

The Phylogeny of the Myrmecophagidae (Mammalia, Xenarthra, Vermilingua) and the Relationship of *Eurotamandua* to the Vermilingua

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A cladistic investigation of the phylogenetic relationships among the three extant anteater genera and the three undoubted extinct myrmecophagid genera is performed based upon osteological characteristics of the skull and postcranial skeleton. One hundred seven discrete morphological characters are analyzed using the computer program PAUP. Characters are polarized via comparison to the successive xenarthran outgroups Tardigrada (represented by the living sloth *Bradypus*) and Cingulata (represented by the recent armadillos *Dasypus* and *Euphractus*). The analysis results in a single most-parsimonious tree (TL = 190, CI = 0.699, RI = 0.713). The tree corroborates the monophyly of the subfamilies Cyclopiinae and Myrmecophaginae, the former including the extant *Cyclopes* and the Pliocene genus *Palaeomyrmidon*. Within the Myrmecophaginae the Miocene genus *Protamandua* is the sister taxon to a clade including the remaining three genera. The recent *Tamandua* is in turn the sister taxon to the extant *Myrmecophaga* plus the Pliocene genus *Neotamandua*. Contrary to the suggestions of recent authors, weak support is provided for the taxonomic distinctiveness of the latter genus from the recent *Myrmecophaga*. The monophyly of the Myrmecophagidae is supported by 15 unequivocal synapomorphies. The monophyly of the Cyclopiinae and Myrmecophaginae is supported by 3 and 13 unambiguous synapomorphies, respectively. The enigmatic Eocene genus *Eurotamandua*, from the Messel fauna of Germany, is coded for the 107 morphological characters above and included in two subsequent PAUP analyses. The palaeodont *Metacheiromys* is also added to these two analyses as a nonxenarthran outgroup to test for the possibility that *Eurotamandua* lies outside the Xenarthra. In the first analysis, *Eurotamandua* is constrained a priori to membership in the Vermilingua. The single most-parsimonious tree (TL = 224, CI = 0.618) that results places *Eurotamandua* as the sister group to the remaining anteater genera, contra Storch and Habersetzer's (1991) assignment of *Eurotamandua* to the vermilinguan subfamily Myrmecophaginae. *Eurotamandua* shares six unequivocal synapomorphies with other anteaters, including the absence of teeth and the presence of a lateral tuberosity on the fifth metatarsal. The remaining vermilinguans are united by 11 unequivocal synapomorphies, plus an additional 10 ambiguous synapomorphies. In the second analysis, the position of *Eurotamandua* is unconstrained. The resulting single most-parsimonious tree (TL = 219, CI = 0.632) places *Eurotamandua* outside Vermilingua as the sister group to the Pilosa (*Vermilingua* plus *Bradypus*). The monophyly of this node is supported by four unambiguous synapomorphies in the unconstrained analysis. Further manipulation of this second analysis shows that placement of *Eurotamandua* as the sister group to the Xenarthra or to the Palaeodonta adds three steps to the shortest tree but is more parsimonious than its placement as a sister group to the Vermilingua is the previous analysis. The addition of pangolins to the analysis does little to alter the major phylogenetic conclusions of the study. The allocation of *Eurotamandua* to the Xen-

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which leaves open the bio-
ring the Eocene.

thran suborder Vermilingua,
era. Extant vermilinguans are
th to Paraguay and northern
ng vermilinguans within the
Cyclopes. Only *Tamandua* has
Cyclophaga tridactyla is the larg-
illy terrestrial (Wetzel, 1985).
e tail and a semiarboreal habi-
the extant anteaters (~230 g)
ile tail and a foot modified for

ecophagidae, *Protamandua* and
tly complete skulls and at least
nta Cruz formation of Patagonia
cludes isolated pedal elements
Cyclophagus and *Promyrmephus*,
(1992) as identical to the same
Myrmecophaga is based on a single nearly
of Argentina (Rovereto, 1914).
Myrmecophaga, has been proposed based on
ombia and the Pliocene Araucano
1976). The high degree of simi-
Myrmecophaga has led Patterson *et al.*
eric. However, we follow Hirsch-
ly as a distinct taxon.

Extremely incomplete. They are first
mammal age of South America (Car-
ter group to Vermilingua, are known
aíno and Scillato-Yané, 1995). This
quity. Excepting the aforementioned
originated in and been confined to
s separation from Africa around 85
anian isthmus around 3 million years
covery of a purported anteater from
rch, 1981), could change this view of

ly complete specimen (Storch, 1981;
ated postcranial elements (Storch and
ed this early European taxon with the
to place *Eurotamandua* within one of

the two vermilinguan subfamilies, the Myrmecophaginae (Storch and Habersetzer, 1991). The latter authors proposed an ancient split between the two vermilinguan subfamilies extending back as far as the Late Cretaceous. Although much of the skeleton of *Eurotamandua* is preserved, critical areas of the skeleton are missing or inadequately preserved. Thus Storch's (1981) assertions about *Eurotamandua*'s taxonomic affinities with Xenarthra, let alone with a particular vermilinguan subfamily (Storch and Habersetzer, 1991), have been difficult to confirm (Rose and Emry, 1993; Szalay and Schrenk, 1994). Indeed, a recently published abstract has suggested that *Eurotamandua* is more closely related to the Pholidota than to the Xenarthra (Shoshani *et al.*, 1997), a suggestion adopted in the recent mammalian classification of McKenna and Bell (1997). As discussed below, *Eurotamandua* has been excluded from recent cladistic studies of vermilinguan phylogeny. Therefore, we have decided to include this taxon in the present study in an attempt to evaluate its purported links with the Vermilingua in general and the Myrmecophaginae in particular. A detailed consideration of the possible nonxenarthran interordinal affinities of *Eurotamandua* would require a broad analysis incorporating numerous taxa and characters representing all three major edentate lineages (Xenarthra, Palaeanodonta, and Pholidota). Such an analysis is beyond the scope of the present study, although the matter receives cursory consideration in the analysis and discussion presented below.

The phylogeny of undoubted myrmecophagids has been reviewed by several recent authors. Hirschfeld (1976), in a noncladistic study based on a survey of postcranial morphological features in all anteater genera known at that time, divided the Myrmecophagidae into two subfamilies, Cyclopininae and Myrmecophaginae. The former included the extant *Cyclopes* and extinct *Palaeomyrmidon*. The latter was comprised of *Protamandua*, *Tamandua*, *Neotamandua*, and *Myrmecophaga*. *Protamandua* was identified as a probable ancestor to the three other Myrmecophaginae genera, whereas *Neotamandua* was allied by Hirschfeld more closely to *Myrmecophaga* than to *Tamandua*.

Subsequent to Hirschfeld's (1976) analysis, several cladistic studies have been published. Like Hirschfeld's study, all limit to some degree the range of morphological characters considered, and none include all the known taxa. Engelmann (1985) examined all the relevant genera except *Eurotamandua* and produced a phylogeny identical to Hirschfeld's, with the sole exception that *Protamandua* formed the sister taxon rather than the ancestor to the remaining myrmecophagines. However, Engelmann (1985) based his findings on only a handful of cranial and postcranial characteristics. The phylogeny produced by Patterson *et al.* (1992) was identical to that of Engelmann (1985), excluding the fact that Patterson *et al.* (1992) did not include *Palaeomyrmidon* or *Neotamandua* in their study. Patterson *et al.* based on their phylogeny exclusively on morphological features taken from the bony anatomy of the ear region. Gaudin's (1993) phylogenetic analysis resulted in several different schemes of myrmecophagid relationships. One of Gaudin's trees arranged anteater taxa as did Patterson *et al.* (1992) and Engelmann (1985). However, using a slightly different set of outgroups, Gaudin (1993) produced a tree in which *Palaeomyrmidon* became the sister taxon to the Myrmecophaginae. Gaudin's analyses did not include *Neotamandua* or *Eurotamandua* and were confined exclusively to cranial morphological characteristics. Further, his characters were primarily chosen to work out the phylogeny of the Tardigrada and are not ideally suited to resolve myrmecophagid relationships.

myrmecophagid phylogenies, relationships among all the relevant primate skeleton. Moreover, none of the proposed relationships between Myrmecophagidae using an analysis of postcranial and cranial skeletal data in an attempt to evaluate the relationships among all known and purported

METHODS

Data for this study were gathered through a review of the primary literature (Weber, 1928; Storch and Haubold, 1989; see Appendix, Table AI). Of the characters used in some analyses (see below) are 107 characters. Fourteen of the 107 characters are used to determine the position of *Eurotamandua* (characters 79, and 106; see Appendix, Table AI). However, as some of the latter characters were used for analyses not including *Eurotamandua*, the consistency index (CI) exclude uninfor-

group taxa considered are based upon information obtained from the primary literature: *Myrmecophaga tridactyla* (FMNH 25261), *Eurotamandua tetradactyla* (FMNH 69969), *Protamandua rothi* (FMNH P 14419). Information on *Myrmecophaga joresi* have been obtained solely from Storch, 1981; Storch and Haubold, 1989; published sources were also consulted as to character state distributions (Pocock (1914), Pocock (1924), Weber (1928), Storch (1981), Engelmann (1985), Storch (1991), Patterson *et al.* (1992), and

outgroup comparison. Three separate analyses were conducted: one including *Eurotamandua*, and two of which were conducted with constraints placed on its phylogenetic position relative to *Bradypus*, and the Cingulata (represented by successive outgroups to the Vermilingua) (Gaudin and Gaudin (1993, 1995). Information on

these outgroup taxa was obtained by direct observation of the following specimens: *Bradypus tridactylus* (FMNH, 16556, 16557, 93297, 140254), *Bradypus variegatus* (FMNH 60164, 69587), *Dasyurus novemcinctus* (UTCM-15, FMNH 18750, 18758, 54245, 55664), and *Euphractus sexcinctus* (FMNH, 28350, 34348, 152051).

In both analyses which incorporate *Eurotamandua*, the palaeodont *Metacheiromys* is employed as a nonxenarthran outgroup. The Palaeodontia is believed by some authors to represent the closest sister taxon to the Xenarthra (Simpson, 1931, 1945; Szalay, 1977; Patterson *et al.*, 1992; Gaudin, 1993, 1995). Furthermore, McKenna (1987) has referred to *Eurotamandua* as a palaeodont, and Rose and Emry (1993) have noted special resemblances between *Eurotamandua* and the Messel pangolin *Eomomys*, which in turn resembles palaeodonts in certain features. The utilization of *Metacheiromys* as an outgroup to the Xenarthra allows us to test for the possibility that *Eurotamandua* could occupy a phylogenetic position outside Xenarthra. Character state assignments for *Metacheiromys* are based upon direct observation of specimens (YPM-PU 18107, AMNH 11549) and information obtained from the primary literature (Simpson, 1931; Schoch, 1984). In the first analysis to include *Eurotamandua*, the latter taxon is constrained to fall within the Vermilingua. In the second such analysis, the phylogenetic position of *Eurotamandua* is not constrained.

Due to the suggestion by Shoshani *et al.* (1997) that *Eurotamandua* is a close relative of pangolins, the genus *Manis* has been included with *Eurotamandua*, *Metacheiromys*, and the Xenarthra in a final analysis which is addressed briefly under the Discussion. Character state assignments for *Manis* are based almost entirely on *M. temminckii* (FMNH 34610, 35682, 38144). Supplementary information on the postcranial skeleton (especially the manus, pes, and scapula) was obtained from specimens of *M. javanica* (FMNH 62918, 68742) and *Manis* sp. (FMNH 13568) and from the primary literature (Weber, 1928; Grassé, 1955; Kingdon, 1971).

The data matrix (Appendix, Table AII) has been analyzed using the computer program PAUP (Swofford, 1993, Version 3.1.1). The data are analyzed using PAUP's branch-and-bound algorithm. Each of the first three separate analyses described above are subjected to four different manipulations involving the weighting and ordering of characters. Following Gaudin (1995), characters are weighted using two schemes. In the first, all the character state changes are assigned equal weight. In the second scheme each character is given equal weight, with character state changes scaled according to the number of states in that character. Thus a character state change between character states in a binary character retains a weight of 1.0. Character state changes in a character with three states are given a weight of 0.5; changes in a four-state character are assigned a weight of 0.333, and so on (Gaudin, 1995). In addition to the two weighting schemes, two character ordering schemes are employed. In the first, all multistate characters are left unordered. In the second, certain multistate characters are ordered along positional, structural, or numerical morphoclines (Appendix, Table AI). The combination of the two ordering and weighting schemes yields four sets of manipulations performed in each analysis: (1) character state changes weighted equally, multistate characters all unordered; (2) characters weighted equally, multistate characters all unordered; (3) characters weighted equally, multistate characters ordered or unordered; and (4) character state changes weighted equally, multistate characters ordered or unordered. Note that the effect of these manipulations is to alter the influence of multistate characters on the analysis,

allowing us to test how ordering and weighting effect phylogenetic results. Manipulation 2 minimizes the effect of multistate characters and manipulation 4 maximizes their effect, whereas 1 and 3 represent intermediate conditions. Note further that each manipulation will, of necessity, change the length of the shortest tree(s), such that manipulation 2 will always yield the shortest tree length (TL) and manipulation 4 the longest. Because tree length is biased in this fashion, it cannot be used to discriminate which manipulation is producing the best set of most parsimonious trees. However, indices of homoplasy, e.g., consistency index (CI) and retention index (RI), are not necessarily biased among the four manipulations, and hence provide a fairer method for selecting the best tree. Therefore, for every one of the three analyses described in the previous paragraph, the preferred tree(s) will be that which results from the one of the four weighting and ordering manipulations yielding the highest CI.

Character state transitions have been optimized using PAUP's DELTRAN option. Although the choice of optimization scheme does not affect tree topology, it does affect character distribution (Wiley *et al.*, 1991). Since the number of reversals is minimized in DELTRAN, the consistency index is maximized. DELTRAN is also preferred as a more conservative optimization scheme, because it only assigns synapomorphies to the basal node of a clade if there is positive evidence that members of that clade share the character primitively (Gaudin, 1995).

In order to assess the robustness of the preferred trees, PAUP's exhaustive search option has been used for each of the three primary analyses (without *Eurotamandua*, with *Eurotamandua* constrained, with *Eurotamandua* unconstrained). The exhaustive search is conducted using the same weighting and ordering scheme as the preferred tree resulting from the previous branch-and-bound searches.

Abbreviations. AMNH, American Museum of Natural History, New York; CI, consistency index; FMNH, Field Museum of Natural History, Chicago; RI, retention index; TL, tree length; UTCM, University of Tennessee at Chattanooga Natural History Museum; YPM—PU, Princeton University collection housed at Peabody Museum, Yale University, New Haven.

RESULTS

Analysis 1: *Eurotamandua* Excluded

Four separate PAUP manipulations have been conducted, using two types of weighting schemes and two different ordering schemes. Three of the four yield a single most-parsimonious tree with an identical tree topology (Fig. 1). The other, manipulation 1 in which all characters are unordered and all character states weighted equally, results in two most parsimonious trees. One of these is identical to the tree in Fig. 1. In the other tree, *Cyclopes* and *Palaeomyrmidon* form successive sister taxa to the Myrmecophaginae (see Fig. 9). TL, CI, and RI vary as follows in the manipulations performed: (1) all unordered, states weighted equally, TL = 186, CI = 0.700, RI = 0.707; (2) all unordered, characters weighted equally, TL = 154, CI = 0.678, RI = 0.697; (3) ordered and unordered, characters weighted equally, TL = 155, CI = 0.676, RI = 0.700; and (4) ordered and unordered, states weighted equally, TL = 190, CI = 0.699, RI = 0.713.

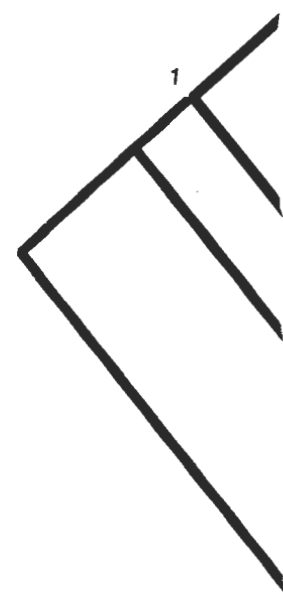


Fig. 1. Hypothesized phylogeny of six extant and extinct anteater genera (*Dasypus* and *E. dypus*) and Cingulata (*Dasypus* and *E. dypus*) (TL = 190, CI = 0.699, RI = 0.713). The two undoubted anteater genera are included in the analysis and ordering scheme 4, in which characters are ordered along with the other characters. Multistate characters are ordered along with the other characters. Nodes are discussed in the text.

The weighting and ordering scheme used in this analysis is equal to that of manipulation 1, and a subset of the weighting and ordering scheme in this analysis, resulting in the same single most parsimonious tree-length frequency distribution (Fig. 2). The analysis is based upon manipulation 4. Character

genetic results. Manipulation 4 maximizes their effect, further that each manipulation such that manipulation 2 will be on 4 the longest. Because tree length is minimized which manipulation is preferred, indices of homoplasy, e.g., CI, are necessarily biased among the alternatives for selecting the best tree. Therefore, in the previous paragraph, the preferred tree is the one with the four weighting and ordering

schemes. PAUP's DELTRAN option affects tree topology, it does affect the number of reversals is minimized. DELTRAN is also preferred as it assigns synapomorphies to the members of that clade share the

same trees, PAUP's exhaustive search analyses (without *Eurotamandua*, and unconstrained). The exhaustive search is preferred as the preferred tree scheme.

See Natural History, New York; CI, see at Chicago; RI, retention index; see at Chattanooga Natural History Museum; housed at Peabody Museum, Yale

Excluded

been conducted, using two types of analyses. Three of the four yield a single topology (Fig. 1). The other, manipulation 4, results in a tree with character states weighted equally, results in a tree identical to the tree in Fig. 1. In the successive sister taxa to the Myrmecophagidae in the manipulations performed: (1) all characters, CI = 0.700, RI = 0.707; (2) all characters, CI = 0.678, RI = 0.697; (3) ordered characters, CI = 0.676, RI = 0.700; and (4) ordered characters, TL = 190, CI = 0.699, RI = 0.713.

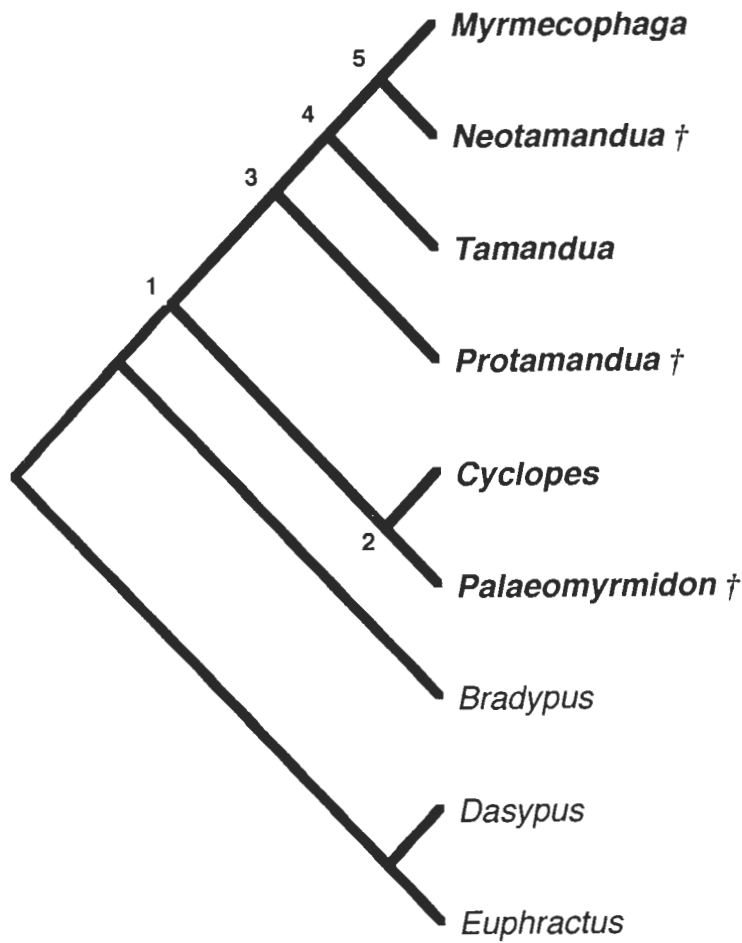


Fig. 1. Hypothesized phylogeny of the Myrmecophagidae based on PAUP analysis of six extant and extinct anteater genera and their outgroups in the Tardigrada (*Bradypus*) and Cingulata (*Dasypus* and *Euphractus*). This single most-parsimonious tree (TL = 190, CI = 0.699, RI = 0.713) results from Analysis 1, in which only undoubted anteater genera are included. The tree statistics are based upon weighting and ordering scheme 4, in which character states are weighted equally and some multistate characters are ordered along structural morphoclines (see text). Numbered nodes are discussed in the text.

The weighting and ordering scheme in which character state changes are weighted equally and some multistate characters are ordered (No. 4) yields a CI essentially identical to that of manipulation 1, and a substantially higher RI. It is thus the preferred weighting and ordering scheme in this analysis. An exhaustive search is run using these settings, resulting in the same single most parsimonious tree, with a strongly right-skewed tree-length frequency distribution (Fig. 2). The discussion of character state distributions follows is based upon manipulation 4. Characters are referred to in this section according

Analysis 1

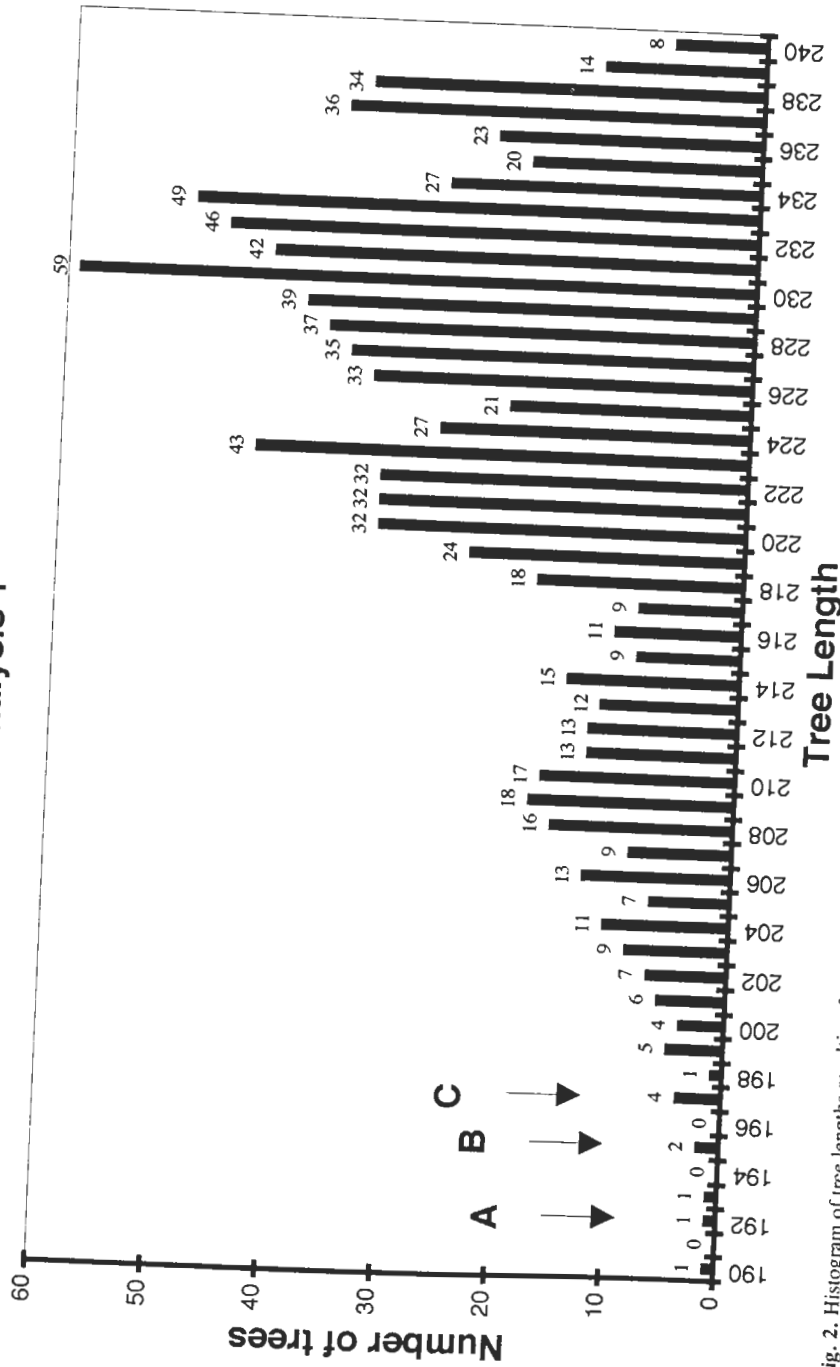


Fig. 2. Histogram of tree lengths resulting from an analysis using PAUP's "exhaustive search" option. The analysis is otherwise identical to the preferred tree in Fig. 1. (A) Point at which the monophyly of Node 2 (subfamily Cyclopininae) collapses in a strict consensus. (B) Point at which Node 3 (subfamily Myrmecophaginae) collapses. (C) Point at which Node 4 (*Tamandua* + *Myrmecophaga* + *Neotamandua*) and Node 5 (*Myrmecophaga* + *Neotamandua*) collapse.

to their number system as presented are those designated in Fig. 1.

Pilosa/Cingulata. There are 1 character state changes at the base of without reference to further outgroups of either *Pilosa* or *Cingulata*.

Node 1. Vermilingua. The morphomorphies (Appendix, Table A 21 synapomorphies are unique, if found in any other taxa included in Twelve of the 21 characters represented (Figs. 3-5): (7) teeth absent, (9) suture well anterior to anterior edge of tympanic cavity, (32) internal auditory oriented posteromedially, (42) basal region of mandible strongly process of the axis extends anteriorly present, (97) tibial sesamoid bone opened proximal lateral tuberosity.

Note 2. Cyclopininae. This clade three are both unique and unambiguous separated from porus acousticus (51) skull strongly tapered anteriorly.

Cyclopes has a particularly essentially surprising given the peculiar that most seem to converge on cyclopinine anteater *Tamandua* (characters 4, 11, 70, 75, 78).

It should be noted that in this analysis is united with the Myrmecophaginae single unambiguous character, (4) on the anterior edge of the nasal process.

Node 3. Myrmecophaginae. This is one of the most strongly supported synapomorphies, all of which are present on the anterior edge of the nasal process situated above supraorbital foramen does not participate in medial wall of tympanic and basioccipital wall (38) internal carotid artery dorsomedial of the petrosal foramen located inside jugular fossa, (51) in view, (74) inferior edge of coronoid with distal concavity on third

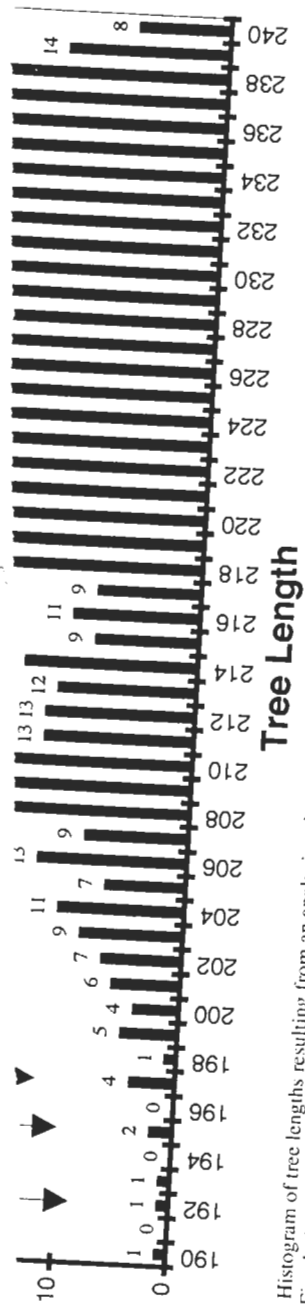


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to their number system as presented in the Appendix (Table AI), and nodes described are those designated in Fig. 1.

Pilosa/Cingulata. There are 11 unambiguously placed features which undergo character state changes at the base of the Xenarthra. These characters cannot be polarized without reference to further outgroups. Therefore, these characters may be synapomorphies of either Pilosa or Cingulata.

Node 1. Vermilingua. The monophyly of anteaters is strongly supported by 21 synapomorphies (Appendix, Table AIII), of which 15 are unambiguous. Sixteen of these 21 synapomorphies are unique, i.e., the character states assigned to this node are not found in any other taxa included in the analysis (note: according to our usage "unique" characteristics may be either ambiguously or unambiguously assigned to a given node). Twelve of the 21 characters represent both unequivocal and unique synapomorphies (Figs. 3–5): (7) teeth absent, (9) small maxillary exposure in orbit, (17) frontal/parietal suture well anterior to anterior edge of glenoid, (22) palate extends posterior to back of tympanic cavity, (32) internal auditory meatus directed medially, (33) eustachian tube oriented posteromedially, (42) basicranial/basifacial axis slightly curved, (55) symphyseal region of mandible strongly downturned ventrally, (57) cranial edge of the spinous process of the axis extends anterior to the level of the dens, (79) entepicondylar notch present, (97) tibial sesamoid bone present, and (101) fifth metatarsal with well-developed proximal lateral tuberosity.

Note 2. Cyclopininae. This clade is supported by only four synapomorphies, although three are both unique and unambiguous. They are as follows (Fig. 3): (40) glenoid well separated from porus acousticus, (42) basicranial/basifacial axis strongly curved, and (51) skull strongly tapered anteriorly in lateral view.

Cyclopes has a particularly large number (20) of autapomorphies. This is not necessarily surprising given the peculiarity of *Cyclopes*' morphology, but it is interesting that most seem to converge on two taxa in particular (see Discussion), the myrmecophagine anteater *Tamandua* (characters 63, 77, 85, 90) and the sloth *Bradypus* (characters 4, 11, 70, 75, 78).

It should be noted that in the second tree resulting from manipulation 1, *Cyclopes* is united with the Myrmecophaginae to the exclusion of *Palaeomyrmidon* by only a single unambiguous character, (6) the presence of distinct lateral and medial processes on the anterior edge of the nasal.

Node 3. Myrmecophaginae. The monophyly of the subfamily Myrmecophaginae is one of the most strongly supported results of this study. This clade is supported by 13 synapomorphies, all of which are both unequivocal and unique. The synapomorphies include eight cranial and five postcranial characters (Figs. 4–6): (16) supraorbital foramen situated above supraorbital crest, (25) weak pterygoid inflation, (30) entotympanic does not participate in medial tympanic cavity, (34) eustachian tube opening comprised of tympanic and basioccipital with minor contribution from pterygoid or entotympanic, (38) internal carotid artery dorsal to entotympanic, (43) distinct groove across the promontorium of the petrosal for internal carotid artery, (49) internal carotid artery foramen located inside jugular fossa, (51) skull nearly cylindrical, not tapered anteriorly in lateral view, (74) inferior edge of coracoid process sigmoidal, (91) large medial dorsal ridge with distal concavity on third metacarpal, (96) lateral condyle of femur wider medio-

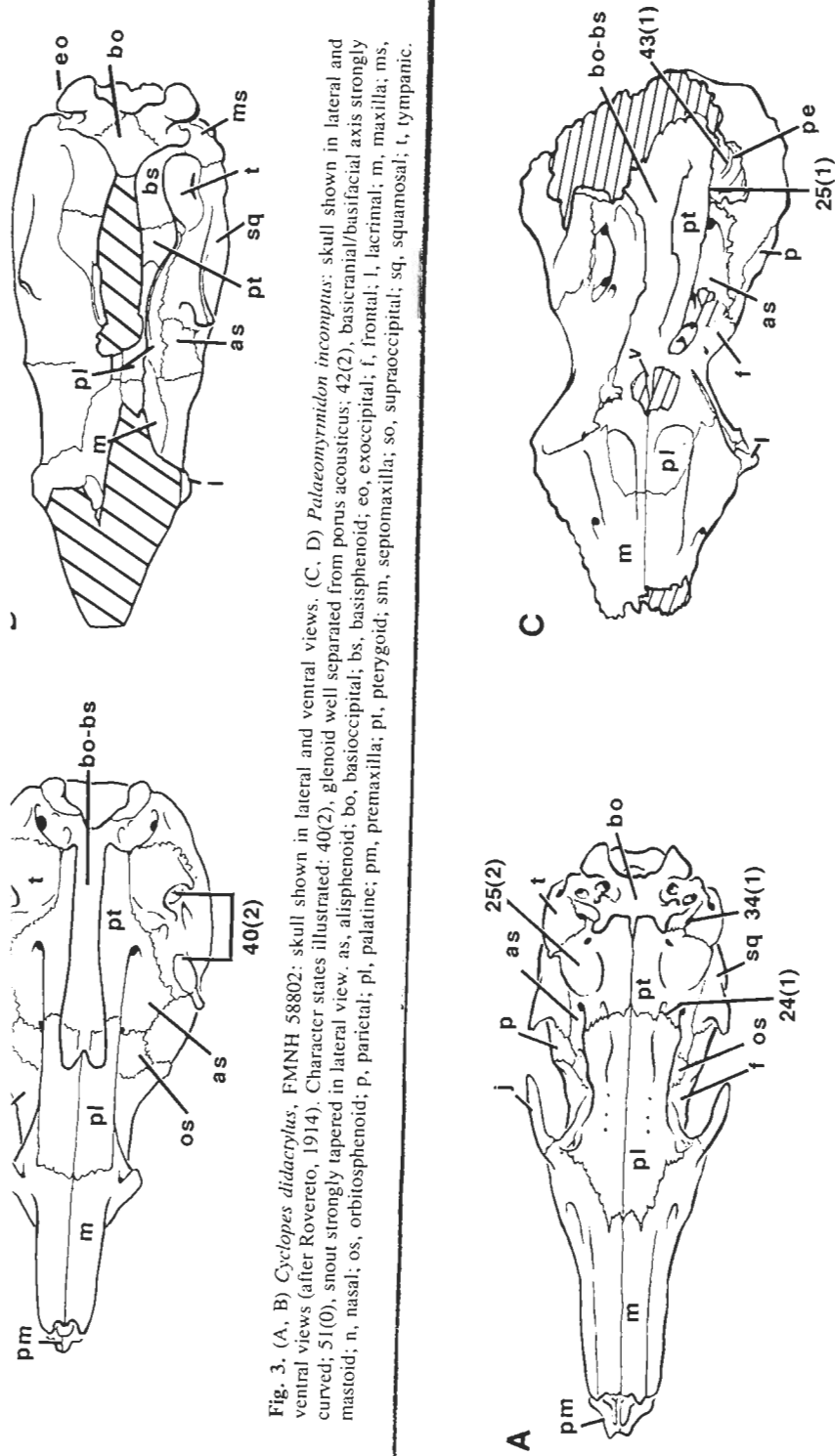


Fig. 3. (A, B) *Cyclopes didactylus*, FMNH 58802: skull shown in lateral and ventral views. (C, D) *Palaeomyrmidon incomptus*: skull shown in lateral and ventral views (after Rovereto, 1914). Character states illustrated: 40(2), glenoid well separated from porus acousticus; 42(2), basicranial/basifacial axis strongly curved; 51(0), snout strongly tapered in lateral view. as, alisphenoid; bo, basioccipital; bs, basisphenoid; eo, exoccipital; f, frontal; i, lacrimal; m, maxilla; ms, mastoid; n, nasal; os, orbitosphenoid; p, parietal; pl, palatine; pm, premaxilla; pt, pterygoid; sm, septomaxilla; so, supraoccipital; sq, squamosal; t, tympanic.

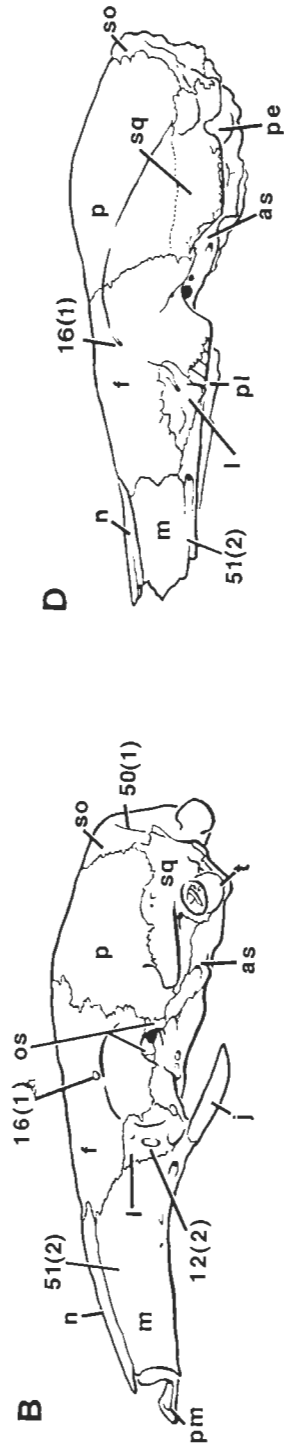


Fig. 4. (A, B) *Tamandua tetradactyla*, FMNH 93176 (jugal added based on *T. mexicana*, FMNH 22397): skull shown in ventral and lateral views. (C, D) *Pratamandua rotii*, FMNH P13134: skull shown in ventral and lateral views. Character states illustrated: 12(2), two lacrimal foramina, the size of the larger foramen being greater than 2 mm anteroposteriorly; 16(1), supraorbital foramen above supraorbital crest; 24(1), pterygoid/palatine suture in line with foramen ovale; 25(1), pterygoid inflation weak; 25(2), large pterygoid sinus present; 34(1), eustachian tube opening lies between tympanic and basioccipital with minor contribution from pterygoid or entotympanic; 43(1), distinct groove across the promontorium of the petrosal for the internal carotid artery; 50(1), nuchal crest weakly developed; 51(2), skull nearly cylindrical in lateral view. j, jugal; pe, petrosal; v, vomer; remainder of abbreviations as in Fig. 3.

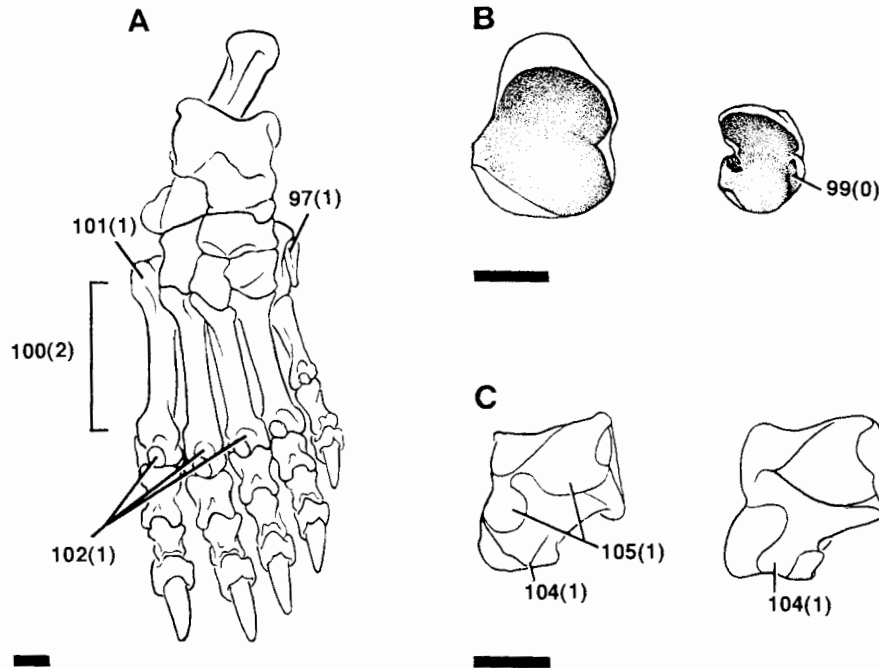


Fig. 5. (A) *Myrmecophaga tridactyla*, FMNH 49342: right pes shown in dorsal view. (B) *Myrmecophaga tridactyla*, FMNH 49342 (left), and *Tamandua mexicana*, FMNH 22397 (right): right navicular in proximal view. (C) *Neotamandua borealis* [left, after Hirschfeld (1976)], and *Tamandua mexicana*, FMNH 22397 (right): right astragalus in ventral view. All scale bars = 1 cm. Character states illustrated: 97(1), tibial sesamoid bone present; 99(0), proximal navicular facet with a ventral concavity extending dorsomedially to the dorsal convexity; 100(2), metatarsals progressively more elongate laterally; 101(1), proximal lateral tuberosity of fifth metatarsal present; 102(1), dorsal concavity on distal end of metatarsals; 104(1), groove lateral to sustentacular facet of astragalus perforates rim of navicular facet; 105(1), astragalocalcaneal and sustentacular facets of astragalus confluent.

laterally than medial condyle, (100) metatarsals progressively more elongate laterally, and (102) dorsal concavity on distal end of metatarsals.

Node 4. The clade comprised of *Tamandua*, *Neotamandua*, and *Myrmecophaga* is supported by a large number of synapomorphies. There are 25 possible synapomorphies, although many are ambiguous because of the incomplete nature of *Protamandua*, the sister taxon to this clade. Fifteen synapomorphies are unique to this group, with one of the remaining characters (13, absence of lateral walls of the lacrimal foramen) representing a reversal, and nine representing convergences on taxa outside Vermilingua. Eight characters can be unambiguously assigned to this node, and five of these are also unique (Figs. 4 and 5): (9) no maxillary exposure in the orbit, (12) two lacrimal foramina, the lower exceeding 2 mm in diameter, (24) pterygoid/palatine suture in line with foramen ovale, (25) pterygoid with large sinus present, and (104) groove lateral to sustentacular facet of astragalus perforating the rim of the navicular facet.

Node 5. *Myrmecophaga* and *Neotamandua* are united by 10 total synapomorphies, 8 of which are unequivocal. Eight synapomorphies are unique, and seven synapomor-

Phylogeny of Anteaters

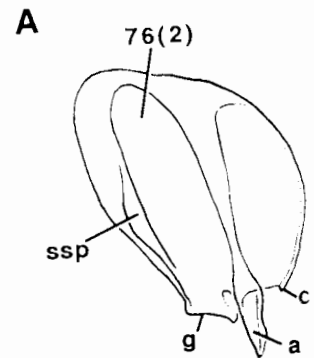


Fig. 6. (A) *Cyclopes didactylus*, FMNH 22397: right scapula with major fossa enlarged, area greater than the area of the minor fossa; extremely concave in lateral view; 76(2), process sigmoidal; 75(1), metacromioclavicular process; g, glenoid fossa; s, scapular spine.

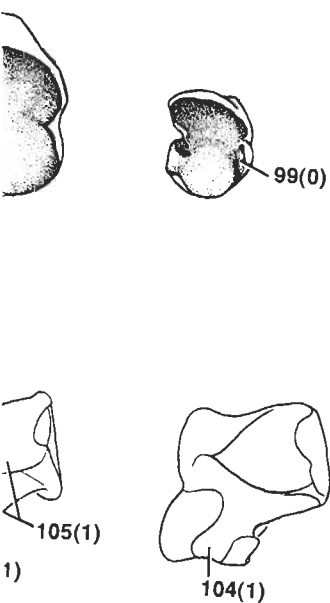
phies are both unique and unambiguous: (81) skull length, (82) radius with a notch, (84) anterior median ridge, (88) pisiform dumbbell shaped, (98) astragalus confluent (Fig. 5), and (103) process separating extensor digitorum longus.

Several characters were also shared by *Myrmecophaga* and *Neotamandua* but not by *Myrmecophaga* alone: (29) horizontal inclination of the scapula, (30) scapular spine, (31) scapular spine, (32) scapular spine, (33) scapular spine, (34) scapular spine, (35) scapular spine, (36) scapular spine, (37) scapular spine, (38) scapular spine, (39) scapular spine, (40) scapular spine, (41) scapular spine, (42) scapular spine, (43) scapular spine, (44) scapular spine, (45) scapular spine, (46) scapular spine, (47) scapular spine, (48) scapular spine, (49) scapular spine, (50) scapular spine, (51) scapular spine, (52) scapular spine, (53) scapular spine, (54) scapular spine, (55) scapular spine, (56) scapular spine, (57) scapular spine, (58) scapular spine, (59) scapular spine, (60) scapular spine, (61) scapular spine, (62) scapular spine, (63) scapular spine, (64) scapular spine, (65) scapular spine, (66) scapular spine, (67) scapular spine, (68) scapular spine, (69) scapular spine, (70) scapular spine, (71) scapular spine, (72) scapular spine, (73) scapular spine, (74) scapular spine, (75) scapular spine, (76) scapular spine, (77) scapular spine, (78) scapular spine, (79) scapular spine, (80) scapular spine, (81) skull length, (82) radius with a notch, (84) anterior median ridge, (88) pisiform dumbbell shaped, (98) astragalus confluent (Fig. 5), and (103) process separating extensor digitorum longus.

Analysis 2: *Eurotamandua*

The same four PAUP manipulations were used in Analysis 2. All result in the same single clade, with its arrangement of the undoubtedly correct sister group to the remaining nodes.

The four manipulations (1) TL = 224, CI = 0.642; (2) TL = 185.5, CI = 0.642; (3) TL = 185.5, CI = 0.656; (4) TL = 185.5, CI = 0.656. Manipulation 1, in v



shown in dorsal view. (B) *Myrmecops* (left) and *Tamandua mexicana* (right): right navicular bone shown in dorsal view. Scale bars = 1 cm. Character states illustrated: 102(1), dorsal concavity on distal edge of astragalus perforates rim of navicular facet; 104(1), dorsal concavity on distal edge of astragalus perforates rim of navicular facet; 105(1), dorsal concavity on distal edge of astragalus perforates rim of navicular facet.

ssively more elongate laterally,

mandua, and *Myrmecophaga* is represented by 25 possible synapomorphies, the nature of *Protamandua*, the nature of this group, with one of the lacrimal foramen) represented by taxa outside Vermilingua. Character state 102(1), dorsal concavity on distal edge of astragalus perforates rim of navicular facet, and five of these are also shared by the group. (12) two lacrimal foramina, (104) groove lateral to sustentacular facet.

represented by 10 total synapomorphies, one unique, and seven synapomor-

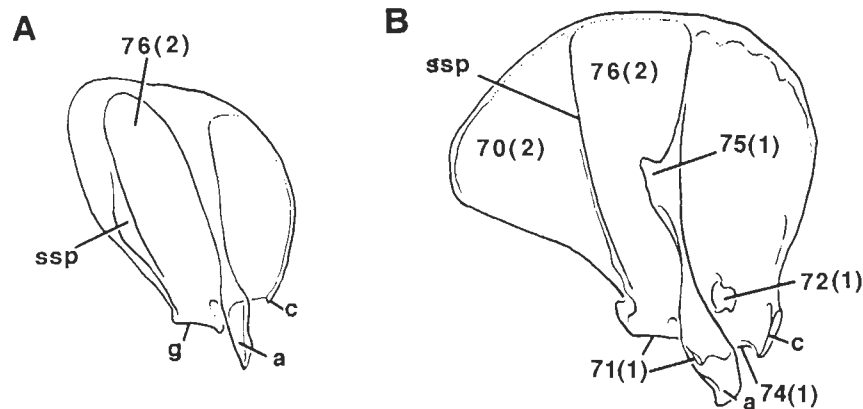


Fig. 6. (A) *Cyclopes didactylus*, FMNH 58802: right scapula shown in lateral view. (B) *Tamandua mexicana*, FMNH 22397: right scapula shown in lateral view. Character states illustrated: 70(2), teres major fossa enlarged, area greater than 50% that of infraspinous fossa; 71(1), scapular glenoid fossa extremely concave in lateral view; 72(1), scapular fenestra present; 74(1), inferior edge of coracoid process sigmoidal; 75(1), metacromion present; 76(2), infraspinous fossa rectangular. a, acromion; c, coracoid process; g, glenoid fossa; ssp, secondary scapular spine. Scale bars = 1 cm.

phies are both unique and unambiguous: (4) nasal elongate, more than 37% of overall skull length, (82) radius with circular head, (83) styloid process of radius distinctly notched, (84) anterior median ridge of radius extending to distal edge of styloid process, (88) pisiform dumbbell shaped, (105) astragalocalcaneal and sustentacular facets of astragalus confluent (Fig. 5), and (107) distinct ridge present on external side of calcaneus separating extensor digitorum brevis from accessorius.

Several characters were also found which indicate that *Neotamandua* and *Myrmecophaga* represent distinct genera. The PAUP analysis assigns nine autapomorphies to *Myrmecophaga*, but none represent characters which are preserved in *Neotamandua*; hence all are ambiguous. However, *Neotamandua* possesses two autapomorphies that support its position as an independent genus, and one of these autapomorphies is unambiguous: (29) horizontal inclination of the glenoid.

Analysis 2: *Eurotamandua* Included, Constrained to Lie Within Vermilingua

The same four PAUP manipulations employed in Analysis 1 are used in Analysis 2. All result in the same single most-parsimonious tree (Fig. 7). This tree is identical in its arrangement of the undoubted vermilinguan genera to the tree in Fig. 1 from the first analysis. Of particular interest in Analysis 2 is the placement of *Eurotamandua* as the sister group to the remaining myrmecophagids, contra Storch and Habersetzer (1991).

The four manipulations (numbered as above) yielded trees with the following statistics: (1) TL = 224, CI = 0.618, RI = 0.649; (2) TL = 181, CI = 0.598, RI = 0.642; (3) TL = 185.5, CI = 0.589, RI = 0.647; and (4) TL = 231, CI = 0.603, RI = 0.656. Manipulation 1, in which all characters are unordered and all character states

ship in the Xenarthra, is a facial exposure of the lacrimal which is smaller than the orbital exposure (Fig. 8). However, Ken Rose (personal communication) has noted several similarities in the humeri of *Eurotamandua* and palaeonodons, including a strikingly similar deltopectoral crest which is not displaced laterally in anteater fashion, contra Storch and Haubold [(1989); also character 77 in the present study, which is coded according to Storch and Haubold]. Although the shortest trees in the two auxiliary runs are three steps longer than the preferred tree from Analysis 3 (in which *Eurotamandua* is allied to the Pilosa), these auxiliary trees (TL = 222 steps) are two steps shorter than the tree length of the most-parsimonious tree resulting from the same weighting and ordering scheme in Analysis 2 (TL = 224). In other words, according to our admittedly limited data set, *Eurotamandua* is as likely to be a sister group to the Palaeonodonta, or to the Xenarthra as a whole, as it is to be a vermilinguan.

As noted in the Introduction, Shoshani *et al.* (1997) have offered a novel suggestion for the phylogenetic affinities of *Eurotamandua*, placing it as a sister group to the Pholidota. In order to evaluate this hypothesis, we coded the 107 characters in this analysis for extant pangolins (see Materials and Methods and Appendix, Table AII). We then reanalyzed the entire data matrix without designating an outgroup (using PAUP's midpoint rooting option instead), employing the same weighting and ordering scheme as that utilized in the preferred tree from Analysis 3.

The two most-parsimonious trees (TL = 240, CI = 0.583) that resulted from an unconstrained analysis of this data placed *Manis*, *Eurotamandua*, and *Metacheiromys* as successive sister groups to the Pilosa (*Bradypus* plus Vermilingua) within the Xenarthra! Because we believe the monophyly of Xenarthra to be well established (Engelmann, 1985; Gaudin, 1993, 1995), we reran the analysis with the monophyly of Xenarthra constrained a priori. If *Eurotamandua* was included in this constrained Xenarthra, it occupied a position as the sister taxon to Pilosa in the single most-parsimonious tree (TL = 241, CI = 0.581). Removing *Eurotamandua* from the constrained Xenarthra added a step relative to the previous run (TL = 242, CI = 0.578), with *Eurotamandua* forming the sister taxon to Xenarthra in the most parsimonious tree. An additional four, five, or seven steps had to be added in order for *Eurotamandua* to occupy a position as the sister taxon to *Manis*, *Metacheiromys*, or the Vermilingua, respectively. Only one unambiguous feature could be found to link *Eurotamandua* to manids in the present analysis, the absence of teeth, with the absence of an alisphenoid/parietal contact and a metacromion serving as equivocal synapomorphies. There were no unambiguous synapomorphies of *Metacheiromys* and *Eurotamandua* if manids were included in the analysis.

The inclusion of *Manis* does not alter the primary conclusion of the previous analyses with regard to the position of *Eurotamandua*. A sister-group relationship between *Eurotamandua* and the Pilosa (*Bradypus* plus Vermilingua) within Xenarthra is still the most-parsimonious phylogenetic arrangement. The results based on the addition of *Manis* differ from previous results, however, in suggesting that a sister-group relationship between *Eurotamandua* and Xenarthra is substantially more parsimonious than a sister group relationship between *Eurotamandua* and manids, palaeonodons, or vermilinguans. Although Shoshani and co-workers' (1997) hypothesis remains appealing on biogeographic grounds, given the presence of the true pangolin *Eomanis* in the same Messel fauna as *Eurotamandua*, we feel that the positive evidence they offer in support of this hypothesis is less than compelling. They employ two features to join *Eurotamandua* to

Pholidota rather than Xenarthra. (2) a dorsal exposure of the lacrimal which is smaller than the orbital exposure of the Pilosa. Shoshani *et al.* (1997) assert that this character is shared by taxa including the same two taxa characteristic of cingulates a second feature is present in the Cingulata (Gaudin, 1993).

What then is the most parsimonious analysis was designed by Storch and Habersetzer (1993) for the subfamily Myrmecophaginae. We found very few characters in common between the two taxa. A number of characters possessed by *Eurotamandua* and *Pholidota* resemble those of true vermilinguans. Furthermore, a number of features that are not present in *Eurotamandua* based on the present analysis including both sloths and true vermilinguans.

As noted in the Introduction, the question of *Eurotamandua*'s phylogenetic position is broadened considerably in the present analysis by the inclusion of ordinal-level characters and the addition of Pholidota, and Palaeonodonta. An alternative answer to the interordinal question is the most critical phylogenetical question: the nearly complete skeleton of the posterior portion of the pelvis (Rose and Emry, 1993) is so distinctive in the Xenarthra that it is found for a full 40% of the characters. This is especially true for basicranial characters, as well as for morphological regions previously defined for Pholidota, Palaeonodonta, and Vermilingua.

Notwithstanding the latter conclusion, it is the largest that while *Eurotamandua* could be placed with equal parsimony with either Pholidota or Palaeonodonta by Szalay and Schrenk (1993), this option is less parsimonious than the arrangement proposed by McKenna (1987). The latter arrangement is appealing because of the presence of the latter group in the Messel fauna by Shoshani *et al.* (1997) and is also appealing on biogeographic grounds. This arrangement is not con-

lacrimal which is smaller than the orbital (communication) has noted several similarities in anteater fashion, contra Storch and his study, which is coded according to the two auxiliary runs are three steps in which *Eurotamandua* is allied to the two steps shorter than the tree length same weighting and ordering scheme linking to our admittedly limited data set, the Palaeonodonta, or to the Xenarthra

(1997) have offered a novel suggestion placing it as a sister group to the Pholidota (the 107 characters in this analysis and Appendix, Table AII). We then used an outgroup (using PAUP's midpoint weighting and ordering scheme as

CI = 0.583) that resulted from an analysis of *Eurotamandua*, and *Metacheiromys* as a sister group to the Xenarthra! (Vermilingua) within the Xenarthra! This relationship is well established (Engelmann, 1997) with the monophyly of Xenarthra. In this constrained Xenarthra, it is the single most-parsimonious tree (TL = 107) in the constrained Xenarthra added (CI = 0.578), with *Eurotamandua* forming a sister group to the Xenarthra in this tree. An additional four, five, or six steps are required to occupy a position as the sister group to the Xenarthra, respectively. Only one unambiguous character in the present analysis, the absence of an alisphenoid-parietal contact and a metacromion, are unambiguous synapomorphies of the Xenarthra included in the analysis.

The conclusion of the previous analysis of a sister-group relationship between *Eurotamandua* and the Xenarthra (Gaudin and Branham, 1997) is still the most parsimonious based on the addition of *Manis* to the analysis that a sister-group relationship between *Eurotamandua* and the Palaeonodonta, or vermilinguans, remains appealing on biogeographic grounds. This thesis remains appealing on biogeographic grounds. The inclusion of *Eomanis* in the same Messel locality they offer in support of this thesis. The inclusion of *Eomanis* to join *Eurotamandua* to

Pholidota rather than Xenarthra: (1) the absence of an alisphenoid/parietal contact and (2) a dorsal exposure of the supraoccipital. Both are found within Xenarthra, but Shoshani *et al.* (1997) assert that they are absent primitively. However, an analysis (Gaudin, 1993) including the same two characters examined in 34 extant and extinct xenarthran taxa shows their polarity to be equivocal at the base of Xenarthra. The first is a primitive character of cingulates and is also found in many sloths, although a contact between alisphenoid and parietal is likely the primitive condition in *Pilosa* (Gaudin, 1993). The second feature is present in all vermilinguans and most sloths, although it is absent in the Cingulata (Gaudin, 1993).

What then is the most probable phylogenetic position for *Eurotamandua*? The present analysis was designed primarily to evaluate the hypothesis of Storch (1981) and Storch and Habersetzer (1991), that *Eurotamandua* is a true vermilinguan belonging to the subfamily Myrmecophaginae. Our results strongly contradict this hypothesis. We found very few characters linking *Eurotamandua* to myrmecophagines, and a large number of characters possessed by undoubted myrmecophagines that are absent in *Eurotamandua*. Furthermore, although *Eurotamandua* does exhibit several derived characters resembling true vermilinguans, all undoubted anteaters share a large number of characters that are not present in the European form. The most-parsimonious allocation of *Eurotamandua* based on the present data set is as a sister taxon to the *Pilosa*, a group including both sloths and true anteaters.

As noted in the Introduction, the present analysis cannot conclusively answer the question of *Eurotamandua*'s ordinal-level affinities. The analysis would have to be broadened considerably in order to address such a question, so that it included more ordinal-level characters and a broader taxonomic representation from the Xenarthra, Pholidota, and Palaeonodonta. Yet even such an expanded analysis would find a definitive answer to the interordinal relationships of *Eurotamandua* elusive, as many of the most critical phylogenetically informative areas are inadequately preserved in the one nearly complete skeleton. Other authors have noted the difficulty in assessing the morphology of the posterior thoracic and lumbar vertebrae and the posterior regions of the pelvis (Rose and Emry, 1993; Szalay and Schrenk, 1994; Gaudin, in press), which are so distinctive in the Xenarthra. In the present analysis, *Eurotamandua* cannot be scored for a full 40% of the characters in the data matrix. These include all the palatal and basicranial characters, as well as many of the characters from the ear region, scapula (especially the ventral region), carpus, tarsus, metacarpus, and metatarsus. Yet these morphological regions provide many of the features that are most diagnostic for the Pholidota, Palaeonodonta, Xenarthra, and Vermilingua.

Notwithstanding the large amount of missing data, the results of this analysis suggest that while *Eurotamandua* does show some derived resemblances to true anteaters, it could with equal parsimony be considered a sister taxon to the Xenarthra, as suggested by Szalay and Schrenk (1994), or even as a sister taxon to the Palaeonodonta (although this option is less parsimonious if pangolins are included in the analysis), following McKenna (1987). The latter is compelling from a biogeographic standpoint, given the presence of the latter group in the European Paleogene (Heissig, 1982). The suggestion by Shoshani *et al.* (1997) that *Eurotamandua* is closely related to the order Pholidota is also appealing on biogeographic grounds, although the morphological evidence for such an arrangement is not convincing. However, our data set implies that the most likely

allocation of *Eurotamandua* is as a somewhat aberrant but true xenarthran closely allied to the Pilosa. Such a phylogenetic position leaves open the mystery of how a group which originated in and purportedly was restricted to the island continent of South America until the emergence of the Panamanian isthmus 2 million years ago managed to land an early member in Western Europe in the middle Eocene some 40–50 million years ago.

ACKNOWLEDGMENTS

Most of the research for this report was conducted at the Field Museum of Natural History, Chicago, IL, or on specimens borrowed from that institution. For providing access to specimens under their care, we would like to thank Larry Heaney, Bruce Patterson and Bill Stanley of the Division of Mammals and John Flynn and Bill Simpson of the Department of Geology. We thank Ken Rose, John Wible, and Pat Luckett for their comments on an early draft of the manuscript. Last, but by no means least, we are grateful to Julia Scott, who prepared the illustrations for this paper.

APPENDIX

Table A1. Listing of Characters and Character States: Characters Marked with a Single Asterisk Are Multistate; Those Marked with Two Asterisks Are Multistate and Ordered in Analysis 1

- *1. Shape of premaxilla in ventral view: (0) plate-like, lacking distinct medial and lateral rami; (1) v-shaped, with distinct medial and lateral rami, anteriormost edge flat or pointed in midline; (2) v-shaped, with distinct medial and lateral rami, anteriormost edge indented in midline.
2. Attachment of premaxilla to skull: (0) firmly sutured; (1) loosely attached.
3. Shape and inclination of dorsal process of premaxilla: (0) extends anterodorsally, elongate anteroposteriorly; (1) erect, short anteroposteriorly.
- **4. Nasal length relative to overall skull length: (0) less than 28%; (1) 29–37%; (2) over 37%.
5. Nasal width: (0) expands posteriorly; (1) uniform along entire length.
- *6. Anterior edge of nasal: (0) convex; (1) with lateral process and medial process separated by a distinct notch; (2) relatively straight.
7. Teeth: (0) present; (1) absent.
8. Length of maxilla anterior to zygoma: (0) short, < 1/3 skull length; (1) elongate, > 1/3 skull length.
- **9. Maxillary exposure in orbit: (0) large; (1) small; (2) absent.
- *10. Medial portion of maxillopalatine suture: (0) not interdigitated—suture flat or slightly v-shaped with apex directed anteriorly; (1) weakly interdigitated—suture v-shaped, apex directed posteriorly; (2) strongly interdigitated—suture w-shaped.
11. Length of infraorbital canal: (0) canal > 5 mm; (1) canal < 2 mm.
- *12. Lacrimal foramen: (0) single foramen, less than 1 mm in diameter; (1) single foramen, greater than 2 mm in diameter; (2) double foramina, with the diameter of the ventral foramen greater than 2 mm anteroposteriorly.
13. Lacrimal foramen with prominent lateral walls: (0) absent; (1) present.
14. Relative size of facial and orbital portions of lacrimal: (0) orbital > facial; (1) facial > orbital.
15. Postorbital process of frontal: (0) present; (1) absent.
16. Supraorbital foramen: (0) below supraorbital crest; (1) above supraorbital crest.
17. Position of frontal/parietal suture: (0) at or behind anterior edge of glenoid; (1) well anterior to anterior edge of glenoid.
18. Zygomatic arch: (0) complete; (1) incomplete.
19. Attachment of jugal to skull: (0) firmly sutured; (1) loosely attached.
20. Orbital process of parietal: (0) absent; (1) present.
- *21. Temporal lines: (0) converge posteriorly, contact nuchal crest; (1) diverge posteriorly, approach but do not contact nuchal crest; (2) diverge posteriorly, widely separated from nuchal crest.
- **22. Posterior extent of palate: (0) to sphenorbital fissure; (1) to front of tympanic cavity; (2) to back of tympanic cavity.
23. Crest at median suture of palatine: (0) absent; (1) present.
24. Position of pterygoid/palatine suture: (0) anterior to foramen ovale; (1) in line with foramen ovale.

- **25. Pterygoid inflation: (0) ut
26. Pterygoid contact in ventr
27. Alisphenoid–parietal cont
28. Foramen rotundum: (0) c
- **29. Glenoid inclination: (0) a
30. Entotympanic participat
31. Entotympanic lateral exte
32. Orientation of internal au
33. Orientation of eustachian
- *34. Elements in eustachian tu basioccipital, with minor ectotympanic.
35. Shape of mallear head in
36. Tympanic contact in ventr
37. Shape of tympanic in late
38. Course of internal carotid
39. Lamina and anterior proce
40. Position of glenoid relativ
41. Subarcuate fossa: (0) sma
- *42. Curvature of the basicran
43. Distinct groove across the (1) present.
44. Tympanic medial expansi
45. Tympanic orientation: (0)
46. Occipital condyles: (0) se
47. Condylloid foramen: (0) s
48. Slope of occiput: (0) ante
49. Position of internal caroti
50. Nuchal crest: (0) strongly
- **51. Relative depth of snout at snout depth < 18% of ma; snout depth 30–35% of n > 38% of maximum bull:
52. Coronoid process: (0) pre
- *53. Shape of condyle in poste
54. Relative position of cond; (1) condyle posterior to au
- **55. Symphyseal region of ma (1) symphysis slightly do
56. Anterior edge of atlas bou
- **57. Position of anterior edge (2) anterior to dens.
58. Spinous process of axis: posteriorly.
59. Shape of neural spine on
- **60. Number of thoracic verte
61. Neural spines of T2–T6 portions sloping craniall
- **62. Number of lumbar verte
63. Number of caudal verte
64. Xenarthrales: (0) absen
- *65. Shape of ribs: (0) unex rib; (2) expanded with
66. Abdominal mammary
67. Fusion of ischium and
68. Position of tuberosity
69. Prehensile tail: (0) abs
- **70. Ratio of the area of th

at aberrant but true xenarthran closely allied
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stricted to the island continent of South Amer-
sthus 2 million years ago managed to land
middle Eocene some 40-50 million years

DISCUSSION

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APPENDIX

Characters Marked with a Single Asterisk Are
Are Multistate and Ordered in Analysis 1

lacking distinct medial and lateral rami;
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anterior-most edge indented in midline.
; (1) loosely attached.
: (0) extends anterodorsally, elongate

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3 skull length; (1) elongate, > 1/3 skull length.
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ure v-shaped, apex directed posteriorly;

al < 2 mm.
in diameter; (1) single foramen, greater than
ter of the ventral foramen greater than 2 mm

nt; (1) present.
) orbital > facial; (1) facial > orbital.

ove supraorbital crest.
r edge of glenoid; (1) well anterior to

y attached.

rest; (1) diverge posteriorly, approach but
separated from nuchal crest.
> front of tympanic cavity; (2) to back of

n ovale; (1) in line with foramen ovale.

Table AI. Continued

-
- **25. Pterygoid inflation: (0) uninflated; (1) weak; (2) large sinus present.
26. Pterygoid contact in ventral midline: (0) absent; (1) present.
27. Alisphenoid-parietal contact: (0) absent; (1) present.
28. Foramen rotundum: (0) confluent with sphenorbital fissure; (1) separate.
**29. Glenoid inclination: (0) anterodorsal; (1) horizontal; (2) posterodorsal.
30. Entotympanic participation in medial wall of tympanic cavity: (0) present; (1) absent.
31. Entotympanic lateral extension contacting tympanohyal: (0) present; (1) absent.
32. Orientation of internal auditory meatus: (0) posteromedial; (1) medial.
33. Orientation of eustachian tube: (0) anteromedial; (1) posteromedial.
*34. Elements in eustachian tube opening: (0) entotympanic, tympanic, and pterygoid; (1) tympanic and basioccipital, with minor contribution from pterygoid or entotympanic; (2) entotympanic and ectotympanic.
35. Shape of malleolar head in dorsal view: (0) rounded; (1) parallel-sided.
36. Tympanic external surface: (0) smooth; (1) rugose.
37. Shape of tympanic in lateral view: (0) elongate dorsoventrally; (1) elongate anteroposteriorly.
38. Course of internal carotid artery: (0) medial to entotympanic; (1) dorsal to entotympanic.
39. Lamina and anterior process of the malleus: (0) small; (1) enlarged.
40. Position of glenoid relative to porus acousticus: (0) just anterior; (1) well separate.
41. Subarcuate fossa: (0) small, forms only shallow depression; (1) deep and large.
**42. Curvature of the basicranial/basifacial axis: (0) flat; (1) slightly curved; (2) strongly curved.
43. Distinct groove across the promontorium of the petrosal for the internal carotid artery: (0) absent; (1) present.
44. Tympanic medial expansion: (0) absent; (1) present.
45. Tympanic orientation: (0) horizontal; (1) vertical.
46. Occipital condyles: (0) sessile; (1) with distinct neck.
47. Condylod foramen: (0) small; (1) enlarged.
48. Slope of occiput: (0) anterosuperior; (1) vertical or posterosuperior.
49. Position of internal carotid artery foramen: (0) outside jugular fossa; (1) inside jugular fossa.
50. Nuchal crest: (0) strongly developed; (1) weakly developed.
**51. Relative depth of snout and braincase in lateral view: (0) skull strongly tapered anteriorly, minimum snout depth < 18% of maximum bullar depth; (1) skull moderately tapered anteriorly, minimum snout depth 30-35% of maximum bullar depth; (2) skull nearly cylindrical, minimum snout depth > 38% of maximum bullar depth.
52. Coronoid process: (0) present; (1) absent.
*53. Shape of condyle in posterior view: (0) flat; (1) evenly convex; (2) concave.
54. Relative position of condyloid process versus angular process: (0) angle posterior to condyle process; (1) condyle posterior to angle.
**55. Symphyseal region of mandible in lateral view: (0) symphysis horizontal, may extend anterodorsally; (1) symphysis slightly downturned ventrally; (2) symphysis strongly downturned ventrally.
56. Anterior edge of atlas body in ventral view: (0) concave; (1) flat or convex.
**57. Position of anterior edge of spinous process of axis: (0) posterior to dens; (1) at level of dens; (2) anterior to dens.
58. Spinous process of axis: (0) extends posteriorly, overlapping C3 and C4; (1) does not expand posteriorly.
59. Shape of neural spine on C6: (0) pointed dorsally; (1) columnar.
**60. Number of thoracic vertebrae: (0) less than 16; (1) 16; (2) 17.
61. Neural spines of T2-T6: (0) inclined caudally; (1) proximal portions inclined caudally with distal portions sloping cranially.
**62. Number of lumbar vertebrae: (0) more than three; (1) three; (2) two.
63. Number of caudal vertebrae: (0) below 30; (1) above 30.
64. Xenarthrales: (0) absent; (1) present.
*65. Shape of ribs: (0) unexpanded; (1) expanded with anterior flange extending along entire length of rib; (2) expanded with distinct posterior flange dorsally.
66. Abdominal mammary glands: (0) present; (1) absent.
67. Fusion of ischium and caudal vertebrae: (0) absent; (1) present.
68. Position of tuberosity of ischium: (0) caudal to pelvic symphysis; (1) cranial to pelvic symphysis.
69. Prehensile tail: (0) absent; (1) present.
**70. Ratio of the area of the teres major fossa to the area of the infraspinous fossa: (0) less than 0.30;
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Table AI. Continued

(1) between 0.35 and 0.45; (2) more than 0.50.
71. Scapular glenoid fossa: (0) moderately concave in lateral view; (1) extremely concave in lateral view.
72. Scapular fenestra: (0) absent; (1) present.
*73. Shape of anterior edge of supraspinous fossa: (0) convex; (1) sigmoidal; (2) concave.
74. Shape of inferior edge of coracoid process: (0) concave; (1) sigmoidal.
75. Metacromion: (0) present; (1) absent.
*76. Shape of infraspinous fossa: (0) triangular, strongly tapered ventrally, does not extend to rim of glenoid; (1) triangular, tapered ventrally but does extend to rim of glenoid; (2) rectangular.
**77. Deltoid tubercle of humerus: (0) medially situated; (1) laterally displaced; (2) laterally displaced, extends distally to contact supinator crest.
78. Distinct fossa on medial epicondyle of humerus in cranial view: (0) absent; (1) present.
79. Entepicondylar notch: (0) absent; (1) present.
80. Trochlear notch of ulna extends medially farther than any element of the olecranon: (0) yes; (1) no.
81. Styloid process of ulna: (0) sessile; (1) distinctly notched proximally in medial view.
82. Shape of radial head in proximal view: (0) oval; (1) circular.
83. Styloid process of radius: (0) short; (1) elongate, distinctly notched proximally.
**84. Anterior median ridge of radius: (0) absent; (1) present, not extending to distal edge of styloid process; (2) present, extending to distal edge of styloid process.
85. Lunate extends farther proximally than scaphoid: (0) yes; (1) no.
86. Dorsal process of lunate extending distal to articular surface: (0) absent; (1) present.
87. Scaphoid: (0) flat or convex distally on dorsal surface; (1) concave distally on dorsal surface.
*88. Pisiform: (0) square or pyramidal, expanded at base; (1) extended distally with ventrolateral crest; (2) dumbbell shaped.
89. Proximal overlap of dorsal surface of third metacarpal on hamate: (0) absent; (1) present.
90. Width of midshaft of third metacarpal: (0) less than twice the width of the midshaft in the next largest metacarpal; (1) greater than twice the width of midshaft in the next largest metacarpal.
91. Large medial dorsal ridge with distal concavity on third metacarpal: (0) absent; (1) present (see Hirschfeld, 1976, Fig. 1A).
**92. Number of claws on manus: (0) 4-5, (1) 3; (2) 2.
*93. Metacarpal length: (0) third metacarpal longest; (1) fourth metacarpal longest; (2) second metacarpal longest.
**94. Ungual phalanx of third digit: (0) claw lacking hood, relatively straight; (1) claw lacking hood, strongly curved; (2) claw hooded, strongly curved.
95. Intercondylar fossa of femur: (0) wider than lateral condyle; (1) narrower than lateral condyle.
96. Lateral condyle of femur: (0) thinner mediolaterally than medial condyle; (1) wider than medial condyle.
97. Tibial sesamoid bone: (0) absent; (1) present.
**98. Tibial sesamoid bone/navicular connection: (0) tibial sesamoid contacts navicular via distinct articular facet; (1) tibial sesamoid abuts navicular; (2) tibial sesamoid separated from navicular by medial cuneiform.
99. Shape of proximal navicular facet: (0) ventral concavity extends dorsomedial to the dorsal convexity; (1) no dorsal extension of ventral concavity (Fig. 5).
*100. Metatarsal length: (0) third metatarsal longest; (1) metatarsals subequal; (2) metatarsals progressively more elongate laterally.
101. Proximal lateral tuberosity of fifth metatarsal: (0) absent; (1) present.
102. Dorsal concavity on distal end of metatarsals in dorsal view: (0) absent; (1) present.
103. Sustentacular and navicular facets of astragalus: (0) separate; (1) confluent.
104. Groove lateral to sustentacular facet of astragalus: (0) does not perforate rim of navicular facet; (1) perforates rim of navicular facet.
105. Astragalocalcaneal and sustentacular facets of astragalus: (0) separate; (1) confluent.
106. Navicular facet of astragalus: (0) convex; (1) concave.
107. Distinct ridge on external side of calcaneus separating extensor digitorum brevis from accessorius: (0) absent; (1) present.

	60	70	
<i>Cyclopes</i>	11100	11010	
<i>Alouemyrmidon</i>	??10	210??	
<i>Rotamandua</i>	??10	?1?11	
<i>Mandua</i>	21111	11122	
<i>Rotamandua</i>	??10	?11??	
<i>Myrmecophaga</i>	11212	11122	
<i>Dasypus</i>	11n0a	20000	
<i>Dasypus</i>	00011	00101	
<i>Lophractis</i>	00011	00000	
<i>Rotamandua</i>	?1010	0102?	
<i>Detacheiromys</i>	21010	10011	
<i>Dasypus</i>	11?10	11010	
	60	70	
00002	11111	02112	00110
0????	?????	?????	?????
2????	?????	??12	??1?
21112	01112	11112	11012
?1012	?????	?????	??10?
21012	02101	12012	11102
10100	0011a	0a010	11100
10200	100n0	00011	01001
10200	10000	01011	01001
20?01	?00??	00010	?1000
10100	?00?0	00000	?0000
110n0	02110	00000	1000n

"The symbol '?' represents missing data to a given taxon. The following a = (0,1); b = (1,2).

Table AIII. The Distribution of Character States in Which Character States Differ Along Structural Lines

Node 1. Vermilingua: 3(1); 6(1); 7(1); 57(1); 60(1); 65(2); 69(1); 79(1)
Node 2. Cyclopininae: 5(0); 40(1); 41(1); 42(1); 43(1); 44(1); 45(1); 46(1); 47(1); 48(1); 49(1); 50(1); 51(1); 52(1); 53(1); 54(1); 55(1); 56(1); 58(1); 59(1); 61(1); 62(1); 63(1); 64(1); 66(1); 67(1); 68(1); 70(1); 71(1); 72(1); 73(1); 74(1); 75(1); 76(1); 77(1); 78(1); 80(1); 81(1); 82(1); 83(1); 84(1); 85(1); 86(1); 87(1); 88(1); 89(1); 90(1); 91(1); 92(1); 93(1); 94(1); 95(1); 96(1); 97(1); 98(1); 99(1); 100(1); 101(1); 102(1); 103(1); 104(1); 105(1); 106(1); 107(1); 108(1); 109(1); 110(1); 111(1); 112(1); 113(1); 114(1); 115(1); 116(1); 117(1); 118(1); 119(1); 120(1); 121(1); 122(1); 123(1); 124(1); 125(1); 126(1); 127(1); 128(1); 129(1); 130(1); 131(1); 132(1); 133(1); 134(1); 135(1); 136(1); 137(1); 138(1); 139(1); 140(1); 141(1); 142(1); 143(1); 144(1); 145(1); 146(1); 147(1); 148(1); 149(1); 150(1); 151(1); 152(1); 153(1); 154(1); 155(1); 156(1); 157(1); 158(1); 159(1); 160(1); 161(1); 162(1); 163(1); 164(1); 165(1); 166(1); 167(1); 168(1); 169(1); 170(1); 171(1); 172(1); 173(1); 174(1); 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1157(1); 1158(1); 1159(1); 1160(1); 1161(1); 1162(1); 1163(1); 1164(1); 1165(1); 1166(1); 1167(1); 1168(1); 1169(1); 1170(1); 1171(1); 1172(1); 1173(1); 1174(1); 1175(1); 1176(1); 1177(1); 1178(1); 1179(1); 1180(1); 1181(1); 1182(1); 1183(1); 1184(1); 1185(1); 1186(1); 1187(1); 1188(1); 1189(1); 1190(1); 1191(1); 1192(1); 1193(1); 1194(1); 1195(1); 1196(1); 1197(1); 1198(1); 1199(1); 1200(1); 1201(1); 1202(1); 1203(1); 1204(1); 1205(1); 1206(1); 1207(1); 1208(1); 1209(1); 1210(1); 1211(1); 1212(1); 1213(1); 1214(1); 1215(1); 1216(1); 1217(1); 1218(1); 1219(1); 1220(1); 1221(1); 1222(1); 1223(1); 1224(1); 1225(1); 1226(1); 1227(1); 1228(1); 1229(1); 1230(1); 1231(1); 1232(1); 1233(1); 1234(1); 1235(1); 1236(1); 1237(1); 1238(1); 1239(1); 1240(1); 1241(1); 1242(1); 1243(1); 1244(1); 1245(1); 1246(1); 1247(1); 1248(1); 1249(1); 1250(1); 1251(1); 1252(1); 1253(1); 1254(1); 1255(1); 1256(1); 1257(1); 1258(1); 1259(1); 1260(1); 1261(1); 1262(1); 1263(1); 1264(1); 1265(1); 1266(1); 1267(1); 1268(1); 1269(1); 1270(1); 1271(1); 1272(1); 1273(1); 1274(1); 1275(1); 1276(1); 1277(1); 1278(1); 1279(1); 1280(1); 1281(1); 1282(1); 1283(1); 1284(1); 1285(1); 1286(1); 1287(1); 1288(1); 1289(1); 1290(1); 1291(1); 1292(1); 1293(1); 1294(1); 1295(1); 1296(1); 1297(1); 1298(1); 1299(1); 1300(1); 1301(1); 1302(1); 1303(1); 1304(1); 1305(1); 1

inued

Table AII. Data Matrix^a

	10	20	30	40	50
lateral view; (1) extremely concave in lateral					
ve; (1) sigmoidal; (2) concave.					
ve; (1) sigmoidal.					
pered ventrally, does not extend to rim of					
nd to rim of glenoid; (2) rectangular.					
) laterally displaced; (2) laterally displaced,					
lateral view: (0) absent; (1) present.					
any element of the olecranon: (0) yes; (1) no.					
ted proximally in medial view.					
rcular.					
ctly notched proximally.					
t, not extending to distal edge of styloid					
l process.					
es; (1) no.					
rface: (0) absent; (1) present.					
(1) concave distally on dorsal surface.					
) extended distally with ventrolateral crest;					
on hamate: (0) absent; (1) present.					
ce the width of the midshaft in the next					
midshaft in the next largest metacarpal.					
metacarpal: (0) abscent; (1) present					
th metacarpal longest; (2) second metacarpal					
latively straight; (1) claw lacking hood,					
yle; (1) narrower than lateral condyle.					
) medial condyle; (1) wider than medial					
amoid contacts navicular via distinct					
ial sesamoid separated from navicular by					
xtends dorsomedial to the dorsal convexity;					
rsals subequal; (2) metatarsals progressively					
(1) present.					
ow: (0) absent; (1) present.					
ate; (1) confluent.					
s not perforate rim of navicular facet;					
(0) separate; (1) confluent.					
nsor digitorum brevis from accessorius:					

^aThe symbol “?” represents missing data; the symbol “n” is used in cases where a character is not applicable to a given taxon. The following symbols are used to represent character states in polymorphic taxa: a = (0,1); b = (1,2).

Table AIII. The Distribution of Apomorphies on the Tree in Fig. 1; Based on Manipulation 4 from Analysis 1, in Which Character States are Weighted Equally and Some Multistate Characters are Ordered Along Structural Morphoclines; Unequivocal Characters in Boldface

Node 1. Vermilingua: 3(1); 6(1); 7(1) ; 9(1); 17(1); 21(2); 22(2); 32(1); 33(1); 41(1); 42(1); 53(0); 55(2); 57(1); 60(1); 65(2); 69(1); 79(1) ; 95(0); 97(1); 101(1).
Node 2. Cyclopinae: 5(0); 40(1) ; 42(2); 51(0).
Node 3. Myrmecophaginae: 16(1) ; 25(1); 30(1); 34(1) ; 38(1); 43(1); 49(1); 51(2); 74(1) ; 91(1); 96(0); 100(2) ; 102(1).
Node 4. <i>Tamandua</i> , <i>Myrmecophaga</i> , and <i>Neotamandua</i> : 1(2); 8(1); 9(2) ; 10(2); 12(2) ; 13(0); 23(0); 24(1) ; 25(2); 31(1); 35(1); 39(1); 50(1) ; 52(1); 54(1); 56(0); 61(1); 66(1); 70(2); 71(1); 72(1); 81(1); 84(1); 98(1); 104(1) .
Node 5. <i>Myrmecophaga</i> and <i>Neotamandua</i> : 4(2) ; 26(1); 69(0); 82(1) ; 83(1) ; 84(2) ; 88(2); 99(1); 105(1) ; 107(1).

Table AIV. The Distribution of Apomorphies on the Tree in Fig. 7; Based on Manipulation 1 from Analysis 2 in Which All Character States Are Weighted Equally and All Multistate Characters Are Unordered; Unequivocal Characters in Boldface

Node 1. Xenarthra: **12(0); 14(1); 17(0); 29(2); 37(0); 64(1); 67(1); 95(1); 96(1).**
Metacheiromys: **12(1); 14(0); 17(1); 29(0); 37(1); 64(0); 67(0); 95(0); 96(0).**
 Pilosa: **13(1); 19(1); 46(1); 47(1); 59(1); 75(1); 93(1); 103(1); 106(1).**
 Node 2. Vermilingua and *Eurotamandua*: **7(1); 15(1); 41(1); 51(2); 101(1).**
 Node 3. Vermilingua: **3(1); 17(1) 18(1); 21(2); 22(2); 28(1); 32(1); 33(1); 55(2); 57(1); 58(1); 60(1); 62(2); 65(2); 69(1); 77(2); 88(1); 94(2); 95(0); 97(1).**
 Node 4. Myrmecophaginae: **16(1); 30(1); 34(1); 38(1); 42(1); 43(1); 49(1); 74(1); 76(1); 86(1); 91(1); 96(0); 100(2); 102(1).**
Eurotamandua: **6(0); 9(2); 14(0); 22(1); 25(2); 27(0); 44(0); 45(0); 55(1); 73(0); 77(1); 87(1).**

Table AV. The Distribution of Apomorphies on the Tree in Fig. 9; Based on Manipulation 1 from Analysis 3 in Which All Character States Are Weighted Equally and All Multistate Characters Are Unordered; Unequivocal Characters in Boldface

Node 1. Xenarthra: **6(0); 12(0); 17(0); 29(2); 37(0); 64(1); 67(1); 95(1); 96(1)**
Metacheiromys: **6(1); 12(1); 17(1); 29(0); 37(1); 64(0); 67(0); 95(0); 96(0).**
 Node 2. Pilosa and *Eurotamandua*: **13(1); 19(1); 75(1); 106(1).**
 Node 3. Pilosa: **6(2); 14(1); 18(1); 28(1); 46(1); 47(1); 58(1); 59(1); 68(1); 76(2); 80(0); 92(1); 93(1); 94(2); 100(1); 103(1).**
 Node 4. Vermilingua: **7(1); 15(1); 17(1); 21(2); 22(2); 32(1); 33(1); 42(2); 51(0).**
 Node 5. All Vermilingua except *Palaeomyrmidon*: **3(1); 6(1); 41(1); 48(1); 55(2); 57(1); 60(1); 62(2); 65(2); 69(1); 77(2); 88(1); 95(0); 97(1); 101(1).**
Eurotamandua: **7(1); 9(2); 15(1); 22(1); 25(2); 27(0); 41(1); 44(0); 45(0); 51(2); 55(1); 73(0); 77(1); 87(1); 101(1).**

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Tree in Fig. 7; Based on Manipulation 1 from
 Ordered Equally and All Multistate Characters Are
 Characters in Boldface

4(1); 67(1); 95(1); 96(1).
 0); 67(0); 95(0); 96(0).
 03(1); 106(1).
 1(1); 51(2); 101(1).
 3(1); 32(1); 33(1); 55(2); 57(1); 58(1); 60(1);
 42(1); 43(1); 49(1); 74(1); 76(1); 86(1); 91(1);
 0); 45(0); 55(1); 73(0); 77(1); 87(1).

in Fig. 9; Based on Manipulation 1 from Analy
 y and All Multistate Characters Are Unordered:
 ers in Boldface

); 67(1); 95(1); 96(1)
 67(0); 95(0); 96(0).
 06(1).
 8(1); 59(1); 68(1); 76(2); 80(0); 92(1); 93(1);
 (1); 33(1); 42(2); 51(0).
 (1); 41(1); 48(1); 55(2); 57(1); 60(1); 62(2);
); 44(0); 45(0); 51(2); 55(1); 73(0); 77(1);

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