its anteroposterior axis than in that dorsoventral. The same bone is proportionally smaller than in *Tamandua* and even more than in *N. conspicua*. It has a triangular outline (at least anteriorly), similar to *Myrmecophaga* and unlike *Tamandua* (irregularly rounded, ovated, or, infrequently, sub-triangular lacrimal). The maxilla is not part of the orbit. The superior wall of the orbit is more laterally expanded than the inferior wall, without forming a conspicuous dome as in *N. conspicua*. This is similar to the condition observed in *Myrmecophaga* and differs from that in *Tamandua*, in which the inferior wall is prominent given that it is more laterally expanded. It is not possible to recognize lacrimal nor orbital foramina. In ventral view, the dorsal border of the orbit is regularly concave. The palatines are less laterally extended than in *Tamandua* and apparently there are no palatine "wings" (noticeable lateral expansions of the palatines), unlike *N. conspicua* [Insert Fig. 3 here].

Taxonomic reanalysis of the genus *Neotamandua*

Taxonomic history and discussion on the taxonomic status of *Neotamandua*

The genus *Neotamandua* was proposed by Rovereto (1914) from a posterior portion of a skull (MACN 8097), which was collected in upper Miocene-to-Pliocene strata of the Catamarca Province, Argentina. The name *Neotamandua*, literally meaning 'new tamandua', was coined by Rovereto in allusion to the cranial similarity of the type species, *N. conspicua*, with the extant genus *Tamandua*, rather than with *Myrmecophaga*. This detail would be historically paradoxical, as will be shown below. It is important to note that Rovereto did not provide a diagnosis for *Neotamandua*, but he just briefly described the holotype of *N. conspicua*, emphasizing its elongated parietals. However, this feature, more comparable with that in *Myrmecophaga* than that in any other myrmecophagid, was correlated with the anteroposterior length of the parietals in *Tamandua*. A few years after the Rovereto's work, Carlos Ameghino (Ameghino 1919) used a pelvis (MPT 58) recovered in contemporary strata of the Tucuman Province, Argentina, to create a new species, *N. magna*. Despite the taxonomic assignment of this pelvis to *Neotamandua*, Ameghino discussed that, alternatively, this species could belong to other genus of larger body size, as Kraglievich (1940) also held. Formally, *N. magna* has not been reevaluated, but McDonald et al. (2008) suggested that, given that this species was transferred to *Nunezia* by Kraglievich (1934), and *Nunezia* is considered a junior synonym of *Myrmecophaga* (Hirschfeld 1976; McKenna & Bell 1997), then *N. magna* should be included in the latter genus, i.e. *Myrmecophaga magna* comb. nov. (unpublished). Indeed, the morphological differences cited by Ameghino (1919) and Kraglievich (1940) between the pelvis of *N. magna* and that of *M. tridactyla* (e.g. greater width and ventral flattening of the intermediate sacral vertebrae) do not seem sufficient to consider a generic distinction between these species.

Two decades later, Kraglievich (1940) proposed a new species from postcranium collected in the upper Miocene of the Catamarca Province. This was initially assigned to *N. conspicua*. According to Kraglievich, the then new species, *N. greslebini*, is easily identifiable by its large size, intermediate between those of *N. conspicua* and *N. magna*. Like Rovereto (1914), this author also correlated his generic assignment of *N. greslebini* to *Neotamandua* from the similarity between the fossil specimens of this species and homologous elements of *Tamandua* (Kraglievich, p. 633). The holotype of *N. greslebini* is missing or mixed up with material labelled with generic names of extinct anteaters (i.e. *Neotamandua* and *Palaeomyrmidon*) in the Museo Argentino de Ciencias Naturales (MACN), in Buenos Aires, Argentina (McDonald et al. 2008).

Already in the second half of the XX century, a controversy about the possible synonymy between *Neotamandua* and *Myrmecophaga* arose. This means that there was a radical paradigmatic shift in myrmecophagid systematics, from that in early XX century, in which *Neotamandua* was considered closely related to *Tamandua*, to that in late XX century, in which *Neotamandua* was even a serious candidate to be a junior synonym of *Myrmecophaga*. This historical change began with the non-cladistic systematic analysis of Hirschfeld (1976), in which *Neotamandua* was originally proposed as the direct ancestor (anagenetic form) of *Myrmecophaga*. In the same work, Hirschfeld created the first and, until now, only nominal extinct species of Vermilingua and Myrmecophagidae for northern South America, *N. borealis* (Middle Miocene of Colombia). Given the scarcity and fragmentation of the specimens referred to *Neotamandua*, Hirschfeld recognized the need to revise the taxonomic validity of *N. conspicua*, *N. magna* and *N. greslebini*. Indeed, she went beyond and stated that *Neotamandua* species could be representatives of more than one single genus. However, her assignment of *N. borealis* to *Neotamandua* was based primarily on the idea that the fossils she studied are 'considerably more advanced than those known from the Santacruzian [late Early Miocene], closer to the Araucanian [Late Miocene-Pliocene] species and…to the line leading to *Myrmecophaga* than *Tamandua*' (Hirschfeld, p. 421). For this author, many postcranial traits of *N. borealis* are intermediate between *Tamandua* and *Myrmecophaga*. As a questionable methodological aspect, it is important to note that Hirschfeld did not make osteological comparisons with the southern species of *Neotamandua*, only with postcranium of *Protamandua*, *Tamandua* and *Myrmecophaga* (extant species of the two latter genera).

In implicit reply to Hirschfeld (1976), Patterson et al. (1992) highlighted the morphological similarities between the unpublished skull FMNH P14419, catalogued as *N. conspicua* in the Field Museum, and the modern skulls of *Myrmecophaga*. For these authors, FMNH P14419 only differs from skulls of the living giant anteater in its smaller size. Consequently, Patterson et al. (1992) suggested synonymize *Neotamandua* and

Myrmecophaga, with nomenclatural priority for the latter. Nevertheless, Gaudin & Branham (1998) provided (weak) support for the validity of *Neotamandua* through a comprehensive phylogenetic analysis of Vermilingua. Their results indicate that *Neotamandua* is an independent taxon based on two autapomorphies, being one of them ambiguous and the other one unambiguous. The latter is the horizontal inclination of the glenoid. In the only most parsimonious tree recovered by Gaudin & Branham (1998), *Neotamandua* is closely related to *Myrmecophaga*, not *Tamandua*, as opposed to Rovereto (1914) and Kraglievich (1940).

Finally, the last species referred, with doubt, to the genus was *N.*? *australis* (Scillato-Yané & Carlini 1998). The holotype of this species consists only of a humerus (MLP 91-IX-6-5) collected in the lower Middle Miocene of the Río Negro Province, Argentina. Scillato-Yané & Carlini (1998) highlighted some similarities of this material with the humerus of *Tamandua*. They also expressed considerably uncertainty in assigning it to *Neotamandua*, not only by its fragmentary nature, but from the idea of Hirschfeld about the non-natural (i.e. non-monophyletic) status of this genus. Without performing a phylogenetic analysis, these authors proposed a hypothesis that *N. borealis* is closely related to *Myrmecophaga*, while *N. conspicua* and *N.*? *australis* are closer to *Tamandua*. If this hypothesis is correct, *N. borealis* does not belong to *Neotamandua* as consequence of the application of the nomenclatural priority principle.

In summary, multiple historical factors, including the lack of a diagnosis, insufficient number of anatomically correlatable/highly diagnostic postcranial elements and, especially, absence of cranial-postcranial associations, aroused the relatively arbitrary use of *Neotamandua* as a wastebasket taxon, i.e. a residual genus deriving from weak and/or inadequate systematic analysis. According to the conceptual model of Plotnick & Warner (2006), *Neotamandua* has five (from a total of seven) properties of a genus potentially classifiable as wastebasket: (1) it is an old name (i.e. more than one century to the present); (2) it is [relatively] rich in species (five species, i.e. the most speciose extinct genus of Vermilingua); (3) it has a [relatively] high number of occurrences; (4) it has wide temporal and geographical distributions; (5) it [primarily] groups together specimens poorly preserved and/or difficult to identify. To these five properties we may add the lack of a diagnosis, which is related in some way to the property number two of the Plotnick-Warner model, i.e. genera diagnosed from generalized characters, probably plesiomophies or easily recognizable characters.

As it was shown, *Neotamandua* has been invoked as a directly ancestral form of *Tamandua*, or, more recently, of *Myrmecophaga*, from its morphological characteristics in common with these two extant genera. But precisely because of this character mosaic, the generic allocation of isolated postcranial remains of myrmecophagids potentially referable to *Neotamandua* should not be reduced or exclusively focused on their comparison with the crown-group, but should also consider the effect of possible homoplasies (e.g. those related to ecological convergences), plesiomorphies and limitations of the fossil record (Plotnick & Warner 2006). In other words, the apparent affinity between isolated postcranial elements of any Neogene anteater and their homologous in *Myrmecophaga* is not enough to make a reliable generic allocation in *Neotamandua*; diagnostic information of the latter genus is needed, preferably autapomorphies, which allow it to be individually identified and not simply as a set of forms similar to *Myrmecophaga*.

Comparisons between northern and southern species referred to *Neotamandua*

***N. borealis* and *N. greslebini*.** See the Table 2 for comparison of postcranial measurements between these species.

Radius. Both *N. borealis* and *N. greslebini* show two longitudinal, parallel radial ridges, of which the lateral ridge is higher and reaches a more distal level than the cranial one. This is similar to the condition observed in *Myrmecophaga* and differs from the distally convergent radial ridges of *Tamandua*. In *N. borealis*, the lateral ridge is even more distally extended than in *N. greslebini,* in such a way that the flanks of this structure contact the lateral border of the styloid process. According to Kraglievich (1940), in the Argentinean species this ridge ends at an intermediate level between the distal end of the cranial ridge and the styloid process.

Tibia. The type material of *N. borealis* includes a proximal epiphysis and part of the diaphysis of a right tibia. According to Kraglievich (1940), the holotype of *N. greslebini* includes two fragments of a tibia, one of them proximal and the other one distal. Both Hirschfeld and Kraglievich claimed greater overall similarity between the tibial fragments of these species and the homologous parts of *Tamandua*, rather than *Myrmecophaga*. This way, the mid-section of the tibias both of *N. borealis* and *N. greslebini* is not as strongly triangular as in *Myrmecophaga*. Rather, this bone segment is from gently triangular to sub-rounded in these two species referred to *Neotamandua*, without being rounded as in *Tamandua*.

Astragalus. Hirschfeld (1976) described the astragalus of *N. borealis* (Fig. 4A-B, 4E-F) as intermediate in morphology and size between those in *Tamandua* and

Myrmecophaga. In contrast, Kraglievich (1940) stated that the astragalus of *N. greslebini* closely resembles that of *Tamandua*. New observations allow to determinate that, in dorsal view, the astragalus of *N. borealis* is more similar to that in *Tamandua* than *Myrmecophaga* as consequence of a lateral side of the trochlea larger than the medial one (trochlear asymmetry). Like *N. greslebini*, the regular concavity in which is inserted the *flexor digitorum fibularis* tendon extends posteroventrally like a well-defined wedge ("pointed shape" in Kraglievich's words) and it contacts the calcaneal facets across the entire width of the latter. In ventral view, the arrangement of the calcaneal facets in *N. borealis* is a kind of 'transition' between that in *Myrmecophaga* and *Tamandua*. In *N. borealis*, the ectal and sustentacular are largely separated by a wide and deep sulcus, but there is an incipient connection. This condition is approximately comparable to that described by Kraglievich (1940) for *N. greslebini* and differs from the fully separated calcaneal facets in *Protamandua* and *Tamandua*. In this sense, Kraglievich was not very explicit in pointing out the degree of development of the connection between these facets, but it is inferred that it is not exactly wide as in *Myrmecophaga* when he wrote that '…these calcaneal articulations are, *apparently*, posteriorly fused…' (italics are ours; Kraglievich, p. 635).

Calcaneum. Like *N. greslebini*, *N. borealis* has a narrow fibular calcaneal facet, which is located laterally and in a slightly different plane with respect to that of the ectal facet (Fig. 4C-D, 4G-H). In both of the former species, the *sustentaculum* is less medially projected than in *Myrmecophaga*. They also show an accessory facet in the anterior end of the calcaneum that articulates with the astragalar head, similarly to *Tamandua*. In all the aforementioned taxa, this facet is closer (even in contact) to the cuboid facet. In *N. borealis* and *N. greslebini*, the cuboid facet is transversely ovate and concave. A unique feature in common for them is the presence of a short tendinous groove (shorter than in *Myrmecophaga*) and strongly concave (Fig. 4H). It is the continuation of the longitudinal and conspicuous ridge that runs the calcaneum in its lateral side. The latter separates tendons of the *fibularis longus* and *accesorius* muscles (Hirschfeld 1976; Gambaryan et al. 2009). In *N. borealis*, this ridge is more conspicuous than in *Tamandua* and less than in *Myrmecophaga* [Insert Fig. 4 here].

***N. borealis* and *Neotamandua* sp.** See the Table 3 for comparison of postcranial measurements between these species.

Radius. The distal epiphysis of the radius in *Neotamandua* sp. (MACN 2408) is more massive than that in *N. borealis*. In the latter species, the distal end of the radius is relatively stylized, like *Tamandua*. However, the morphologies of *N. borealis* and *Neotamandua* sp. are more comparable between them. In distal view, the styloid process of these species is more elongated and posteriorly oriented than in *Tamandua*. In the latter extant genus, the transverse axis (longer axis) of the facet for distal articulation is forming an angle close to 45° with respect to the plane of the anterior side of the radius, while this axis is nearly parallel with respect that plane in *N. borealis* and *Neotamandua* sp. This difference gives to the distal radius of the compared *Neotamandua* species a non-rotated appearance, unlike the same epiphysis in *Tamandua*. In anterior view, the distal articulation facet of *N. borealis* and *Neotamandua* sp. is visible in wedge shape pointing towards the medial border. Additionally, in the same view, this facet exhibits comparable exposures in both of the latter species, considerably more than in *Tamandua*. The posterior side of the distal epiphysis is from flat to slightly concave in *N. borealis* and *Neotamandua* sp., unlike the convex posterior side in *N. greslebini* (this observation could suggest that the material of *Neotamandua* sp. is not the holotype of *N. greslebini*, as speculated by McDonald et al. 2008) and *Tamandua*. The distal extension of the lateral ridge in *N. borealis* and *Neotamandua* sp. is similar.

Astragalus. The astragalus of *Neotamandua* sp. (MACN 2406) is only represented by the astragalar body. The medial trochlea is smaller than the lateral trochlea, but this asymmetry is less than in *N. borealis*. In addition, these sections of the trochlea are proportionally less separated in the latter species than in *Neotamandua* sp.

Calcaneum. The calcaneum is fragmentary in *Neotamandua* sp. (MACN 2411). As in the case of the astragalus, the preserved portion is the bone body. The ectal facet is sub-triangular in shape in *Neotamandua* sp., while it is approximately sub-oval in *N. borealis*. The sustentacular facet is more medially extended in the latter species than in *Neotamandua* sp. In both species, the cuboid facet is partially visible in dorsal view, particularly in *Neotamandua* sp. In the same view, the lateral ridge is slightly exposed in *N. borealis*, but not so in *Neotamandua* sp.

Discussion. The former comparisons allow to recognize a few morphological similarities and differences between homologous postcranial elements of *N. borealis*, *N. greslebini* and *Neotamandua* sp. It is considered that some similarities in these species are potentially diagnostic at the genus level, namely the sub-rounded to gently triangular shape of the tibial mid-section; ectal and sustentacular facets incipiently connected in the astragalus; and a short tendinous groove in the lateral side of the calcaneum (Table 4). These similarities seem to provide support to the hypothesis that these northern and southern South American species referred to *Neotamandua* are closely related and, consequently, that they are correctly included in the same genus. Alternatively, these common features could be symplesiomorphies of a hypothetical lineage of myrmecophagids more late diverging than *Protamandua* and apparently closer to *Myrmecophaga* than *Tamandua*. Provisionally, from the analysis presented, it is proposed to circumscribe the genus *Neotamandua* to the nominal species *N. conspicua* (type species), *N. greslebini* and *N. borealis*. Since *N. magna* and *N.*? *australis* are doubtfully assigned to *Neotamandua* or its allocation in this genus has been seriously questioned (McDonald et al. 2008; this work), they are considered *species inquirendae*, following the International Code of Zoological Nomenclature (Ride et al. 1999). To denote the questionable generic allocation of *N. magna* is suggested the use of inverted commas, i.e. '*N.*' *magna*. The material referred to *Neotamandua* sp. seems correctly referred to this genus, but it should be further tested. It is possible that these specimens correspond to a new species.

The diagnosis for *Neotamandua* proposed below is largely based on the designation of the specimen FMNH P14419 as epitype for the type species, *N. conspicua*, after considering the fragmentary nature of the holotype of this taxon (MACN 8097; Rovereto 1914), and, consequently, its ambiguity or lack of some taxonomically relevant features, particularly in the rostrum. In addition, the potentially diagnostic postcranial features for *Neotamandua* that has been identified above are also incorporated in the new diagnosis until cranial-postcranial associations are found and studied.

Neotamandua Rovereto, 1914

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

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

Other referred species. *N. greslebini* Kraglievich 1940; *N. borealis* Hirschfeld 1976.

Related *species inquirendae*. '*N.*' *magna* Ameghino 1919 (*Myrmecophaga magna* new combination? See McDonald et al. 2008); *N.*? *australis* Scillato-Yané & Carlini 1998.

Diagnosis. Middle-to-large sized myrmecophagid, larger than *Tamandua* but smaller than *Myrmecophaga*. It can be differentiated from other vermilinguans by the following combination of characteristics: in dorsal view, rostrum strongly tapered towards its anterior end (more than in any other myrmecophagid), with a regular transition in width from the anterior portion of frontals to the anterior end of nasals; reduced lacrimal which is not part of the orbit; jugal inserted in posteroventral position with respect to the lacrimal and slightly projected in posterodorsal direction; frontal forming a dorsal dome at the orbit level; hard palate well extended towards the posterior end of the skull, close to the ventral border of the occipital condyles; squamosal (= posterior) zygomatic process dorsally inclined; presence of palatine "wings"; horizontal inclination of the glenoid (Gaudin & Branham 1998); sub-oval to gently triangular shape of the tibial mid-section; ectal and sustentacular facets incipiently connected in the astragalus; short tendinous groove in the lateral side of the calcaneum.

Neotamandua conspicua Rovereto, 1914

(Fig. 5)

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

Holotype. MACN 8097, posterior portion of a skull.

Epitype. FMNH P14419, nearly complete skull but with fractured rostrum and partially eroded frontals and parietals.

Geographical and stratigraphic provenance. MACN 8097 is from an indeterminate locality in the Santa María Valley, Catamarca Province, Argentina (Rovereto 1914). Probably Andalhuala Formation. Upper Miocene (McDonald et al. 2008; Bonini 2014; Esteban et al. 2014).

FMNH P 14419 is from the Corral Quemado area, Catamarca Province, Argentina. Corral Quemado Formation. Lower Pliocene (Bonini 2014; Esteban et al. 2014). This specimen was collected by Robert Thorne and Felipe Méndez during the Second Captain Marshall Field Palaeontological Expedition, which was led by Elmer S. Riggs and developed in Argentina and Bolivia in 1926□1927 (Simpson, pers. comm.; Riggs 1928). In the Field Museum, where it is deposited, has been catalogued as *N. conspicua*. No known reference publication exists as support for the taxonomic assignation to this species, except in Gaudin & Branham (1998) and, now, in this work from direct comparison with the holotype.

Diagnosis. See the diagnosis for *Neotamandua* above. The postcranial diagnostic features included there do not belong to material known for this species.

Comparative description of the epitype. The skull FMNH P14419 is anteroposteriorly elongated, with a general architecture more similar to that in *Myrmecophaga* than *Tamandua*. The cranial measurements taken for this specimen are shown in the Table 1. In dorsal view, both the rostrum, in general, as well as the nasals, in particular, are anteriorly tapered. The pre-orbital section of the frontals is proportionally less elongated than in *Myrmecophaga*. The lacrimal has a sub-triangular outline and its anteroposterior and dorsoventral lengths are similar, unlike *Myrmecophaga*, in which the lacrimal is triangular and more anteroposteriorly elongated. The insertion of the jugals is more ventral and posterior than in *Myrmecophaga* and even more than *Tamandua*. Each jugal is slightly tapered by mediolateral compression in its posterior end and it is posterodorsally projected, instead of posteroventrally like *Myrmecophaga*. The posterolateral process of the maxilla contacts the entire anterior and ventral borders of the lacrimal. The orbital ridge is less prominent than in *Myrmecophaga*. The superior orbital wall is laterally expanded, forming a roof more developed than in *Myrmecophaga*. At the orbit level, the palatines are also laterally expanded, forming palatine "wings". These structures make the anterior hard palate look wider than the posterior palate. The posterior end of the hard palate is less ventrally projected, unlike *Tamandua* and *Myrmecophaga*. In lateral view, the squamosal zygomatic processes are dorsally inclined, unlike the ventral inclination of the same bone projection in *Tamandua* and *Myrmecophaga*. This feature would be a convergence with *Cyclopes*. The braincase is proportionally larger than in *Myrmecophaga*, but smaller than in *Tamandua*. The tympanic bulla is less developed than in *Tamandua*. The external auditory meatus has subcircular to circular shape, like *Myrmecophaga* (ovated in *Tamandua*). In *N. conspicua* the same opening is located in a posterodorsal position, like *Myrmecophaga* and in contrast with *Tamandua*, in which it has an anterodorsal position. Despite the palatopterygoid suture is not well preserved, appears to be more similar to the irregular suture in *Myrmecophaga*, with a posteriorly opened, asymmetrical "V" shape, than the regular suture in *Tamandua*, with an anteriorly opened, symmetrical "V" shape. There is no interpterygoid vacuity in which it could be established a soft palate, like *Myrmecophaga*. The occipital condyles are proportionally larger than in *Myrmecophaga* [Insert Fig. 5 here].

Discussion

Systematic implications

This works includes the first description of a new, valid extinct genus for Myrmecophagidae in the last century, i.e. *Myrmedioctes* gen. nov. Likewise, it constitutes a novel taxonomic comprehensive reassessment for *Neotamandua* from Hirschfeld (1976). The results suggest that there are still critical gaps in our knowledge on the composition and diversity of the Neogene assemblages of these xenartrans, particularly in the tropical region of South America. With the inclusion of Gen. et sp. nov. (Fig. 6), Myrmecophagidae now comprises at least five genera (three of them fully extinct) and 11 nominal species (eight extinct species), namely [the dagger means extinct species]: *Protamandua rothi*†; *Neotamandua*? *australis*†; *Neotamandua borealis*†; Gen. et sp. nov.†; '*Neotamandua*' *magna*†; *Neotamandua greslebini*†; *Neotamandua conspicua*†; *Myrmecophaga caroloameghinoi*†; *Myrmecophaga tridactyla*; *Tamandua tetradactyla*; and *Tamandua mexicana*. Of these taxa, only two genera and two species have fossil occurrence in northern South America: *N. borealis* (Middle Miocene of Colombia; Hirschfeld 1976) and Gen. et sp. nov. (Middle Miocene of Colombia; this work) (Fig. 7). The latter taxon is a small-to-middle sized myrmecophagid, comparable but slightly smaller than *Tamandua*. The general morphology of the skull of this new anteater resembles more to that of *Tamandua* than any other known taxon. It shows remarkable features such as: (1) strongly tapered nasals toward its anterior rostrum; (2) relatively low rostrum and anterior section of frontals; (3) large pre-orbital section of frontals; and (4) strongly triangulated (anterior) lacrimal. The tapering of nasals is a characteristic in common with *N. conspicua*, but in the latter species the entire rostrum is tapered, not only the nasals, like Gen. et sp. nov. The relatively low rostrum and anterior section of frontals seems to indicate a plesiomorphy, given that this feature is apparently present in *P. rothi*. A large pre-orbital section of frontals is shared, in (nearly) extreme condition, by *N. conspicua* and, especially, *Myrmecophaga*, but it should be noted that in Gen. et sp. nov. there is no such as elongated skull. And, finally, the strongly triangulated (anterior) lacrimal in the latter species is superficially similar to that in *Myrmecophaga*. Estimates of cranial measurements and features (rostrum length, exposure of the maxilla in the orbit and curvature of the basicranial-basifacial axis) used for coding the characters with numbers 4, 8, 9 and 42 of the character list by Gaudin & Branham (1998), allow tentatively infer the phylogenetic position of Gen. et sp. nov. as a taxon included within the clade *Tamandua* + *Neotamandua* + *Myrmecophaga* and located in a polytomy with *Tamandua*. Under this preliminary phylogenetic analysis, which is not presented in the results section because there is no enough information for coding the new taxon, *Protamandua* is well supported as the most basal myrmecophagid as consequence of sharing several character states with non-Myrmecophagidae Vermilingua (i.e. *Cyclopes* and *Palaeomyrmidon*; for more details, see Gaudin & Branham 1998). For future studies, it is tentatively suggested the subfamilial name “Myrmecophaginae” for all the Myrmecophagidae more late diverging than *Protamandua*, including possibly Gen. et sp. nov. In this sense, new and more complete material referable to the latter taxon is required to shed light on its phylogenetic position [Insert Fig. 6 here].

On other hand, the taxonomic analysis of *Neotamandua* and its referred species indicates that these taxa were based on a poorly supported taxonomy. Other case of extinct vermilinguans with flawed systematics in low levels of the taxonomic hierarchy was noted by McDonald et al. (2008) with regard to genera and species proposed from isolated postcranial elements of putative myrmecophagids or even members of new, distinct families from the Early Miocene of Santa Cruz, southern Argentina. These authors, partially based on comparisons by Hirschfeld (1976), argued that the number of taxa claimed for that area and interval (seven genera and nine species; e.g. *Promyrmephagus*, *Adiastaltus*; Ameghino 1894) has been artificially inflated, even though it is still possible to revalidate taxa other than the well validated species *P. rothi* (McDonald et al. 2008). All these research problems in systematics imply the need to regularly reevaluate the taxonomy of extinct anteaters through reexamination, when possible, of previously described material and the study of new specimens. While it is true that the fossil record of Vermilingua is poor and fragmentary in comparison, for instance, with that of other xenartrans such as Tardigrada, the sampling effort should be increased in order to have greater recovery of fossil material for this group, especially in areas known for their preservation potential (e.g. southern and northwestern Argentina, southwestern Colombia).

The reevaluation of the taxonomic status of *Neotamandua* found that there was no diagnosis for this genus. The newly proposed diagnosis includes multiple cranial and potential postcranial characteristics, which uphold that *Neotamandua*, independently whether it is a natural group or not, certainly contains species that do not belong to *Myrmecophaga*, despite their great resemblance with the latter. This outcome is congruent with the taxonomic opinion of Gaudin & Branham (1998) and is at odds with Patterson et al. (1992). Now, can we confidently say that *Neotamandua* is monophyletic from current evidence? *Neotamandua*, as previously defined by other workers, may be composed of successive basal species or genera in relation to the hypothetical clade of *Myrmecophaga* (i.e. *My. tridactyla* + *My. caroloameghinoi*). If that is correct, *Neotamandua* would be paraphyletic by definition, since it excludes some of its descendants (Sereno et al. 1991). This possible pattern of basal paraphyly is consequence of a taxonomy not defined by clades, but grades (Huxley 1958; Wood & Lonergan 2008). The monophyly of *Neotamandua*, as was redefined here (i.e. *N. conspicua* + *N. greslebini* + *N. borealis*), is tentatively supported by three potential synapomorphies shared by two of its species whose postcranium is known (*N. greslebini* and *N. borealis*): (1) sub-oval to gently triangular mid-section of the tibia; (2) ectal and sustentacular facets incipiently connected in the astragalus; (3) short tendinous groove in the lateral side of the calcaneum. However, the synapomorphic condition of these features for *Neotamandua* need to be further tested from systematic analysis of new, more complete and/or associated material of Gen. et sp. nov. and species referred to *Neotamandua*. That would allow to assess more adequately the global morphological variability and character distribution in Miocene myrmecophagids more late diverging than *Protamandua*. In turn, knowing this distribution better, it is more likely to disentangle the taxonomic identities and affinities of the *Neotamandua* species in order to corroborate the monophyly of this genus. For the moment, the hypothesis of Hirschfeld (1976) that *Neotamandua* is not monophyletic is, in principle, less probable if the *species inquirendae* ‘*N.*’ *magna* and *N.*? *australis* are excluded from the genus, as it was decided here, than if they are retained within it. The exclusion of the *species inquirendae* does not affect the hypothesis that *Neotamandua* is closer to *Myrmecophaga* than any other known nominal genus. Consequently, the type species of *Neotamandua*, *N.*

conspicua, is reiterated as closer to *Myrmecophaga* than *Tamandua*, in line with the phylogeny of Gaudin & Branham (1998) and unlike the hypothesis of Carlini & Scillato-Yané (1998).

Finally, the material referred to *Neotamandua* sp. and used in this study to make comparisons with *N. borealis*, seems correctly allocated in that genus, but it might eventually be assigned to a new species with very large body size, larger than *N. greslebini*. This is partially conditioned to the clarification of the taxonomic status of '*N.*' *magna*, which is a species comparable in body size to *Neotamandua* sp., so they could be (or not) the same taxon.

The diversification of Myrmecophagidae

McDonald et al. (2008) pointed out that since the highly incomplete fossil record of Vermilingua, several fundamental questions on the evolution of this group, including morphological trends and the acquisition of ecological preferences in its distinct taxa, are largely unknown. Likewise, they highlighted some uncertainty related to the divergence times of possible sub-clades. However, several inferences and hypotheses about the evolutionary history of anteaters and, particularly, the myrmecophagids, can be outlined from the current evidence, including that presented in this work. Following to Pascual & Ortiz-Jaureguizar (1990), McDonald et al. (2008) and Toledo et al. (2017), the next discussion is based on multiple palaeobiological, ecological and biogeographical aspects as major constraints and/or consequences of the myrmecophagid evolution.

The diversification of Myrmecophagidae was an macroevolutionary event that occurred through the Neogene, at least as early as the Burdigalian (Early Miocene), according to the minimal age estimated for the most basal genus, i.e. *Protamandua*. The beginning of this diversification is approximately overlapped in time with the onset or development of similar events in other higher taxa in South America, such as the xenartrans Megatherioidea, Mylodontidae, Glyptodontidae and Dasypodini (Croft et al. 2007; McDonald & De Iuliis 2008; Bargo et al. 2012; Carlini et al. 2014; Boscaini et al. 2019), or the South American native ungulates Pachyrukhinae, Mesotheriinae and Toxodontidae related to *Pericotoxodon* and *Mixotoxodon* (Seoane et al. 2017; Armella et al. 2018a; Armella et al. 2018b). This pattern shows the importance of the Early Miocene, particularly the Burdigalian, as a critical interval for the diversification of multiple South American land mammal lineages. In light of the geographical provenance of *Protamandua*, the most probable ancestral area for Myrmecophagidae is southern South America (Fig. 7). The palaeonvironmental conditions inferred for the Early Miocene of this area are considerably warmer and more humid (1000□1500 mm/year) than today, with presence of a subtropical dry forest (Iglesias et al. 2011; Quattrocchio et al. 2011; Kay et al. 2012; Brea et al. 2017; Raigenborm et al. 2018). In line with this reconstruction, Palazzesi et al. (2014), using a rarefied richness analysis from palynological evidence, reported that southern Argentina harboured in the Early Miocene a plant richness comparable to that documented today for the Brazilian Atlantic Forest, in southeastern Brazil. Similar to *Tamandua*, *Protamandua* would have preferred forested habitats and would have had semiarboreal habits (Gaudin & Branham 1998; McDonald et al. 2008; Kay et al. 2012). Whether the ancestral condition of substrate use in Myrmecophagidae is arboreal, as held by Gaudin & Branham (1998), the preference for open biomes (e.g. savannah) and terrestriality in *Myrmecophaga* (and possibly in *Neotamandua*) is a derived condition (McDonald et al. 2008; Toledo et al. 2017). The semiarboreal habits of *Tamandua* are explained from niche conservatism or, alternatively, from convergence with *Protamandua* if the ancestor of *Tamandua* was hypothetically terrestrial [Insert Fig. 7 here].

Since their particular, low basal metabolic rates and myrmecophagous diets (McNab 1984, 1985), it is likely that the global warm recovery during the early Neogene (Early Miocene to early Middle Miocene; including the Middle Miocene Climatic Optimum or MMCO; Fig. 8), linked to latitudinal temperature gradient reduction and expansion of the tropical (warm) forest belt towards higher latitudes in the continents (including South America; see Anderson 2009; Herold et al. 2011; Morley 2011; Palazzesi et al. 2014), has influenced on the evolutionary differentiation of the myrmecophagids, maybe predominantly *in situ* as in the climatically-induced evolution of other small Cenozoic mammals (Fortelius et al. 2014), such as *Protamandua*. This differentiation would have been triggered by increase in suitable area in terms of preferred biomes (warm forests in this case) and, especially, temporarily sustained availability of social insects for their feeding (McDonald et al. 2008; Kay et al. 2012; Toledo et al. 2017). Indeed, extant termites and ants (Termitidae and Formicidae, respectively) concentrate the vast majority of their biomass (and species richness) in the tropics and warm subtropical regions (Hölldobler & Wilson 1990; Tobin 1995; Davidson & Patrell-Kim 1996; Eggleton et al. 1996; Davidson et al. 2003; Ellwood & Foster 2004; Keller & Gordon 2009). This ecogeographical pattern is consistent with the fossil record of the former higher taxa, which shows a strong tropical niche conservatism from their respective evolutionary origins in the Late Cretaceous/Early Paleogene (see below; Archibald et al. 2011; LaPolla et al. 2013; Guénard et al. 2015; Bourguignon et al. 2017).

According to Blois & Hadly (2009), the responses of mammalian taxa to climate change throughout the Cenozoic are causally interconnected. These responses at the level of individual taxa may include changes in abundance, genetics, morphology and/or distributional range, and they may instigate multitaxa responses such as diversification events comparable to that placed on the root of the evolutionary tree of Myrmecophagidae. This case of a cladogenetic event possibly induced by climate contrasts in kind of biome with those that have been repeatedly documented for intervals of grassland expansion (e.g. Equidae, Bovidae, Cervidae, Ochotonidae, Hippopotaminae; MacFadden 2000; Bouchenak-Khelladi et al. 2009; Boisserie & Merceron, 2011; Ge et al. 2013).

In the Middle Miocene, *N.*? *australis*, *N. borealis* and Gen. et sp. nov. exhibit a mosaic of morphological features in common with *Tamandua* and/or *Myrmecophaga*, as well as some exclusive characteristics, which suggest an early, important increase in morphological disparity in Myrmecophagidae and possibly the evolutionary divergence of those lineages comprising its crown-group. This coincides with the interpretation of Hirschfeld (1976), according to which the lineages including the extant genera of Myrmecophagidae differentiated morphologically at least from the Friasian (Middle Miocene). Same way, it is compatible with the results of the molecular phylogenies by Delsuc et al. (2001, 2012) and Gibb et al. (2016), which estimated that the evolutionary divergence of *Tamandua* and *Myrmecophaga* occurred in the late Middle Miocene, c. 13 mya. On the other hand, relative body sizes inferred for the Middle Miocene taxa show an apparent trend towards increase in body size in comparison with the basal taxon *Protamandua*. During this interval, the myrmecophagids have a wide geographical distribution in South America (Fig. 7), from low to medium-high latitudes. This is in line with the evolution of larger body sizes since when this attribute increases, the foraging area also increases and, with it, the distributional range, according the general foraging strategy of the extant myrmecophagids (Naples 1999; Toledo et al. 2017; Gaudin et al. 2018). The co-occurrence pattern of *N. borealis* and Gen. et sp. nov. in La Venta area in Colombia constitutes the earliest pattern of this kind for Myrmecophagidae until pending systematic revisions for putative taxa from the Early Miocene of Santa Cruz, Argentina, are carried out. These revisions would allow to determine whether there are two or more co-occurrent myrmecophagid taxa in the latter area. Given that *N. borealis* and Gen. et sp. nov. probably are not sister taxa, it would imply a non-sympatric diversification followed by dispersal of at least one of the involved taxa. The habitat preference of Gen. et sp. nov. in the palaeoenvironmental mosaic of La Venta area (Kay & Madden 1997; Spradley et al. 2019) is speculated as tropical forest (semiarboreal?) by analogy with *Protamandua*, while it is proposed a more generalized habitat selection for *N. borealis* in line with the palaeobiological inference of predominantly terrestrial locomotion for the latter taxon by Hirschfeld (1976). If this hold true, opens the possibility that *N. borealis* is the oldest myrmecophagid inhabiting zones with semi-open or even open vegetation (see below).

The morphological and probably taxonomic diversification of Myrmecophagidae continued in the Late Miocene. Inferred body sizes range from larger than *Tamandua* and nearly comparable to *Myrmecophaga*. Considering the wide geographical distribution during the Middle Miocene, there is probably a geographical bias in the fossil record of the myrmecophagids during the Late Miocene as the only known occurrences are

Myrmecophaga-like forms from northwestern Argentina (Fig. 7). If *N. borealis* and *N. greslebini* are sister taxa, as it seems, that means there was a biogeographical connection for Myrmecophagidae between northern and southern South America in the late Middle/early Late Miocene. This inference is congruent with the palaeobiogeographical analyses of Cozzuol (2006) and Carrillo et al. (2015), according to which the affinities between several Late Miocene, northern and southern South American land mammal assemblages are strong or, at least, not so distant as those between Middle Miocene assemblages from the same regions. This pattern might be explained from the geographical shrinks of the Pebas Mega-Wetland System and the Paranean Sea in the Middle-Late Miocene transition (Aceñolaza & Sprechmann 2002; Cozzuol 2006; Salas-Gismondi et al. 2015). It is also possible that the expansion of open biomes in South America during the Late Miocene has facilitated this biotic connection, as has been acknowledged in the case of other mammal taxa (e.g. Glyptodontinae, a xenartran group like Myrmecophagidae; Ortiz-Jaureguizar & Cladera 2008; Oliva et al. 2010). Indeed, from a palaeoenvironmental viewpoint, the (partial?) co-occurrence of '*N.*' *magna*, *N. greslebini* and *N. conspicua* in northwestern Argentina is important inasmuch as this pattern is related, for the first time in the evolutionary history of Myrmecophagidae, to savannahs well developed with respect to other kinds of vegetation cover (Latorre et al. 1997; Brandoni et al. 2012; Cotton et al. 2014; Amidon et al. 2017; Zimicz et al. 2018). On the basis of the foregoing and by generalization of morphological and ecological features of the living vermilinguans, e.g. less dependence on trees related to greater taxonomic and/or ecological diversity of consumed insects (Hirschfeld 1976; Montgomery 1985a; Rodrigues et al. 2008; Toledo et al. 2017; Table 5), it is hypothesized that, as early as the late Middle Miocene, with the triggering of a global cooling (Fig. 8), *Neotamandua* was involved in a niche evolution process within Myrmecophagidae which implied a significative increase in dietary diversity as myrmecophagous and expansion of substrate use and biome selection. Probably the species of this genus preferred the frequent use of the ground by biomechanical constraints and made inroads into largely open environments as humid savannahs, without excluding use of forested environments, like *Myrmecophaga* (Fuster et al. 2018; Gaudin et al. 2018). The former model is further supported from the evolutionary response pattern to major climatic-vegetational changes documented by Badgley et al. (2008) in a faunal sequence of mammals from the Late Miocene of southern Asia, according to which the trophic niche evolution and, particularly the expansion of this attribute, in conjunction with habitat changes, is related to increase in the probabilities of local and regional survivorship in the studied lineages [Insert Fig. 8 here].

On other hand, the fossil record of the crown-group genera, *Tamandua* and *Myrmecophaga*, is confined to the Pliocene-Pleistocene, but the evolutionary (morphological) divergence of *Myrmecophaga* would date back at least to the late Middle Miocene according the first appearance of *Neotamandua*, i.e. *N. borealis*. Under this assumption, the hypothesis of '*N.*' *magna* as a species of *Myrmecophaga* is perfectly feasible. In any case, the biogeographical dynamics of the two extant myrmecophagid genera may have been constrained by their respective ecological tolerances and, they, in turn, by the rapidly changing habitat and biome distribution in the Americas during at least the last five or six million years (de Vivo & Carmignotto 2004; Salzmann et al. 2011; Sniderman et al. 2016; Amidon et al. 2017; Roberts et al. 2018; Grimmer et al. 2018). This applies especially to the case of *Tamandua* since this taxon is less generalist in relation to habitat selection than *Myrmecophaga* (McDonald 2005). Considering the hypothesis of niche expansion for *Neotamandua*, the differentiation of *Myrmecophaga* would have accentuated this putative evolutionary trend through stronger preference for open environments, which is consistent with the general palaeoenvironment of savannah in the Early Pliocene of the area where occurs the oldest species of the latter genus, i.e. *My. caroloameghinoi* (Zavala & Navarro 1993; McDonald et al. 2008).

The myrmecophagid evolution has a late episode with the complete formation of the Panama Land Bridge (PLB) in the terminal Neogene (Coates & Stallard 2013; O'dea et al. 2016; Jaramillo 2018). *Myrmecophaga tridactyla* invaded and colonized Central- and southern North America (northern Mexico) at least as early as the Early Pleistocene (Shaw & McDonald 1987; Fig. 7). This dispersal event is part of the Great American Biotic Interchange (GABI), specifically the episode referred as GABI 2 (Woodburne 2010). Today, the northern boundary of this species is located in northern Central America, over 3000 Km to the south of the northernmost fossil record (Gaudin et al. 2018). This distributional difference was interpreted by Shaw & McDonald (1987) from the occurrence of warmer and more humid conditions in the Early Pleistocene of southern North America (southern United States-northern Mexico) than today in the same area. These conditions would have allowed that *Myrmecophaga* colonize subtropical savannahs with permanent availability of insects included in its diet (Croxen III et al. 2007; McDonald 2005), but subsequent climatic-vegetational shifts (desertification) during the Late Pleistocene would have forced from extirpation a range shrinkage of this taxon towards lower latitudes (McDonald 2005; Ferrusquía-Villafranca et al. 2017). The distributional range pattern of tropical taxa expanded towards southern North America during some intervals of the Pleistocene has been well supported from the records of multiple taxa other than

Myrmecophaga, including mammals and sauropsids (Shaw & McDonald 1987; Moscato & Jasinski 2016; Ferrusquía-Villafranca et al. 2017).

Like *Myrmecophaga*, *Tamandua* also colonized (or evolved in) northern continental territories outside South America. This is supported from the occurrence of *Tamandua* sp. in the terminal Pleistocene of Central Mexico (Arroyo-Cabrales et al. 2004; Ferrusquía-Villafranca et al. 2010; Fig. 7). In its northern zone, the current distributional area of *T. mexicana* includes latitudes comparable with that of the referred fossil record for this species (Navarrete & Ortega 2011). Central Mexico is part of the transitional area between the current Neotropical and Neartic regions, called Mexican Transition Zone (MTZ; Halffter & Morrone 2017). All these observations, in conjunction with the above interpretation of the Neogene biogeographical and environmental patterns, suggest that Myrmecophagidae kept throughout its evolutionary history a niche conservatism associated with tropical (warm) habitats (a case of phylogenetic niche conservatism or PNC; see Cooper et al. 2011; Fig. 8), possibly in parallel with the same pattern in species groups of its prey insects (Thompson 1994). Even more, the fact that Myrmecophagidae currently accumulates its highest species richness in the warmest and wettest belt of the Americas (Hayssen 2011; Navarrete & Ortega 2011; Miranda et al. 2017; Gaudin et al. 2018) is further interpreted as evidence that this higher taxon represents support for the tropical niche conservatism hypothesis (TCH; Wiens & Donoghue 2004; Wiens & Graham 2005). However, in line with the discussion above, this major ecological constraint in Myrmecophagidae is not only related to environmental thermal tolerance (see McNab [1985] for an analysis on the thermophysiological constraints of the Xenarthra; McNab [1984] also discussed the same issue for myrmecophagous mammals), as emphasized by

TCH, but it is also driven by food availability, at least by limiting or preventing historical colonization of low-productivity regions far from the tropics (Shaw & McDonald 1987; McDonald 2005; Šímová & Storch 2017; Fig. 8).

Conclusion

The systematic evidence presented here suggests that probably the diversification of Myrmecophagidae is taxonomically and biogeographically more complex than previously thought. This insight is based on the description of the new taxon Gen. et sp. nov. for the Middle Miocene of Colombia (co-occurrent species of *N. borealis*) and the determination of *Neotamandua*, as previously defined, as a wastebasket taxon which is probably formed by species belonging to more than one single genus. While Gen. et sp. nov. possibly has affinities with *Tamandua*, more information is needed to test its phylogenetic position within Myrmecophagidae. On the other hand, *N. borealis*, *N. greslebini* and *Neotamandua* sp. share postcranial features (potential synapomorphies) that imply some grade of kinship between them. Therefore, the two nominal species among the former ones are provisionally kept within *Neotamandua*. Alternatively, these features also may constitute symplesiomorphies of a hypothetical lineage which is apparently close to *Myrmecophaga*. The remaining nominal species referred to *Neotamandua*, i.e. '*N.*' *magna* and *N.*? *australis* were designated as *species inquirendae*. Overall, it is necessary to develop new systematic revisions, including new phylogenetic analyses similar to that of Gaudin & Branham (1998), from new material referable to Gen. et sp. nov. and the referred species to *Neotamandua*, so as to obtain enough evidence to solidly determine the phylogenetic position of the new species from La Venta and corroborate the putative monophyletic status of *Neotamandua*. In line with the foregoing considerations, the paleontological exploration of Neogene sedimentary units in northern South America and northern Argentina is crucial to improve our understanding of the diversification of Myrmecophagidae.

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Statement of data archiving

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

[identifier Gen. et sp. nov.]

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

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

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Figure captions

Figure 1. Geographical and stratigraphic provenance of the skull VPPLT 975 of the new taxon described here and the holotype of *Neotamandua borealis* (Hirschfeld 1976). **A**, location of the Department of Huila in Colombia; **B**, location of the fossil area of interest, i.e. northern of La Venta area, in the Department of Huila (small rectangle); **C**, location of

the fossil site (black star), near the La Victoria town; **D**, 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 are based on Hossotani et al. (2017). Nomenclatural modifications from these measurements are shown in the section of Anatomical Abbreviations. **A**, skull of *Tamandua* in dorsal view; **B**, 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. **A**, dorsal view; **B**, right lateral view; **C**, ventral view; **D**, left lateral view; **E**, anatomical drawing in dorsal view; **F**, anatomical drawing in right lateral view. **Abbreviations: fr,** frontals; **ji,** jugal insertion; **la,** lacrimal; **mx,** maxilla; **na,** nasals; **or,** orbit. Scale bar equal to 30 mm.

Figure 4. Epitype (FMNH P14419) of *Neotamandua conspicua*. **A**, dorsal view; **B**, right lateral view; **C**, ventral view; **D**, left lateral view; **E**, right hemimandible; **F**, left hemimandible; **G**, anatomical drawing in dorsal view; **H**, anatomical drawing in ventral view; **I**, anatomical drawing in left lateral view. **Abbreviations: ab**, auditory bullae; **fr**, frontals; **j**, jugal; **mx**, maxilla; **na**, nasals; **oc**, occipital condyles; **pal**, palatines; **ptb**, pterygoid bullae; **pte**, pterygoids; **szp**, squamosal zygomatic process. Scale bar equal to 80 mm.

Figure 5. Two very informative postcranial bones of the holotype (UCMP 39847) of *Neotamandua borealis* (Hirschfeld 1976). **A**, right astragalus, dorsal view; **B**, right

astragalus, ventral view; **C**, left calcaneum, dorsal view; **D**, left calcaneum, lateral view; **E**, anatomical drawing of the astragalus in dorsal view; **F**, anatomical drawing of the astragalus in ventral view; **G**, anatomical drawing of the calcaneum in dorsal view; **H**, anatomical drawing of the calcaneum in lateral view. **Abbreviations: af**, calcaneal accessory 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 6. Reconstruction 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 *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: **A**, biochrons of the myrmecophagid genera or questionable grouping (horizontal solid bars and dashed line); **B**, 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); **C**, 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. Palaeocological data used for the plot in 'B' is from the following references: Huntley & 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.

TABLES

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

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

Measurement	*N. borealis*	*N. greslebini*
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.

Measurement	*N. borealis*	*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

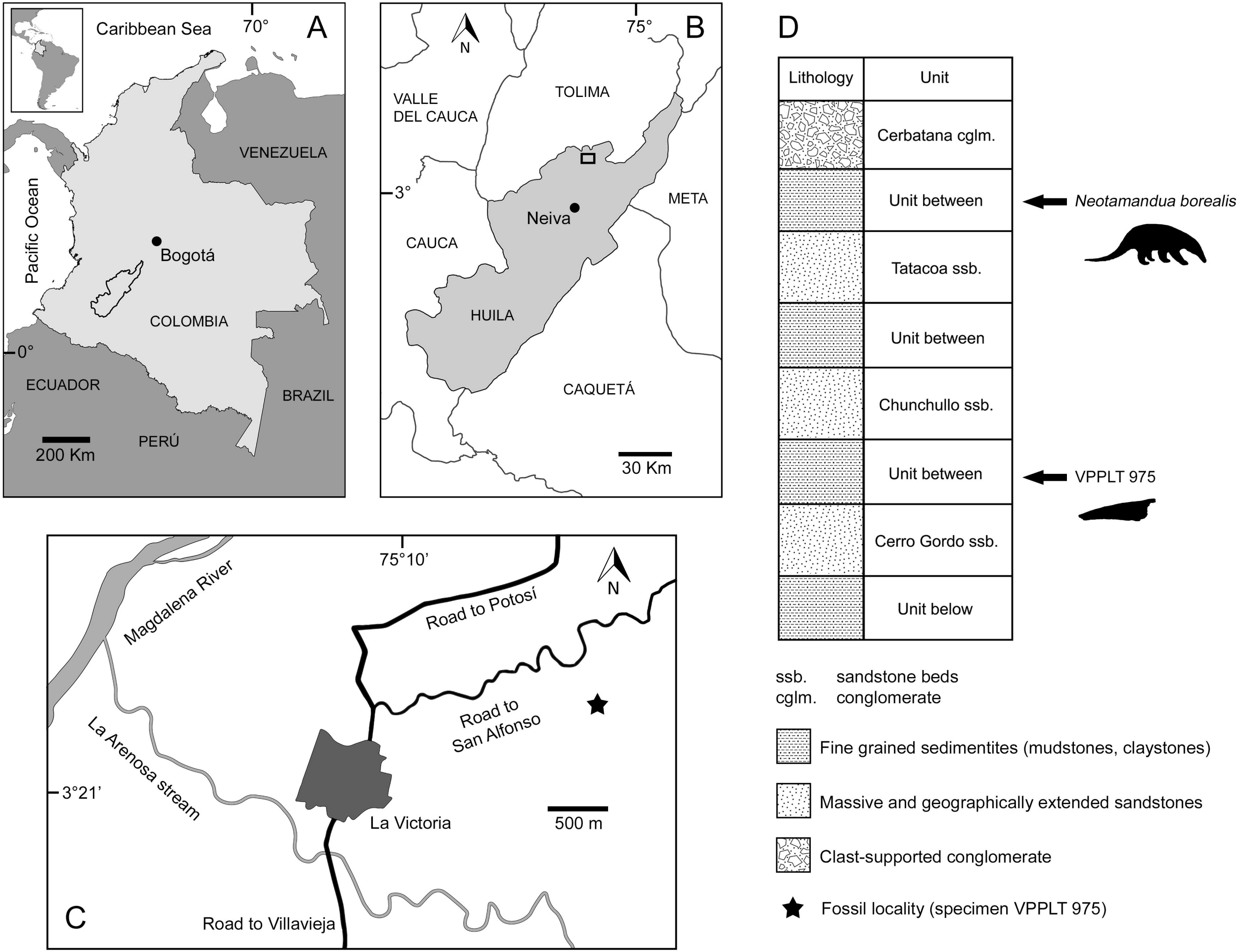
Table 4. Distribution of some postcranial characters of species referred to *Neotamandua* and other myrmecophagid taxa. The

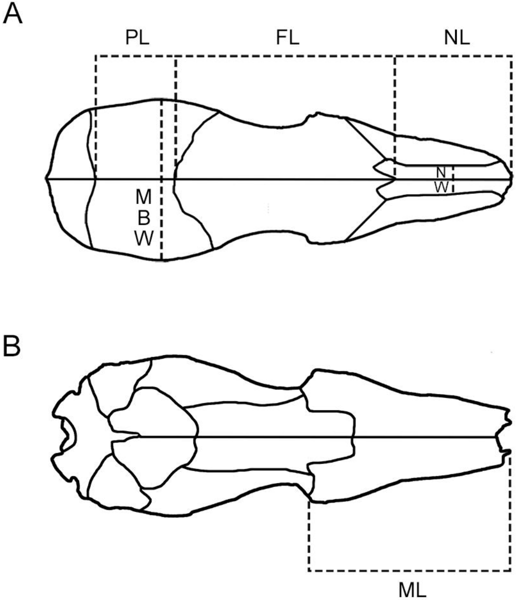
	N. borealis	*N. greslebini*	*Neotamandua* sp.	*Protamandua*	*Tamandua*	*Myrmecophaga*
Relative body size	Medium to large	Large	Very large	Small	Medium	Very large
Character						
1. Arrangement of the radial ridges	Parallel ridges	Parallel ridges	Parallel ridges	NA	Distally convergent ridges	Parallel 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

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 & 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 & 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 & 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


A
Caribbean Sea
70°
Pacific Ocean
VENEZUELA
Bogotá
COLOMBIA
0°
ECUADOR
BRAZIL
PERÚ
200 Km
B
N
75°
VALLE
DEL CAUCA
TOLIMA
3°
Neiva
META
CAUCA
HUILA
CAQUETÁ
30 Km
C
75°10'
N
Magdalena River
Road to Potosí
Road to
San Alfonso
La Arenosa stream
3°21'
La Victoria
500 m
Road to Villavieja
D
Lithology
Unit
Cerbatana cglm.
Unit between
Neotamandua borealis
Tatacoa ssb.
Unit between
Chunchullo ssb.
Unit between
VPPLT 975
Cerro Gordo ssb.
Unit below
ssb. sandstone beds
cglm. conglomerate
Fine grained sedimentites (mudstones, claystones)
Massive and geographically extended sandstones
Clast-supported conglomerate
Fossil locality (specimen VPPLT 975)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PL
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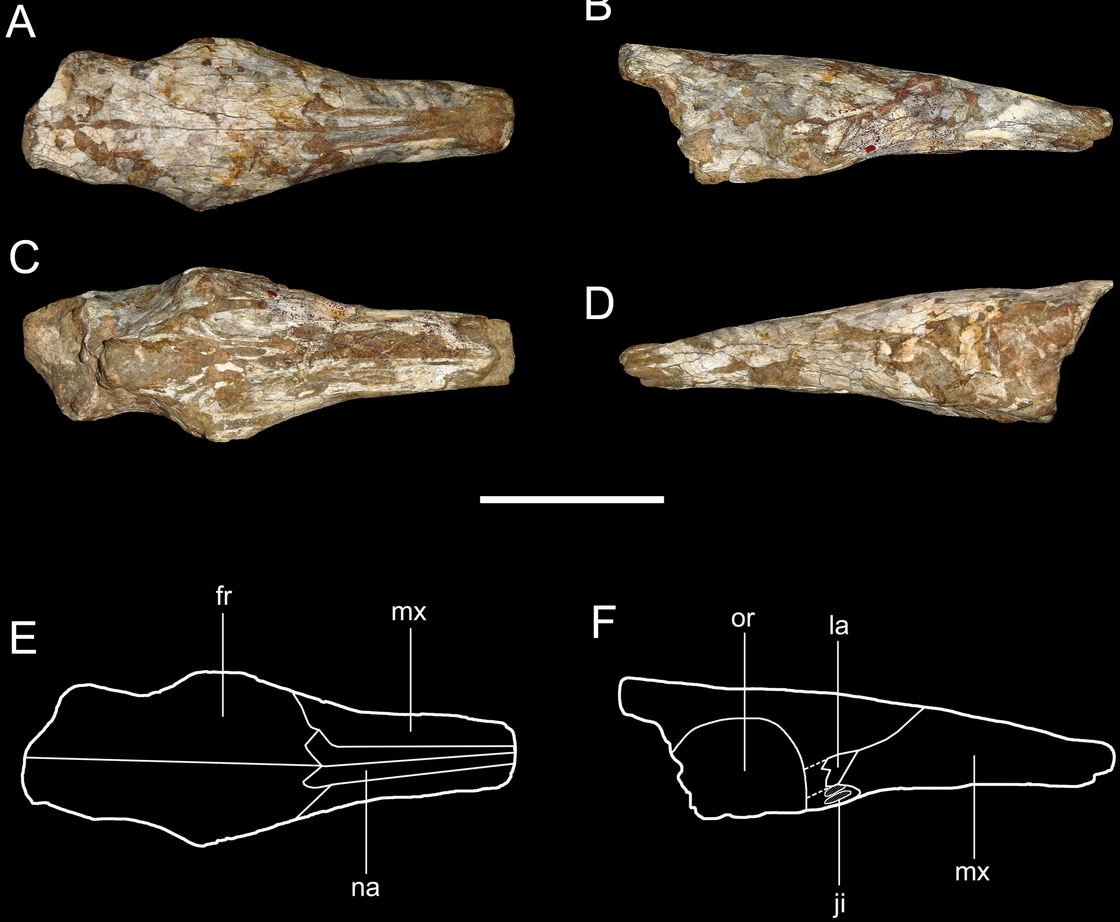
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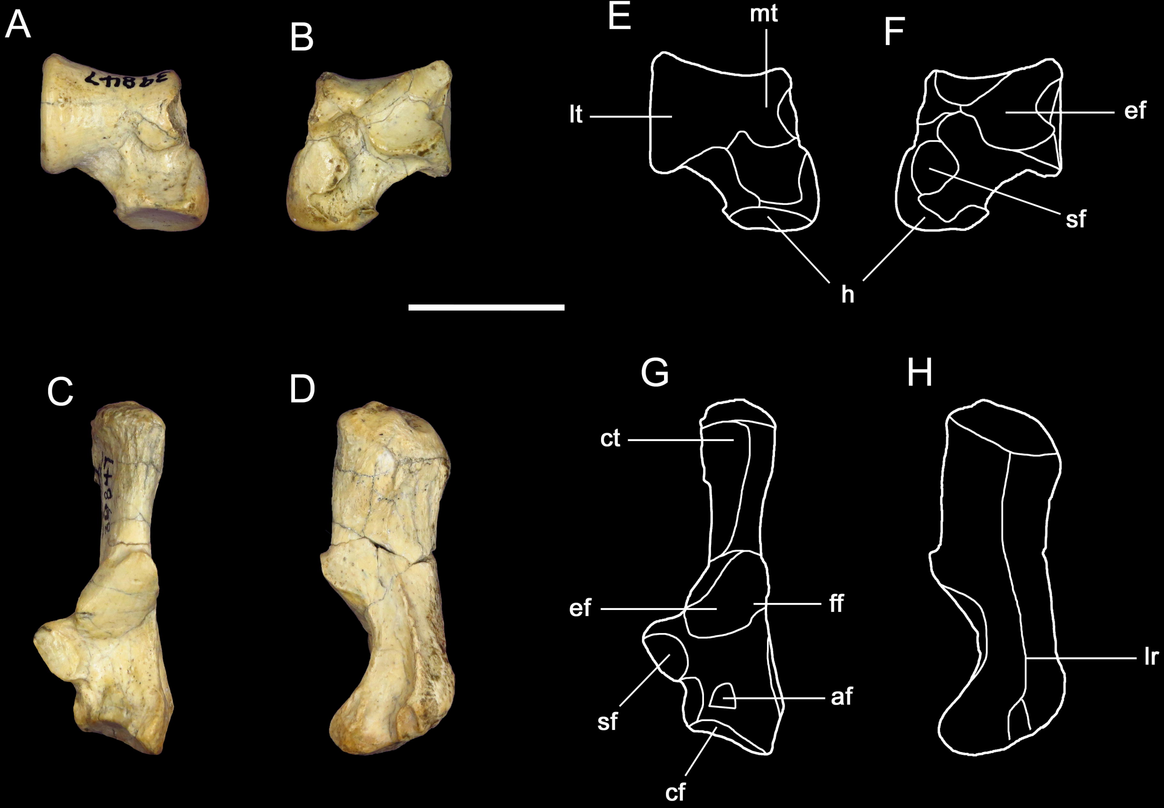
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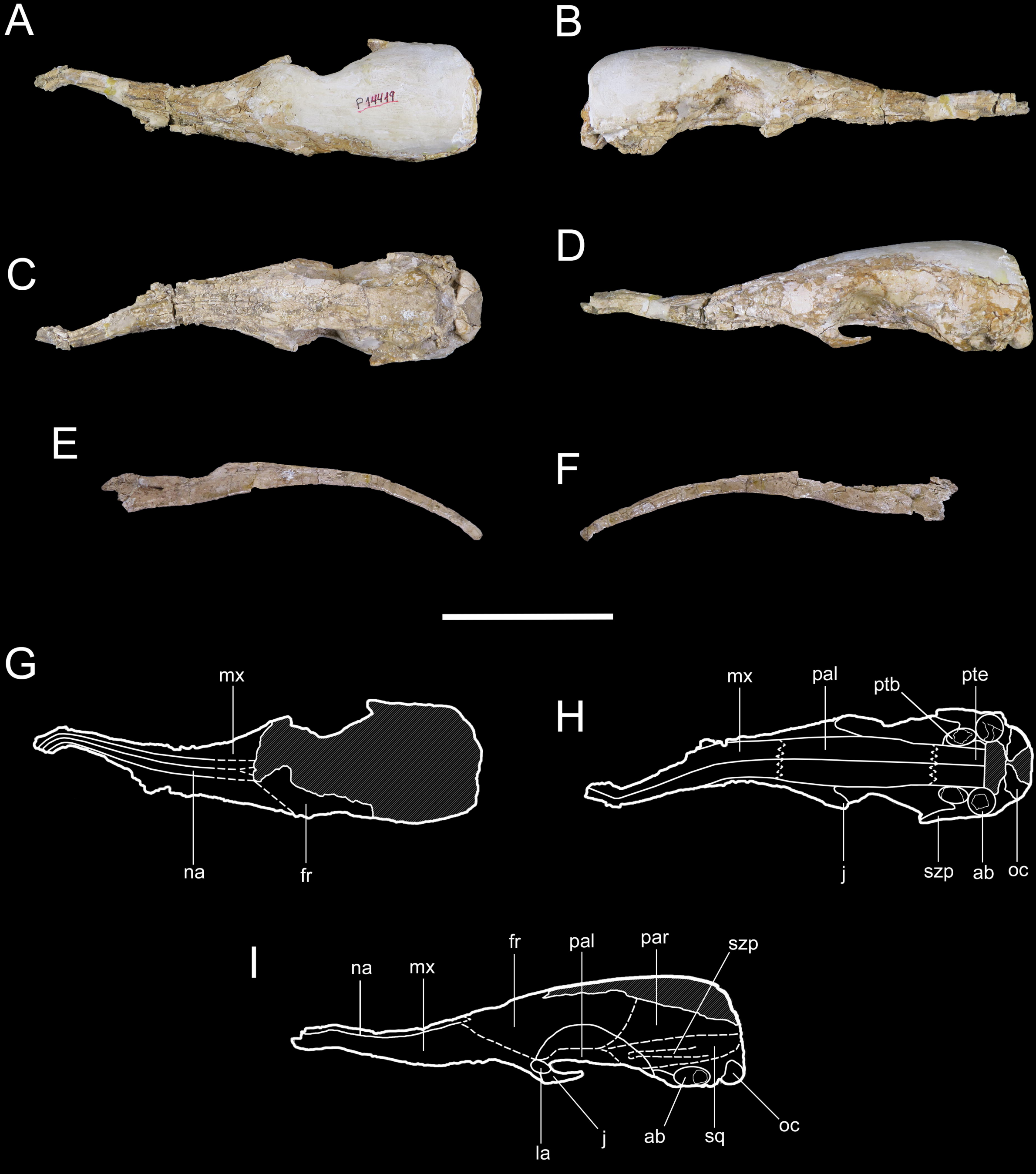
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P14419
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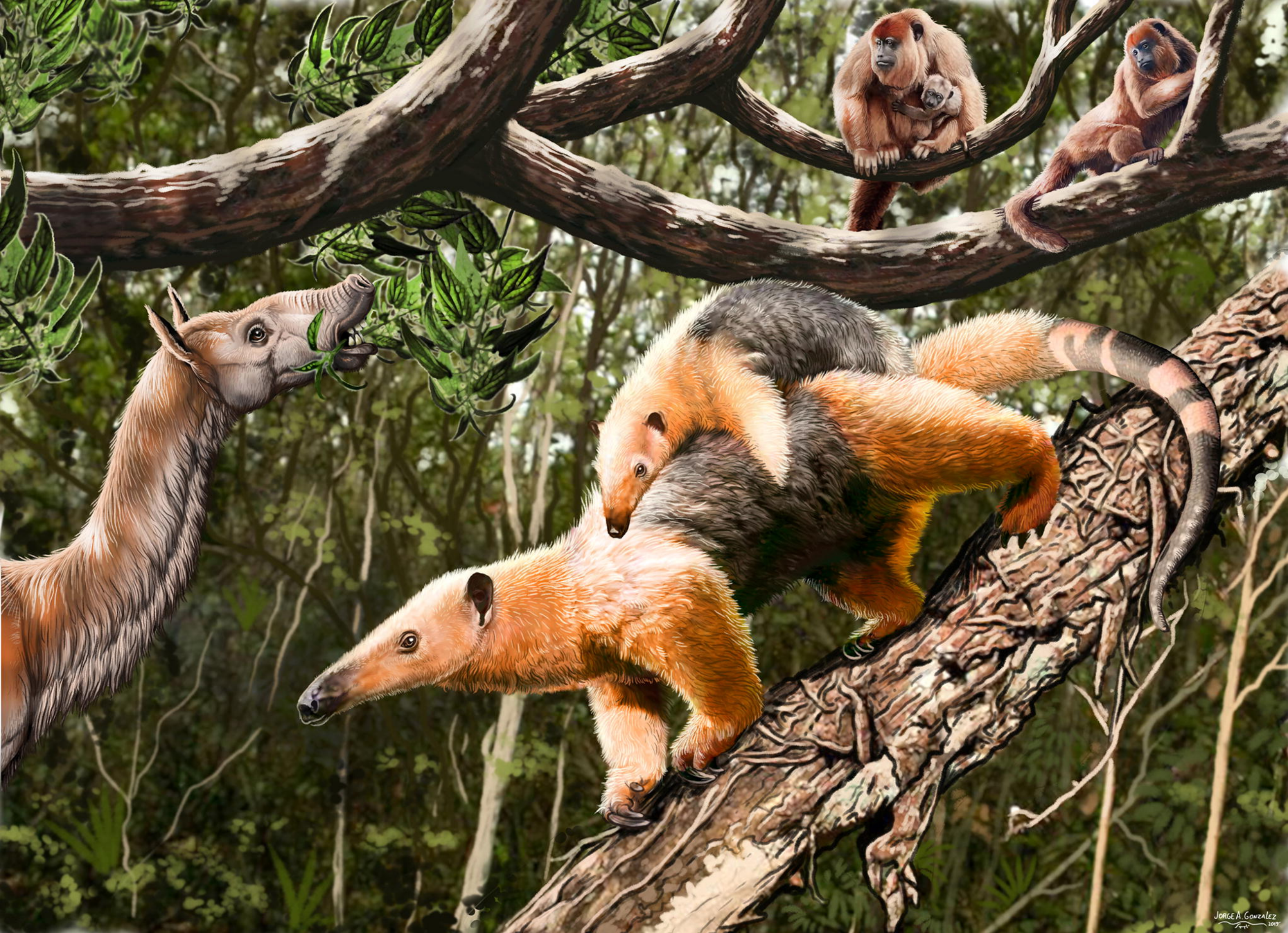
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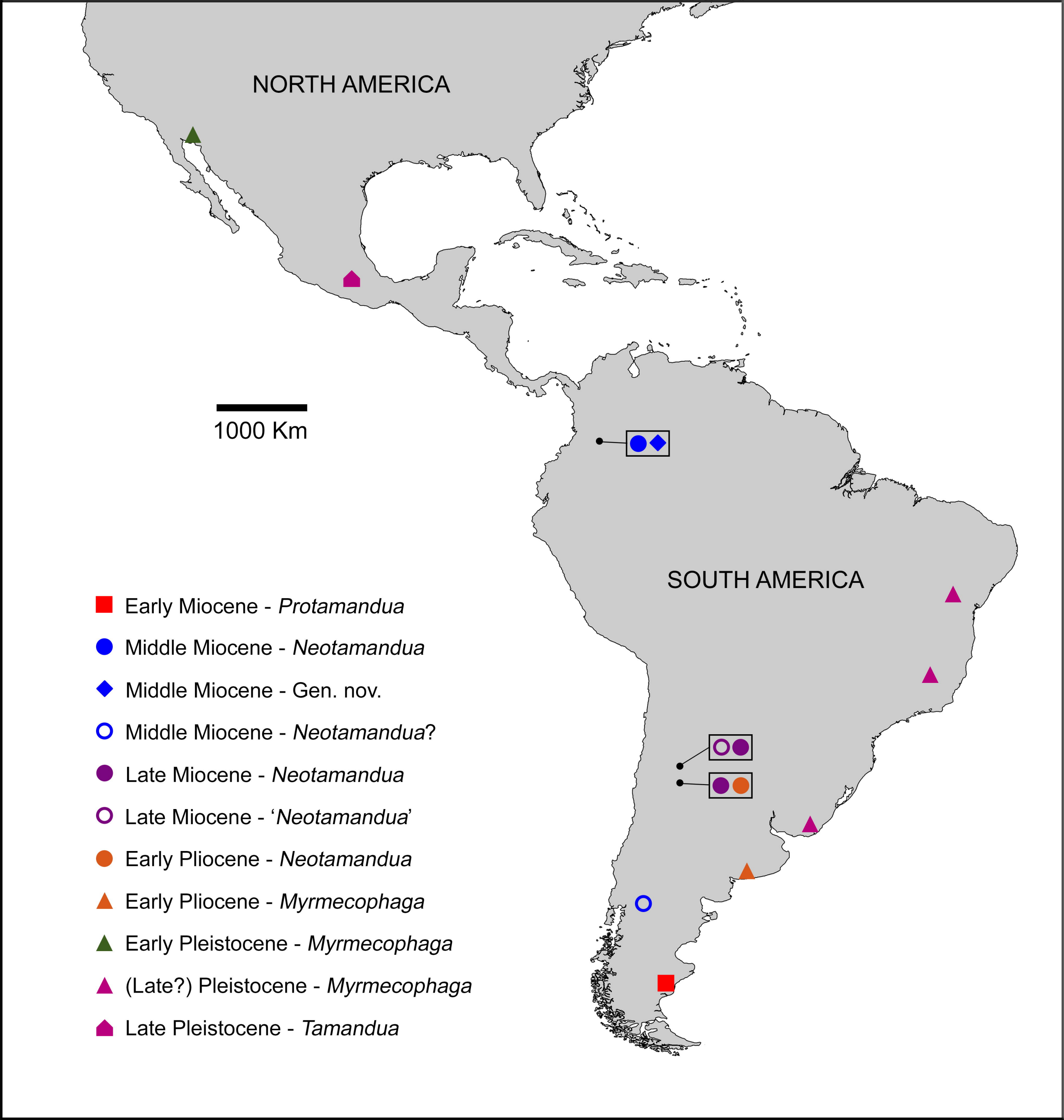
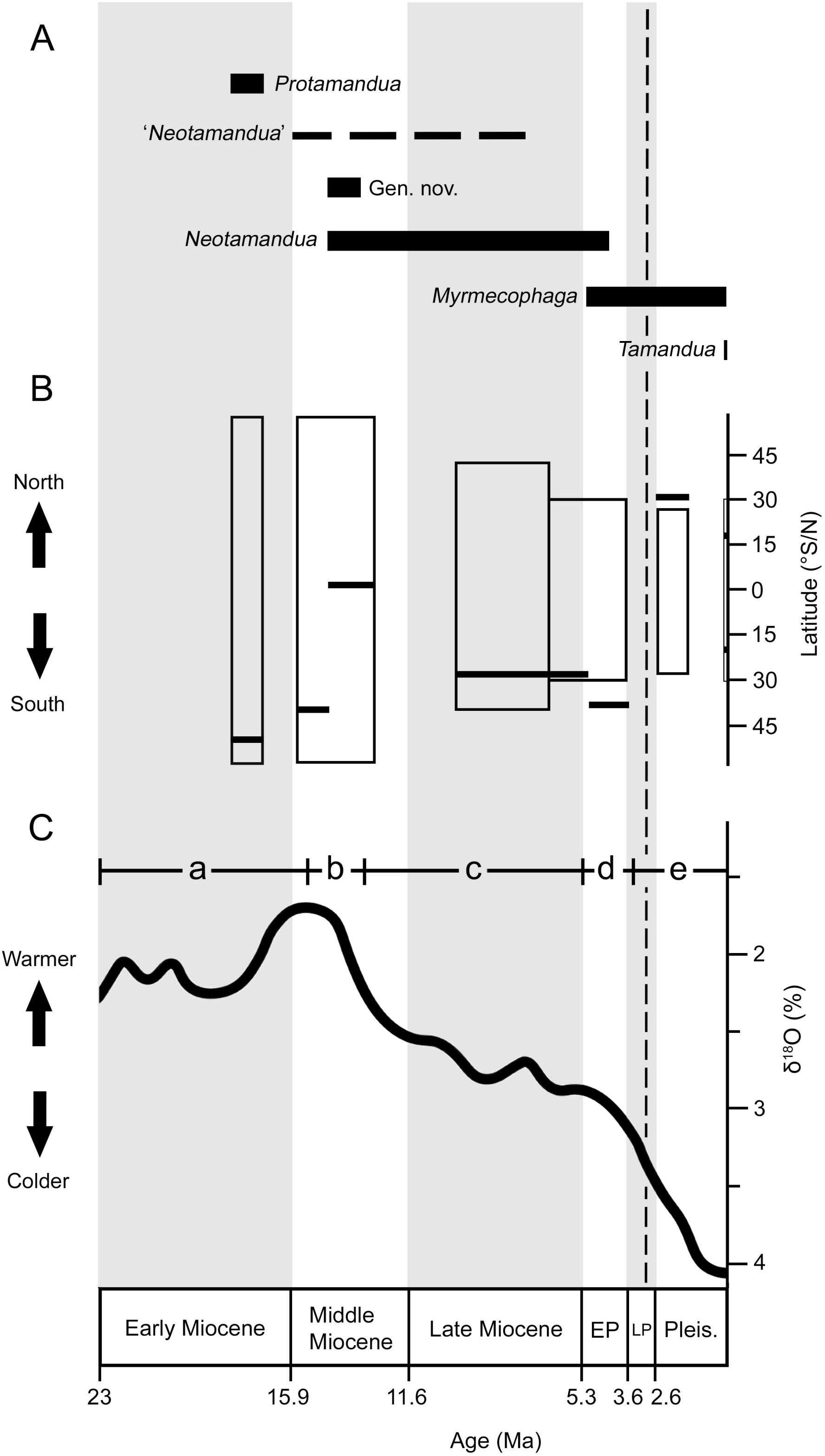
2019


NORTH AMERICA
SOUTH AMERICA
1000 Km
■ Early Miocene - *Protamandua*
● Middle Miocene - *Neotamandua*
◆ Middle Miocene - Gen. nov.
○ Middle Miocene - *Neotamandua*?
● Late Miocene - *Neotamandua*
○ Late Miocene - '*Neotamandua*'
● Early Pliocene - *Neotamandua*
▲ Early Pliocene - *Myrmecophaga*
▲ Early Pleistocene - *Myrmecophaga*
▲ (Late?) Pleistocene - *Myrmecophaga*
⬟ Late Pleistocene - *Tamandua*


A
Protamandua
'Neotamandua'
Gen. nov.
Neotamandua
Myrmecophaga
Tamandua
B
North
South
45
30
15
0
15
30
45
Latitude (°S/N)
C
a
b
c
d
e
Warmer
Colder
2
3
4
δ18O (%)
Early Miocene
Middle Miocene
Late Miocene
EP
LP
Pleis.
23
15.9
11.6
5.3
3.6
2.6
Age (Ma)