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Myrmecophaga tridactyla (Pilosa: Myrmecophagidae)

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Abstract: The monospecific giant anteater, *Myrmecophaga tridactyla* Linnaeus, 1758, is the largest of the 4 species of New World vermilinguans. A feeding specialist on ants and termites, it occupies a broad range of lowland habitats, from dry scrub and savannah to rainforests. Its geographic range extends throughout southern Central America and northern South America, from Honduras in the north to Bolivia and northern Argentina in the south. *M. tridactyla* is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and is identified as "Vulnerable" on the International Union for Conservation of Nature and Natural Resources Red List.

Key words: giant anteater, myrmecophagy, South America, Vermilingua, Xenarthra

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Myrmecophaga Linnaeus, 1758

Myrmecophaga Linnaeus, 1758:35. Type species *Myrmecophaga tridactyla* Linnaeus, 1758 by subsequent selection (Thomas, 1901:143); placed on Official List of Generic Names in Zoology (International Commission on Zoological Nomenclature 1926).

Myrmecophata Bechstein, 1801:209. Incorrect subsequent spelling of *Myrmecophaga* Linnaeus, 1758.

Nyrmecophaga Bechstein, 1801:1346. Incorrect subsequent spelling of *Myrmecophaga* Linnaeus, 1758.

Myrmecopha G. Fischer, 1803:333. Incorrect subsequent spelling of *Myrmecophaga* Linnaeus, 1758.

Myrmecophagus Gray, 1825:343. Unjustified emendation of *Myrmecophaga* Linnaeus, 1758.

Falcifer Rehn, 1900:576. Type species *Myrmecophaga jubata* Linnaeus, 1766 by monotypy.

CONTEXT AND CONTENT. Order Pilosa, suborder Vermilingua, family Myrmecophagidae. *Myrmecophaga* is monotypic. The name derives from the Greek for "anteater." The generic synonymy is modified from Gardner (2007).

Myrmecophaga tridactyla Linnaeus, 1758

Giant Anteater

[*Myrmecophaga*] *tridactyla* Linnaeus, 1758:35. Type locality "America meridionali;" restricted to Pernambuco, Pernambuco, Brazil by Thomas (1911:132).

[*Myrmecophaga*] *jubata* Linnaeus, 1766:52. Type locality "Brasilia."

Myrmecopha didactyla G. Fischer, 1803:333. Incorrect subsequent spelling.

M[*yrmecophaga*]. *iubata* Wied-Neuwied, 1826:537. Incorrect subsequent spelling of *M. jubata* Linnaeus, 1766.

Tamandua tridactyla: Matschie, 1894:63. Name combination.

Falcifer jubata: Rehn, 1900:576. Name combination.

Myrmecophaga centralis Lyon, 1906:570. Type locality "Pacuare," Limón, Costa Rica.

Myrmecophaga tridactyla artatus Osgood, 1912:40. Type locality "Empalado Savannas, 30 miles east of Maracaibo, [Zulia], Venezuela."

Fig. 1.—Adult *Myrmecophaga tridactyla*, photographed at Iberá, Corrientes, Argentina (~ −28.62042°S, 057.36244°W, 72 m elevation). The animal above shows the bushy tail and elongated rostrum characteristic of this species, and the animal below (shown with the head of a 2nd individual) illustrates the dramatic black striping at the end of the white forelimbs. Photos used with the permission of photographer Juan Ramon Diaz Colodrero (www.iberaphotosafari.com).

Myrmecophaga tridactyla centralis: Goldman, 1920:64. First use of current name combination.

Myrmecophaga tridactyla artata Pittier and Tate, 1932:255. Corrected gender concordance.

Myrmecophaga trydactyla Utrera and Ramo, 1989: 65. Incorrect subsequent spelling *Myrmecophaga tridactyla* Linnaeus, 1758.

Context and Content. Context as for genus. As noted above, *Myrmecophaga* is monotypic at least as far as living taxa are concerned. The specific epithet "*tridactyla*" refers to the fact that there are typically 3 well-developed claws on the manus, the unguals on the 4th and 5th digits being strongly reduced or absent. It is possible that several extinct species pertain to the genus, though none have been formally designated (see "Fossil Record"). The species-level synonymy is modified from Gardner (2007). Common names for *M. tridactyla* include ant bear, gran hormiguero, oso hormiguero (o.h. común, o.h. mayor, o.h. real, o.h. palmero, o.h. gigante), tamanduá bandera, oso bandera, oso comilón, oso caballuno, oso pajizo, oso caballo, oso banderón, tamanduá de occidente, tamandua de bandera, hormiguero gigante, oso palmero, papa-formigas, tamanduá-açú, tamanduá-bandeira, and tamanduá cavalho, grosser amiesenbär, grand fourmilier, tamanoir, grote miereneter, mierenbeer, and reuzenmeiereneter (Superina and Aguiar 2006). Superina and Aguiar (2006) also provide an extensive list of names in a variety of indigenous South American languages. Gardner (2007:172) "tentatively" recognizes 3 extant subspecies, for populations in northeastern Colombia and northwestern Venezuela, in central America and Columbia and Ecuador west of the Andes Mountains, and in the remainder of northern South America (see "Distribution").

M. t. artata Osgood, 1912:40. See above.
M. t. centralis Lyon, 1906:570. See above.
M. t. tridactyla Linnaeus, 1758:35. See above.

DIAGNOSIS

Myrmecophaga tridactyla is easily distinguished from the other 2 genera (3 species) of anteaters within the suborder Vermilingua by size alone. With an average total length of roughly 2,000 mm, it is twice as long as the 2 species of *Tamandua*, and it dwarfs the silky anteater *Cyclopes didactylus*, which has an average total length of 433–450 mm. *M. tridactyla* has an average mass of 33 kg. *Tamandua* and *Cyclopes* are much smaller, weighing in at 3.2–7.0 kg and 175–400 g, respectively (Montgomery 1985; Wetzel 1985; Eisenberg et al. 1999). The coloration of *M. tridactyla* is also distinctive. Dark brown or black hairs cover the majority of the body, with conspicuous elongated triangular black stripes extending from below the ear and the throat toward the forelimbs and continuing posterodorsally, ending at mid-body (Fig. 1). In the other 2 genera the pelage is generally a lighter golden brown, although both species of *Tamandua* may be marked by a black vest around the neck and anterior trunk (Wetzel 1985; Eisenberg et al. 1999; Gardner 2007). This pattern is quite distinct from the diagonal stripe of *M. tridactyla*. The tail of *M. tridactyla* is not prehensile like that of other anteaters and is covered with long coarse hairs (Wetzel 1985; Eisenberg et al. 1999; Gardner 2007).

Skeletal characters may also be used to diagnose this species. Anteriorly, the greatly elongated rostrum of *M. tridactyla* generally constitutes more than 65% of the condylonasal length of the long, tapering skull (Fig. 2; Gardner 2007), whereas in other anteaters the rostrum comprises less than 50% of skull length (Gardner 2007). The braincase wall is markedly thickened relative to other anteaters (Patterson et al. 1992:41, 47, figures 13 and 15). The jugal bones are sharply pointed posteriorly (Grassé 1955), whereas the jugal is rounded posteriorly in *Tamandua* and is absent in *Cyclopes* (Gaudin and Branham

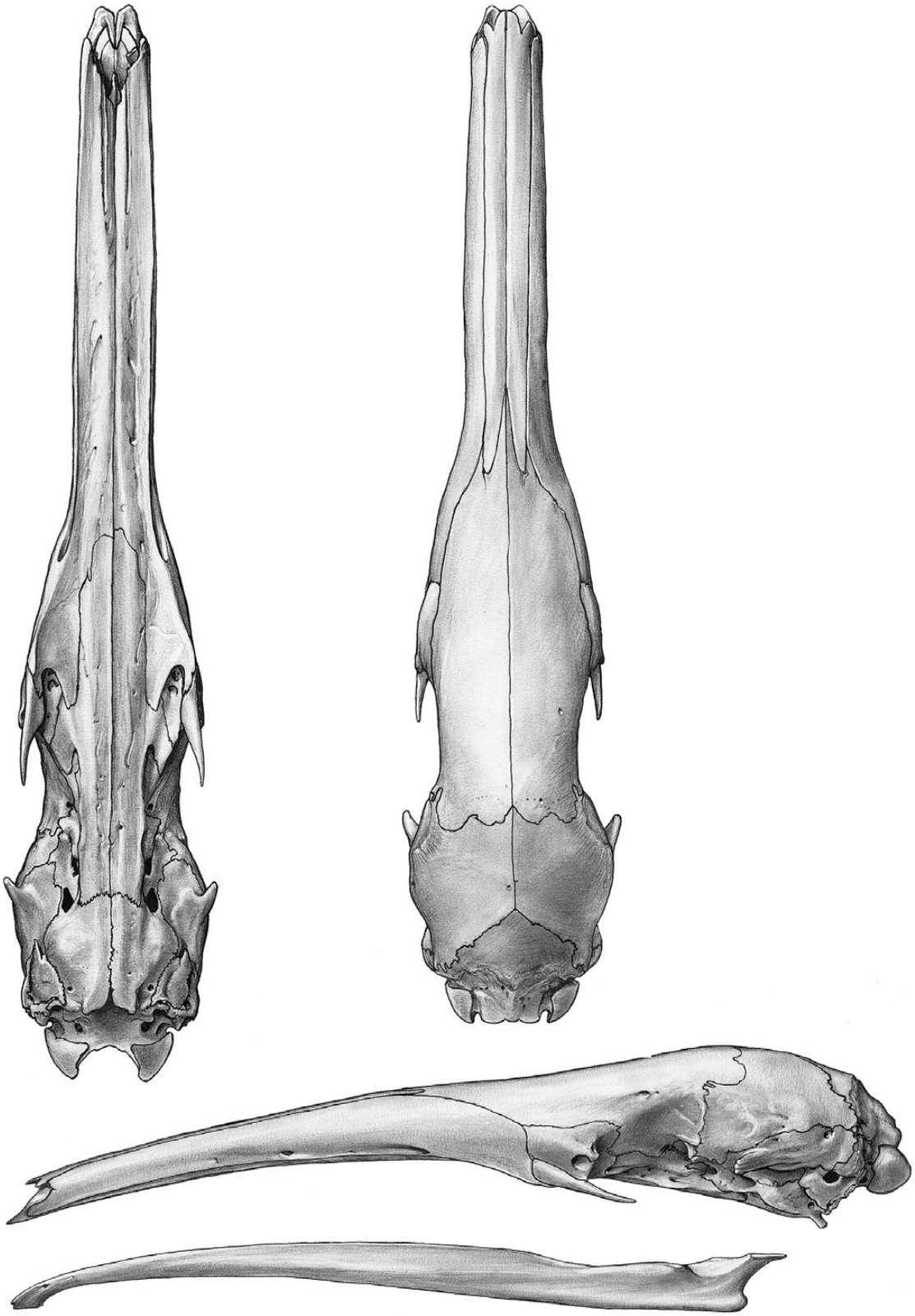

Fig. 2.—Dorsal (top left) and ventral (top right) views, with cranium and mandible shown in left lateral view (bottom) of a skull of an adult (gender unknown) *Myrmecophaga tridactyla* (UTCM [University of Tennessee at Chattanooga Natural History Museum] 1590), commercially obtained specimen lacking locality data. Occipitonasal length is 351.4 mm. Illustration by Julia Morgan Scott used with permission.

1998). The lumbar vertebrae possess an extra xenarthrous facet not found in other anteaters (Gaudin 1999), between the ventral surface of the accessory process and the dorsal surface of the transverse process. *M. tridactyla* is the only anteater species to have a fused pubic symphysis, and an elongated crest connecting the 3rd trochanter of the femur to the lateral epicondyle distally.

GENERAL CHARACTERS

Myrmecophaga tridactyla exhibits little sexual dimorphism (Eisenberg et al. 1999). Its narrow body is covered by long, coarse, dark brown or black hair, and its long tail is uniformly brown (Fig. 1). The hairs covering the tail are even more coarse and longer than those of the body. Its flanks are marked by elongated, triangular black stripes with white borders, beginning just below the ears, covering the throat, and continuing diagonally back above the shoulders, tapering to a point posteriorly. The powerful forelimbs are predominantly white except for 2 black bands, one present above the wrists and the other above the claws (Wetzel 1985; Eisenberg et al. 1999; Gardner 2007).

Mean external measurements (mm; with parenthetical *SE*, range, and *n*) based on adults from northern South America (Wetzel 1985) were: total length 2,000 (241, 1,740–2,817, 16); tail length 734 (76, 645–900, 16); pes length 165 (8, 150–180, 13), ear length 46.7 (4.7, 35–50, 9). Redford and Eisenberg (1992) reported a much smaller mean total length of 1,265.5 (1,100–2,000, 16), but other external measurements were identical to Wetzel (1985). Mean skull measurements (mm; with parenthetical *SE*, range, and *n*) based on adults from northern South America (Wetzel 1985) were: cranionasal length 359 (19, 313–409, 52); ratio of rostral length/cranionasal length 0.65 (0.02, 0.63–0.73, 49). Reeve (1940) reported similar values, with a range of total skull lengths from 360 to 380 based on 23 adult individuals from Brazil, Bolivia, Peru, and Ecuador. Mean body mass (kg; with parenthetical *SE*, range, and *n*) based on adults from northern South America (Wetzel 1985) was: 32.9 (7.1, 22–39, 5). Similar masses of 26.2 kg and 30.6 kg, respectively, were reported by Montgomery (1985—based on an unspecified number of individuals from Panama) and by McNab (1984—based on a commercially obtained individual). Redford and Eisenberg (1992) reported 3 different values for mean body mass (kg; with parenthetical range), 32.9 (22–39) for 5 individuals of unspecified gender, 32.1 (26.4–36.4) for 12 males from Brazil, and 29.2 (25.5–31.8) for 12 females, presumably also from Brazil.

DISTRIBUTION

Myrmecophaga tridactyla is a Neotropical species found at low elevations (Medri and Mourão 2005). It has a wide distribution from Honduras, south to Bolivia and northern Argentina (Fig. 3; Gardner 2007; Aguiar and da Fonseca 2008). Guatemala, southern Belize, and Costa Rica were once part of its distribution, but *M. tridactyla* is now most likely extirpated in these countries (IUCN/SSC Anteater, Sloth and Armadillo Specialist Group 2012). Reyes et al. (2010) have suggested that within Honduras, *M. tridactyla* has been eradicated from the Caribbean, and now can only be found further inland in the departments of Olancho and Gracias a Dios.

The distribution of *M. tridactyla* within South America extends east of the Andes and as far south as the Gran Chaco region of Bolivia, Paraguay, and Argentina (Gardner 2007; Aguiar and da Fonseca 2008). Only within Colombia and possibly Ecuador, can they be found west of the Andes (Gardner 2007; Aguiar and da Fonseca 2008). *Myrmecophaga tridactyla* is now likely extirpated from parts of its historical range in northern Argentina, eastern Paraguay, and southern Brazil (IUCN/SSC Anteater, Sloth and Armadillo Specialist Group 2012).

FOSSIL RECORD

The 1st record of the genus *Myrmecophaga* may go as far back as the Colloncuran South American Land Mammal Age (middle Miocene, 15.5–14 million years ago—McDonald et al. 2008), based on a suggestion made by Patterson et al. (1992) that the extinct anteater genus *Neotamandua* is congeneric with *Myrmecophaga*. However, both Engelmann (1985) and Gaudin and Branham (1998) treat *Neotamandua* as a separate genus closely related to *Myrmecophaga*. A younger extinct anteater species from the Montehermosan South American Land Mammal Age (late Miocene; 7–4 million years ago), *Nunezia caroloameghinoi* (Kraglievich 1934), was later assigned to *Myrmecophaga* by McKenna and Bell (1997). The slightly older *Neotamandua magna* (Ameghino 1919) was transferred to *Nunezia* by Kraglievich (1934), and therefore should also be considered *Myrmecophaga*. The latter 2 taxa represent the oldest definitive *Myrmecophaga*, and suggest that the genus extends back at least as far as the Huayquerian South American Land Mammal Age (late Miocene, 9–7 million years ago). This date is slightly younger but not inconsistent with the molecular estimate of divergence between *Myrmecophaga* and *Tamandua*, determined by Delsuc et al. (2001) to occur roughly 13 million years ago.

A large gap of at least 2 million years exists between the late Miocene specimens of *M. caroloameghinoi* and younger specimens of *M. tridactyla*, which are first known from the Irvingtonian North American Land Mammal Age (early Pleistocene, 1.9–1 million years ago) in northern Mexico (Shaw and McDonald 1987). Additional fossil material of *M. tridactyla* is known from late Pleistocene cave deposits in Brazil, and from late Pleistocene sites in eastern Brazil and Uruguay (McDonald et al. 2008).

FORM AND FUNCTION

Form.—A distinguishing feature of *Myrmecophaga tridactyla* is its long, tubular skull, with its particularly elongated rostrum (Fig. 2; Reeve 1940; Grassé 1955). Reeve's (1940) study of cranial allometry demonstrated strong positive

Fig. 3.—Geographic range of *Myrmecophaga tridactyla* in Central and South America (modified from Gardner 2007; IUCN/SSC Anteater, Sloth and Armadillo Specialist Group 2012). Subspecies are: 1, *M. t. centralis* (darkest gray area); 2, *M. t. artata* (lightest gray area); and 3, *M. t. tridactyla* (medium gray). Areas marked by vertical lines are those from which the species is likely extirpated recently. The region of Ecuador (west of the Andes) marked by horizontal lines and a question mark represents an area where the presence of *M. tridactyla* is in need of confirmation (IUCN/SSC Anteater, Sloth and Armadillo Specialist Group 2012).

allometry in the growth of the facial region of the skull. Reeve (1940:72) noted that the rostrum is "hardly wider or deeper in *Myrmecophaga* than at its widest point in *Tamandua*," despite the fact that overall skull length and rostral length is much greater in the former. The skull is also unusual for its longitudinal curvature (Reeve 1940; Grassé 1955), and its very thick braincase, a unique and somewhat puzzling feature not found in other anteaters or in ant-eating mammals in general. The jugal bones are sharply pointed posteriorly, and the zygomatic arch is incomplete (Grassé 1955). The hard palate is comprised by not only the premaxilla, maxilla, and palatine bones, but also by horizontal palatal processes of the pterygoids that meet in the midline and form the ventral edge to the choanae (Patterson et al. 1992; Gaudin 1995; Gaudin and Branham 1998). It is greatly elongated, covering the nasopharynx and basicranium in ventral view (Patterson et al. 1992). The auditory bulla is fully ossified, formed by a large ectotympanic and small entotympanic element with a medial contribution from the basioccipital, and the tympanic cavity is expanded into both an epitympanic sinus in the squamosal bone (Guth 1961; Patterson et al. 1992), and a hypotympanic sinus that forms a superficially visible inflation within the pterygoids (Guth 1961; Patterson et al. 1992; Storch and Habersetzer 1992). The eustachian tube opens at the posterior margins of the auditory bulla, a unique feature of anteaters (Patterson et al. 1992; Gaudin 1995; Gaudin and Branham 1998). The malleus has an anteroposteriorly elongated head, and the manubrium forms roughly a 150° angle to the neck in lateral view (Doran 1878;

Guth 1961; Fleischer 1973; Patterson et al. 1992). The stapes is horseshoe-shaped, or with slightly convex crura, and is perforated by a large stapedial foramen (Doran 1878; Guth 1961; Fleischer 1973; Gaudin et al. 1996), though the stapedial artery itself is absent (Guth 1961). The promontorium of the petrosal is crossed by a groove for the internal carotid artery (Guth 1961; Patterson et al. 1992).

The jaws bear no teeth. The long dentary bones are slight and strongly compressed mediolaterally, and rather loosely joined at an unfused mandibular symphysis (Grassé 1955; McDonald et al. 2008).

The cervical vertebrae are elongated anteroposteriorly in *M. tridactyla*, in particular the atlas and axis, although even in the remaining cervicals, the centra are longer than they are wide in ventral view. Thoracic vertebral counts vary from 15 to 16, and lumbar counts of 2–3 have been reported (Gaudin 1999). There are generally 4 sacral vertebrae, with tall neural spines. The first 3 sacrals attach to the ilium, the 4th to the ishium. The 1st caudal also attaches to the ischium (McDonald et al. 2008). The anterior caudal vertebrae are robust with deep zygapophyses limiting lateral movement (McDonald et al. 2008), and the anterior and posterior faces of the centra are slanted rather than vertical (Hirschfeld 1976). Flower (1885) reports 29 caudal vertebrae for *M. tridactyla.* Original descriptions of the vertebrae of *Myrmecophaga* are found in Owen (1851; see also Flower 1885; Jenkins 1970). He states that within the Edentata (a term that is roughly equivalent to the modern Xenarthra) the development of vertebral processes is at its greatest complexity among placental mammals, with large neural spines, transverse processes, metapophyses, and anapophyses. As in other xenarthrans, these processes form extra intervertebral articulations, the xenarthrous articulations, between the posterior thoracic, lumbar, and 1st sacral vertebrae. In *Myrmecophaga*, these form as joints between the dorsal surface of anapophysis of the anterior vertebra and the metapophysis of the succeeding vertebra, and, in the lumbar vertebrae only, between the ventral anapophysis and dorsal surface of the succeeding transverse process (Gaudin 1999). The posterior thoracic, lumbar, and 1st sacral vertebrae are also characterized by medial and lateral zygapophyseal articulations, divided from one another by enlarged metapophyses (Gaudin 1999). To help visualize these xenarthrales, and the vertebrae in general, 3-dimensional reconstructions of *M. tridactyla* vertebrae based on CT scans can be found in Endo et al. (2009). It has been suggested that the xenarthrous articulations stabilize the trunk while feeding in a bipedal standing posture without unduly restricting dorsal and lateral mobility of the trunk (Endo et al. 2009). The rib shafts of *Myrmecophaga* are greatly expanded anteroposteriorly (Jenkins 1970). Jenkins (1970) asserts that these expanded ribs also provide trunk support crucial to the fossorial lifestyle of *M. tridactyla*.

The scapula of *Myrmecophaga* is nearly quadrangular in shape, due to an enlarged posterior fossa for the teres major muscle, separated from the infraspinous fossa by a tall, elongated secondary scapular spine (Taylor 1985; McDonald et al. 2008). It has a large acromion process and a large process that has been termed a metacromion (Gaudin and Branham 1998; McDonald et al. 2008), though it lies at the midpoint of the scapular spine rather than at its ventral extremity. A scapular foramen, a feature characteristic of pilosan xenarthrans, is present between the glenoid region and the procoracoid (= anterior coracoid), which initially develops as a separate center of ossification (Rose and Emry 1993; Gaudin and Branham 1998; McDonald et al. 2008). The clavicle is vestigial (Taylor 1985). The humerus is marked by very large muscular processes, including an expanded, posterior curved deltoid tubercle, connected distally by a ligament to the strong supinator crest (Hildebrand 1985:96, figure 6-4G; Taylor 1985; McDonald et al. 2008). The entepicondylar process is flared distally and also curves posteriorly, and the entepicondylar canal is well-developed (McDonald et al. 2008). The olecranon of the ulna is robust and markedly flared medially, though less elongated than in other fossorial xenarthrans (Hildebrand 1985; Vizcaíno and Milne 2002). The distal end of the radius lies well anterior to the proximal end, the dorsal tubercle at the distal end is enlarged, and the distal articular surface is deeply concave (McDonald et al. 2008). The latter 2 features serve to brace the wrist in its vertical standing posture (Orr 2005). Orr (2005) provides radiographs of the phalanges and wrists of the anteater taken in dorsovolar and radioulnar planes. The 3rd digit of the manus is greatly enlarged (*M. tridactyla*, UTCM [University of Tennessee at Chattanooga Natural History Museum] 1900: midshaft width of metacarpal III = 15.4 mm; midshaft width of next largest digit, metacarpal IV = 8.8 mm), with a large, medially offset keel on the metacarpal. The 3rd ungual is both the primary digging claw and the primary weight-bearing surface on the manus (Hildebrand 1985; Orr 2005).

The pelvis of *M. tridactyla* is distinctive. The medial dorsal flange of the ilium is tall and sharp, creating a deep gluteal fossa. The anteroventral edge of the ilium and pubis is aligned in lateral view and the ischial tuberosity lies anterior to the posterior edge of the pubic symphysis. The femoral head is directed medially in *Myrmecophaga*, and the conspicuous 3rd trochanter is elongated proximodistally, spanning the lateral margin of the femur from the greater trochanter to the lateral epicondyle (McDonald et al. 2008). The distal end of the tibia is marked by strong posterior grooves for the flexor tendons. The distal end of the fibula has 2 separate anterior and posterior facets that articulate with the tibia. *Tamandua* has only 1 facet, and the tibia and fibula of *Cyclopes* are fused distally (McDonald et al. 2008). The astragalar head is concave distally, and the pes is plantigrade (Rose and Emry 1993; McDonald et al. 2008).

The facial muscles of *M. tridactyla* are greatly reduced compared to those of most placental mammals, a feature that likely evolved to allow precise control over their mouths and noses while feeding (Naples 1985). The m. buccinatorius is divided into 2 parts, the pars externus, which has fibers oriented dorsoventrally, and the pars internus, whose fibers are anteroventrally oriented (Naples 1985). This is a unique arrangement not found in other mammals, and is important in executing control over the cheek region while feeding.

The jaw musculature is also strongly diminished (Owen 1854; Windle and Parsons 1899; Lubosch 1907; Kühlhorn 1940; Guth 1961; Naples 1985, 1999). *M. tridactyla* lacks deep masseter (M. masseter profundus) and zygomaticomandubularis muscles, and the superficial masseter is thin (Naples 1999). The origin of the temporalis muscle is restricted to the posterodorsal region of the orbit, and does not extend onto the dorsal surface of the braincase (Guth 1961; Naples 1999). The tongue is long, narrow, and protrusible, with a diameter of only 10–15 mm at its widest point, and is comprised of highly developed tongue musculature (Reiss 1997; Naples 1999). The tongue muscles originate on the posterior end of the sternum instead of the hyoid (Reiss 1997). This allows the tongue to be extended up to 610 mm beyond the mouth (Nowak 1999). Reiss (1997) notes the elongation of the soft palate, the loss of the interhyoideus tendon, and the increased robustness of the M. medialis veli palatini in *M. tridactyla* relative to other anteaters. Reiss (1997) also depicts the relationships among pharyngeal spaces and musculoskeletal structures of the tongue and hyoid in *M. tridactyla.*

Taylor (1985) notes the enlargement of the digital flexors in the manus of *M. tridactyla*. Digital flexion is supplemented by an elongate, distally divided supinator muscle (Hildebrand and Goslow 2001), and the medial head of the triceps, which lacks an ulnar insertion and instead shares a tendon of insertion with the m. flexor digitorum profundus (Taylor 1985). The latter is a feature shared with the closely related genus *Tamandua*, and is unique to these 2 genera among mammals. *M. tridactyla* also shows expansion of the teres major muscle and the dorsal forearm muscles, associated with powerful flexion of the elbow and retraction of the humerus, but lacks fusion of the clavotrapezius and clavodeltoid muscles into a common cephalohumeralis, as is common in aclaviculate mammals (Taylor 1985). Gambaryan et al. (2009) note that the forelimb musculature has twice the weight of the hindlimb muscles, and that the weight of the hindlimb musculature active during the support phase of locomotion (including the gastrocnemius, soleus, and digital flexors) is greater than that of the muscles active during the swing phase (tibialis anterior, peroneus muscles, and digital extensors). Gambaryan et al. (2009:1) also assert that *M. tridactyla* "has a complete set of short pes muscles."

The small eyes and ears of *M. tridactyla* rest upon a cylindrical head which is elongated and narrow. The manual claws are quite conspicuous, and are much larger than the 5 pedal claws. The 3rd ungual of the manus is especially large. It is curled posteromedially under the manus and is weight bearing on its dorsolateral surface during standing and walking (Wetzel 1985; Orr 2005; Gardner 2007). Manual digits 4 and 5 are syndactylous and are covered by an external pad that contacts the substrate when standing and serves as the primary weight-bearing structure (Pocock 1924; Orr 2005). Manual digit 5 lacks a claw (Grassé 1955). The tail of *M. tridactyla* is covered by alternating rows of horny epidermal scales, the bushy hairs emerging behind each scale (Weber 1928).

Few recent reports on the nonmuscular, nonintegumentary soft tissues of *M. tridactyla* exist. Forbes (1882) notes that the olfactory lobes of the brain are quite large and must be essential to an animal that is led by smell while foraging. Forbes (1882) also notes the prominence of the vermis of the cerebellum, and the presence of distinct cerebrellar flocculi and a well-developed corpus callosum. Sherwood et al. (2009) describe the anatomy of neocortical neurons, noting the predominance of nonphosphorylated neurofilament proteinimmunoreactive neurons, frequently with nonpyramidal shapes, in layer V of the neocortex. The soft palate is elongated in *M. tridactyla*. In the closely related genus *Tamandua*, the soft palate extends posteriorly to the level of the 5th cervical vertebra (Reiss 1997), and Reiss (1997) asserts that the anatomy of this region in *M. tridactyla* is quite similar. Therefore, like *Tamandua*, the nasopharynx and oropharynx would lie primarily within the neck (Reiss 1997). Grassé (1955) commented briefly on the "dent musculaire," small muscular projections of the lining of the pylorus that extend into the lumen of the stomach. They are most likely used to crush ants and other insects, which are not chewed before being swallowed. The intestine is divided into discrete large and small intestines, but there is no cecum or ileocecal valve (Owen 1854). The right lateral and caudate lobes of the liver are fused, and the unlobed kidneys are pelvic in position (Weber 1928; Grassé 1955). The lung has an accessory lobe on the right side (Owen 1854; Weber 1928).

Grassé (1955) and Owen (1854) emphasize the unusual nature of the salivary glands of *M. tridactyla*. The salivary glands are very large and produce copious amounts of glue-like saliva. The volume of the submaxillary salivary gland alone is roughly equal to that of the entire head. The parotid and submaxillary salivary glands together form an almost continuous mass extending from the ear to the shoulder. A sublingual salivary gland is lacking in *M. tridactyla*, but it is functionally replaced by numerous mucus glands that open within the mouth, especially on the hard palate and between the mandibular rami, where they form a continuous layer (Grassé 1955).

The female reproductive organs of *M. tridactyla* and other anteaters are peculiar in that there is no well-defined cervix and there are 2 vaginal outlets (Forbes 1882; Wislocki 1928; Grassé 1955; Novacek and Wyss 1986). *M. tridactyla* also lacks a free-standing clitoris or visible labia minora (Forbes 1882), and has a single pair of pectoral nipples (Owen 1854). *Myrmecophaga tridactyla* males are characterized by intra-abdominal testes, well-developed prostatic glands, and a short penis without a baculum (Weber 1928; Rodrigues et al. 2008).

Function.—*Myrmecophaga tridactyla* is a terrestrial quadrupedal animal that rarely uses its ability to climb (Montgomery 1985; Young et al. 2003). Its hindlimbs exhibit a plantigrade posture during normal locomotion, but the forelimb posture is typically characterized as "knuckle-walking" (Vaughan et al. 2015).

Orr (2005) examines the knuckle-walking of *M. tridactyla*, providing detailed analysis of the osteological features and the actions of articulations and joints of the manus and wrist, and how weight is borne upon them during standing and walking. *M. tridactyla* holds the manus vertically during locomotion, and exhibits digit hyperextension at the metacarpophalangeal joints. Weight is borne upon the manus and is transferred to the substrate

primarily through the fatty pad that unites flexed digits 4 and 5, with a contribution through the dorsal surface of the greatly enlarged 3rd ungual phalanx. Gambaryan et al. (2009) also study myrmecophagid locomotion, but focus on the myology of the pes and its adaptive properties. They note that although *M. tridactyla* is a specialized fossorial animal, it has rear feet that are adapted to walking like other plantigrade mammals.

Although the anatomy and function of the forelimb of *Tamandua* is very similar to that of *M. tridactyla*, their behavior is quite distinct in several ways (Taylor 1985). *M. tridactyla*, unlike *Tamandua*, has generally been thought to prefer ants to termites, and has rarely been observed climbing or ripping open termite nests (Montgomery and Lubin 1977; Montgomery 1985; Shaw et al. 1985), yet it still retains great grasping and tearing power. This is generally concentrated on the greatly enlarged 3rd digit, the power being provided by the muscular flexion of large forelimb muscles, as well as the medial head of the triceps and the supinator muscle (Taylor 1985; Hildebrand and Goslow 2001). Taylor (1985) concludes that because *M. tridactyla* rarely climbs or tears open termite mounds, the retention of this power must be primarily associated with defense against predators. More recent information provided by Rodrigues et al. (2008), however, shows that feeding preference in *M. tridactyla* is dependent upon season and location. In grassland areas with a high density of termite mounds, *M. tridactyla* will consume a much greater proportion of termites, and therefore will use their large 3rd digits more frequently to open termite nests.

The mode of digging utilized by *M. tridactyla* has been described by Hildebrand (1985) as "hook-and-pull" digging. Once an individual has found a termite or ant nest, it will insert the 2nd and 3rd digit into a hole or crevice, and then pull the manus back toward the body. Hildebrand (1985) also notes the unusual arrangement of the medial head of the triceps, and affirms that the claws can be flexed against the palm, creating a grip that can be used to manipulate the material of a termite or ant nest.

Masticatory function of *M. tridactyla* has been investigated by Naples (1999). Modifications of the head contribute to the acquisition of ants and termites through the contraction and concomitant protrusion of the tongue, unusual rotational movements of the mandible to form a mouth opening, and movement of the anterior tip of the rostrum in order to aim the tongue toward prey. The masticatory system is marked by rapid tongue protrusion–retraction cycles (up to 160 cycles/min), and high associated food transport rates, coupled with nearly continuous swallowing. After retracting the prey-covered tongue into the mouth, prey is removed from the tongue as it moves anteriorly, rubbing against transverse ridges running along the roof of the mouth (Naples 1999). Naples (1999) asserts that the tongue of *M. tridactyla* can be extended about the length of its head, over 350 mm beyond the mouth opening in some adults, but Nowak (1999) reports that it can be extended nearly twice as far, some 610 mm. This extraordinary extensibility is made possible by an overall increase in the length of the tongue via loss of attachment to the hyoid and attachment instead to the sternum (Windle and Parsons 1899; Engelmann 1985; Reiss 1997). While feeding, the tongue is aimed by cervical muscles which control head orientation (Naples 1999). Like many mammals, *M. tridactyla* has unfused mandibular symphyses, though the symphysis is particularly loose in *M. tridactyla*, and assumes a highly unusual horizontal orientation at rest (Naples 1999). Masseter and temporalis muscles are used in closing the jaw in most mammals, but in *M. tridactyla*, they function to spread and depress the mandibular symphysis via rotation of the mandibular rami medially around their long axes (Naples 1999). There is very little mandibular depression during mouth opening due in part to a decrease in the size of the digastric muscle, but more importantly, to an anteroposterior expansion of the buccinator that limits jaw depression. Nevertheless, mandibular rotation allows *M. tridactyla* to produce an opening sufficiently large for protrusion and retraction of the tongue.

A body temperature of 32.7°C for a captive *M. tridactyla* was noted by McNab (1984), but he also recorded measurements of 34–36.7°C during activity in the field. The basal metabolic rate is quite low, averaging 0.085 $cm^3O_2/g{\cdot}h$ (± 0.002, $n = 29$), only 34% of the expected value based on body mass (McNab 1984). Its thermal conductance is also low, however, averaging 0.0054 $cm^3O_2/g{\cdot}h{\cdot}°C$ (± 0.0003, $n = 18$), some 94% of expectations for body size (McNab 1984), due to its coarse pelage and the use of its large bushy tail as an aid for thermoregulation (McNab 1984; Rodrigues et al. 2008). The combination of its low conductance, large body mass, and high metabolic scope make it an able thermoregulator over a wide range of ambient temperatures (McNab 1985), with a lower thermoneutrality limit of 15.0°C (McNab 1984).

ONTOGENY AND REPRODUCTION

Reproductive behavior has been little documented in wild-living *Myrmecophaga tridactyla* (Shaw et al. 1987; Medri et al. 2006; Rodrigues et al. 2008), though a recent report suggests males will aggressively pursue females even if the female is not receptive (Júnior and Bertassoni 2014). Their exceptional olfactory sense is used by males to pick up chemical cues revealing the reproductive status of females (Rodrigues et al. 2008). Estrus cycles occur at approximately 7-week intervals, with each cycle lasting 47–62 days (Knott et al. 2013). Estrus may be marked by vaginal discharge (Shaw et al. 1987). The onset of ovarian cyclic activity takes place within 4–11 weeks after pregnancy occurs (Patzl et al. 1998; Knott et al. 2013). Cycles are not seasonal, and females are normally polyestrous, with slight vaginal bleeding marking the proestrus period (Schauerte 2005). During intercourse, the male is positioned over the female while she lies on her side. Copulations can occur several times for a period of approximately 3 days (Medri et al. 2006).

Gestation typically lasts 170–190 days (Bartmann 1983; Shaw et al. 1987; Medri et al. 2006; Gardner 2007; Knott et al. 2013). The placenta is hemochorial, discoid, and lobulated (Benirschke 2008). *M. tridactyla* usually produces only 1 offspring (Gardner 2007) with a body mass between 1.1 and 1.6 kg at birth (Byrne 1962). Breeding can occur throughout the year (Patzl et al. 1998),

but evidence exists for seasonality in courtship and in giving birth in captive animals (Merrett 1983; Shaw et al. 1987). Shaw et al. (1987) observed courtship repeatedly in January and recorded births inconsistent with the gestation periods recorded in captivity, and suggested the possibility of delayed implantation in *M. tridactyla*, a characteristic known in *Dasypus* (Loughry and McDonough 2013) but not in other xenarthrans (Benirschke 2008). The case for delayed implantation in *M. tridactyla* is strongly disputed by other researchers (S. Nofs, pers. comm.), but received support from the work of Knott et al. (2013).

Lactation lasts 6 months and young are carried on the mother's back for 6–9 months until the female is pregnant again, enabling intense parental care in this species (Bartmann 1983; Rodrigues et al. 2008). The interval between consecutive births is typically 9 months. Offspring typically reach sexual maturity in 2–4 years, but have been recorded as soon as 1.6 years (Knott et al. 2013). Yearlings exhibit rapid growth during the second half of their 2nd year, and require at least 3 years to reach full size in the wild (Shaw et al. 1987). *Myrmecophaga tridactyla* lives up to 15 years in the wild, but can live from 25 to more than 30 years in captivity (Jones 1982; Weigl 2005; Medri et al. 2006; Knott et al. 2013).

ECOLOGY

Unless stated otherwise, the following information is drawn from the work of Rodrigues et al. (2008), who have provided a comprehensive survey of the literature on the ecology and behavior of *Myrmecophaga tridactyla*. *M. tridactyla* has the ability to climb but prefers a terrestrial existence as opposed to the purely arboreal *Cyclopes* and the 2 species of *Tamandua* that may be found foraging on the ground or in the trees (Gardner 2007). The diet of *M. tridactyla* consists of almost entirely ants and termites, although it may feed on the occasional beetle larva, social insect mimic, or European bee that has created a hive within a termite nest. As many as 35,000 ants or termites may be consumed in a single day (Moeller 1990). Montgomery (1985) notes that *M. tridactyla* studied in Venezuela consumed 23 different ant morphospecies, preferring large or medium-sized ants. The proportion of ants or termites consumed depends on the geographic region and the season, with termites forming a greater proportion of the diet in drier habitats, and during the dry season (Rodrigues et al. 2008). *M. tridactyla* is able to limit its exposure to the varied physical and chemical defenses of ants and termites by feeding only briefly at any one site and then moving to another. Feeding bouts may last as little as 38 seconds per ant or termite nest (Montgomery 1985).

Myrmecophaga tridactyla is generally solitary except during the breeding season or when females are carrying young. Mean home ranges can vary from 2.7 to 11.9 km^2 (Rodrigues et al. 2008). Overlapping of individual home ranges from these studies was considerable, as density reached up to 2 animals per km^2. Higher densities at certain sites were attributable to abundant resources and to a lack of natural predators (primarily jaguars), human hunting, and road kills. Sex ratios vary among regions from 1:1 to as many as 3 males per female (Sampaio et al. 2006). Antagonistic interactions between males, ranging from circling to serious fighting, have been observed and may indicate territorial defense behavior (Rodrigues et al. 2008). Tree scratching may be used by *M. tridactyla* to communicate with conspecifics and was found to be associated with higher stress levels attributed to anthropogenic disturbance or fire (Braga et al. 2010).

Myrmecophaga tridactyla can be found at night or during the day roaming diverse habitats ranging from very wet rainforests to dry savannas and thorn scrub. The home ranges of individuals also consist of a variety of habitats, with varying habitat preferences depending upon its activity and the region where it lives. There is some interindividual variation as well. For example, some *M. tridactyla* of the Pantanal wetlands in Brazil have been observed resting in both savanna and forest, whereas other studies conducted in the same region found that *M. tridactyla* preferred resting in open areas. It was observed foraging in many habitat types including scrub savanna, grasslands, forest patches, savanna, and near lakes. Foraging frequency in a given habitat among *M. tridactyla* in the Pantanal generally correlated to percent cover of that habitat. Shaw et al. (1987) rarely observed *M. tridactyla* foraging in brushland within Serra da Canastra National Park in Brazil, though termite mounds were abundant. Instead, it was unexpectedly found foraging in gallery forests, an area of fewer termite mounds. In a study conducted within Emas National Park in the Brazilian Cerrado, Vynne et al. (2011) found that *M. tridactyla* utilizes agricultural areas and is generally found close to roads. It may use them as corridors as it travels through the croplands, an activity that increased as more of these areas appeared within its habitats. From the few examples above, it is clear that generalizations regarding *M. tridactyla* habitat preferences may be unreliable because of the abundant intraspecific variation, though future studies of its habitat preferences may provide more clarification (Rodrigues et al. 2008).

Temperature influences daily activity patterns. During very hot periods, *M. tridactyla* prefers to forage at night. Midday foraging increases as temperatures decrease. To conserve heat, it may be seen wrapping itself with its giant tail while it sleeps, or it may fully extend the tail to absorb the sun's rays. Bathing is often associated with cooling off, but this may not be the reason *M. tridactyla* participates in this activity—it may bathe to remove ants or termites (Emmons et al. 2004).

Many female *M. tridactyla*, and to a lesser extent males, will return to their area of birth to breed (Collevatti et al. 2007). The population of *M. tridactyla* studied by Collevatti et al. (2007) in Emas National Park, Brazil, has been greatly reduced due to recurrent fire events. Collevatti et al. (2007) estimate a population of 300 individuals in the park, or 0.23 per km^2, but suggest that a 1994 fire may have reduced the population to as few as 43 individuals. This kind of bottleneck, combined with their philopatric nature, may contribute to a high level of inbreeding and a loss of genetic variation.

GENETICS

Myrmecophaga tridactyla has a diploid number (2n) of 60 chromosomes and a fundamental number (FN) of 104

(Hsu 1965; Pereira Júnior et al. 2004). It has an extra group of acrocentrics (group V), as compared to the 2 species of *Tamandua*. The karyotype comprises pairs of 2 large metacentric chromosomes (group I), 3 submetacentric chromosomes (group II), 8 medium submetacentric chromosomes (group III), 11 medium to small metacentric chromosomes (group IV), and 5 acrocentric chromosomes (group V). Sex-determining chromosomes X and Y comprise a large metacentric and small acrocentric morphology, respectively (Pereira Júnior et al. 2004).

Population genetic studies of *M. tridactyla* are rare. Collevatti et al. (2007) conducted one such study, and found a high level of inbreeding in the population of *M. tridactyla* in Emas National Park, with a low level of genetic diversity, especially in males, in spite of the more philopatric behavior of females. Males with adjacent home ranges showed low levels of relatedness (Prodöhl et al. 2008). Garcia et al. (2005) reported the identification of 6 microsatellite loci that may be useful in future studies.

CONSERVATION

Myrmecophaga tridactyla is broadly distributed from Honduras to northern Argentina and take advantage of a wide variety of habitats. Because of this, extinction is not likely in the near future. However, its existence is in peril in many portions of its range, as it is subject to the threat of human activities. Domestic dogs, highway collisions, burning, and destruction of its habitat, and sport and subsistence hunting all take their toll on populations. Low reproductive rates and a highly specialized diet also contribute to its decline (Aguiar and da Fonseca 2008). *M. tridactyla* is listed on Appendix II of CITES and is identified as "Vulnerable" on the International Union for Conservation of Nature and Natural Resources Red List (International Union for Conservation of Nature and Natural Resources 2014).

Habitat destruction and fragmentation are the primary cause for the decrease in *M. tridactyla* numbers. The species may survive this loss of habitat by foraging in agricultural fields and pasturelands that contain many termite mounds and mimic the undisturbed grasslands in which *M. tridactyla* thrives. However, these pastoral areas must be in close proximity to covered habitats to meet the thermoregulatory needs of the animals, especially during the hotter times of the year (Rodrigues et al. 2008; Vynne et al. 2011).

Myrmecophaga tridactyla is actively hunted throughout its range, as it is an easy target and provides a fair amount of meat (Aguiar and da Fonseca 2008). It may be hunted for illegal trade and to be kept as a pet in certain parts of its range (International Union for Conservation of Nature and Natural Resources 2014). In Bosawas Biosphere Reserve in Nicaragua, hunters do not actively seek *M. tridactyla*, but kill them because they pose a threat to their hunting dogs (Koster 2008). Others feel they should be killed on sight due to superstitions or out of fear of the animal's presumed hostility and aggressive nature. The latter represents a misinterpretation of the defensive behavior of *M. tridactyla*, designed to ward off predators before any physical interactions occur. *M. tridactyla* has been taken for its thick, tough hide, which provides durable leather for equestrian purposes (Aguiar and da Fonseca 2008); and, in Venezuela, it is killed for its large foreclaws.

Myrmecophaga tridactyla has been extirpated from certain parts of its historical range, especially in Central America (IUCN/SSC Anteater, Sloth and Armadillo Specialist Group 2012), as a consequence of the human activities mentioned above. In La Selva, Costa Rica, the last individual of *M. tridactyla* was seen in the 1960s or 1970s (Clark 2007). As mentioned above, *M. tridactyla* is endangered in Honduras, and Reyes et al. (2010) found that the Honduran Caribbean is now devoid of *M. tridactyla*.

With a typical birth interval of no more than 1 offspring every 9 months (Rodrigues et al. 2008; see above), *M. tridactyla* populations grow slowly, are they are currently being killed at a much higher rate than can be replenished through natural breeding efforts, contributing to declining numbers and a reduced gene pool in the smaller remnant populations. Population bottlenecks, created primarily through habitat destruction, may eventually lead to a reduction in evolutionary potential. Corridors connecting the fragmented populations and preventing bottlenecks are critical in insuring that genetic variability is maintained (Rodrigues et al. 2008).

Scientific conservation efforts are led by the IUCN/SSC Edentate Specialist Group whose primary mission is the preservation of *M. tridactyla* and all other xenarthran species. They provide grants for short-term field projects with a conservation emphasis and produce the open access journal Edentata, which is available to publish the findings of these field projects (IUCN/SSC Anteater, Sloth and Armadillo Specialist Group 2012).

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