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Choloepus hoffmanni (Pilosa: Megalonychidae)

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Abstract: *Choloepus hoffmanni* Peters, 1858 (Hoffmann's two-toed sloth) is 1 of 2 extant two-toed sloths. A high-canopy folivore, *C. hoffmanni* has a disjunct range with a northern population in Central America and northern South America and a southern population in South America. *C. hoffmanni* is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources because of its wide distribution.

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

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Choloepus Illiger, 1811

Bradypus Linnaeus, 1758:34. Part.

Myrmecophaga Linnaeus, 1758:35. Part.

Choloepus Illiger, 1811:108. Type species *Bradypus didactylus* Linnaeus, 1758, by subsequent designation (Gray 1827:275).

Unaues Rafinesque, 1815:57. No type species mentioned; spelling corrected by Gardner and Naples (2007).

Unaus Gray, 1821:305. Type species *Bradypus didactylus* Linnaeus, 1758, by monotypy.

Cholaepus Schinz, 1821:328. Incorrect subsequent spelling of *Choloepus* Illiger, 1811.

Chaelopus Gray, 1827:275. Incorrect subsequent spelling of *Choloepus* Illiger, 1811.

Choelopus Tschudi, 1844:253. Incorrect subsequent spelling of *Choloepus* Illiger, 1811.

Cholopus Agassiz, 1846:83. Unjustified emendation of *Choloepus* Illiger, 1811.

Cholaepus Cornalia, 1849:4. Incorrect subsequent spelling of *Choloepus* Illiger, 1811.

Choloppus Stocker, 1987:1. Incorrect subsequent spelling of *Choloepus* Illiger, 1811.

CONTEXT AND CONTENT. Order Pilosa, suborder Folivora, family Megalonychidae. Synonymy modified from Cabrera (1958), Gardner (2005), and Gardner and Naples (2007).

Choloepus hoffmanni Peters, 1858
Hoffmann's Two-toed Sloth

Choloepus hoffmanni Peters, 1858:128. Type locality "Costa Rica" restricted to "Escazú," by Goodwin (1946:353);

Fig. 1.—Young adult male *Choloepus hoffmanni* from Aburrá Valley, Colombia. Used with permission of the photographer, T. Plese.

corrected to "Heredia, Volcán Barba," by Wetzel and Ávila-Pires (1980:835).

Choloepus didactylus Sclater, 1856:139. Type locality "near David," Chiriqui, Panama. Not *Bradypus didactylus* Linnaeus, 1758.

Choloepus hoffmanni peruvianus Menegaux, 1906:460. Type locality "Pérou."

Choloepus agustinus Allen, 1913:470. Type locality "near San Agustin (alt. 5000 ft.), Huila, Colombia."

Choloepus andinus Allen, 1913:472. Type locality "Salento, West Quindio Andes (alt. 7000 ft.), Cauca, Colombia."

Choloepus capitalis Allen, 1913:472. Type locality "Barbacoas, Colombia."

Choloepus didactylus pallescens Lönnberg, 1928:12. Type locality "Calavera, a place near Roque on the way to Moyabamba," San Martín, Peru.

Choloepus juruanus Lönnberg, 1942:29. Type locality "Santo Antonio, E. of Rio Eiru, S. of Rio Juruá," Brazil.

Choloepus hoffmanni agustinus: Cabrera, 1958:211. Name combination.

Choloepus hoffmanni capitalis: Cabrera, 1958:212. Name combination.

Choloepus hoffmanni juruanus: Cabrera, 1958:212. Name combination.

Choloepus hoffmanni pallescens: Cabrera, 1958:212. Name combination.

Choloepus augustinus Wetzel and Ávila-Pires, 1980:834. Incorrect subsequent spelling of *agustinus* Allen, 1913.

Choloepus hoffmani Swartz 1985:13A. Incorrect subsequent spelling of *hoffmanni* Peters, 1858.

CONTEXT AND CONTENT. Context as for genus. Synonymy modified from Cabrera (1958), Gardner (2005), and Gardner and Naples (2007). *Choloepus hoffmanni* has 5 subspecies with much intergradation (Gardner and Naples 2007). Cabrera (1958) treated *florenciae* Allen, 1913, as a subspecies of *C. hoffmanni* but Wetzel and Ávila-Pires (1980) correctly identified *florenciae* Allen, 1913, as a subspecies of *C. didactylus*. Thus, *augustinus* Allen, 1913, which had been treated as a synonym of *florenciae*, retains subspecific status. The following 5 subspecies are currently recognized (Gardner and Naples 2007):

C. h. agustinus Allen, 1913:470. See above; *andinus* Allen is a synonym.

C. h. capitalis Allen, 1913:472. See above.

C. h. hoffmanni Peters, 1858:128. See above.

C. h. juruanus Lönnberg, 1942:29. See above.

C. h. pallescens Lönnberg, 1928:12. See above; *peruvianus* Menegaux is a synonym.

NOMENCLATURAL NOTES. The generic name *Choloepus* is from the Greek for maimed-footed perhaps in comparison with the three-toed sloth (Borror 1960; Gotch 1979). The species name *hoffmanni* is in honor of the German naturalist Carl Hoffmann. Other common names are perezoso, unau, unau d'Hoffmann (Meritt et al. 2008), and preguiça real (Lönnberg 1942).

DIAGNOSIS

The distribution of *Choloepus hoffmanni* (Fig. 1) may overlap that of the three-toed sloths *Bradypus pygmaeus* (pygmy three-toed sloth—Hayssen 2008) and *B. variegatus* (brown-throated sloth—Hayssen 2010). *Choloepus* is usually stockier and larger than *Bradypus* (Langworthy 1935). The faces of the 2 genera have striking visual differences: that of *Choloepus* is much more elongated, with a more-prominent fleshy nose, whereas that of *Bradypus* is much blunter (Langworthy 1935; Webb 1985). *Bradypus* has a long neck, whereas that of *Choloepus* is short (Wislocki 1928b). *Choloepus* has an anterior caniniform tooth (Fig. 2) that *Bradypus* lacks (Webb 1985). *Bradypus* has 3 digits on the manus that are partially fused and hairy volar pads (Mendel 1985), whereas *Choloepus* has only 2 unfused digits and hairless volar pads (Mendel 1981b). *Bradypus* has a tail, but *Choloepus* does not (Langworthy 1935). *Bradypus* has 8 or 9 cervical vertebrae compared with 6 in *C. hoffmanni* (Mendel 1985). The throat of *C. hoffmanni* is paler in color than that of Linné's two-toed sloth (*C. didactylus*—Adam 1999). In addition, hairs on the cheek and throat hairs in *C. hoffmanni* are shorter and finer than those on the neck and shoulder but are not shorter on the neck and throat in *C. didactylus* (Wetzel 1985; Wetzel and Ávila-Pires 1980). In *C. hoffmanni* the anterior maximal interpterygoid width is less than double the minimum posterior interpterygoid width (double in *C. didactylus*) and 3 pairs of foramina penetrate the anterodorsal portion of the interpterygoid space (2 pairs in *C. didactylus*—Wetzel 1985; Wetzel and Ávila-Pires 1980). *C. hoffmanni* usually has fewer cervical vertebrae than *C. didactylus* (6, range 5 or 6 versus 7, range 6–8—Maslin et al. 2007; Wetzel 1985). *C. hoffmanni* also has fewer precaudal vertebrae than *C. didactylus* (39 versus 41—Maslin et al. 2007).

GENERAL CHARACTERS

Mean external measurements (mm [*SE*, range, *n*]) for Nicaraguan male and female *Choloepus hoffmanni*, respectively, were: total length, 607 (25.9, 570–680, 4), 635 (11.1, 570–710, 10); length of hind foot, 132 (4.1, 120–137, 4), 132 (3.4, 115–153, 13); and length of ear, 26.5 (0.86, 25–28, 4), 22.8 (0.95, 15–27, 13—Genoways and Timm 2003). Mean external measurements (mm or kg [*SD*, range, *n*]) for adults of mixed sex collected from Costa Rica to Brazil were: total length, 621 (48, 540–720, 52); length of tail, 21 (5, 14–30, 12); length of hind foot, 123 (27, 100–150, 45); length of ear, 25 (4, 20–37, 33); and mass, 5.72 (0.69, 4.54–6.69, 13—Wetzel 1985). Measurements (mm) for 2 adult female and 1 adult

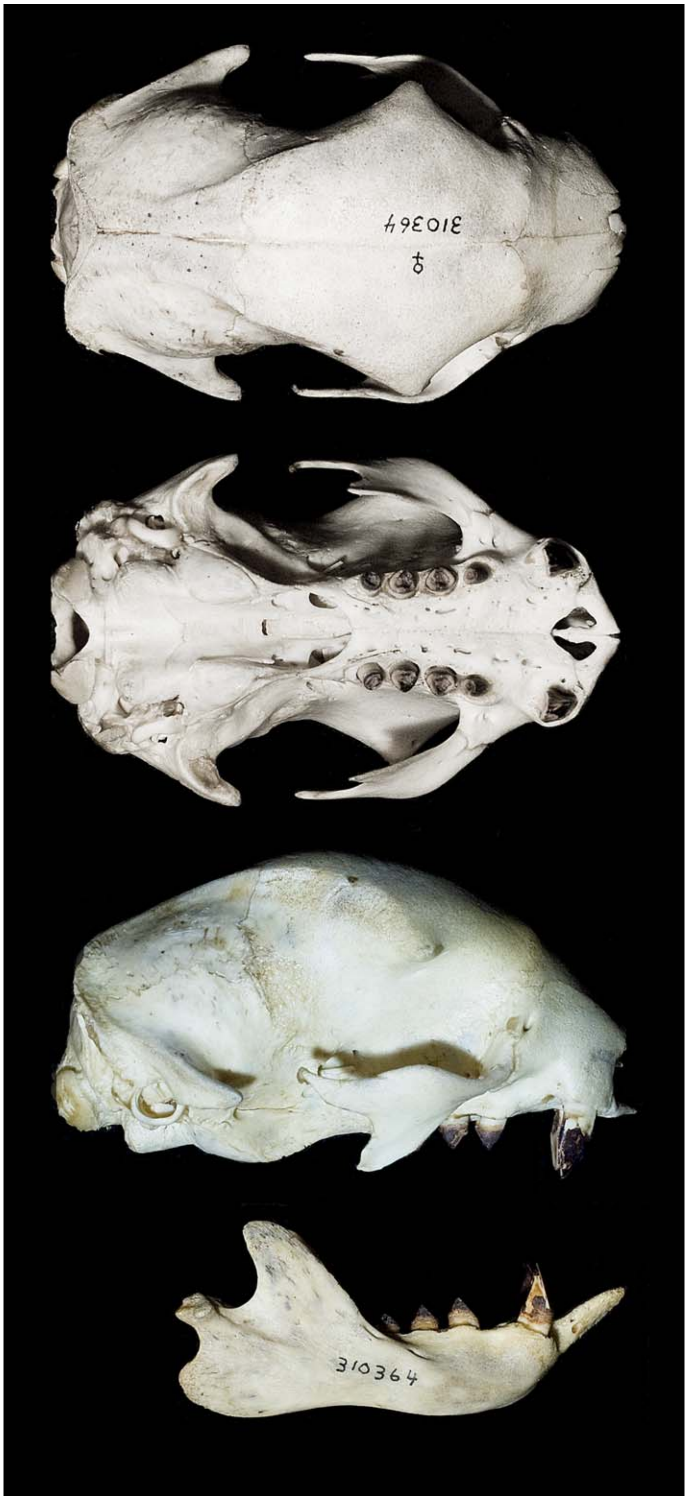

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult *Choloepus hoffmanni* (United States National Museum 310364) from Arraijan, Panama. Greatest length of skull is 92.6 mm.

male *C. h. augustinus* were, respectively: total length, 600, 640, 637; length of hind foot without claws, 82, 102, —; length of front nails in a straight line, 57, —, —; length of front nails over the curvature, 68, —, —; length of middle hind nail in a straight line, 46, —, —; and length of middle hind nail over the curvature, 53, —, — (Allen 1913). Measurements (mm) for 1 adult female *C. h. capitalis* were: total length, 690; length of hind foot without claws, 90; length of front claws in a straight line, 48; length of front claws over the curvature, 58; length of middle hind claw in a straight line, 44; and length of middle hind claw over the curvature, 53 (Allen 1913). An adult male *C. h. juruanus* was 520 mm in length (Lönnberg 1942). An adult female *C. h. pallescens* was 570 mm in length with a length of hind foot to end of middle toe pad of 93 mm; length of longest front claw from base of sheath, 53 mm; and length of middle hind claw, 46 mm (Lönnberg 1928).

Average body mass of *C. hoffmanni* was 5.72 kg (Gilmore et al. 2001) or 7.0–9.0 kg (Gillespie 2003). Body mass of 7 adult *C. hoffmanni* ranged from 3.3 to 6.4 kg (Goffart et al. 1967) and that of 20 *C. hoffmanni* was from 2.1 to 6.85 kg (Goffart 1971). Adult mass was 2.7–8.1 kg for captive and Panamanian animals (Meritt 1985). Two young *C. hoffmanni* collected in Barro Colorado Island, Panama, were 600–700 g in mass (Enders 1935). Animals from Costa Rica ($n = 26$) ranged from 2.0 to 7.0 kg in mass (Hanley et al. 2008). In Nicaragua, mean mass of 4 males was 6.7 kg (range, 5.9–7.2 kg) and that of 13 females was 5.8 kg (range, 4.7–7.2 kg—Genoways and Timm 2003). Two females from Costa Rica had body masses of 2.8 and 3.3 kg (Callens et al. 1965). Masses of 5 females and 4 males from Costa Rica were 3.45–6.0 kg (Betz et al. 1967). A female from Recife, Brazil, had a mass of 4.6 kg (Goffart et al. 1962). One pregnant female ranged from 5.0 to 5.4 kg in mass, and 1 male ranged from 5.3 to 5.7 kg (Hill and Tenney 1974). Postpartum, the female had a mass of 4.2 kg (Hill and Tenney 1974).

Skulls are variable in external characteristics across individuals from the same locality (Gray 1871). X-ray computed tomography coronal scans of the skull and mandible of an adult are available (American Museum of Natural History 30765—Digimorph 2003). Greatest length of skull for 51 adults of mixed sex from Costa Rica to Brazil was 106.3 mm (*SE*, 0.6 mm; range, 97.8–116.5 mm, $n = 51$—Wetzel 1985). Mean cranial measurements (mm [*SE*, range, *n*]) for male and female *C. hoffmanni*, respectively, from Nicaragua were: greatest skull length, 107.6 (1.18, 103.8–110.8, 5), 104.1 (1.08, 97.7–111.1, 13); anterior zygomatic breadth, 67.2 (0.74, 64.2–68.8, 5), 63.3 (1.26, 58.8–71.3, 14); posterior zygomatic breadth, 67.9 (0.31, 67.2–68.6, 5), 63.6 (1.04, 58.6–69.3, 13); postorbital breadth, 35.0 (0.45, 33.8–35.9, 5), 33.9 (0.49, 29.9–36.4, 14); length of squamosal process, 23.1 (1.15, 19.5–25.8, 5), 22.7 (0.85, 18.4–28.5, 14); length of maxillary toothrow, 24.1 (0.35, 22.7–24.5, 5), 23.5

(0.33, 20.3–25.1, 14); postpalatal length, 47.0 (0.49, 45.6–48.1, 5), 46.3 (0.52, 41.1–49.9, 14); palatal breadth, 24.8 (0.29, 24.1–25.5, 5), 24.6 (0.25, 23.0–26.2, 14); braincase depth, 39.9 (0.50, 38.3–41.1, 5), 38.1 (0.54, 34.8–41.9, 14); breadth of antorbital bar, 8.0 (0.28, 7.5–9.1, 5), 7.0 (0.17, 5.8–8.0, 14); and length of descending jugal process, 29.4 (0.58, 27.6–30.7, 5), 26.4 (0.73, 21.8–32.2, 14—Genoways and Timm 2003). Cranial measurements (mm) from 3 adult females, 2 *C. h. agustinus* and 1 *C. h. capitalis*, respectively, were: occipitonasal length, 93, 111, —; condylobasal length, —, 112, 106; zygomatic breadth, 60, 65, 64; interorbital breadth, 31, 32.5, 30.5; breadth across postorbital processes, 53, 53.5, 55.5; least postorbital breadth, 38, 36, 33; mastoid breadth, 45, 47, 40; palatal length, 45, 50, 50; length of nasals, 27, —, 32; greatest width of nasals, 24, —, 30; least width of nasals, 15, —, 15; diastema, 9, 10, 10; length of upper toothrow, 21, 25, 23; breadth of rostrum at canines, 34.5, 35.2, 34.5; length of mandible, —, 84, —; height at condyle, —, 20, —; and height at coronoid, —, 35, — (Allen 1913). Greatest length of skull for 107 adults was 75.8 mm (*SD*, 4.9 mm; range, 65.1–87.4 mm) and mean length of mandibular spout of 108 animals was 1.4 mm (*SD*, 1.0 mm; range, 0.004–3.6 mm—Wetzel 1985). Skull measurements (mm) for 1 *C. h. juruanus* were: occipitonasal length, 110; condylobasal length, 110; zygomatic width, 72; interorbital breadth, 72; breadth across postorbital processes, 55.5; distance from foramin lacrymal to nasal opening, 22; least postorbital breadth, 35; mastoid breadth, 49; length of palate, 51; postpalatal length, 51; breadth of rostrum at canines, 36.5; diastema, 11; length of upper toothrow, 23; length of mandibular toothrow, 20; breadth of bulla, 7; breadth of fossa pterygoidea in front of bulla, 15; and least interspace between bullae, 12.5 (Lönnberg 1942). Skull measurements (mm) for 1 *C. h. pallescens* were: occipitonasal length, 100; condylobasal length, 106; zygomatic width, 61; interorbital breadth, 30.5; breadth across postorbital processes, 49; least postorbital breadth, 33; mastoid breadth, 47.7; length of palate, 45.5; mesial length of nasals, 31.2; greatest breadth of nasals, 23; least breadth of nasals, 12; diastema, 8; alveolar length of upper toothrow, 23; breadth of rostrum at canines, 32.7; distance between alveolar margins of 1st pair of cheek teeth, 16; and distance between alveolar margins of last pair of cheek teeth, 11.5 (Lönnberg 1928). Males are larger than females in posterior zygomatic breadth, antorbital bar breadth, and descending jugal process length (Genoways and Timm 2003).

DISTRIBUTION

Choloepus hoffmanni occurs in 2 disjunct areas. The northern population ranges from Honduras and Nicaragua south into western Venezuela, and the southern population ranges from north-central Peru through southwestern Brazil to central Bolivia (Fig. 3; McCarthy et al. 1999; Meritt et al. 2008; Salazar-Bravo et al. 1990). It occurs from sea level to 3,328 m (Enders 1940; McCarthy et al. 1999; Ureña et al. 1986). *C. hoffmanni* lives at elevations higher than 2,400 m in Braulio Carrillo National Park, Costa Rica (Ureña et al. 1986). The skull of one animal was found at 3,328 m above sea level on Turrialba Volcano, Costa Rica (Ureña et al. 1986). A single *C. hoffmanni* was captured 1,100 m above sea level in Guayas, Ecuador (Grimaldi et al. 1992), and 2 others were caught in Guyaramerin and Mururata, Bolivia (Le Pont and Desjeux 1992; Wetzel 1985). No fossils are known (Patterson and Pascual 1968).

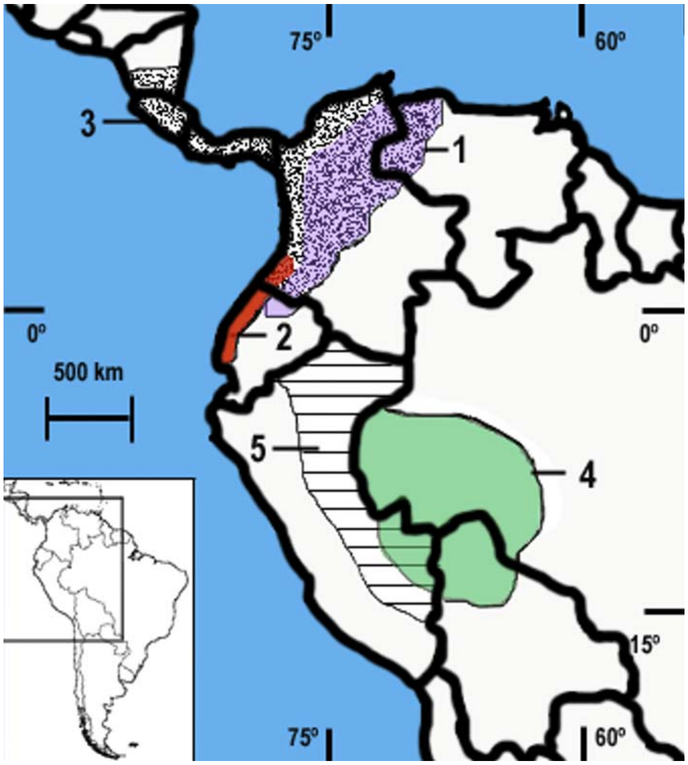

Fig. 3.—Geographic distribution of *Choloepus hoffmanni* (modified from Gardner and Naples 2007). Subspecies are: 1, *C. h. agustinus*; 2, *C. h. capitalis*; 3, *C. h. hoffmanni*; 4, *C. h. juruanus*; 5, *C. h. pallescens*. *C. h. hoffmanni* intergrades with *C. h. agustinus* in central Colombia and western Venezuela and intergrades with *C. h. capitalis* in southwestern Colombia. *C. h. juruanus* and *C. h. pallescens* intergrade in southeastern Peru.

FORM AND FUNCTION

Form.—General body hair is blond, buff, tan, or light brown in adults but may appear shaded pale green from algae that grows on the hairs (Gilmore et al. 2001; Meritt 1985). Facial hair is usually lighter than the hair on the rest of the body (Gilmore et al. 2001). *Choloepus hoffmanni* lacks a dense undercoat (McNab 1978). Abdominal hair is parted in the middle and flows toward the midback (Gilmore et al. 2001; Meritt 1985). A photomicrograph of a strand of hair shows 5 longitudinal ribs, each of which is enclosed within a scaly cuticle (Aiello 1985:figure 1e); the 3–9 furrows and ridges extend the length of each hair (Wujek and Cocuzza 1986). The maximum width of hairs is 0.16 mm (Wujek and Cocuzza 1986). Longest hairs on upper back are 17 cm (Lönnberg 1928). The cuticle is discontinuous around the hair shaft (Wujek and Cocuzza 1986). Hair is shaded from light to dark over the head and back (Gilmore et al. 2001). Sweat glands are present on the hairy portion of the body as well as being extremely large and abundant over the hairless snout, but are absent from the naked soles (Wislocki 1928b).

A tail remnant is palpable but not visible through the fur (Meritt 1985). Ears are round, thick, and covered with hair (Gilmore et al. 2001; Meritt 1985).

Incisors are absent; premolars and molars are indistinguishable, thus dental formula is i 0/0, c 1/1, p-m 4/3, total 18. The origin of the anteriormost tooth, counted here as a canine, is unclear and is usually described as caniniform (Webb 1985). The caniniform tooth may be visible when the mouth is closed and may cause a groove in the lower lip (Meritt 1985).

Facial muscles include musculus buccinatorius, m. cervico-auricularis, m. dilator, m. mandibulo-auricularis, m. nasolabialis, m. orbicularis, m. platysma, m. sphincter, and m. zygomaticolabialis (Naples 1985).

The eye has a wide, vascular, convex cornea with a deep anterior chamber and a thick lens. The cilary muscle is absent as is a Bowman's membrane. The pseudoangiotic membrane has only rods, and no macula (Goffart 1971; Watillon and Goffart 1969). Diameter of the optic fibers is less than 6 µm (Meulders et al. 1966). The retinal rods converge to ganglion cells and the axons make up a slender optic nerve about 1 mm thick (Goffart 1971). The retina lacks a central artery, and the optic papilla is small, round, and pale (Goffart 1971).

The ectotympanic is often poorly ossified (Patterson et al. 1992). An opening is present from the pterygoid sinus into the nasal passage (Patterson et al. 1992). Most specimens have a small to rudimentary mastoid process (Patterson et al. 1992). An illustration of the ear region of the cranium is available (Patterson et al. 1992).

The mean cochlear height is 4 mm and the width at the base of the cochlea is 4,040 µm (Pye 1979). The cochlea is completely surrounded by thick bone, and the perilymphatic and endolymphatic spaces are small (Pye 1979).

Fore- and hind legs are nearly equal in length (Wislocki 1928b). Forelegs have 2 large, curved claws, whereas hind limbs have 3 (Meritt 1985). Each hind claw has a thick layer of unguis over the dorsum and sides of the distal phalanxes (Mendel 1981a). Fore claws average 5.5–6.5 cm and hind claws average 5.0–6.5 cm (Britton 1941). Average hind-claw length was digit II, 3.6 cm; digit III, 5.1 cm; and digit IV, 4.2 cm; but hind claws on living animals are typically 9–10 cm (Mendel 1981a). Digits II and III are functional in the forefoot, whereas digits I and IV are splint-like metapodials. In the hind foot, digits II, III, and IV are functional, whereas I and V are splint-like (Mendel 1981a, 1981b). Digits of both forefeet and hind feet are syndactylus up to the distal interphalangeal joints and the volar surface has rubbery, thick-skinned, glabrous pads (Mendel 1981a, 1981b; Wislocki 1928b). On the hind feet, the plantar pad extends from the tip of the calcaneal tuberosity to the distal interphalangeal joint. Skin on the plantar is smooth and callus free (Mendel 1981a). Extensive anatomical description of the hind leg is available (Mendel 1981a).

Choloepus hoffmanni has 21 rib pairs forming a relatively noncompliant rib cage (Hoffman and Ritman 1984). Vertebral formula is 6 C, 23–25 T, 3–4 L, 5–6 S, 4–5 Ca, total 41–46 (Goffart et al. 1967).

Tissue composition (%) of 2 animals was: bone, 14.4–18.9; muscle, 26.2–27.4; and skin, 15.0–15.8 (Grand 1978). Body mass distribution (%) of 1 animal was: hind limbs, 12.8; trunk, 76.2; and forelimbs 11.0 (Grand 1978). Skin thickness (mm) is throat, 4; back of neck, 4; back, 3; dorsum of head, 3; legs, 1–2; abdomen, 1.5–2.0; and over sacrum, 1 (Wislocki 1928a).

In 8 *C. hoffmanni* weighing 3.1–4.7 kg, average mass of the brain was 28.5 g or 0.73% of body mass (Goffart 1971). The auditory area of the cerebral cortex is small and located in the posterior part of the ectosylvian gyrus (Meulders et al. 1966). "[N]ear the anterior end of the pallium, a vertical transverse fissure extends upwards from the rhinal fissure, and turns round the upper margin of the hemisphere to the mesial surface. … Behind this fissure a longitudinal fissure extends backwards, which separates a marginal saggital convolution … from a second longitudinal convolution" lower on the cranial surface. Below this an arched fissure "forms the upper limit of a third convolution" (Turner 1890:121). A Sylvian fissure is not obvious (Turner 1890). The cerebral motor cortex has been mapped with respect to facial and neck musculature, mouth, foreleg, and hind-leg movements (Langworthy 1935). The allocortex is well developed but the isocortex is poorly differentiated (Callens et al. 1965; Gerebtzoff 1962). *C. hoffmanni* has 2 large olfactory bulbs and the piriform lobe is developed but limited by the posterior rhinal fissure (Callens et al. 1965).

The spinal cord of *C. hoffmanni* is 34 cm in length (Gómez-Osorio 1964). Nerve cells measure 30 µm in diameter, and glial cells range 4–7 µm (Gómez-Osorio 1964). The vertebral canal holds a large intravertebral vein, which shifts the spinal cord to the left (Goffart et al. 1967). Spinal roots on the right cross the dorsal surface of the intravertebral vein in the middle and lower thoracic area (Wislocki 1928b). The cervical roots in 4 fetuses and 1 newborn *C. hoffmanni* were horizontal and become right angles lower down the spinal cord (Goffart et al. 1967). Anterior roots of myelinated fibers are 1–16 µm in diameter, but fibers < 2 µm and > 14 µm are rare (Goffart et al. 1967).

The pyramidal tract is located in the lateral funiculus (Strominger 1969). Figures of neurons in the lumbar region in the nucleus of Clarke, and neurons and satellite cells in the pyriform lobe of the brain are available (Gómez-Osorio 1964). A diagram of the brachial plexus illustrates the positions of the cervical and thoracic vertebrae relative to the median, musculocutaneous, radial, and ulnar nerves (Giffin and Gillett 1996).

The pituitary gland lies in a noticeable shallow depression in the sphenoid bone, is markedly flattened, and is encapsulated by a heavy sheath of pigmented dura (Wislocki 1938). The pars tuberalis is completely missing; the pars intermedia is well developed; and the infundibular recess is extensive. Melanophores in the hypophysial region penetrate the hypophysis tissues (Wislocki 1938). Wet mass of the pituitary gland of 5 *C. hoffmanni* (1 male and 4 females) ranged from 57.0 to 77.0 mg, whereas dry mass was 11.2–15.2 mg (Fontaine and Goffart 1963). The adenohypophysis contains many colloid vesicles (Duchesne 1967).

Choloepus hoffmanni has little subcutaneous or abdominal fat (Wislocki 1928b), but extradural fat occurs in the spinal canal (Goffart et al. 1967) as well as around the aorta, kidneys, and urogenital passages (Wislocki 1928b). Body fat is orange or buff in color (Wislocki 1928b).

The external carotid artery contributes to the dura supply (Bugge 1979). The internal carotid artery departs from the common carotid artery and connects with the anterior carotid foramen. The anterior carotid foramen is between the petrosal and basioccipital bones. Intracranial circulation is established with spinal branches from the vertebral artery (Bugge 1979). Arterial and venous plexuses are present in the extremities (Wislocki 1928b). *C. hoffmanni* has a double vena cava, in addition blood from the hind limbs returns to the heart via both the venae cavae and also the infravertebral vein (Wislocki 1928b).

The heart is wide at the base relative to its length. The left ventricle forms the apex of the heart, and the axis from base to apex deviates from the midline by 35°. Little or no epicardial fat is present (Rowlatt 1980). The lungs have no lobes in the adult (Wislocki 1928b). The trachea is short, 9–10.5 cm in length, and bifurcates upon entry to the thoracic cavity (Wislocki 1928b).

The large, 3-chambered stomach (Britton and Atkinson 1938) takes up much of the abdominal cavity (Wislocki 1928b). In a 4,134-g young adult, the stomach contents weighed 570 g, whereas the liver weighed 96.2 g; the spleen, 1.8 g; the pancreas, 5.3 g; the adrenals, 0.7 g; the kidneys, 23 g; the heart, 14.6 g; and the thyroid, 0.25 g (Wislocki 1928b). The cardiac portion of the stomach and the fundus are homologous to the rumen of ruminants although the fundus secretes mucus (Denis et al. 1967). A glandular prepyloric chamber is homologous to the ruminant abomasum (Denis et al. 1967). The gastric content of *C. hoffmanni* is rich in bacteria (Goffart 1971).

The gall bladder is small with a simple, straight neck and is buried in the parenchyma of the liver (Wislocki 1928b). It contains about 1 ml of dark green bile (Wislocki 1928b). Internally the walls are thin and the mucosa is "thrown everywhere into delicate elevations" (Wislocki 1928b:345).

The spleen is roughly triangular, flattened, and fused at the hilum with the pancreas (Wislocki 1928b). The pancreas is fleshy, compact, and yellowish orange with microscopic islets of Langerhans (Wislocki 1928b).

The gray-brown adrenals measure 30 mm by 7 mm and lie in an anterior to posterior axis (Betz et al. 1967). Adrenals are located on both sides of the aorta (Dresse and Gerebtzoff 1962). Kidneys are not associated with the adrenals (Dresse and Gerebtzoff 1962). Mass of adrenal glands is 0.015–0.02% of total body mass (Betz et al. 1967) or 334 mg/kg (Philippot et al. 1965). Adrenal glands as a percentage of adult mass for 7 females (range, 2,950–5,150 g) and 10 males (range, 2,250–5,200 g), respectively, were on average (*SE*): 0.014%, 0.016% (0.0006, 0.0006—Hartman 1959). The adrenals are encapsulated by connective tissue, and the adrenal cortex and medula are separated by a thin layer of connective tissue (Betz et al. 1967). The cortex is bright yellowish orange (Wislocki 1928a). Distinct clusters of large cells are grouped around a central axis in the medulla (Hartman 1959). Cells with noradrenaline are grouped in islets on the periphery of the adrenal medulla (Dresse and Gerebtzoff 1962). Dopa, dopamine, and adrenaline also are present in the adrenal medulla (Dresse and Gerebtzoff 1962). Descriptions of the fasciculata, glomerular, and reticular zones of the adrenal cortex are available (Betz et al. 1967).

Average mass of the thyroid gland is 346 mg, or 72 mg/kg gross body mass (Goffart 1971). The ratio of thyroid mass to body mass is 0.109 (Goffart 1971). The paired glands are orange, spindle-shaped, and gelatinous (Wislocki 1928b).

External genitalia are inconspicuous (Meritt 1985). Both sexes have a small genital protuberance that is smaller in females (Meritt 1985). Testes are within the abdomen (Meritt 1985) with abundant interstitial tissue with large, polygonal, yellow cells (Wislocki 1928b). Paired seminal vesicles are large: the tubes reach 10 cm in length when straightened (Wislocki 1928b). A prostate gland is present (Wislocki 1928b). The pear-shaped uterus has a single cavity with fallopian tubes coiled to either side that open through a "fringe of fimbria" to the pouched, bilobed ovaries (Wislocki 1928b:349).

A freshly delivered, lobular placenta measured 200 by 160 by 10 mm (Benirschke and Powell 1985). The umbilicus is about 100 mm at term and contains 2 arteries and 1 vein (Benirschke 2008). The endotheliochorial placenta is laminar with multiple cotyledons separated by thin maternal septa with large maternal blood vessels (Benirschke 2008; Soma 1976; Wislocki 1928a). Vitelline tissue is absent and the amnionic sac lies against the chorion (Benirschke 2008). An image of a placenta and a photomicrograph of an implantation site and the placental labyrinth are available (Benirschke 2008).

All the muscles of *C. hoffmanni* are red and the deep muscles (i.e., leg) are darker (Goffart 1971; Wislocki 1928b). Thick filaments of the limb muscles are organized in a hexagonal array and the thin filaments are arranged in an orthogonal array. Thick filaments and thin filaments are about 1.5 μm and 2.6 μm long, respectively (Goffart 1971). Contraction time of hind-limb muscles is 100–150 ms (Goffart 1968) and isometric contraction time for a single twitch was 100–175 ms (Enger and Bullock 1965). The twitch time increased from 70 to 350 ms when the temperature decreased from 36°C to 9°C (Enger and Bullock 1965).

Function.—Eyes are mobile and partially retractable (Gilmore et al. 2001; Meritt 1985). This trait is why *Choloepus hoffmanni* sometimes appears pop-eyed when stressed or threatened (Gilmore et al. 2001). The circular pupil never fully dilates (Meritt 1985). Due to a very convex cornea and thick lens, the shortsightedness of *C. hoffmanni* is about 3–4 diopters (Goffart 1971). The actions of the vestibular-ocular system are qualitatively similar to those of rabbits and cats but less intense (Demanez et al. 1968). The pupils of *C. hoffmanni* can be paralyzed with 0.2% atropine (Meulders et al. 1966).

Partitions of the abdominal hair allow for efficient water runoff (Gilmore et al. 2001). The rib cage maintains a constant shape prone versus supine as the diaphragm shift is pistonlike (Hoffman and Ritman 1984). During bending, limb bones are loaded with either tension or compression superimposed on the bending (Swartz 1985). Myoglobin is slightly heterogeneous and the isoelectric pH of oxymyoglobin is 6.75 with 10% of the myoglobin having an isoelectric point of 7.15–7.20 (Jammaers 1965). The tetanus to twitch ratio varies between 3.5 and 5.8 (Goffart 1971) or 4–5.8 (Goffart et al. 1962). A fused tetanus exerts a maximum of 1.62–4.65 kg/cm^2 of force (Goffart et al. 1962). Leg muscle time reactions in response to electrical shocks are: extensor digitorum longus, 122–135 ms; tibialis anticus, 120–122 ms; gastrocnemius internus, 109 ms; and gastrocnemius externus, 96–152 ms (Goffart et al. 1962).

The descending portion of the zygomatic arch allows attachment of the masseter muscles in a horizontal plane such that forward and backward movements of the mandible occur during mastication (Sicher 1944). Flexor muscles of the limbs, torso, and neck are powerful (Toole and Bullock 1973). Modifications of limb and trunk muscles and joints facilitate suspensory posture and locomotion (Grand 1978). An ergographic recording of muscle contraction is available (Toole and Bullock 1973). Activities of myosin (ethylenediaminetetraacetic acid–activated adenosine triphosphatase and calcium-activated adenosine triphosphatase) and glycolytic (hexosephosphate isomerase, phosphoglucokinase, aldolase, triosephosphate isomerase, glyceraldehyde-3-phosphatedehydrase, lactatedehydrogenase, phosphoglycerate kinase, and pyruvatekinase) enzymes from the biceps gracilis, subcutaneous muscle of the abdominal wall, pectoralis major, biceps femoralis and adductor magnus, and ventricle have been measured (Toole and Bullock 1973). Actin-activated, Ca^{2+}-activated, and ethylenediaminetetraacetic acid–activated adenosine triphosphatase activities of myosins from extensor digitorum longus, gastrocnemius medialis, gastrocnemius lateralis, tibialis anterior, claw flexor (anterior limb), diaphram, and tibialis anterior muscles are available (Bárány et al. 1967).

Two *C. hoffmanni* had normal clinging and climbing locomotion after removal of their cerebella (Murphy and O'Leary 1973). In decerebrated animals, flexor rigidity occurs in the limbs, claws, and trunk; reflex hanging also occurs. Removal of red nuclei results in rigidity in the trunk and limbs, and the animal's posture resembles the "resting position." Removals made above the red nuclei result in rigidity in the claws, and the animals are able to hang in normal active positions (Richter and Bartemeier 1926).

Mean rectal body temperature is 34.2°C (Enders and Davis 1936), 34.4°C (range, 33.4–35.7°C—Britton and Atkinson 1938), 34.5°C (McNab 1978), and 34.6°C (Britton and Kline 1939a). Rectal temperatures ranged from 31.8°C to 33.8°C for 2 animals (Hill and Tenney 1974), from 32.6°C to 34.4°C for 5 animals (Enger and Bullock 1965), and from 34.5°C to 35.5°C for 4 animals (Goffart et al. 1962). A 2-week record of body temperature of 2 males and 2 females between 0730 and 1600 h provided a mean of 32.9°C (range, 30.5–34.2°C—Meritt 1985). In animals from Panama, body temperature was 29.4–32.8°C (Richter and Bartemeier 1926) and rectal temperature was 33.4–35.7°C (Britton and Atkinson 1938; Enders and Davis 1936). Rectal temperature of 1 pregnant *C. hoffmanni* varied from 32.2°C to 32.8°C prepartum, and from 31.8°C to 32.2°C postpartum (Hill and Tenney 1974). In *C. hoffmanni* body temperature varies 2.6°C in 24 h when ambient temperature is kept constant (Goffart 1971). Body temperature of a single, free-living *C. hoffmanni* over 2 days ranged from 33.3°C to 40.6°C (Montgomery and Sunquist 1978). Body temperature rose 0.5°C after 3 min of threatened attack (Britton and Kline 1939a). Subcutaneous limb temperature was 27.2–30.9°C and deep in the muscle was 0.5°C higher (Enger and Bullock 1965).

In 3 *C. hoffmanni* the body temperature dropped 10°C when exposed to cold but pH of the blood did not change significantly (Marder and Reeves 1967). The alveolar carbon dioxide level decreased; oxygen content and arterial blood pressure remained stable; but heart rate dropped (Marder and Reeves 1967). Normal arterial pH was 7.441 and normal partial pressure of carbon dioxide was 36.1 mm Hg (Marder and Reeves 1967).

The metabolic rate (ml O_2 kg^{-1} min^{-1}) of *C. hoffmanni* was 3.51, range, 3.08–4.04 (Lemaire et al. 1969) and 3.1–3.8 (Irving et al. 1942). Mean basal metabolism of 3 animals was 0.188 ml O_2 g^{-1} h^{-1} (McNab 1978). The metabolic rate of 1 lightly anesthetized *C. hoffmanni* was 3.5 ml O_2 kg^{-1} min^{-1} (Hill and Tenney 1974). Thermal conductance is estimated at 0.010–0.018 ml O_2 g^{-1} h^{-1} $°C^{-1}$ depending on the estimate of the lower limit of thermoneutrality (12°C versus 24°C, respectively—McNab 1978).

Respiratory rate is 13–14 breaths/min; average ventilation is 190 ml kg^{-1} min^{-1}; the average tidal volume per kilogram body weight is 19.0 ml; heart rate is 0–100 beats/min (Goffart 1971; Goffart et al. 1962). Mean respiration rate for free-ranging and captive animals in Panama was 9 breaths/min (range 8–11 breaths/min—Meritt 1985). The mean respiratory rate of anesthetized *C. hoffmanni* was 8.0–11.0 breaths/min compared with 27.0–39.2 breaths/min just prior to anesthesia (Hanley et al. 2008). Awake, resting animals used 13–14 breaths/min and used 150–220 ml air kg^{-1} min^{-1} (Irving et al. 1942). Mean respiratory values for a pregnant female and the same female postpartum followed by a range of values for 1 male are: alveolar carbon dioxide level/partial pressure of carbon dioxide in arterial gas (torr), 32.5, 35.0, 37.3–40.0; alveolar oxygen level/partial pressure of oxygen in alveoli (torr), 117, 114, 109–110; respiratory frequency (breaths/min), 10.9, 11.1, 14.2–16.1; tidal volume (ml), 147, 103, 47–51; and ventilation rate (ml/min), 1.57, 1.09, 0.67–0.82 (Hill and Tenney 1974).

When carbon dioxide in the air was increased from 33 to 60 torr, respiratory frequency of a male *C. hoffmanni* increased from 16.1 to 17.5 breaths/min and his tidal volume increased from 47.7 to 166 ml (Hill and Tenney 1974). When oxygen in the room decreased from 109 to 47 torr, respiratory frequency of the male increased from 16.1 to 20.3 breaths/min and tidal volume increased from 47.6 to 115 ml (Hill and Tenney 1974). For a female *C. hoffmanni*, respiratory frequency increased from 10.3 to 12.6 breaths/min and tidal volume increased from 175 to 542 ml when carbon dioxide in the air level increased from 33 to 53 torr. When oxygen fell from 117 to 43 torr, respiratory frequency of a female increased from 10.3 to 13.3 breaths/min, while tidal volume decreased from 175 to 140 ml; a further decrease of oxygen to 28 torr increased tidal volume to 251 ml, while respiration frequency was 10.9 breaths/min (Hill and Tenney 1974).

After 45 min of anesthesia, respiratory rate (*SD*) dropped in males and females from 27.0 (8.7) to 11.0 (5.7) breaths/min and 39.2 (20.1) to 9.7 (5.2) breaths/min, respectively. Prior to anesthesia, heart rates were 94.9 (17.5) beats/min. Mean systolic blood pressure was 104.6 (19.7) mm Hg. Heart rate (beats/min) dropped from 90.5 (16.6) to 60.8 (7.4) and 95.3 (16.7) to 59.8 (9.3) in males and females, respectively. Systolic blood pressure (mm Hg) dropped from 121.4 (22.2) to 96.4 (21.0) and 129.7 (13.0) to 96.6 (15.6) in males and females, respectively (Hanley et al. 2008).

Choloepus hoffmanni cannot go without breathing for more than 20 min (Irving et al. 1942). In one *C. hoffmanni* arterial blood level (ml O_2) decreased from about 16 to 1 after 13 min of arrested breathing. The blood lactate level (mg%) increased from less than 10% to greater than 50% after 10 min, and then increased to about 60% during early recovery from arrested breathing before decreasing again. During rebreathing, the oxygen level in alveolar air (vol% O_2) decreased from 16% to 2%, while carbon dioxide level (vol% CO_2) increased from about 4% to 12% (Irving et al. 1942).

Strychnine (1 mg/kg) injected into the heart rapidly causes tonic flexor convulsions, whereas pentobarbital (35 mg/kg) results in relaxation from tonic flexion but causes flexor jerks (Esplin and Woodbury 1961).

Bacteria break down cellulose into sugars that are converted to volatile short-chain fatty acids by microbial fermentation in the 3-chambered stomach (Denis et al. 1967; Jeuniaux 1962). The fatty acids are absorbed by the gastric mucosa and then moved into the gastric veins (Denis et al. 1967). Water reabsorption occurs in the prepyloric muscular chamber of the stomach (Denis et al. 1967).

The adrenals of *C. hoffmanni* contain ascorbic acid at 90 mg/100 g, cholesterol at 300 mg/100 g, and hydroxycorticosteroids at 889 mg/100 g (Palem-Vliers et al. 1962). Plasma corticosterone is 18 μg/100 ml and plasma cells in the adrenals contain hydroxycorticosteroids at 120 μg/100 ml (Palem-Vliers et al. 1962). In late pregnancy, adrenaline levels exceed noradrenaline levels in the adrenals (375 μg versus 285 μg—Dresse and Goffart 1963). In nongravid animals, 1 adult female had adrenaline at 334 μg/g and noradrenaline at 103 μg/g; another adult female had adrenaline at 854 μg/g and noradrenaline at 108 μg/g (Dresse and Goffart 1963). Adrenals of fetal and neonatal *C. hoffmanni* have more dopamine and adrenaline than noradrenaline (Dresse and Goffart 1963).

Elimination occurs every 3–8 days (Enders 1940; Meritt 1985). Animals descend to the forest floor to defecate and usually leave their pellets on the leaf litter without covering them (Montgomery and Sunquist 1975). Feces are a firm and compact mass of individual pellets with a usual volume greater than 500 ml (Meritt 1985). The copious urine is clear to brown with a penetrating odor, a mean specific gravity of 1.023 (range, 1.020–1.031), mean pH of 7.1 (range, 7.0–9.0), mean volume of 808 ml (range, 340–1,600 ml, or about 178 ml/kg body mass), and contains no sugar, protein, urobilinogen, ketones, blood, or bilirubin (Meritt 1985). After elimination 1 animal was $>$ 30% lighter in mass (Meritt 1985). Urinary ketosteroids vary between 0.24 and 1.94 mg (Palem-Vliers et al. 1962). The urine magnesium concentration of 9 *C. hoffmanni* was 21 mEq/l (Goffart 1971). The kidney reabsorbs Na^+, Ca^{++}, Cl^-, and glucose and concentrates K^+, Mg^{++}, P, bicarbonate, creatinine, urea, and uric acid, and the pH of the urine is 7.5–8.5 (Goffart 1971).

Choloepus hoffmanni has a histamine content varying between 6 and 15 μg/g in liver, lungs, skin, and spleen (Cession-Fossion and Lecomte 1963). The intestines contain substance P up to 14 units/g with little histamine (Cession-Fossion and Lecomte 1963).

General ranges of hematological parameters are: erythrocytes × 10^6/ml, 2.53–3.55; packed cell volume (%), 33.2–46.6; hemoglobin (g/dl), 10.6–16.8; mean corpuscular volume (fl), 109.5–140.7; mean corpuscular hemoglobin (pg), 40.8–52.2; mean corpuscular hemoglobin concentration (g/dl), 34.7–40.5; leukocytes (ml^{-1}), 7,220–18,360; neutrophils (ml^{-1}), 1,439–7,419; band neutrophils (ml^{-1}), 35–1,320; lymphocytes (ml^{-1}), 3,210–10,982; eosinophils (ml^{-1}), 87–749; monocytes (ml^{-1}), 74–4,119; basophils (ml^{-1}), 27–1,757; platelets (ml^{-1}), 133,000–347,000; and nucleated red blood cells per 100 white blood cells, 2.0–8.0 (Gillespie 2003). Blood measures from a single animal were: hemoglobin, 11.2 g/100 ml; hematocrit, 30%; red blood cells, 3.46 × 10^6; white blood cells, 16 × 10^3/ml; platelets, 246 × 10^3–248 × 10^3; segmented cells, 30; lymphocytes, 61; band forms, 7; monocytes, 2; eosinophils, 0; basophils, 0; red blood cell fragility, began at 0.4% NaCl, complete at 0.3% NaCl; whole blood clotting time, 100 min; recalcification time of platelet-rich plasma, 54 min; recalcification time of platelet-poor plasma, 110 min; and partial thromboplastin time, 95 min with cephalin and m/40 $CaCl_2$ (Toole 1972). Ranges for blood measures from 3 females and 1 male were: hemoglobin, 11.7–13.6 g/100 ml; hematocrit, 33–38.7%; red blood cells, 3.85 × 10^6–5.04 × 10^6; and white blood cells, 13.4 × 10^3–21.0 × 10^3/ml (Meritt 1985). Differential counts for the same 4 animals were: basophils, 1–3; eosinophils, 0–5; myelocytes, 0; juveniles, 0; stab cells, 0–3; segmented cells, 40–49; lymphocytes, 40–49; and monocytes, 0–3 (Meritt 1985). Medians (and ranges) for blood measures from 8 female and 9 male adults, respectively, were: hemoglobin (g/100 ml), 12.1 (11.3–15.1), 13.5 (11.8–14.2); hematocrit (%), 36.9 (34.5–43.8), 42.9 (34.4–45.8); red blood cells (× 10^6), 3.0 (2.9–3.6), 3.3 (2.9–3.5); white blood cells (× 10^3), 13.5 (4.6–23.6), 15.5 (12.0–18.9); mean corpuscular hemoglobin (pg), 41.1 (38.7–42.3), 40.9 (38.2–42.9); and mean corpuscular hemoglobin concentration (g/100 ml), 33.4 (29.6–35.5), 33.1 (29.5–34.3—Wallace and Oppenheim 1996). Hematologic counts (× 10^3 and % of white blood cells) for the same 8 female and 7 male adults, respectively, were; segmented neutrophils, 2.4, 20 (0.4–10.1, 10–43), 3.6, 29 (1.8–5.4, 11–31); lymphocytes, 9.7, 72 (3.8–13.9, 45–84), 10.8, 67 (7.7–14.4, 46–85); monocytes, 0.4, 4 (0.0–0.9, 0–7), 0.1, 1 (0.1–0.2, 0–2); eosinophils, 0.4, 4.5 (0.0–1.0, 0–7), 0.3, 2 (0.0–3.3, 0–20); band neutrophils were not present; and platelets were adequate for both sexes (Wallace and Oppenheim 1996). Values for 7 female and 7 male juveniles did not differ significantly from those of adults (Wallace and Oppenheim 1996).

General ranges of serum biochemistry are: total protein (g/dl), 7.1–8.7; albumin (g/dl), 3.5–4.5; globulin (g/dl), 3.2–4.8; albumin : globulin ratio, 0.94–1.09; calcium total (mg/dl), 8.5–10.5; phosphorus (mg/dl), 3.1–6.9; sodium (mEq/l), 123–133; potassium (mEq/l), 4.6–7.6; chloride (mEq/l), 85–95; creatinine (mg/dl), 0.7–1.3; urea nitrogen (mg/dl), 17–43; cholesterol (mg/dl), 114–274; glucose (mg/dl), 34–82; and total carbon dioxide (mm/l), 13–25 (Gillespie 2003). Serum chemistry for 10 animals of mixed sex was (average with parenthetical range): sodium, 131.0 mEq/l (122.1–141.8 mEq/l); potassium, 7.73 mEq/l (5.82–10.30 mEq/l); chloride, 99.7 mEq/l (92.8–103.8 mEq/l); urea, 106 mg% (64–166 mg%); and sugar, 88 mg% (59–137 mg%—Britton et al. 1938). Ranges from standard metabolic screening of serum for 1–4 animals were: sodium, 133–139 mEq/l; potassum, 3.8–6.2 mEq/l; chloride, 94–96 mEq/l; magnesium, 1.1–1.9 mEq/l; calcium, 2.1–3.0 mEq/l; phosphorus, 2.7–5.4 mg/100 ml; glucose, 34–51 mg/100 ml; blood urea nitrogen, 20.5–33.0 mg/100 ml; uric acid, 2.1–6.3 mg/100 ml; cholesterol, 132–218 mg/100 ml; bilirubin, 0.3–0.6 mg/100 ml; alkaline phosphatase, 27–51 mU/ml; lactate dehydrogenase, 270 mU/ml; creatinine phosphokinase, 17–20 creatinine phosphokinase units; serum glutamic-oxaloacetic transaminase, 90 mU/ml; total protein, 7.2–7.8 g/100 ml; albumin, 2.0–2.1 g/100 ml; globulin, 4.8–5.9 g/100 ml; tetraiodothyronine, 1.1–3.3 μg/100 ml; triiodothryonine, 46.1–48.6%; no thyroid binding globulin; protein-bound iodine, 2.0–4.5; acid phosphatase, 0.2 Shinowara–Jones–Reinhart units; triglycerides, 76 mg/100 ml; and plasma osmolar concentration, 262 milliosmols (Toole 1972). Serum chemistry (median and range) for 8 female and 7 male adults, respectively, was: glucose (mg/100 ml), 44 (35–56), 47 (35–65); blood urea nitrogen (mg/100 ml), 19 (12–24), 16 (8–21); creatinine (mg/100 ml), 1 (0.7–1.5), 0.8 (0.7–1.2); uric acid (mg/100 ml), 2.6 (1.5–3.9), 3.2 (2.2–3.7); calcium (mg/100 ml), 9 (8.8–9.9), 9.5 (8.4–9.7); phosphorus (mg/100 ml), 4.3 (2.7–5.8), 3.8 (3.0–5.1); sodium (mEq/l), 127 (123–131), 127 (124–129); chloride (mEq/l), 91.5 (86–96), 90 (87–92); potassium (mEq/l), 5.2 (4.4–8.3), 5.6 (4.6–6.3); triglycerides (mg/100 ml), 106 (39–140), 107 (46–129); cholesterol (mg/100 ml), 186 (124–259), 197 (136–202); total protein (g/100 ml), 7.9 (7.5–8.8), 7.9 (6.3–8.7); albumin (g/100 ml), 3.7 (3.5–4.7), 3.9 (3.4–4.3); globulin (g/100 ml), 4 (3.8–5.2), 4 (2.9–4.4); serum glutamic-oxaloacetic transaminase (IU/l), 64 (47–109), 82 (67–92); serum glutamic pyruvic transaminase (IU/l), 5 (1–7), 2 (1–4); gamma-glutamyl transpeptidase (IU/l), 2.5 (2–8), 4 (1–8); total bilirubin (mg/100 ml), 0.2 (0.1–0.8), 0.3 (0.1–0.5); conjugated bilirubin (mg/100 ml), 0.1 (0.06–0.48), 0.17 (0.06–0.28); unconjugated bilirubin (mg/100 ml), 0.13 (0.01–0.40), 0.13 (0.04–0.22); alkaline phosphatase (IU/l), 276 (131–841), 483 (249–973); and lactate dehydrogenase (IU/l), 274 (191–325), 239 (78–393—Wallace and Oppenheim 1996). Ranges for serum enzymes are (IU/l): lactic dehydrogenase, 174–552; alkaline phosphatase, 272–1,192; gamma-glutamyl transferase, 0–10; creatine kinase, 0–547; aspartate aminotransferase, 82–156; alanine aminotransferase, 6.0–24; total bilirubin (mg/dl), 0.0–0.6; and triglycerides (mg/dl), 81–135

(Gillespie 2003). Mean ionic composition of blood serum (mEq/l) in 4 *C. hoffmanni* was: sodium, 133 (range, 125–147); potassium, 5.78 (range, 1.05–11.10); chlorine, 97.5 (range, 92–106); and calcium, 4.33 (range, 3.55–4.80—Goffart 1971).

Mean blood glucose from 11 samples was 79 mg/100 ml (range, 57–120 mg/100 ml) and rose 54 mg/100 ml after 3 min of threatened attack (Britton and Kline 1939a). Blood cholesterol was 1.72 g/L (range, 1.32–2.46 g/l—Lemaire et al. 1969). The average oxygen content of the blood in 3 *C. hoffmanni* was 14.6 volume % (Irving et al. 1942). Arterial blood pH of an anesthetized male *C. hoffmanni* was 7.46; alveolar oxygen level, 95 torr; and alveolar carbon dioxide level, 36 torr (Hill and Tenney 1974). The blood of *C. hoffmanni* contains kininogens (Lecomte 1964).

Average percent glycogen with parenthetical range from 10 animals was: liver, 0.50 (0.23–0.72); muscle, 0.42 (0.22–0.72); and heart, 0.48 (0.29–0.71—Britton et al. 1938). For 10 animals, muscle was 74.7% water on average (range, 73.1–75.6%—Britton et al. 1938). Bile contained biliverdin at 200–450 mg/l (Barac 1963).

The thyroids of 8 animals had iodine at 1.79 mg/g tissue, range, 0.54–3.84 mg/g tissue (Lemaire et al. 1969). The thyroxine secretion rate was 0.18 $\mu g\ kg^{-1}\ 24\ h^{-1}$ (Lemaire et al. 1969). Maximal uptake of manually injected radioactive iodine by the thyroid occurred after 3–14 days with a mean maximal uptake of 1 week (Goffart 1971). After 1 week 19–54% of the iodides were excreted, but 25–65% of the iodine injected was still present outside the thyroid gland (Lemaire et al. 1969). Protein-bound iodine in the plasma of 12 animals was 1.67 µg%, range, 1.2–2.5 µg% (Lemaire et al. 1969). The ratio of mono- to di-iodinated tyrosine was lower in a fetus (0.5) than in its mother (0.6—Closon and Wankenne 1962). Thyroid-stimulating hormone was 10–29 µU/mg dry pituitary (Fontaine and Goffart 1963).

Uterine and trachael smooth muscle contain alpha and beta adrenaline receptors (Philippot and Goffart 1963). Adrenaline increases muscle tone and contractions of the uterus (Philippot and Goffart 1963).

Stimulation of the olfactory bulbs causes posttetanic potentiation and a small-amplitude response (Callens et al. 1965). Seizures were induced in *C. hoffmanni* by electroshock. After supramaximal brain stimulation, the seizure pattern consisted of "weak extension, followed by rigid tonic flexion of limbs, trunk, and neck" (Esplin and Woodbury 1961:1426). After relaxation terminal clonus primarily of the claws and jaw occurred (Esplin and Woodbury 1961).

Electroencephalographic studies have recorded sinusoidal activity at 32–40 cycles/s (Goffart 1971). The glial index of *C. hoffmanni* increases as axon length increases and varies in the pyriform lobe, fascia dentata, hypothalamus, and somatosensory areas of the brain (Gómez-Osorio 1964). Auditory stimuli cause cortical potentials in the ectosylvian gyrus limited superiorly and posteriorly by the suprasylvian sulcus (Goffart 1971). The evoked potentials of auditory origin have a short latency of 18–20 ms (Goffart 1971).

ONTOGENY AND REPRODUCTION

***Reproduction.*—**Litter size is 1 (Genoways and Timm 2003; Hayssen et al. 1993; Meritt 1985). Menses lasts 5–7 days (Meritt 1985). Gestation is between 11 months 10 days and 12 months 12 days (Taube et al. 2001) or 350 days (Partridge 1991).

Interbirth interval is 15 months 5 days (Taube et al. 2001). Sexual maturity is at 2–4 years (Taube et al. 2001). In Costa Rica, adults with single young were observed in January and March (Timm et al. 1989). In Panama, 2 adults were pregnant and nursing young of 600–700 g in late December (Enders 1935). During pregnancy, abdominal fullness increases until birth or abortion. The abdominal girth of *Choloepus hoffmanni* decreases 2 days after parturition (Moore and Moore 1985).

During parturition contractions are visible and the vulvar region becomes distended. Mammary development does not occur until after the neonate nurses, but nipples are visible (Merrit 1976; Moore and Moore 1985). In the first 24 h after birth, the milk starts to flow after the infant begins to suckle. Female *C. hoffmanni* are anemic directly after parturition or presumptive abortion (Moore and Moore 1985).

Copulation takes place shortly after parturition (Enders 1935). In 1 observed mating, 2 bouts of thrusting each of 55 s were separated by a 2-min interval (Moore and Moore 1985).

Newborns have a body mass of 340–454 g at birth (Meritt 1985) and have open eyes, pigmented teeth, patent ear pinnae, fully formed and hard claws, a full coat of hair, and loud vocalizations (Meritt 1985). One term fetus weighed 400 g (Maréchal et al. 1963), whereas a neonate weighed 375 g at 5 days (Dresse and Goffart 1963; Philippot et al. 1965). A 193-g neonate survived 2 days (Moore and Moore 1985). A midgestational fetus was 136 mm along the spine and without hair or epitrichial membranes (Wislocki 1928a).

The caudal edge of the adrenals in fetal *C. hoffmanni* touches the kidneys (Goffart et al. 1967). After growth, the adrenals are found above the kidneys (Goffart et al. 1967). Adrenals are proportionately larger in young (450–1,600 g) animals and change with age (chiefly elongation, anterior migration, and shrinkage relative to kidneys—Hartman 1959). The paired adrenals of a newborn and term fetus were 2,024 and 1,796 mg, respectively, whereas adult glands range from 711 to 1,479 mg (Philippot et al. 1965).

Newborns are alert, mobile, and strong (Meritt 1985). They have coordinated movement, can hold their heads erect, and have strong grasping reflexes (Meritt 1985). Newborns are spread against the mother's abdomen with the newborn's head against the mother's chest (Meritt 1985). Newborns nurse 6–15 min at at time several times a day (Meritt 1985). Water is 1st consumed at 7 days and solid food at 15–27 days (Meritt 1985). Play began at 15–19 days, hanging upside down at 20–25 days, sleeping off the mother at 50 days, independent exploration at 41–54 days, regularly feeding away from the mother at 5 months, and eliminating in an adult fashion at 6 months (Meritt 1985). Young are independent at 5–9 weeks (Taube et al. 2001). A young animal, 220 mm in total length, is described as being "in the first pelage" (Allen 1910:93). One female became sexually mature at about 2 years (Meritt 1985).

ECOLOGY

Population characteristics.—In captivity, a *Choloepus hoffmanni* lived at least 32 years 1 month (Jones 1982). Adults comprise 94% of captured animals and juveniles comprise 6% (Montgomery and Sunquist 1975). Sex ratio of 72 animals from 3 Panamanian sources was 93% females, but sex ratio of animals born in captivity was closer to equality (6 females and 5 males—Meritt 1985; Meritt and Meritt 1976).

Estimated densities are 1.1–2.7 animals/ha (Montgomery and Sunquist 1975). Biomass estimates per hectare are 3.5 kg for adults and 0.1 kg for juveniles (Montgomery and Sunquist 1975). In Panama, *C. hoffmanni* accounts for 12.3–14.7% of the estimated biomass of nonvolant mammals (Eisenberg and Thorington 1973).

Space use.—*Choloepus hoffmanni* uses many tree species in Panama (*Alchornea costaricensis*, *Alseis blackiana*, *Anacardium excelsum*, *Apeiba membranacia*, *Astronium graveolens*, *Beilschmiedia pendula*, *Bombacopsis sessilis*, *Brosium bernadetteae*, *Calophyllum longifolium*, *Cavanillesia platanifolia*, *Ceiba pentandra*, *Chrysophyllum panamensis*, *Cordia alliodora*, *Diptery panamensis*, *Eugenia nesiotica*, *Ficus insipida*, *Ficus obtusifolia*, *Ficus yoponensis*, *Genipa americana*, *Gustavia superba*, *Heisteria concinna*, *Hyeronima laxiflora*, *Inga goldmanii*, *Lacmellea panamensis*, *Licania platypus*, *Luehea seemannii*, *Macrocnemum glabrescens*, *Mangifera indica*, *Platymiscium polystachyum*, *Platypodium elegans*, *Poulsenia armata*, *Pouteria stipitata*, *Prioria copaifera*, *Protium tenuifolium*, *Pterocarpus hayesii*, *Quararibea asterolepis*, *Sapium caudatum*, *Slonea terniflora*, *Solanum hayesii*, *Spondias mombin*, *Spondias nigrescens*, *Sterculia apetala*, *Terminalia amazonica*, *Tetragastris panamensis*, *Trattinickia aspera*, *Trichanthera gigantean*, *Trichilia cipo*, *Virola nobilis*, *Virola sebifera*, *Zanthoxylum panamense*, and *Zanthoxylum procerum* (Montgomery and Sunquist 1975, 1978).

In Panama, *C. hoffmanni* tended to choose trees with masses of lianas in the tree crown as well as trees with direct exposure to sunlight; in addition, 4 of 6 individuals used *A. excelsum* as a modal tree (Montgomery and Sunquist 1975, 1978). Six sloths were radiolocated on 4 or fewer species of trees almost 50% of the time (Montgomery and Sunquist 1975). Average home range size is 1.97 hectare, in which animals use an average of 24.7 trees (18–27 m tall) from 16 different tree species (Montgomery et al. 1973; Montgomery and Sunquist 1975). *C. hoffmanni* moved more than 125 feet (38 m)/day and was located 80 feet (24.4 m) above the ground 20% of the time (Montgomery and Sunquist 1975). The annual cropping rate is 4.29 kg of leaves/ha with 1.1 sloths/ha (Montgomery and Sunquist 1975).

In Venezuela, all animals were caught only in trees; most captures were in moist areas (75%) rather than dry areas (25%); 75% of captures were in evergreen forest versus 25% in orchards; and captures were at 24–460 m above the ground (Handley 1976). A young *C. hoffmanni* was living on *Fuchsia arborescens* in Costa Rica (Ureña et al. 1986).

In an organic cacao farm in Costa Rica, mean home-range size (ha; mean, *SD*) for 6 males (21.52, 56.59) and 6 females (1.69, 24.71) differed, but was not significant; median home-range size for all 12 animals was 4.4 ha (Vaughan et al. 2007). On the cacao farm 3 habitats were used more than expected (living fence, riparian forest, and secondary forest) and 6 habitats were used less than expected (banana, cacao, corn, forest fragment, pasture, and pineapple—Vaughan et al. 2007).

Diet.—*Choloepus hoffmanni* is primarily an arboreal herbivore and eats buds, leaves, flowers, fruit, twig tips, and young stems (Meritt 1985). In Costa Rica, *C. hoffmanni* visited 101 tree species and used 34 species as food (Vaughan et al. 2007). Tree species used as food were fresh leaves and inflorescences of *Cecropia obtusifolia*, *Cestrum racemosa*, *Cordia alliodora*, *Coussapoa villosa*, *Erythrina poeppigiana*, *Eucalyptus globulus*, *Ficus werckleana*, *Hieronyma alchorneoides*, *Hura crepitans*, *Inga oerstediana*, *Leucaena leucocephala*, *Luehea seemannii*, *Ocotea sinuate*, *Piper auratum*, *Spondias mombin*, *Theobroma cacao*, and *Trophis racemosa* (Vaughan et al. 2007).

Diseases and parasites.—Ectoparasites include mites (Acaria, Psoroptidae): *Edentalges* (Christensen and Herrer 1976), *Sarcoptes scabiei* (Sibaja-Morales et al. 2009); ticks (Acaria, Ixodidae): *Amblyomma varium* (Marques et al. 2002; Sibaja-Morales et al. 2009); mosquitoes (Diptera, Culicidae, Culicini): *Aedes terrens*, *A. angustivittatus*, *A. fulvus*, *Haemagogus lucifer*, *Mansonia venezuelensis*, *Psorophora ferox*; (Sabethini) *Trichoprosopon magnus*, *Wyeomyia*; (Anophelini) *Anopheles apicimacula*, *A. eiseni*, *A. punctimacula*, *A. neivai*, *Chagasia bathanus* (Shaw 1969); sand flies (Diptera, Psychodidae): *Lutzomyia gomezi*, *L. ovallesi*, *L. sanguinaria*, *L. shannoni*, *L. trapidoi*, *L. trinidadensis*, *L. ylephiletor* (Christensen and de Vasquez 1982; Christensen and Herrer 1976; Shaw 1964; Thatcher and Hertig 1966); horse flies (Diptera, Tabanidae): *Dichelacera fasciata*, *Philobanus magnificus* (Shaw 1969); triatomines (Hemiptera, Reduviidae): *Triatoma dimidiata* (Shaw 1969); and moths (Lepidoptera, Pyraloidea): *Cryptoses* *choloepi* (Gilmore et al. 2001). Of 65 captive animals in Costa Rica, 19 had pruritic lesions, scabby skin with erythema, hypokeratosis, and alopecia (Sibaja-Morales et al. 2009); no evidence of fungi was present on these 65 animals.

Endoparasites include hemoflagelates *Endotrypanum monterogeii*, *E. schaudinni*, *Leishmania braziliensis*, *L. colombiensis*, *L. equatorensis*, *L. guyanensis*, *L. herreri*, *L. panamensis*, *Trypanosoma cruzi*, *T. leeuwenhoeki*, *T. rangeli*, *T. preguici* (Christensen and Herrer 1976, 1979; Delgado et al. 1993; Franco et al. 1996; Grimaldi et al. 1992; Herrer and Christensen 1976, 1980; Herrer et al. 1973; Katakura et al. 2003; Salazar-Antón et al. 2009; Shaw 1964, 1985; Travi et al. 1989; Zeledón et al. 1975, 1979), *Endotrypanum* (in 7 Costa Rican animals—Zeledón et al. 1975), *L. braziliensis* sensu lato (in 12 of 85 Panamanian animals—Herrer and Telford 1969), *L. braziliensis* (in 8 of 47 Costa Rican animals [Zeledón et al. 1975], in 14 of 18 Costa Rican animals [Zeledon et al. 1975], in 93 of 498 Panamanian animals [Herrer and Christensen 1975], and 86 strains isolated from *C. hoffmanni* [Herrer et al. 1979]), *L. colombiensis* (in 1 Panamanian animal—Kreutzer et al. 1991), *L. herreri* (in 24 of 63 animals—Zeledón et al. 1979); as well as cestode helminths (in 3 of 65 Costa Rican, captive animals—Sibaja-Morales et al. 2009) and coccidian protists (in 10 of 65 Costa Rican, captive animals—Sibaja-Morales et al. 2009). *T. leeuwenhoeki*, also was identified in a Colombian animal (Travi et al. 1989). *C. hoffmanni* (58 of 72) had single or multiple trypanosomatid infections of *L. braziliensis*, *E. schaudinni*, *T. rangeli*, and *T. cruzi* in Panama (Christensen and Herrer 1979). *C. hoffmanni* is the reservoir host of *L. braziliensis* (Christensen and Herrer 1976, 1979; Herrer and Christensen 1976, 1980; Herrer et al. 1973), but does not exhibit skin lesions (Herrer and Christensen 1975). Infection rates of *L. braziliensis* in *C. hoffmanni* are up to 59% in Panama (Herrer and Christensen 1980).

Vesicular stomatitis virus was found in 34 of 94 *C. hoffmanni* from Panama (Srihongse 1969). Six of 29 *C. hoffmanni* had antibodies to a South American subtype of Venezuelan encephalitis (Seymour 1985). None of 29 Panamanian *C. hoffmanni* tested positive for Mayaro or Anhanga viruses nor did any of 57 animals test positive for the yellow fever virus but 39% (of 99 individuals) were positive for the St. Louis encephalitis virus, 1 of 99 was positive for the Ilheus virus, 52% of 23 were positive for Utinga virus, 1 of 5 was positive for the Utive virus, 1 of 29 was positive for the Itaporanga virus, and 25 of 59 were positive for the Changuinola virus (Seymour 1985; Seymour et al. 1983b). In response to experimental infection with St. Louis encephalitis virus detectable viremia ranged from 7 to 27 days with a median of 11 days, and *C. hoffmanni* did not become overtly ill (Seymour et al. 1983a). A virus from the Changuinola complex was isolated from *C. hoffmanni* (Seymour 1985). Two animals from Nicaragua were negative for leptospirosis (Clark et al. 1966). One captive animal recovered from a *Bordetella bronchiseptica* infection after treatment (Hammond et al. 2009). Of 9 animals from Panama, none was positive for *Salmonella* and 1 was positive for *Arizona hinsawii* (Kourany et al. 1976). Zero of 21 *C. hoffmanni* had antibodies against *Toxoplasma* (Frenkel and Sousa 1983). Sera of *C. hoffmanni* was used as an antigen to prepare antisera to determine the host range, vector potential, and general feeding habits of phlebotomine sandflies in central Panama (Tesh et al. 1971).

***Interspecific interactions.*—**Sympatry with the three-toed sloth *Bradypus variegatus* occurs over nearly the entire range of *Choloepus hoffmanni*, but sympatry with the conspecific two-toed sloth, *C. didactylus*, is restricted to small portions of western South America between 0°S and 12°S latitude (Gardner and Naples 2007; Gilmore et al. 2000).

A red alga (*Rufusia pilicola*) and 2 green algae (*Dictyococcus bradypodis* and *Chlorococcum choloepodis*) live on hairs of *C. hoffmanni* (Wujek and Timpano 1986). Commensal invertebrates include the sloth moth (*Cryptosis choloepi*), which lives in the fur (Dyar 1908; Waage and Montgomery 1976). Coprophagic beetles (Coleoptera, Scarabaeidae, *Ontoophagus*) occurred in feces (Sibaja-Morales et al. 2009).

Harpy eagles (*Harpia harpyja*) prey on *C. hoffmanni* (Touchton et al. 2002) as do ocelots (*Leopardus pardalis*—Moreno et al. 2006) and jaguars (*Panthera onca*—Carrillo et al. 2009). Margays (*Leopardus wiedii*) and anacondas (*Eunectes*) also are predators (Goffart 1971). Indigenous peoples hunt *C. hoffmanni* for diverse purposes including for sale as pets to tourists (Meritt et al. 2008).

HUSBANDRY

Captive *Choloepus hoffmanni* eat diverse fruits and vegetables and will also eat meat products (Enders 1935; Meritt 1970, 1973, 1985). *C. hoffmanni* will feed on apples (diced), bananas, bread, carrots, cecropia leaves, citrus, grapes, green beans, ground meat, ground smelt, lettuce, mango, oranges, peas, salmon (canned), spinach, sweet potatoes, and yucca (Enders 1935; Esplin and Woodbury 1961; Gilmore et al. 2001; Herrer and Christensen 1980; Hill and Tenney 1974; Seymour et al. 1983a). The diet of *C. hoffmanni* in the Burnet Park Zoo consists of 90% vegetable matter and 10% animal protein (Moore and Moore 1985). Vegetable matter was romaine, spinach, broccoli, green beans, carrots, apples, yams, potatoes, beets, and turnips. The additives include cod liver oil, hard-boiled eggs, honey, molasses, feline kibble, peanut oil, vitamins, and protein powder. Daily consumption averaged 78% (Moore and Moore 1985). Newly captured adults ate an average of 340 g/day (range, 150–507 g/day; mean, 85 g/kg body mass). Adult zoo animals ate an average of 250 g/day (range, 150–400 g/day) and drank an average of 170 ml of water per day (Meritt 1985).

Capture of *C. hoffmanni* entails placing a noose around the animal while it is still in the tree, pulling the animal toward oneself, putting the animal in a bag, and lowering the bag to the ground (Montgomery and Sunquist 1975).

A colony of *C. hoffmanni* lived in an enclosure measuring 6 feet wide by 12 feet long and 6.5 feet from floor to ceiling (Moore and Moore 1985). The enclosure was made of 1-inch chain link. Plastic milk crates (12 by 12 inches) were placed on the sides for resting sites. Temperature in the cage averaged 25°C (Moore and Moore 1985). A movement sensitive cage for *C. hoffmanni* was constructed from spring-tempered beryllium copper 0.03 inches thick (Howarth and Toole 1973). *C. hoffmanni* were kept in 4 by 6 m cages with 2 sides and a roof fenced with wire mesh (Herrer and Christensen 1980).

Chloralose (80 mg/kg), chloroform, ether, halothane, ketamine (5–10 mg/kg), and pentobarbital have been used to anesthetize *C. hoffmanni* (Callens et al. 1965; Dresse and Gerebtzoff 1962; Goffart et al. 1962; Gómez-Osorio 1964; Hill and Tenney 1974; Langworthy 1935; Meulders et al. 1966; Montgomery and Sunquist 1975; Richter and Bartemeier 1926). Ketamine (2.5 mg/kg)–medetomidine (0.02 mg/kg) combination administered intramuscularly will anesthetize sloths, but bradycardia may occur (Hanley et al. 2008). Atipamazole (0.1 mg/kg) will counteract the anesthetic effects of medetomidine (Hanley et al. 2008).

Choloepus hoffmanni can be immobilized with phencylidine hydrochloride at 1.65 mg/kg in combination with 0.85 mg/kg of promazine hydrochloride (Meritt 1974, 1985). Immobilization was complete within 21 min (range, 15–26 min) and recovery was complete within 5 h (Meritt 1974, 1985).

BEHAVIOR

Choloepus hoffmanni is nocturnal and solitary, and 2 or more are rarely seen in the same tree (Montgomery and Sunquist 1975). *C. hoffmanni* habitually hangs suspended equally by all 4 limbs with its trunk nearly horizontal to the ground (Wislocki 1928b). *C. hoffmanni* tends to sleep in tangled masses of lianas in the canopy (Montgomery and Sunquist 1978). Captive animals rest or sleep about 20 h/day (Goffart 1968), but in the wild are active about 11 h/day through most of the night (Sunquist and Montgomery 1973). Continuous activity of 6 adults ranged from 0.5 to 10 h with an average of 7.6 h (Sunquist and Montgomery 1973). Activity usually begins around 1930 h and continues until about 0530 h (Howarth and Toole 1973). *C. hoffmanni* moves between trees at night via interconnecting tree crowns and vines (Montgomery and Sunquist 1975). Five of 6 animals changed trees on successive nights and some animals moved as much as 300 m (Sunquist and Montgomery 1973). Captive *C. hoffmanni* drank from a hose during bathing (Moore and Moore 1985). *C. hoffmanni* ate an average of 350 g/day or 85 g/kg of body mass (Gilmore et al. 2001). *C. hoffmanni* will hiss, bare its teeth, and try to slash with the claws when disturbed (Enders 1935; Hill and Tenney 1974).

Choloepus hoffmanni easily traverses horizontal supports 13–39 mm in diameter by hooking its claws "over the supports and clasping them between distal ends of volar pads and volar surfaces of claws" (Mendel 1981b:413). On larger supports (52–78 mm in diameter) "volar pads of hands and feet were placed in contact over much of their surfaces with sides of the supports but distal phalanges and claws were held at roughly right angles (Mendel 1981b:413). On even larger supports, "hands were flexed at wrists and feet were hyperflexed at ankles so that volar pads were arched over supports, but friction between them and supports was insufficient to prevent falling" as an animal attempting to traverse a 91-mm-diameter support fell (Mendel 1981b:413).

Feet function similar to clasps (Mendel 1981a). Foot configurations vary with the size of the support as follows: with 13-mm support, flexion of foot at ankle is 41–130°; with 26-mm support, flexion of foot at ankle is 41–100°; with 39-mm support, flexion of foot at ankle is 61–130°; with 52-mm support, flexion of foot at ankle is 11–130°; with 65-mm support, flexion of foot at ankle is 61–130°; with 78-mm support, flexion of foot at ankle is 11–130°; and with 91-mm support, flexion of foot at ankle is 81–130° (Mendel 1981a).

Average rate of locomotion across a branch is 0.14 m/s (range, 0.10–0.16 m/s—Britton and Kline 1939b). Rate of locomotion across a branch is increased 35–48% after excitement or warming in the sun and increased 18–33% after injection with either corticoadrenal extract, adrenalin, or prostigmin (Britton and Kline 1939b). For terrestrial locomotion, animals rise themselves on their soles and palms and use short (mean, 21 cm, range, 10–30 cm) steps (Mendel 1981b). Some animals support themselves with their forelimbs as well as the soles of their feet while on the ground (Mendel 1981b). Usually 3 feet are in contact with the ground during terrestrial locomotion although contralateral fore- and hind limbs are simultaneously in swing phase (Mendel 1981b). Limb movements and sequences as well as the positions of joints during climbing were similar to those during terrestrial locomotion but more uniform and with more time during which the animals were supported by 2 limbs (Mendel 1981b). Animals either back down trees or descend headfirst (Mendel 1981b). *C. hoffmanni* is able to swim (Enders 1935).

Under manipulated conditions with the temperature 25–27°C, *C. hoffmanni* squatted "on the floor or in the fork of a tree, grasping the trunk with the hind or all four limbs" (Goffart 1971:18). *C. hoffmanni* also curled its body. When the temperature was raised to 30°C, *C. hoffmanni* spread out on the floor on its back (Goffart 1971).

Self-grooming is of 2 forms: use of foreclaws to remove food from the head or fur and use of hind limbs to scratch areas of the body, often for 1–6 min (Meritt 1985). Allogrooming is rare except between mothers and infants (Meritt 1985). For several days after birth mothers vigorously lick the head and face of the newborn (Meritt 1985). The anogenital region of the infant is licked daily and any material eliminated was consumed by the mother (Meritt 1985; Moore and Moore 1985). However, after a birth the mother allowed other *C. hoffmanni* to approach and sniff and lick the faces of both the mother and the infant (Moore and Moore 1985). Females stayed close to the mother and licked her face, nipples, and cloaca (Moore and Moore 1985). Infants cling to their mother's venter for the 1st few weeks after birth with mutual licking of face and head (Meritt 1985). When young start exploring they bleat if they cannot easily return to their mothers. Mothers respond to these calls until young are about 6 months of age (Meritt 1985).

In estrus, captive females actively solicit males by pressing close, rubbing their anogenital region against the male, and licking the face (Meritt 1985; Moore and Moore 1985). Estrous behavior lasted 10–14 days (Meritt 1985). Copulation between 1 male and 1 female *C. hoffmanni* took place 31 days postpartum (Moore and Moore 1985). Thrusting during intromissions lasted 45–55 s. Mating activity between 1 pair continued throughout 1 day. Pregnant *C. hoffmanni* change from curled positions to stretched-out positions while resting. Lethargy is experienced 2 days before giving birth. One day before birth, females are in active states (Moore and Moore 1985).

Calls of young *C. hoffmanni* when separated from their mothers are bleats with most energy in 3 bands below 1.4 kHz. The average length of 22 calls was 0.483 s (Montgomery and Sunquist 1974).

In captivity, *C. hoffmanni* shows tolerance when kept in cages of 2 animals (Montgomery and Sunquist 1975). Captive *C. hoffmanni* will share nest boxes, with one resting inside the box while the other rests on top of the box (Moore and Moore 1985). After a male *C. hoffmanni* was introduced into a colony of 7 females, threat behavior ensued (i.e., hissing and slashing) but contact was limited. One female licked the male's face. The male sustained a bite to the lower lip and scratches to both forefeet (Moore and Moore 1985).

GENETICS

Choloepus hoffmanni has a diploid number (2n) of 49–51 chromosomes and a fundamental number (FN) of 61. There are 4 metacentric, 5–11 submetacentric, and 10–15 acrocentric autosomal pairs (Corin-Frederic 1969; Jorge et al. 1985; Svartman et al. 2006). Sex chromosomes are variable (Corin-Frederic 1969; Frederic 1962; Jorge et al. 1978; Jorge and Pereira 2008). In the female 24 pairs of homologous autosomes are found plus only 1 gonosome X; thus, the female is XO (Goffart 1971). The male has 23 pairs of homologous autosomes plus 3 chromosomes without a counterpart: 1 chromosome 23, 1 gonosome X, and 1 chromosome of peculiar shape probably the Y translocated to the 2nd chromosome 23 (Goffart 1971). The Y chromosome may be independent and large or translocated to autosome 21 (Corin-Frederic 1968, 1969; Jorge et al. 1985). One or 2 × chromosomes are present (Jorge and Pereira 2008). Chromatids have a spiral arrangement (Goffart 1971). G-banded and C-banded karyotypes are available (Jorge et al. 1978).

The amino-acid sequence of the α-crystallin A-chain has been determined (de Jong et al. 1985). *C. hoffmanni* has a sequence of DNA that is similar to the exons of caspace-15 (Eckhart et al. 2006). The genome of *C. hoffmanni* has hundreds of foamy virus (a retrovirus) insertions (Katzourakis et al. 2009).

Extracted ribonuclease (13 mg) from the pancreas of 4 *C. hoffmanni* contained about 9 mannose equivalents/mol enzyme of carbohydrates (Havinga and Beintema 1980). The carbohydrate chain in the ribonuclease contains mannose and *N*-acetylglucosamine. The ribonucleases of *C. hoffmanni* are glycoproteins with a carbohydrate attached to Asn-34. The C-terminus of peptide T19C3 is Thr-128. Replacements in the ribonuclease of *C. hoffmanni* are Asp-24 (usually Asn or Thr) and Lys-28 (usually Gln or Glu), which occur in an alpha helix and form salt bridges with each other. The ribonucleases have a histidine at position 73 and an isoleucine at position 108, and an addition of residues at the C-terminus (-Val-Glu-Asp-Ser-Thr).

CONSERVATION

Choloepus hoffmanni is in Appendix III of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (2009) for Costa Rica and is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources (Meritt et al. 2008). This ranking is due to its wide distribution, presumed large population, occurrence in a number of protected areas, tolerance of habitat modification, and the unlikelihood of a precipitous decline (Arita et al. 1990; Moreno and Plese 2006). However, severe deforestation in the range of the northern population could lead to this population being listed as "Near Threatened" (Aguiar and Fonseca 2008; Meritt et al. 2008). The eastern piedmont region of the Andes mountain range is considered by locals a refuge for *C. hoffmanni* (Le Pont and Desjeux 1992).

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LITERATURE CITED

Adam, P. 1999. *Choloepus didactylus*. Mammalian Species 621:1–8.

Agassiz, L. 1846. Nomenclatis zoologigi index universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum deposita, adjectis homonymiis plantarum, nec non variis adnotationibus et emendationibus. Fasciculus XII. Jent et Gassmann, Soloduri.

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.

Allen, J. A. 1910. Additional mammals from Nicaragua. Bulletin of the American Museum of Natural History 28:87–115.

Allen, J. A. 1913. New mammals from Colombia and Ecuador. Bulletin of the American Museum of Natural History 32:469–484.

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.

Barac, G. 1963. Recherches sur la bile de l'unau. Archives Internationales de Physiologie et de Biochimie 71:117–118.

Bárány, M., T. E. Conover, L. H. Schliselfeld, E. Gaetjens, and M. Goffart. 1967. Relation of properties of isolated myosin to those of intact muscles of the cat and sloth. European Journal of Biochemistry 2:156–164.

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 of Florida Press, Gainesville.

Benirschke, K., and H. C. Powell. 1985. On the placentation of sloths. Pp. 237–241 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Betz, E. H., G. Booz, and M. Goffart. 1967. La corticosurréanale chez l'unau (*Choloepus hoffmanni* Peters). Comptes Rendus des Séances de la Société de Biologie et de ses Filiales 161:1132–1134.

Borror, D. J. 1960. Dictionary of word roots and combining forms. Mayfield Publishing Co., Mountain View, California.

Britton, S. W. [W. S.]. 1941. Form and function in the sloth (concluded). Quarterly Review of Biology 16:190–207.

Britton, S. W., and W. E. Atkinson. 1938. Poikilothermism in the sloth. Journal of Mammalogy 19:94–99.

Britton, S. W., and R. F. Kline. 1939a. Emotional hyperglycemia and hyperthermia in tropical mammals and reptiles. American Journal of Physiology 126:730–734.

Britton, S. W., and R. F. Kline. 1939b. Augmentation of activity in the sloth by adrenal extract, emotion and other conditions. American Journal of Physiology 127:127–130.

Britton, S. W., R. F. Kline, and H. Silvette. 1938. Blood-chemical and other conditions in normal and adrenalectomized sloths. American Journal of Physiology 123:701–704.

Bugge, J. 1979. Cephalic arterial pattern in New World edentates and Old World pangolins with special reference to their phylogenetic relationships and taxonomy. Acta Anatomica 105:37–46.

Cabrera, A. 1958. Catalogo de los mamiferos de America del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoologicas 4:1–308. (dated 1957 but published in 1958; see notice on page 308 of the publication).

Callens, M., J. Colle, M. A. Gerebtzoff, and M. Goffart. 1965. Excitatory and depressive phenomena in the olfactory system of the sloth (*Choloepus hoffmanni* Peters). Archives Internationals de Physiologie et de Biochimie 73:748–761.

Carrillo, E., T. K. Fuller, and J. C. Saenz. 2009. Jaguar (*Panthera onca*) hunting activity: effects of prey distribution and availability. Journal of Tropical Ecology 25:563–567.

Cession-Fossion, A., and J. Lecomte. 1963. Présence d'histamine et de substance P dans certains tissus de l'unau (*Choloepus hoffmanni*). Archives Internationales de Physiologie et de Biochimie 70: 397–400.

Christensen, H. A., and A. M. de Vasquez. 1982. The tree buttress biotope: a pathobiocenosis of *Leishmania braziliensis*. American Journal of Tropical Medicine and Hygiene 31:243–251.

Christensen, H. A., and A. Herrer. 1976. Neotropical sand flies (Diptera: Psychodidae), invertebrate hosts of *Endotrypanum schaudini* (Kinetoplastida: Trypanosomatidae). Journal of Medical Entomology 13:299–303.

Christensen, H. A., and A. Herrer. 1979. Susceptibility of sand flies (Diptera: Psychodidae) to Trypanosomatidae from two-toed sloths (Edentata: Bradypodidae). Journal of Medical Entomology 16:424–427.

Clark, L. G., V. M. Varela-Diaz, C. R. Sulzer, R. R. Marshak, and C. J. Hollister. 1966. Lepospirosis in Nicaragua: preliminary report on the first year of study. American Journal of Tropical Medicine and Hygiene 15:735–742.

Closon, J., and H. Wankenne. 1962. Etude de la function thyroïdienne au moyen de $Na^{131}I$, chez *Choloepus hoffmanni* Peters. II. Iodoaminoacides marques thyroglobuliniques. Archives Internationales de Physiologie et Biochimie 70:312–313.

Convention on International Trade in Endangered Species of Wild Fauna and Flora. 2009. Appendix III. http://www.cites.org/eng/app/appendices.shtml, accessed 7 August 2010.

Corin-Frederic, J. 1968. Technique amelioree pour l'etude des meioses males et en particulier du mode d'association des gonosomes. Genetica 39:345–350.

Corin-Frederic, J. 1969. Les formulas gonosomiques dites aberrants chez les mammifères euteries. Chromosoma 27:268–287.

Cornalia, E. 1849. Vertebratorium synopsis in Musaeo Mediolanensis extantium quae per novam orbem Cajetanas Osculati collegit annis 1846–47–1848 speciebus novis vel minus cognitis adjectis nec non discriptionibus atque iconibus illustratis. Typogaphia Corbetta, Modoetiae, Italy.

de Jong, W. W., A. Zweers, K. A. Joysey, J. T. Gleaves, and D. Boulter. 1985. Protein sequence analysis applied to xenarthran and pholidote phylogeny. Pp. 65–76 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Delgado, O., M. Castes, A. C. White Jr., and R. D. Kreutzer. 1993. *Leishmania colombiensis* in Venezuela. American Journal of Tropical Medicine and Hygiene 48:143–147.

Demanez, J. P., M. Goffart, and A. Ledoux. 1968. La fonction vestibulaire chez l'unau (*Choloepus hoffmani* Peters). Archives Internationales de Physiologie et de Biochimie 76:253–267.

Denis, C., C. Jeuniaux, M. A. Gerebtzoff, and M. Goffart. 1967. La digestion stomacale chez un paresseux: l'anau *Choloepus hoffmanni* Peters. Annales de la Société Royale Zoologique de Beligique 97:9–29.

Digimorph. 2003. *Choloepus hoffmanni*, two-toed sloth. http://digimorph.org/specimens/Choloepus_hoffmanni/, accessed 7 August 2010.

Dresse, A., and M. A. Gerebtzoff. 1962. Occurrence of dopa, dopamine, noradrenaline and adrenaline in the adrenal medulla of the sloth (*Choloepus hoffmanni* Peters). Archives Internationals de Physiologie et de Biochimie 70:313–315.

Dresse, A., and M. Goffart. 1963. Les catécholamines de la médullosurréale de l'unau (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 71:271–273.

Duchesne, P. Y. 1967. Le complexe hypothalamo–hypophysaire des paresseux (*Choloepus hoffmanni* Pet. et *Bradypus tridactylus* L.). Acta Anatomica 67:452–464.

Dyar, H. G. 1908. A pyralid inhabiting the fur of the living sloth. Proceedings of the Entomological Society of Washington 9: 142–144.

Eckhart, L., A. Uthman, W. Sipos, and E. Taschachler. 2006. Genome sequence comparison reveals independent inactivation of the caspase-15 gene in different evolutionary lineages of mammals. Molecular Biology and Evolution 23:2081–2089.

Eisenberg, J. F., and R. W. Thorington, Jr. 1973. A preliminary analysis of a Neotropical mammal fauna. Biotropica 5:150–161.

Enders, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panama. Bulletin of the Museum of Comparative Zoology 78:383–502.

Enders, R. K. 1940. Observations of sloths in captivity at higher altitudes in the tropics and in Pennsylvania. Journal of Mammalogy 21:5–7.

Enders, R. K., and D. E. Davis. 1936. Body temperatures of some Central American mammals. Journal of Mammalogy 17:165–166.

Enger, S., and T. H. Bullock. 1965. Physiological basis of slothfulness in the sloth. Hvalrådets Skriftet 48:143–160.

Esplin, D. W., and D. M. Woodbury. 1961. Spinal reflexes and seizure patterns in the two-toed sloth. Science 133:1426–1427.

Fontaine, Y. A., and M. Goffart. 1963. Teneur en hormone thyréotrope de l'hypophyse de l'unau (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 71:462–465.

Franco, A. M. R., H. Momen, R. D. Naiff, C. F. S. Moreira, M. P. Deane, and G. Grimaldi, Jr. 1996. Enzyme polymorphism in *Endotrypanum* and numerical analysis of isoenzyme data. Parasitology 113:39–48.

Frederic, J. 1962. Recherches préliminaries sur l'assortiment chromosomique chez *Choloepus hoffmanni* Peters. Archives Internationales de Physiologie et de Biochimie 70:317–319.

Frenkel, J. K., and O. E. Sousa. 1983. Antibodies to toxoplasma in Panamanian mammals. Journal of Parasitology 69:244–245.

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., and V. L. Naples. 2007. Family Megalonychidae P. Gerais, 1855. Pp. 165–168 in Mammals of South America. Vol. 1. Marsupials, xenarthrans, shrews, and bats (A. L. Gardner, ed.). University of Chicago Press, Chicago, Illinois. (Dated 2007 but published in 2008.)

Genoways, H. H., and R. M. Timm. 2003. The xenarthrans of Nicaragua. Journal of Neotropical Mammalogy 10:231–253.

Gerebtzoff, M. A. 1962. Caractères structuraux primitifs de l'isocortex du paresseux, *Choloepus hoffmanni* Peters. Archives Internationales de Physiologie et de Biochimie 70:315–317.

Giffin, E. B., and M. Gillett. 1996. Neurological and osteological definitions of cervical vertebrae in mammals. Brain, Behavior, and Evolution 47:214–218.

Gillespie, D. S. 2003. Xenarthra: Edentata. Pp. 397–407 in Zoo and wild animal medicine (M. E. Fower and E. Miller, eds.). W. B. Saunders Company, Philadelphia, Pennsylvania.

Gilmore, D. P., C. P. Costa, and D. P. F. Duarte. 2000. An update on the physiology of two- and three-toed sloths. Brazilian Journal of Medical and Biological Research 33:129–146.

Gilmore, D. P., C. P. Costa, and D. P. F. Duarte. 2001. Sloth biology: an update on their physiological ecology, behaviour and role as vectors of arthropods and arboviruses. Brazilian Journal of Medical Biological Research 34:9–25.

Goffart, M. 1968. The problem of slothfulness in the didactyl sloth (*Choloepus hoffmannii* Pet.). Electromyography 8:245–251.

Goffart, M. 1971. Function and form in the sloth. Pergamon Press, New York.

Goffart, M., M. A. Gerebtzoff, and P. Y. Duchesne. 1967. The spinal roots in the sloth (*Choloepus hoffmanni* Peters). Journal of Comparative Neurology 131:393–404.

Goffart, M., O. Holmes, and Z. M. Bacq. 1962. Some mechanical properties of skeletal muscle in the sloth (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 70:103–106.

Gómez-Osorio, H. 1964. Bases anatomicas de la unidad functional neuroña glia. Antioquia Medica 14:275–284.

Goodwin, G. G. 1946. Mammals of Costa Rica. Bulletin of the American Museum of Natural History 87:271–473.

Gotch, A. F. 1979. Mammals: their Latin names explained. Blandford Press, Poole, Dorset, United Kingdom.

Grand, T. I. 1978. Adaptations of tissue and limb segments to facilitate moving and feeding in arboreal folivores. Pp. 231–241 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. London Medical Repository 15:297–311.

Gray, J. E. 1827. Synopsis of the species of the class Mammalia as arranged with reference to their organization by Cuvier and other naturalists, volume the fifth, of The animal kingdom arranged in conformity with its organization, by the Baron Cuvier, with additional descriptions of all the species hitherto named, and of many not before noticed, by Edward Griffith … and others (E. Griffith, ed.). Geo. B. Whitaker, 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.

Grimaldi, G., R. D. Kreutzer, Y. Hashiguchi, E. A. Gomez, T. Mimory, and R. B. Tesh. 1992. Description of *Leishmania equatorensis*, sp. n. (Kinetoplastida: Trypanosomatidae), a new parasite infecting arboreal mammals in Ecuador. Memorias do Instituto Oswaldo Cruz Rio de Janeiro 87:221–228.

Hammond, E. E., D. Sosa, R. Beckerman, and R. F. Aguilar. 2009. Respiratory disease associated with *Bordetella bronchiseptica* in a Hoffmann's two-toed sloth (*Choloepus hoffmanni*). Journal of Zoo and Wildlife Medicine 40:369–372.

Handley, C. O., Jr. 1976. Mammals of the Smithsonian Venezuelan project. Brigham Young University Science Bulletin, Biological Series 20:1–89.

Hanley, C. S., et al. 2008. Immobilization of the free-ranging Hoffmann's two-toed and brown-throated three-toed sloths using ketamine and medetomidine: a comparison of physiologic parameters. Journal of Wildlife Diseases 44:938–945.

Hartman, F. A. 1959. Notes on the adrenal of the sloth. Anatomical Record 133:105–113.

Havinga, J., and J. J. Beintema. 1980. Pancreatic ribonucleases of mammals with ruminant-like digestion: amino-acid sequences of hippopotamus and sloth ribonucleases. European Journal of Biochemistry 110:131–142.

Hayssen, V. 2008. *Bradypus pygmaeus* (Pilosa: Bradypodidae). Mammalian Species 812:1–4.

Hayssen, V. 2010. *Bradypus variegatus* (Pilosa: Bradypodidae). Mammalian Species 42(850):19–32.

Hayssen, V., A. van Tienhoven, and A. van Tienhoven. 1993. Asdell's patterns of mammalian reproduction. Cornell University Press, Ithaca, New York.

Herrer, A., and H. A. Christensen. 1975. Infrequency of gross skin lesions among Panamanian forest mammals with cutaneous leishmaniasis. Parasitology 71:87–92.

Herrer, A., and H. A. Christensen. 1976. Epidemiological patterns of cutaneous leishmaniasis in Panama. III. Endemic persistence of the disease. American Journal of Tropical Medicine and Hygiene 25:54–58.

Herrer, A., and H. A. Christensen. 1980. *Leishmania braziliensis* in the Panamanian two-toed sloth, *Choloepus hoffmanni*. American Journal of Tropical Medicine and Hygiene 29:1196–1200.

Herrer, A., H. A. Christensen, and R. J. Beumer. 1973. Reservoir hosts of cutaneous leishmaniasis among Panamanian forest mammals. American Journal of Tropical Medicine and Hygiene 22:585–591.

Herrer, A., and S. R. Telford, Jr. 1969. *Leishmania braziliensis* isolated from sloths in Panama. Science 164:1419–1420.

Herrer, A., S. R. Teldford, and H. A. Christensen. 1979. *Leishmania braziliensis*: dissemination of Panamanian strains in golden hamsters. Experimental Parasitology 48:359–363.

Hill, N., and S. M. Tenney. 1974. Ventilatory responses to CO_2 and hypoxia in the two-toed sloth (*Choloepus hoffmanni*). Respiration Physiology 22:311–323.

Hoffman, E. A., and E. L. Ritman. 1984. Three-dimensional lung geometry and function of dog and sloth. American Review of Respiratory Disease 129:A267.

Howarth, S. T., and J. F. Toole. 1973. Some observations on the circadian rhythm of *Choloepus hoffmanni*, the two-toed sloth. Laboratory Animal Science 23:377–379.

Illiger, K. 1811. Prodromus systematis mammalium et avium. Salfield, Berlin, Germany.

Irving, L., P. F. Scholander, and S. W. Grinnell. 1942. Experimental studies of the respiration of sloths. Journal of Cellular and Comparative Physiology 20:189–210.

Jammaers, C. 1965. Isolement et propriétés de la myoglobine de l'unau (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 73:651–672.

Jeuniaux, C. 1962. Recherche de polysaccharidases dans l'estomac d'un paresseux, *Choloepus hoffmanni* Pet. (mammifère edenté). Archives Internationales de Physiologie et de Biochimie 70:407–408.

Jones, M. L. 1982. Longevity of captive mammals. Der Zoologische Garten 52:113–128.

Jorge, W., D. A. Meritt, and K. Benirschke. 1978. Chromosome studies in Edentata. Cytobios 18:157–172.

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. Vizcaíno and W. J. Loughry, eds.). University Press of Florida, Gainesville.

Katakura, K., et al. 2003. Identification of *Endotrypanum* species from a sloth, a squirrel and *Lutzomyia* sandflies in Ecuador by PCR amplification and sequencing of the mini-exon gene. Journal of Veterinary Medical Science 65:649–653.

Katzourakis, A., R. J. Gifford, M. Tristem, M. T. P. Gilbert, and O. G. Pybus. 2009. Macroevolution of complex retroviruses. Science 325:1512.

Kourany, M., L. Bowdre, and A. Herrer. 1976. Panamanian forest mammals as carriers of *Salmonella*. American Journal of Tropical Medicine and Hygiene 25:449–455.

Kreutzer, R. D., et al. 1991. Characterization of *Leishmania colombiensis* sp. n (Kinetoplastida: Trypanosomatidae), a new parasite infecting humans, animals, and phlebotomine sand flies in Colombia and Panama. American Journal of Tropical Medicine and Hygiene 44:662–675.

Langworthy, O. R. 1935. A physiological study of the cerebral motor cortex and the control of posture in the sloth. Journal of Comparative Neurology 62:333–348.

Le Pont, F., and P. Desjeux. 1992. Présence de *Choloepus hoffmanni* dans les Yungas de la Paz (Bolivie). Mammalia 56:484–485.

Lecomte, J. 1964. Kininogénes et enzymes kinino-formateurs chez le paresseux (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 72:926–928.

Lemaire, M., M. Goffart, J. Closon, and R. Winand. 1969. La fonction thyroidienne chez l'unau (*Choloepus hoffmanni* Peters). General and Comparative Endocrinology 12:181–199.

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.

Lönnberg, E. 1928. Notes on some South American edentates. Arkiv fur Zoologi Stockholm 20(10):1–17.

Lönnberg, E. 1942. Notes on Xenarthra from Brazil and Bolivia. Arkiv fur Zoologi Stockholm 34A(9):1–58.

Marder, J., and R. B. Reeves. 1967. Acid–base status of the two-toed sloth (*Choloepus hoffmanni*) in acute hypothermia. Physiologist 10: 243.

Maréchal, G., M. Goffart, and X. Aubert. 1963. Nouvelles recherches sur les propriétés du muscle squelettique du paresseux (*Choloepus hoffmanni* Peters). Archives Internationales de Physiolgie et de Biochimie 71:236–240.

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). Memórias do Instituto Oswaldo Cruz, Rio de Janeiro 97:1141–1146.

Maslin, A., C. Stepien, and E. Bucholtz. 2007. Morphological and molecular analysis of vertebral variants in the two-toed sloths *Choloepus hoffmanni* and *Choloepus didactylus*. Journal of Vertebrate Paleontology 27:113A.

McCarthy, T. J., D. L. Anderson, and G. A. Cruz D. 1999. Tree sloths (Mammalia: Xenarthra) in Nicaragua and Honduras, Central America. Southwestern Naturalist 44:410–414.

McNab, B. K. 1978. Energetics of arboreal folivores: physiological problems and ecological consequences of feeding on an ubiquitous food supply. Pp. 153–162 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Mendel, F. C. 1981a. Foot of two-toed sloths: its anatomy and potential uses relative to size of support. Journal of Morphology 170:357–372.

Mendel, F. C. 1981b. Use of hands and feet of two-toed sloths (*Choloepus hoffmanni*) during climbing and terrestrial locomotion. Journal of Mammalogy 62:413–421.

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.

Menegaux, A. 1906. Description of d'un bradypodidé nouveau (*Choloepus hoffmanni peruvianus* subsp. nov.) provenant du Pérou. Bulletin du Museum D'Histoire Naturelle 1906:460–464.

Meritt, D. A., Jr. 1970. Edentate diets currently in use at Lincoln Park Zoo, Chicago. International Zoo Yearbook 10:136–138.

Meritt, D. A., Jr. 1973. Edentate diets II. Two-toed sloths. Laboratory Animal Science 23:543–545.

Meritt, D. A., Jr. 1974. A further note on the immobilization of sloths. International Zoo Yearbook 14:160–161.

Meritt, D. A., Jr. 1976. A simplified method for diagnosing parturition in Hoffmann's sloth, *Choloepus hoffmanni*. International Zoo Yearbook 16:152–153.

Meritt, D. A., Jr. 1985. The two-toed Hoffmann's sloth, *Choloepus hoffmanni* Peters. Pp. 333–341 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Meritt, D. A., Jr., and G. F. Meritt. 1976. Sex ratios of Hoffmann's sloth, *Choloepus hoffmanni* Peters and three-toed sloth, *Bradypus infuscatus* Wagler in Panama. American Midland Naturalist 96: 472–473.

Meritt, M., Members of the International Union for Conservation of Nature and Natural Resources Species Survival Commission Edentate Specialist Group. 2008. *Choloepus hoffmanni*. In International Union for Conservation of Nature and Natural Resources 2009. International Union for Conservation of Nature and Natural Resources Red list of threatened species. Version 2009.1. www.iucnredlist.org/details/4778/0, accessed 4 August 2010.

Meulders, M., J. Gybels, J. Bergmans, M. A. Gerebtzoff, and M. Goffart. 1966. Sensory projections of somatic, auditory and visual origin to the cerebral cortex of the sloth (*Choloepus hoffmanni* Peters). Journal of Comparative Neurology 126: 535–546.

Montgomery, G. G., W. W. Cochran, and M. E. Sunquist. 1973. Radiolocating arboreal vertebrates in tropical forest. Journal of Wildlife Management 37:426–428.

Montgomery, G. G., and M. E. Sunquist. 1974. Contact–distress calls of young sloths. Journal of Mammalogy 55:211–213.

Montgomery, G. G., and M. E. Sunquist. 1975. Impact of sloths on Neotropical forest energy flow and nutrient cycling. Pp. 69–98 in Tropical ecological systems: trends in terrestrial and aquatic research (F. B. Golley and E. Medina, eds.). Springer-Verlag, New York.

Montgomery, G. G., and M. E. Sunquist. 1978. Habitat selection and use by two-toed and three-toed sloths. Pp. 329–359 in The ecology of arboreal folivores (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Moore, A. W., and D. E. Moore. 1985. Behavioral aspects of mating, parturition, and pregnancy in a colony of Hoffmann's two-toed sloths. Pp. 453–461 in Proceedings of the Meeting of the Northeast Regional American Association of Zoological Parks and Aquariums.

Moreno, R. S., R. W. Kays, and R. S. Samudio, Jr. 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. Journal of Mammalogy 87:808–816.

Moreno, S., and T. Plese. 2006. The illegal traffic in sloths and threats to their survival in Colombia. Edentata 7:10–18.

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.

Naples, V. L. 1985. The superficial facial musculature in sloths and vermilinguas (anteaters). Pp. 173–189 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Palem-Vliers, M., N. Brouhon, J. Buret, C. Heusghem, and H. Van Cauwenberge. 1962. Activité surrénalienne chez l'anau, *Choloepus hoffmanni* Pet. Archives Internationales de Physiologie et de Biochimie 70:412–414.

Partridge, J. 1991. The two-toed sloth. International Zoo News 38: 23–28.

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), palaeanodonts, and a miscellany. Fieldiana, Geology (New Series) 24:1–79.

Peters, W. 1858. [Charakterist eines neuen zweizehigen Faulthiers.] Monatsberichte der Königlichen Preuss. Akademie der Wissenschaften zu Berlin 1858:128.

Philippot, E., and M. Goffart. 1963. Nouvelles recherches sur les récepteurs α and β à l'adrénaline chez l'unau (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 71:241–244.

Philippot, E., M. Goffart, and A. Dresse. 1965. Le systeme surrenalo-sympathique chez le paresseux (*Choloepus hoffmanni* Peters). Archives Internationales de Physiologie et de Biochimie 73: 476–504.

Pye, A. 1979. The structure of the cochlea in some mammals. Journal of Zoology (London) 187:39–53.

Rafinesque, C. S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. L'Imprimerie de Jean Barravecchia, Palermo, Italy.

Richter, C. P., and L. H. Bartemeier. 1926. Decerebrate rigidity of the sloth. Brain 49:207–225.

Rowlatt, U. 1980. Functional and nonfunctional determinants of mammalian cardiac anatomy. Pp. 259–300 in Hearts and heart-like organs: comparative anatomy and development (G. H. Bourne, ed.). Academic Press, Inc., New York.

Salazar-Antón, F., et al. 2009. *Trypanosoma rangeli* genotypes association with *Rhodnius prolixus* and *R. pallescens* allopatric distributions in Central America. Infection, Genetics, and Evolution 9:1306–1310.

Salazar-Bravo, J. A., K. H. Redford, and A. M. Stearman. 1990. El perezoso de dos dedos de Hoffmann (*Choloepus hoffmanni* Peters, 1859; Megalonychidae) en Bolivia. Museo Nacional de Historia Natural (Bolivia) Comunicación 9:18–21.

Schinz, H. R. 1821. Das Thierreich eingetheilt-nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Erster band. Säugethiere und Vógel. J. G. Cotta'schen Buchhandlung, Stuttgart and Tübingen, Germany.

Sclater, P. L. 1856. List of mammals and birds collected by Mr. Bridges in the vicinity of the town of David in the province of Chiriqui in the state of Panama. Proceedings of the Zoological Society of London 1856:138–143.

Seymour, C. 1985. Sloths as hosts of arboviruses. Pp. 269–278 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Seymour, C., L. D. Kramer, and P. H. Peralta. 1983a. Experimental St. Louis encephalitis virus infection of sloths and cormorants. American Journal of Tropical Medicine and Hygiene 32:844–853.

Seymour, C., P. H. Peralta, and G. C. Montgomery. 1983b. Serologic evidence of natural togavirus infections in Panamanian sloths and other vertebrates. American Journal of Tropical Medicine and Hygiene 32:854–861.

Shaw, J. J. 1964. A possible vector of *Endotrypanum schaudinni* of the sloth *Choloepus hoffmanni*, in Panama. Nature 201:417–418.

Shaw, J. J. 1969. The haemoflagellates of sloths. London School of Hygiene and Tropical Medicine 13:1–132.

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.

Sibaja-Morales, K. D., et al. 2009. Gastrointestinal parasites and ectoparasites of *Bradypus variegatus* and *Choloepus hoffmanni* sloths in captivity from Costa Rica. Journal of Zoo and Wildlife Medicine 40:86–90.

Sicher, H. 1944. Masticatory apparatus of the sloths. Field Museum of Natural History, Zoology Series 29:161–168.

Soma, H. 1976. Trophoblast: a comparison between human and other mammalian placentas. Journal of Tokyo Medical College 34: 873–883. (In Japanese.)

Srihongse, S. 1969. Vesicular stomatitis virus infections in Panamanian primates and other vertebrates. American Journal of Epidemiology 90:69–76.

Stocker, G. 1987. Order Edentata/family Megalonychidae. *Choloepus hoffmanni*. http://www.cites.org/eng/resources/id/fauna/volume1/a-107.002.002.002%20choloepus%20hoffmanni_e.pdf, accessed 7 August 2010.

Strominger, N. L. 1969. A comparison of the pyramidal tracts in two species of edentate. Brain Research 15:259–262.

Sunquist, M. E., and G. G. Montgomery. 1973. Activity patterns and rates of movement of two-toed and three-toed sloths (*Choloepus hoffmanni* and *Bradypus infuscatus*). Journal of Mammalogy 54: 946–954.

Svartman, M., G. Stone, and R. Stanyon. 2006. The ancestral eutherian karyotype is present in Xenarthra. PLoS Genetics 2: 1006–1011.

Swartz, S. M. 1985. Suspensory support and skeletal loading: an in-vivo bone strain analysis of two-toed sloths. American Zoologist 25:13A.

Taube, E., J. Keravec, 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.

Tesh, R. B., B. N. Chaniotis, M. D. Aronson, and K. M. Johnson. 1971. Natural host preferences of Panamanian phlebotomine sandflies as determined by precipitin test. American Journal of Tropical Medicine and Hygiene 20:150–156.

Thatcher, V. E., and M. Hertig. 1966. Field studies on the feeding habits and diurnal shelters of some *Phlebotomus* sandflies (Diptera: Psychodidae) in Panama. Annals of the Entomological Society of America 59:46–52.

Timm, R. M., D. E. Wilson, B. L. Clauson, R. K. Laval, and C. S. Vaughn. 1989. Mammals of the La Selva–Braulio Carrillo complex, Costa Rica. North American Fauna 75:1–162.

Toole, J. F. 1972. Blood chemistry of the sloth (*Choloepus hoffmanni* and *Bradypus tridactylus*). Laboratory Animal Science 22: 118–121.

Toole, J. F., and T. H. Bullock. 1973. Neuromuscular responses of sloths. Journal of Comparative Neurology 149:259–270.

Touchton, J. M., Y.-C. Hsu, and A. Palleroni. 2002. Foraging ecology of reintroduced captive-bred subadult harpy eagles (*Harpia harpyja*) on Barro Colorado Island, Panama. Ornitologica Neotropical 13:365–379.

Travi, B. L., A. Zea, and A. D'Alessandro. 1989. *Trypanosoma* (*Herpetosoma*) *leeuwenhoeki* in *Choloepus hoffmanni* and *Didelphis marsupialis* of the Pacific coast of Colombia. Journal of Parasitology 75:218–224.

Tschudi, J. J., von. 1844. Mammalium conspectus. Archiv für Naturgeschichte 10:244–255.

Turner, W. 1890. The convolutions of the brain: a study in comparative anatomy. Journal of Anatomy and Physiology 25: 105–153.

Ureña, H. M., C. R. Chacón, A. S. Faerrón, and S. T. Lizano. 1986. Hallazgo de *Bradypus griseus* y *Choloepus hoffmannii* (Edentata: Bradypodidae) en tierras altas de Costa Rica. Revista de Biología Tropical 34:165–166.

Vaughan, C., O. Ramírez, G. Herrera, and R. Guries. 2007. Spatial ecology and conservation of two sloth species in a cacao landscape in Limón, Costa Rica. Biodiversity and Conservation 16: 2293–2310.

Waage, J. K., and G. G. Montgomery. 1976. *Cryptosis choloepi*: a coprophagous moth that lives on a sloth. Science 192:157–158.

Wallace, C., and Y. C. Oppenheim. 1996. Hematology and serum chemistry profiles of captive Hoffmann's two-toed sloths (*Choloepus hoffmanni*). Journal of Zoo and Wildlife Medicine 27: 339–345.

Watillon, M., and M. Goffart. 1969. The eye of the sloth (*Choloepus hoffmanni* Peters). Acta Zoologica et Pathologica Antverpiensia 49:107–122.

Webb, S. D. 1985. The interrelationships of tree sloths and ground sloths. Pp. 105–112 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Wetzel, R. M. 1985. The identification and distribution of recent Xenarthra (= Edentata). Pp. 5–21 in The evolution and ecology of armadillos, sloths, and vermilinguas (G. G. Montgomery, ed.). Smithsonian Institution Press, Washington, D.C.

Wetzel, R. M., and F. D. de Ávila-Pires. 1980. Identification and distribution of the Recent sloths of Brazil (Edentata). Revista Brasileira de Biologia 40:831–836.

Wislocki, G. B. 1928a. Further observations upon the minute structure of the labyrinth in the placenta of the sloths. Anatomical Record 40:385–395.

Wislocki, G. B. 1928b. Observations on the gross and microscopic anatomy of the sloths (*Bradypus griseus griseus* Gray and *Choloepus hoffmanni* Peters). Journal of Morphology and Physiology 46:317–377.

Wislocki, G. B. 1938. The topography of the hypophysis in the Xenarthra. Anatomical Record 70:451–463.

Wujek, D. E., and J. M. Cocuzza. 1986. Morphology of hair of two- and three-toed sloths (Edentata: Bradypodidae). Revista de Biología Tropical 34:243–246.

Wujek, D. E., and P. Timpano. 1986. *Rufusia* (Porphyridiales, Phragmonemataceae), a new red alga from sloth hair. Brenesia 25–26:163–168.

Zeledón, R., C. Ponce, and E. de Ponce. 1975. The isolation of *Leishmania braziliensis* from sloths in Costa Rica. American Journal of Tropical Medicine and Hygiene 24:706–707.

Zeledón, R., C. Ponce, and J. Murillo. 1979. *Leishmania herreri* sp. n. from sloths and sandflies of Costa Rica. Journal of Parasitology 65:275–279.

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