

## *Bradypus tridactylus* (Pilosa: Bradypodidae)

VIRGINIA HAYSSEN

Department of Biology, Smith College, Northampton, MA 01063, USA; vhayssen@email.smith.edu

**Abstract:** *Bradypus tridactylus* Linnaeus, 1758, is commonly called the pale-throated sloth. Males have a middorsal speculum. *B. tridactylus* is endemic to rain forests of northeastern South America. Like other sloths, *B. tridactylus* is a high-canopy folivore. It has a commensal relationship with the algae and invertebrates that live in its abundant pelage. It is listed as “Least Concern” by the International Union for Conservation of Nature and Natural Resources because of its distribution in pristine areas of the Amazon Basin. It does not adapt to zoo settings. DOI: 10.1644/839.1.

**Key words:** commensal, Edentata, edentate, folivory, sloth, South America, Xenarthra

Published 27 July 2009 by the American Society of Mammalogists  
Synonymy completed 22 September 2008

www.mammalogy.org



### *Bradypus tridactylus* Linnaeus, 1758 Pale-throated Sloth

[*Bradypus*] *tridactylus* Linnaeus, 1758:34. Type locality “Americae meridionalis arboribus;” restricted to “Surinam” by Thomas 1911:132.

[*Ignavus*] *tridactylus*: Blumenbach, 1779:71. Name combination.

*Acheus ai* Lesson, 1827:306. Type localities “Brésil, à Cayenne, à la Nouvelle-Espagne, dans toute l’Amérique intertropicale.”

*Bradypus cuculliger* Wagler, 1831:column 605. Type localities “Surinamo, Cayenna et Guiana.”

[*Bradypus* (Acheus)] *cummunis* Lesson, 1840:268. Type locality “Le Brésil.”

[*Bradypus*] *tridactylus* (*Guianensis*) de Blainville, 1840:figs. 3, 4, 6. Type locality unknown.

*Bradypus gularis* Rüppell, 1842:138. Type locality “die Wälder von Guiana.”

*Arctopithecus gularis*: Gray, 1850:70. Name combination.

*Arctopithecus Blainvillii* Gray, 1850:71. Type locality “Tropical America;” restricted to Brazil by O. Thomas (1917:354).

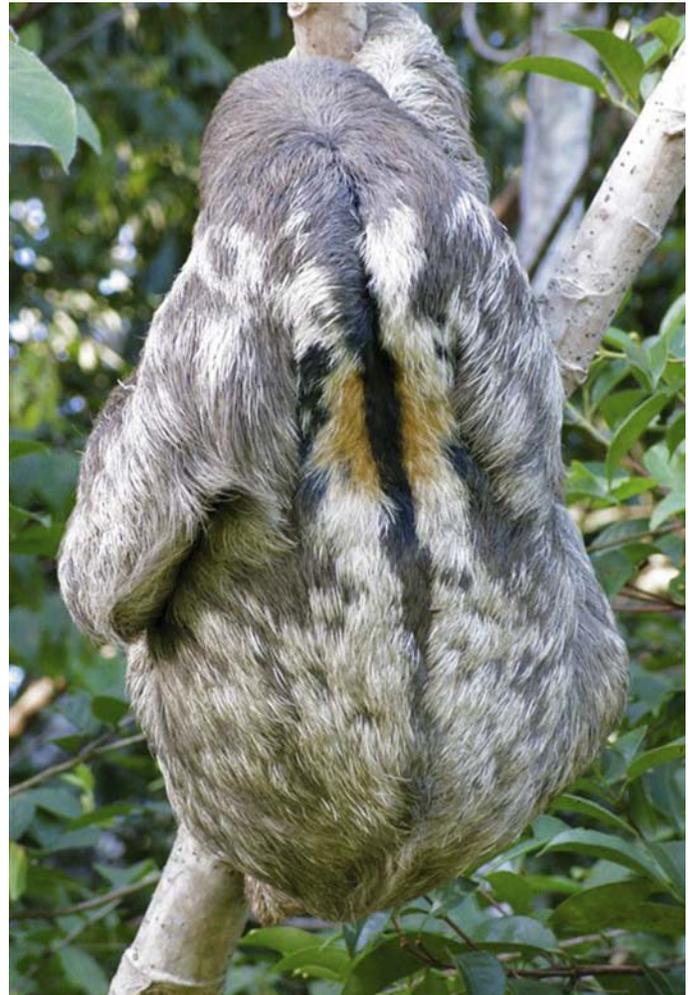
*Arctopithecus flaccidus* Gray, 1850:72. Type locality “Venezuela.”

[*Arctopithecus flaccidus*] Var. 1. *Dysonii* Gray, 1869:365. Type locality “Venezuela.”

[*Arctopithecus flaccidus*] Var. 2. *Smithii* Gray, 1869:365. Type locality “Para” = Pará, Brazil.

*Arctopithecus blainvillei* Gray, 1871:439. Incorrect subsequent spelling of *blainvillii* Gray, 1850.

*Arctopithecus cuculliger*: Gray, 1871:440. Name combination.



**Fig. 1.**—Adult male *Bradypus tridactylus* from Suriname showing the sex-specific dorsal speculum. Used with permission of the photographer M. Pool.

- [*Bradypus tridactylus*] Var. *Blainvillei*: Trouessart, 1898:1095. Name combination.
- [*Bradypus tridactylus*] Var. *flaccidus*: Trouessart, 1898:1096. Name combination.
- Bradypus didactylus* Elliot Smith, 1899:296, fig. 11. Incorrect subsequent spelling of *tridactylus*.
- Bradypus flaccidus*: Krumbiegel, 1941:55. Name combination.
- Bradypus flaccions* Sanderson, 1949:783. Incorrect subsequent spelling of *flaccidus* Gray, 1850.
- Arctopithecus blainvillii* Cabrera, 1958:208. Incorrect subsequent spelling of *blainvillii* Gray, 1850.
- Bradypus* [(*Bradypus*)] *infuscatus flaccidus*: Cabrera, 1958:209. Name combination.
- Bradypus tlaccidus* Convention on International Trade in Endangered Species of Wild Fauna and Flora, 1987:appendix II. Incorrect subsequent spelling of *flaccidus* Gray, 1850.

CONTEXT AND CONTENT. Order Pilosa, suborder Folivora, family Bradypodidae. *B. tridactylus* is monotypic. Synonymy is modified from Gardner (2005, 2007).

NOMENCLATURE NOTES. The generic name, *Bradypus*, is from the Greek for slow-footed. The species name, *tridactylus*, refers to the 3 claws present on both the forefeet and hind feet. Common names include ai-ai and preguiça de bentinho (Wetzel and de Avila-Pires 1980), yellow-throated ai (Gray 1871), and son-loiri (Sanderson 1949). Some researchers incorrectly referred to *Bradypus variegatus* as *Bradypus tridactylus*, but *B. variegatus* has a much wider distribution (Hayssen 2009). Thus, much literature that reportedly describes *B. tridactylus* actually pertains to *B. variegatus*. For instance, the National Center for Biotechnology Information ([www.ncbi.nlm.nih.gov/](http://www.ncbi.nlm.nih.gov/)) provides a gateway to genetic and other molecular sequences but does not include geographic information; thus, sequences attributed to *B. tridactylus* may actually be for *B. variegatus* and cannot be used.

## DIAGNOSIS

*Bradypus tridactylus* is sympatric with both two-toed sloths *Choloepus didactylus* and *C. hoffmanni*. *B. tridactylus* has 3 digits on the manus that are partially fused and hairy volar pads, whereas both *Choloepus* have only 2 unfused digits and hairless volar pads (Mendel 1985; Pocock 1924). *B. tridactylus* has 8 or 9 cervical vertebrae compared with 6 in *Choloepus hoffmanni* (Mendel 1985). Compared with *B. variegatus*, *B. tridactylus* has a yellow throat (that of *B. variegatus* is brown) and distinct foramina in the anterodorsal nasopharynx (lacking in *B. variegatus*—Wetzel and Avila-Pires 1980); however, the 2 species are difficult to distinguish in the field.

## GENERAL CHARACTERS

Adults are blackish with close, large, black spots on shoulders, back, and haunches and have a yellow head and throat (Gray 1871). Males have a dorsal orange-yellow patch with a broad, tapering, black central streak and a black spot (Fig. 1; Gray 1871). Juveniles are grayer than adults (Gray 1871).

Males are smaller than females (Beebe 1926). External measurements (mm) for 500 adults (*SD*, range) from French Guiana were: length of head and body, 548 (42, 450–755); length of tail, 59 (11, 22–110); shoulder height, 457 (31, 300–540); length of hind foot, 91 (7, 40–116); length of head, 84 (11, 60–150); length of ear, 13 (3, 5–21); mass (kg), 4.62 (0.59, 3.42–6.50—Richard-Hansen et al. 1999). In French Guiana, length of head and body of females is 8 mm longer than that of males, whereas shoulder height in males is 5 mm longer than in females (Richard-Hansen et al. 1999). In Suriname, external measurements (mm) for 2 males and 3 females, respectively, were: total length, 475, 555; length of tail, 65, 51; length of hind foot, 83, 75; length of ear, 17, 19; mass (g) 3,233, 2,949 (Sanderson 1949). External measurements (mm) of males and females, respectively, from Suriname at Naturalis (Leiden) were (mean, *SD*, range, *n*): length of head and body, 508.1, 33.03, 445–550, 9; 527.4, 17.92, 505–550, 7; length of tail, 48.4, 9.40, 39–65, 9; 44.3, 10.55, 31–65, 7; length of hind foot (without nail), 100.4, 11.13, 90–120, 8; 102.1, 5.64, 95–108, 7; mass (g), 3,925.0, 913.4, 3,250–6,000, 8; 4,164.3, 565.47, 3,750–4,500, 7.

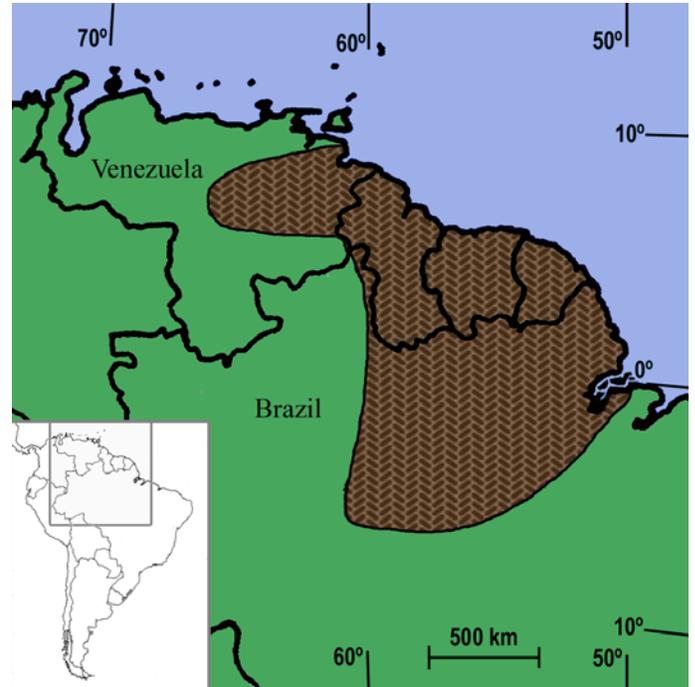
Average cranial (Fig. 2) measurements (*SE*, range, mm, as illustrated by Anderson and Handley [2001]) for 5 adults of mixed sex (from the United States National Museum) were: greatest length of skull, 72.59 (2.87, 69.88–76.84); anterior zygomatic breadth, 44.59 (1.63, 42.89–47.30); posterior zygomatic breadth, 40.28 (1.63, 37.54–41.86); postorbital breadth, 23.59 (0.94, 22.01–24.51); length of squamosal process, 25.61 (0.577, 24.93–26.53); breadth of squamosal process, 5.54 (0.544, 4.57–5.84); length of maxillary toothrow, 23.75 (1.37, 22.29–25.92); postpalatal length, 36.69 (1.965, 34.46–38.60); palatal breadth, 16.92 (0.887, 16.08–18.40); depth of braincase, 31.52 (1.795, 29.64–33.75); breadth of antorbital bar, 4.32 (0.693, 3.42–5.30); length of descending jugal process, 17.58 (2.10, 14.46–20.31); diameter of external auditory meatus, 5.16 (0.435, 4.72–5.66); breadth of ascending mandibular ramus, 15.66 (1.534, 13.70–17.06).

## DISTRIBUTION

*Bradypus tridactylus* lives in the northern Neotropics in Venezuela, Guyana, Suriname, French Guiana (Guyane), and northeastern Brazil (Fig. 3; Wetzel and Avila-Pires 1980) from the delta of the Orinoco River to the Amazon River along both banks of the Amazon from the Negro



**Fig. 2.**—Dorsal, ventral, and lateral views of skull (with atlas attached) and lateral view of mandible of an adult female *Bradypus tridactylus* (United States National Museum 362241) from the upper Takutu River region of Guyana. Greatest length of skull is 69.96 mm.



**Fig. 3.**—Geographic distribution (brown, hatched) of *Bradypus tridactylus* in Venezuela, Guyana, Suriname, French Guiana (Guyane), and northeastern Brazil (modified from Gardner 2007).

River to the mouth (Wetzel 1982). No fossils are known (Patterson and Pascual 1968).

### FORM AND FUNCTION

Pelage color of *Bradypus tridactylus* provides good camouflage (Sanderson 1949). The fur has long guard hairs and a fine, wavy undercoat (Beebe 1926). “The long hairs are flattened to an oval or almost a ribbon, presenting very distinctly broad and narrow sides. The longer, white hairs are more than twice as wide as they are deep averaging .25 by .11 millimeter. ... The hair as a whole grows very closely together from small tufts, closely resembling the down of nestling birds. These are .2 to .6 of a millimeter apart, and each clump consists of six to twenty separate hairs. ... The relative average lengths of the short and long hairs are twenty five and fifty millimeters ... between the eye and ear the hair is thirteen millimeters long, while its maximum length is on the nuchal cape, and on the upper arm, where it may reach one hundred millimeters” (Beebe 1926:28–29). Hairs of *B. tridactylus* have neither a medulla nor pigment granules (Aiello 1985). Individual hairs have moderate transverse cracking (Aiello 1985). Algae colonize the outer hair but not the underfur (Aiello 1985). Alga occur between the cuticular scales (Aiello 1985). The surface of the hair becomes mucilaginous and sticky when wet (Aiello 1985).

Vertebral formula for *Bradypus tridactylus* is 9 C, 16 T, 3 L, 6 S, 11 Ca, total 45 (Narita and Kuratani 2005). The dorsal–ventral flexibility of the head and neck is 270°; the lateral flexibility is 330°. Forelimbs are more flexible than hind limbs. The body can curl forward into a ball but a back bend is not possible. The tail is mobile up through its tip (Beebe 1926). The myology of the limbs has been detailed (Humphry 1870).

Eyes are set about 30 mm apart and look forward (Piggins and Muntz 1985). One eyeball was 14 mm in diameter (Beebe 1926). Eye movements were not observed but blinking was. Eyes are of moderate size with a wide, convex cornea and a rounded, crystalline lens. Irises are medium brown and centrally located; they contract to a pinhole pupil under daylight conditions and the pupil is circular as it contracts. The horizontal monocular fields were 70° with a binocular overlap of 35°. The retina has only rods (Piggins and Muntz 1985). Pinna are small, circular, and buried in fur (Beebe 1926). The hyoid is dissected from the ear with difficulty (Beebe 1926). *B. tridactylus* has acute hearing (Hoke 1987). Smell is used during locomotion to detect rotten branches (Beebe 1926). Details of ocular anatomy, retinal histology (Piggins and Muntz 1985), ear region (Patterson et al. 1992), encephalon (Pouchet 1869), and telencephalon (as *B. tridactylus*—Anthony 1953) are available.

The oral cavity is adapted for folivory (Beebe 1926). The lips are thick, leathery, with low tubercles as well as 2 larger projections that hold leaves in place while foraging. The tongue is large (11 by 35 mm), thick, soft, with deep longitudinal furrows, shallow transverse grooves, minute, backward-directed spines (25/mm<sup>2</sup>—Beebe 1926), and 2 vallate papillae (Sonntag 1923). The palate is rugose. The oral cavity except the tongue is black. Each upper jaw has 5 teeth: 4 molarlike and 1 peglike anterior tooth. The anterior teeth are separated by an 8-mm gap. Each lower jaw has 4 molarlike cheek teeth (Beebe 1926).

The esophagus is small and short but the stomach is large (100 by 120 mm; 60 mm thick) and complex (Beebe 1926). A detailed description of the anatomy of the complex stomach is available in German (Klinkowström 1895). A large cecal diverticulum is present. The small intestine is 1,925–3,825 mm long, and the large intestine is 80–120 mm long ( $n = 2$ ). The trilobed liver is small (55 by 75 mm or 80 by 90 mm; 20–25 mm thick) with closely united lobes (Beebe 1926).

Gut contents of 6 individuals were 17–37% of body mass; rate of fermentation was 6–12 mmol l<sup>-1</sup> h<sup>-1</sup>; and mean retention time for particle and liquid markers was 147–152 h (Foley et al. 1995). Dung pellets are small, dense, angular or ovoid, and about 8–12 mm in diameter (Waage and Best 1985). About a cup of pellets is defecated in a pile (Waage and Best 1985). The bladder can be up to 120 mm in diameter (Beebe 1926).

Lungs of an adult female were 85 mm long, the larynx was 55 mm long, and the recurved tracheal loop was 36 mm long (Beebe 1926). Respiration is irregular; after swimming about 30 m, one animal exhaled 25 times in 25 s (Beebe 1926).

A small clitoris is present; the vagina is duplex (Klinkowström 1895). The simplex uterus is pear shaped (Benirschke and Powell 1985). Fallopian tubes of 1 pregnant female were 7.5 cm long, and ovaries were located in a 8-by-3-cm bursa (Benirschke 2008). One pregnant uterus was 12 by 5 cm (Benirschke and Powell 1985). An 11-by-7-cm (greatest diameters), fundally implanted, near-term placenta was 60 g with about 20 nodular discs held in place by membranes and fetal vessels (Benirschke 2008; Benirschke and Powell 1985). The amnion lacks nodules and is firmly attached to the chorion (Benirschke and Powell 1985). An umbilical cord from a near-term pregnancy was 15 cm long, was diffusely keratinized, and had 2 arteries and 1 vein (Benirschke and Powell 1985). Histological images of the placenta have been published (Benirschke and Powell 1985). Males, attributed to *B. tridactylus*, have rudimentary seminal vesicles, a disseminate prostate gland, and a pair of bulbourethral glands (Klinkowström 1895 in Engle 1926). Testes are abdominal (Klinkowström 1895).

The early literature contains extensive details and illustrations of hair (Sonntag and Duncan 1922), musculature (Zieger 1925), muscles of the limbs including forefeet and hind feet (Jouffroy et al. 1961; Miller 1935; Vassal et al. 1962), digestive tract including histological sections (Sonntag 1921; Sonntag and Duncan 1922), brachial plexus (Harris 1939), and brain (Elliot Smith 1899). This literature is primarily from animals attributed to *B. tridactylus*, but which may actually be *B. variegatus*. The source of the animals is unclear because most were transported from locations unknown to the scientist.

*Bradypus tridactylus* is somewhat poikilothermic (Kredel 1928). Two animals reported as *B. tridactylus* had normal clinging and climbing locomotion after removal of their cerebellum (Murphy and O’Leary 1973).

## ONTOGENY AND REPRODUCTION

Litter size is 1 (Beebe 1926). Two reports of gestation length are divergent: 106 days (Hoke 1987) and 6 months (Taube et al. 2001). In French Guiana, pregnant females were found in March–September (Richard-Hansen and Taube 1997) or January–April (Taube et al. 2001). In Guyana, mating occurs in March and April and 10 births occurred in July–September (Beebe 1926). In Suriname, a pregnant female was collected in March (Naturalis 10460, Leiden). Lactating and nonlactating females do not differ in body mass (Taube et al. 2001). Lactating females are found April–September in French Guiana (Taube et al. 2001). Females can gestate and lactate simultaneously (Taube et al.

2001). First solid food is licked from the mother's lips at 3 weeks, and leaves are 1st eaten at 5 weeks (Beebe 1926). Lactation continues for  $\geq 1$  month (Beebe 1926). Physical characteristics of semen, but not the morphology of spermatozoa, differ in wet and dry seasons (Peres et al. 2008).

Late-term embryos are nearly identical to neonatal sloths up to 1 or 2 weeks old (Beebe 1926; de Beaux 1931). "The hairs are very soft and fine, even softer than in the adult. As to length, on the top of the head the length is 23 mm, at the elbow 30, on the midbreast 26, on the knee 23, and on the midback 30 mm. With the exception of the nostrils, the sub-nasal lip area and a narrow line down the sole, from claw base to heel, every part of body and limbs is clothed densely with hair" (Beebe 1926:45). Adrenals of a near-term fetus had a large cortex (Benirschke and Powell 1985). A full-grown male fetus was 185 g in mass and 27 cm from snout to tail (Benirschke and Powell 1985). Newborns have fur and open eyes; they cling to their mothers immediately (Hoke 1987; Sanderson 1949). "The normal position of the infant after birth is flat upon the mother's ventral body, with limbs wide-spread sideways, gripping her long hair on the sides of the body. From this point of vantage, by a turn and twist of his mobile neck, he can reach either breast, the glands being placed high up and well to each side of the middle line. ... On the sixth or seventh day the young sloth begins a series of gymnastics, by freeing one or both his front limbs and leaning backward, sometimes completely reversed or also stretching far to one side ... often hanging with his head dangling far out between the mother's knees and body" (Beebe 1926:46). Young will take chewed food from their mother's mouth at about 3 weeks (Beebe 1926). The following measurements are from a 4-week-old male: diameter of eyeball, 8 mm; weight of skin, 75 g; weight of skinned body, 235 g; total weight, 310 g; tongue 23 by 10 mm; a square millimeter of tongue contained 72 "teeth" for a total of about 17,500 on the entire tongue; heart, 21 by 44 mm; 8 teeth per jaw (the 2 upper anterior teeth not functional); lungs, 31 mm wide by 13 mm thick by 25 mm long anteriorly and 44 mm long posteriorly; larynx, 35 mm behind snout with 2 concave cartilages against the roof of the mouth; trachea, 95 mm long with about 100 tracheal rings 3 mm in diameter; bladder (diameter, 33 mm; length, 55 mm) fills the lower half of the coelom; large intestine, 35 mm long; small intestine 800 mm long and 5 mm in diameter; liver, trilobed and 43 mm long by 33 mm wide by 12 mm thick; and kidneys, 18 by 13 mm (Beebe 1926). Head-body length versus body mass data were plotted for 500 animals up to 7 kg; head-body length (20–55 mm) curves convexly downward from 0 to 3.5 kg, then slowly increases to 65–70 mm with animals up to 7 kg (Richard-Hansen et al. 1999). Sexual maturity is at about 3 years for both sexes (Taube et al. 2001).

Young seldom leave their mother's ventrum during the 1st month or so of their lives, after which the infant will crawl all over her body (Beebe 1926). Play has been observed (Beebe 1926). Young have long, soft, flaccid, gray-brown fur with a mottled whitish dorsum, a yellowish face and throat, a black eye-streak, and a black circumference around head and neck (Gray 1871).

## ECOLOGY

In French Guiana, density of *Bradypus tridactylus* was 1.7 individuals/km<sup>2</sup> and the species is sympatric with *Choloepus didactylus* (Taube et al. 1999). In Guyana, density was 31 individuals/km<sup>2</sup> (Beebe 1926). In Suriname, *B. tridactylus* accounts for 14.7% of the nonvolant, terrestrial, mammalian biomass (Walsh and Gannon 1967 in Eisenberg and Thorington 1973:table 1). *B. tridactylus* is sympatric with *B. variegatus* along both banks of the Amazon River from the Río Negro to the Río Tapajós and along the left bank to the mouth of the Amazon (Wetzel and Avila-Pires 1980). In Manaus, Brazil, sex ratio of *B. tridactylus* was 1:1 (Jorge et al. 1985). *B. tridactylus* readily eats leaves of *Cecropia* (Cecropiaceae), *Ceiba summa* (Bombacaceae), *Elizabetha paraense* (Leguminosae), and *Hevea viridis* (Euphorbiaceae—Carvalho 1960).

Endoparasites include *Endotrypanum schaudini* (from 1 of 23 animals—Shaw 1985). *Trypanosoma rangeli* occurred in a wild animal (Dereure et al. 2001) as did an unidentified *Trypanosoma* (Miles et al. 1983). The internal parasite *Pneumocystis carinii* occurred in a captive animal reported to be *B. tridactylus* (Lainson and Shaw 1975; Poelma 1975). External parasites include ticks (*Amblyomma geayi* [Waage and Best 1985] and *Amblyomma varium* [Marques et al. 2002]), mites (*Edentalges bradypus*, *Lobalges trouessarti*, and *Psoralges andrei* [Fain 1965]), mosquitoes (*Aedes serratus* [Pinheiro et al. 1962]), and Acaridada (Waage and Best 1985). In Manaus, most (99%) of *B. tridactylus* were infested with an average of 33 ticks/individual (females, 32.9 ticks/individual and males, 34.7 ticks/individual—Waage and Best 1985).

*Bradypus tridactylus* has a commensal relationship with sloth moths (*Cryptosis choloepi* [Hoke 1987], *Bradypodicola hahneli*, *C. rufipictus*, and *C. waagei* [Sanderson 1949; Waage and Best 1985]). Sloth moths inhabit the fur of *B. tridactylus* and their larvae feed on dung. Trace elements for *B. tridactylus* are obtained by incidental ingestion of cecropia ants (*Azteca*—Hoke 1987). The beetle *Trichillum adisi* resides near elbows and knees deep within the fur, and larval stages are found within dung pellets (Waage and Best 1985). Other beetles (*Uroxys batesi* and *U. besti*) also occur in the fur (Waage and Best 1985). The mites *Macrocheles impae* and *M. uroxys* are part of a complex commensal relationship between mites, dung beetles, and *B. tridactylus* (Waage and Best 1985).



**Fig. 4.**—Adult female in typical arboreal habitat in Suriname showing the ability to turn the head 180°. Used with permission of the photographer M. Pool.

*Bradypus tridactylus* is vulnerable to cats (jaguar [*Panthera onca*] and margay [*Leopardus wiedii*]), snakes (anaconda [*Eunectes*]), and harpy eagles (*Harpia harpyja*)—Beebe 1926; Hoke 1987; Izor 1985). *B. tridactylus* is difficult to keep in captivity except where the animal is endemic (Hoke 1987). They succumb to viral infections and trace element deficiencies (Hoke 1987). Electroejaculation has been successful (Peres et al. 2008).

## BEHAVIOR

*Bradypus tridactylus* is not active; 1 animal slept an average of 18.5 h/day (Beebe 1926). The crook of a tree is the preferred sleeping location. The preferred sleeping posture is to sit on the horizontal branch, hold the vertical stem with the rear limbs, curl the head and neck flat on the breast, and curl both forelimbs around the head and body (Beebe 1926). *B. tridactylus* suns itself, stretched out, on top of canopy vegetation (Hoke 1987). It readily swims, with propulsion coming mainly from the forefeet. When swimming, three-fourths of its head and much of its dorsum are out of the water. When foraging, *B. tridactylus* suspends itself beneath branches hanging by its claws. It can

straighten its claws (Beebe 1926), but claws remain flexed in death (Beebe 1926).

*Bradypus tridactylus* is predominantly solitary (Beebe 1926; Hoke 1987; Taube et al. 1999). Aggression occurs between members of the same sex and is predominantly striking with claws and rarely by biting (Beebe 1926).

An observed mating sequence was arboreal, with 3 copulations of 1.5–3 min, and mating occurred either face-to-face or with the male on the female's back (Richard-Hansen and Taube 1997). An observed birth included the mother pulling the neonate from her vagina, severing the umbilical cord with her claws, and grooming and massaging the neonate (Sanderson 1949). A dependent young (3–4 months old) remained on the female's venter during the sequence (Richard-Hansen and Taube 1997).

*Bradypus tridactylus* is curious and will explore minutia in its surroundings (Hoke 1987). It learns the spatial location of, for example, food and nest trees quickly but these engrams are lost if the animal is moved (Beebe 1926). While foraging, leaves are hooked by the claws and brought to the mouth or the head is moved directly to the leaves. Chewing is continuous with 1–2 bites/s; swallowing does not interrupt chewing. During chewing the bite is direct with no lateral movement of the jaws. Leaf tissue is moved by forward and back movements of the tongue (Beebe 1926). Foraging may occur at any time of day but is more frequent morning and afternoon (Beebe 1926).

Predator defense includes the animal staying very still and letting its well-camouflaged, alga-rich fur hide the animal among arboreal vegetation (Hoke 1987). *B. tridactylus* also lives most of its life high in the canopy (Fig. 4) often on small-branched trees and moves very slowly (Beebe 1926). They are aided by their tough skin and broad ribs (Beebe 1926). Behavioral defenses are not effective against most predators (Beebe 1926). If the weather is dry, *B. tridactylus* defecates on the ground using its tail to dig a hole. Defecation is from above during rain (Hoke 1987).

The sole documented vocalization is a whistle represented as “ai” or “ai-ai.” This whistle is described as bird- or cicadalike and ventriloquial (Beebe 1926; Hoke 1987).

## GENETICS

*Bradypus tridactylus* has a diploid number (2n) of 52 chromosomes with 5 metacentric pairs, including X and Y, and 21 acrocentric pairs generating a fundamental number (FN) of 56 (Dobigny et al. 2005; Jorge et al. 1985; Jorge and Pereira 2008). C- and G-banded karyotypes have been illustrated (Dobigny et al. 2005). A 1,200+-base pair sequence of exon 28 of the von Willebrand factor gene has been sequenced (attributed to *B. tridactylus*—Porter et al. 1996), as has the  $\alpha$ A-crystallin of a putative *B. tridactylus* (Van Dijk et al. 1999). The 16S mitochondrial DNA from 3

*B. variegatus* and 1 *B. tridactylus* estimates a split between the lineages 0.4 million years ago (Barros et al. 2003).

## CONSERVATION

*Bradypus tridactylus* is listed as Least Concern by the International Union for Conservation of Nature and Natural Resources (2008) because of its distribution in pristine areas of the Amazon Basin, where it is locally abundant (Aguilar and da Fonseca 2008; Arita et al. 1990; Chiarello et al. 2006).

## ACKNOWLEDGMENTS

A. Keller provided bibliographic support for this monograph. T. Plese and M. Superina were instrumental in finding an image of the animal. H. van Grouw facilitated use of the Naturalis collection (Nationaal Natuurhistorisch Museum, Leiden, Netherlands). D. Fish and T. J. Leach photographed the skull. A. Ward created the map. Funding was from the Blakeslee Grant for Genetics Research at Smith College.

## LITERATURE CITED

- AGUIAR, J. M., AND G. A. B. DA FONSECA. 2008. Conservation status of the Xenarthra. Pp. 215–231 in *The biology of the Xenarthra* (S. F. Vizcaíno and W. J. Loughry, eds.). University Press of Florida, Gainesville.
- AIELLO, A. 1985. Sloth hair: unanswered questions. Pp. 213–218 in *The evolution and ecology of armadillos, sloths, and vermilinguas* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- ANDERSON, R. P., AND C. O. HANDLEY, JR. 2001. A new species of three-toed sloth (Mammalia: Xenarthra) from Panamá, with a review of *Bradypus*. *Proceedings of the Biological Society of Washington* 114:1–33.
- ANTHONY, J. 1953. Morphologie externe du telencéphale dans le genre *Bradypus* L. (Edentata). *Mammalia* 17:149–163.
- ARITA, H. T., J. G. ROBINSON, AND K. H. REDFORD. 1990. Rarity in neotropical forest mammals and its ecological correlates. *Conservation Biology* 4:181–192.
- BARROS, M. C., I. SAMPAIO, AND H. SCHNEIDER. 2003. Phylogenetic analysis of 16S mitochondrial DNA data in sloths and anteaters. *Genetics and Molecular Biology* 26:5–11.
- BEEBE, W. 1926. The three-toed sloth (*Bradypus cuculliger cuculliger* Wagler). *Zoologica* 7:1–67.
- BENIRSCHKE, K. 2008. Reproductive parameters and placentation in anteaters and sloths. Pp. 160–171 in *The biology of the Xenarthra* (S. F. Vizcaíno and W. J. Loughry, eds.). University Press of Florida, Gainesville.
- BENIRSCHKE, K., AND H. C. POWELL. 1985. Sloth hair: unanswered questions. Pp. 237–241 in *The evolution and ecology of armadillos, sloths, and vermilinguas* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- BLUMENBACH, J. F. 1779. *Handbuch der Naturgeschichte*. Johann Christian Dieterich, Göttingen, Germany.
- CABRERA, A. 1958. Catalogo de los mamíferos de America del Sur. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,”* Buenos Aires, Argentina.
- CARVALHO, C. T. 1960. Notes on the three-toed sloth, *Bradypus tridactylus*. *Mammalia* 24:155–156.
- CHIARELLO, A., AND MEMBERS OF THE EDENTATE SPECIALIST GROUP. 2006. *Bradypus tridactylus*. 2006 International Union for Conservation of Nature and Natural Resources Red list of threatened species. [www.iucnredlist.org](http://www.iucnredlist.org), accessed 12 March 2007.
- CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA. 1987. Appendix II. *Bradypus variegatus*. [www.cites.org](http://www.cites.org), accessed 20 April 2008.
- DE BEAUX, O. 1931. Studi sui neonati dei mammiferi. Il neonato di *Bradypus tridactylus*, L. *Archivo Zoologico Italiano* 15:35–82.
- DE BLAINVILLE, M. H. M. D. 1840. *Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d’animaux vertébrés récents et fossiles pour servir de base a la zoologie et a la géologie. Mammifères.—Paresseux.—G. Bradypus*. Arthus Bertrand, Part 4 (fasciculus 5, atlas [fasciculus 4]), Arthus Bertrand, Paris, France.
- DEREURE, J., C. BARNABÉ, J.-V. VIÉ, F. MADÉLENAT, AND C. RACCURT. 2001. Trypanosomatidae from wild mammals in the neotropical rainforest of French Guiana. *Annals of Tropical Medicine and Parasitology* 95:157–166.
- DOBIGNY, G., ET AL. 2005. Low rate of genomic repatterning in *Xenarthra* inferred from chromosome painting data. *Chromosome Research* 13:651–663.
- DUNCAN, F. M. 1937. On the dates of publications of the Society’s ‘Proceedings,’ 1859–1926. With an appendix containing the dates of publication of ‘Proceedings,’ 1830–1858, compiled by the late F. H. Waterhouse, and of the ‘Transactions,’ 1833–1869, by the late Henry Peavot, originally published in P. Z. S. 1893, 1913. *Proceedings of the Zoological Society of London* 107, Series A, General, 71–84.
- EISENBERG, J. F., AND R. W. THORINGTON, JR. 1973. A preliminary analysis of a neotropical mammal fauna. *Biotropica* 5:150–161.
- ELLIOT SMITH, G. 1899. The brain in the Edentata. *Transactions of the Linnean Society of London, Second Series, Zoology* 7(7):277–394.
- ENGLE, E. T. 1926. The copulation plug and the accessory genital glands of mammals. *Journal of Mammalogy* 7:119–126.
- FAIN, A. 1965. Les acariens producteurs de gale chez les edentes et les marsupiaux (Psoroptidae et Lobalgidae: Sarcoptiformes). *Bulletin Institute Royal Sciences Naturelles de Belgique* 41:1–41.
- FOLEY, W. J., W. V. ENGELHARDT, AND P. CHARLES-DOMINIQUE. 1995. The passage of digesta, particle size, and in vitro fermentation rate in the three-toed sloth *Bradypus tridactylus* (Edentata: Bradypodidae). *Journal of Zoology (London)* 236:681–696.
- GARDNER, A. L. 2005. Order Pilosa. Pp. 100–103 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- GARDNER, A. L. 2007. Order Pilosa. Pp. 157–177 in *Mammals of South America. Vol. 1. Marsupials, xenarthrans, shrews, and bats*. University of Chicago Press, Chicago, Illinois.
- GRAY, J. E. 1850. On the genus *Bradypus* of Linnaeus. *Proceedings of the Zoological Society of London* 1849:64–73. [Dated 1849 but published 1850, see Duncan (1937) for dates of publications for the *Proceedings*.]
- GRAY, J. E. 1869. Catalogue of carnivorous, pachydermatous, and edentate mammals in the British Museum. *British Museum (Natural History) Publications*, London, United Kingdom.
- GRAY, J. E. 1871. Notes on the species of Bradypodidae in the British Museum. *Proceedings of the Zoological Society of London* 1871: 428–449.
- HARRIS, W. 1939. *The morphology of the brachial plexus*. Oxford University Press, London, United Kingdom.
- HAYSEN, V. 2009. *Bradypus torquatus* (Pilosa: Bradypodidae). *Mammalian Species* 829:1–5.
- HOKE, J. 1987. Oh, it’s so nice to have a sloth around the house. *Smithsonian Magazine* April, 88–98.
- HUMPHRY, G. M. 1870. The myology of the limbs of the unau, the ai, the two-toed anteater, and the pangolin. *Journal of Anatomy and Physiology* 4:17–78.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 2008. 2008 IUCN Red list of threatened species. [www.iucnredlist.org](http://www.iucnredlist.org), accessed 1 January 2009.
- IZOR, R. J. 1985. Sloths and other mammalian prey of the harpy eagle. Pp. 343–346 in *The evolution and ecology of armadillos, sloths,*

- and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- JORGE, W., A. T. ORSI-SOUZA, AND R. BEST. 1985. The somatic chromosomes of *Xenarthra*. Pp. 121–129 in *The evolution and ecology of armadillos, sloths, and vermilinguas* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- JORGE, W., AND H. R. J. PEREIRA, JR. 2008. Chromosomal studies in the *Xenarthra*. Pp. 196–204 in *The biology of the Xenarthra* (S. F. Vizcaino and W. J. Loughry, eds.). University Press of Florida, Gainesville.
- JOUFFROY, F.-K., J. LESSERTISSEUR, AND P. VASSAL. 1961. Particularités musculaires des extrémités du bradype ai (*Bradypus tridactylus* L.) dans leurs rapports avec la suspension arboricole. *Comptes Rendus de l'Association des Anatomistes* 47:392–400.
- KLINKOWSTRÖM, A. 1895. Zur Anatomie der Edentaten. I. Beiträge zur Anatomie des Magens der Edentaten. II. Beiträge zur vergleichenden Anatomie der Geschlechtsorgane der Edentaten. *Zoologische Jahrbücher, Anatomie Abtheilung* 8:481–519.
- KREDEL, F. E. 1928. Note on the temperature of the sloth. *Journal of Mammalogy* 9:48–51.
- KRUMBIEGEL, I. 1941. Die Säugetiere der Südamerika-Expeditionen Prof. Dr. Kriegs. 14 Faultiere. *Zoologischer Anzeiger* 136:53–62.
- LAINSON, R., AND J. J. SHAW. 1975. *Pneumocystis* and *Histoplasma* infections in wild animals from the Amazon region of Brazil. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 69:505–508.
- LESSON, R. P. 1827. *Manuel de mammalogie ou histoire naturelle des mammifères*. Roret, Paris, France.
- LESSON, R. P. 1840. *Species des mammifères bimanés et quadrumanes; suivie d'un mémoire sur les oryctéropes*. J. B. Baillière, Paris, France.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Vol. 1. Laurentii Salvii, Stockholm, Sweden.*
- MARQUES, S., D. M. BARROS-BATTESTI, J. L. H. FACCINI, AND V. C. ONOFRIO. 2002. Brazilian distribution of *Amblyomma varium* Koch, 1844 (Acari: Ixodidae), a common parasite of sloths (Mammalia: Xenarthra). *Memorias do Instituto Oswaldo Cruz, Rio de Janeiro* 97:1141–1146.
- MENDEL, F. C. 1985. Use of hands and feet of three-toed sloths (*Bradypus variegatus*) during climbing and terrestrial locomotion. *Journal of Mammalogy* 66:359–366.
- MILES, M. A., ET AL. 1983. Vertebrate hosts and vectors of *Trypanosoma rangeli* in the Amazon Basin of Brazil. *American Journal of Tropical Medicine and Hygiene* 32:1251–1259.
- MILLER, R. A. 1935. Functional adaptations in the forelimb of sloths. *Journal of Mammalogy* 16:38–51.
- MURPHY, M. G., AND J. L. O'LEARY. 1973. Hanging and climbing functions in raccoon and sloth after total cerebellectomy. *Archives of Neurology* 28:111–117.
- NARITA, Y., AND S. KURATANI. 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. *Journal of Experimental Zoology* 304B:91–106.
- PATTERSON, B., AND R. PASCUAL. 1968. The fossil mammal fauna of South America. *Quarterly Review of Biology* 43:409–451.
- PATTERSON, B., W. SEGALL, W. D. TURNBULL, AND T. J. GAUDIN. 1992. The ear region in xenarthrans (= Edentata, Mammalia). Part. II. Pilosa (sloths, anteaters), palaeonodons, and a miscellany. *Fieldiana: Geology (New Series)* 24:1–79.
- PERES, M. A., E. J. BENEITI, M. P. MILAZZOTTO, J. A. VISINTIN, M. A. MIGLINO, AND M. E. ASSUMPCÃO. 2008. Collection and evaluation of semen from the three-toed sloth (*Bradypus tridactylus*). *Tissue and Cell* 40:325–331.
- PIGGINS, D., AND W. R. A. MUNTZ. 1985. The eye of the three-toed sloth. Pp. 191–197 in *The evolution and ecology of armadillos, sloths, and vermilinguas* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- PINHEIRO, F., M. PINHEIRO, G. BENSABATH, O. R. CAUSEY, AND R. SHOPE. 1962. Epidemia de virus oropouche em Belém. *Revista de Servico Especial de Saude Publica* 12:15–23.
- POCOCK, R. I. 1924. The external characters of some South American edentates. *Proceedings of the Zoological Society of London* 1924: 983–1031.
- POELMA, F. G. 1975. *Pneumocystis carinii* infections in zoo animals. *Zentralblatt für Bakteriologie, Parasitenkunde, Infektionskrankheiten und Hygiene* 46:61–68.
- PORTER, C. A., M. GOODMAN, AND M. J. STANHOPE. 1996. Evidence on mammalian phylogeny from sequences of exon 28 of the von Willebrand factor gene. *Molecular Phylogenetics and Evolution* 5: 89–101.
- POUCHET, G. 1869. Mémoire sur l'encéphale des edentés. *Journal l'Anatomie et de la Physiologie Normales et Pathologiques de l'Homme et des Animaux* 6:1–18.
- RICHARD-HANSEN, C., AND E. TAUBE. 1997. Note on the reproductive behavior of the three-toed sloth, *Bradypus tridactylus*, in French Guiana. *Mammalia* 61:259–263.
- RICHARD-HANSEN, C., J.-C. VIÉ, N. VIDAL, AND J. KÉRAVEC. 1999. Body measurements on 40 species of mammals from French Guiana. *Journal of Zoology (London)* 247:419–428.
- RÜPPELL, E. 1842. Beschreibung mehrerer neuer Säugethiere, in der zoologischen Sammlung der Senckenbergischen naturforschenden Gesellschaft befindlich. *Museum Senckenbergianum* 1842 (1845) 3:129–144.
- SANDERSON, I. T. 1949. A brief review of the mammals of Suriname (Dutch Guiana), based upon a collection made in 1938. *Proceedings of the Zoological Society of London* 119:755–789.
- SHAW, J. J. 1985. The hemoflagellates of sloths, vermilinguas (anteaters), and armadillos. Pp. 279–292 in *The evolution and ecology of armadillos, sloths, and vermilinguas* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- SONNTAG, C. F. 1921. A contribution to the anatomy of the three-toed sloth (*Bradypus tridactylus*). *Proceedings of the Zoological Society of London* 1921:157–177.
- SONNTAG, C. F. 1923. The comparative anatomy of the tongues of the Mammalia. IX. Edentata, Dermoptera, and Insectivora. *Proceedings of the Zoological Society of London* 1923:515–529.
- SONNTAG, C. F., AND F. M. DUNCAN. 1922. Contributions to the histology of the three-toed sloth (*Bradypus tridactylus*). *Journal of the Royal Microscopical Society* 1:37–46.
- TAUBE, E., J. KÉRAVEC, J.-C. VIÉ, AND J.-M. DUPLANTIER. 2001. Reproductive biology and postnatal development in sloths, *Bradypus* and *Choloepus*: review with original data from the field (French Guiana) and from captivity. *Mammal Review* 31:173–188.
- TAUBE, E., J.-C. VIÉ, P. FOURNIER, AND C. GENTY. 1999. Distribution of two sympatric species of sloths (*Choloepus didactylus* and *Bradypus tridactylus*) along the Sinnamary River, French Guiana. *Biotropica* 31:686–691.
- THOMAS, O. 1911. The mammals of the tenth edition of Linnaeus; an attempt to fix the types of the genera and the exact bases and localities of the species. *Proceedings of the Zoological Society of London* 1911:120–158.
- THOMAS, O. 1917. Some notes on three-toed sloths. *Annals and Magazine of Natural History, Series 8* 19:352–357.
- TROUESSART, E. L. 1898. *Catalogus mammalium tam viventium quam fossilium. Fasciculus V. Sirenia, Cetacea, Edentata, Marsupialia, Allotheria, Monotremata*. R. Friedländer & Son, Berlin, Germany.
- VAN DIJK, M. A. M., E. PARADIS, F. CATZEFELIS, AND W. W. DE JONG. 1999. The virtues of gaps: xenarthran (edentate) monophyly supported by a unique deletion in  $\alpha$ A-crystallin. *Systematic Biology* 48:94–106.
- VASSAL, P. A., F. K. JOUFFROY, AND J. LESSERTISSEUR. 1962. Musculature de la main et du pied du paresseux ai (*Bradypus tridactylus* L.). *Folia Clinica et Biologica* 31:142–153.
- WAAGE, J. K., AND R. C. BEST. 1985. Arthropod associates of sloths. Pp. 297–311 in *The evolution and ecology of armadillos, sloths, and vermilinguas* (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.
- WAGLER, J. G. 1831. Mittheilungen über die Gattungen der Sippe *Bradypus*. *Isis von Oken* 24:columns 604–612.
- WALSH, J., AND R. GANNON. 1967. Time is short and the water rises. Thomas Nelson and Sons, Camden, New Jersey. (not seen, cited in Eisenberg and Thorington 1973)

- WETZEL, R. M. 1982. Systematics, distribution, ecology, and conservation of South American edentates. Pp. 345–375 in *Mammalian biology in South America* (M. A. Mares and H. H. Genoways, eds.). Special Publication Series of the Pymtuning Laboratory of Ecology, University of Pittsburgh 6:1–539.
- WETZEL, R. M., AND R. D. DE AVILA-PIRES. 1980. Identification and distribution of the Recent sloths of Brazil (Edentata). *Revista Brasileira de Biologia* 40:831–836.
- ZIEGER, K. 1925. Beiträge zur Kenntnis der Hautmuskulature der Säugetiere. I. Mitteilung: die Hauttrumpfmuskeln der Xenarthra. *Gegenbaurs Morphologisches Jahrbuch* 54:205–238.

Associate editors of this account were DAVID M. LESLIE, JR. and PAMELA OWEN. Editor was MEREDITH J. HAMILTON.