

## A new species of three-toed sloth (Mammalia: Xenarthra) from Panamá, with a review of the genus *Bradypus*

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**Abstract.**—Morphological and morphometric analyses of three-toed sloths (*Bradypus*) from the islands of Bocas del Toro reveal rapid differentiation of several populations during the Holocene. These islands, lying off the Caribbean coast of western Panamá, were separated from the adjacent mainland by rising sea levels during the past 10,000 years. The sequence of island formation and the approximate ages of the islands are known. In at least four independent events, sloths on five of the islands evolved smaller size following insularization. Sloths on the younger islands remain conspecific with mainland populations of *Bradypus variegatus*. On Isla Escudo de Veraguas—the oldest and most remote island of the archipelago—however, the three-toed sloth has differentiated to the species level, and we here describe it as *Bradypus pygmaeus*. We provide updated diagnoses and distributions for the species of *Bradypus*, including a key to the genus.

**Resumen.**—Se realizaron análisis morfológicos y morfométricos de los perezosos de tres dedos (*Bradypus*) de las islas de Bocas del Toro, que mostraron una diferenciación rápida de varias de las poblaciones durante el Holoceno. Estas islas, que se ubican en la costa caribeña del occidente de Panamá, se separaron de tierra firme debido a aumentos en los niveles del mar durante los últimos 10.000 años. Se conoce la secuencia de formación de las islas y sus edades aproximadas. Los perezosos de cinco de las islas evolucionaron hacia un tamaño corporal menor en por lo menos cuatro eventos independientes, siguiendo el proceso de insularización. Consideramos que tanto los perezosos de tierra firme como los de las islas jóvenes son representantes de la especie *Bradypus variegatus*; sin embargo en la Isla Escudo de Veraguas, la más vieja y más remota del archipiélago, el perezoso de tres dedos ha logrado el nivel de especie y lo describimos acá como una especie nueva, *Bradypus pygmaeus*. Presentamos caracteres diagnósticos y distribuciones para las especies de *Bradypus*, incluyendo una clave de las especies del género.

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Together with armadillos and anteaters, sloths make up the Neotropical order Xenarthra (Gardner 1993, or magnorder Xenarthra sensu McKenna & Bell 1997). Two distantly related genera of sloths, *Choloepus* (two-toed sloths) and *Bradypus* (three-toed sloths) are extant. Over much of their

ranges, one species of *Choloepus* and one species of *Bradypus* occur together in the same habitat, exhibiting biotic sympatry (= syntopy; Sunquist & Montgomery 1973, Wetzell 1985, Taube et al. 1999). The two genera are easily distinguished by the number of clawed digits on their forelimbs (two

for *Choloepus*; three in *Bradypus*), by the blunter muzzle of *Bradypus*, and by dentition—stronger and more complex in *Choloepus*, while simple and peg-like in *Bradypus* (Naples 1982, Wetzel 1985). Here we consider only the three-toed sloths, *Bradypus*.

The three nominal species of *Bradypus* can be distinguished both externally and cranially (Wetzel & Avila-Pires 1980, Wetzel 1985). The maned sloth (*Bradypus torquatus*) of southeastern Brazil has a distinctive plume or mane of long, jet-black hair from its nape to the middle of its back, and its skull is characterized by inflated pterygoid sinuses (illustrated by Wetzel 1985:10). Both the pale-throated sloth, *Bradypus tridactylus* (Guianas, eastcentral Venezuela, and northcentral Brazil), and the brown-throated sloth, *B. variegatus* (Honduras to Argentina), lack the mane and inflated pterygoids. Adult males of these two species also have a large orange patch (speculum) on the dorsum. They may be distinguished from each other by the bright golden-yellow throat and face in *B. tridactylus*, whereas the throat is brownish, at least at the base of the hairs, in *B. variegatus*. Most *B. variegatus* also possess a facial stripe not present in *B. tridactylus*. A single pair of large foramina in the anterodorsal nasopharynx in *B. tridactylus* are lacking in *B. variegatus* (illustrated in Wetzel 1985:10). Emmons & Feer (1997) provided external color illustrations of these sloths.

Three-toed sloths are arboreal folivores. They eat leaves of a variety of trees, including, but by no means limited to, *Cecropia* spp., which is a common early successional tree in Neotropical rainforests (Carvalho 1960, Montgomery & Sunquist 1975, Chiarello 1998b). Concomitant with their energy-poor diet, they have low metabolic rates and are not fully homeothermic (Britton & Atkinson 1938). Interestingly, temperature regulation is more effective in pregnant females (Morrison 1945). The percent of body weight made up of muscle in

*Bradypus* is about half that of most mammals (Britton & Kline 1939); its muscle mass to surface area ratio may not be enough to create sufficient heat to maintain a constant body temperature. Clearly, the low level of energy expenditure by three-toed sloths for both movement and thermoregulation directly relates to their diet of leaves.

The natural history of *Bradypus* indicates a low potential for dispersal. Sloths avoid predation largely by avoiding detection, moving very slowly in trees (Brattstrom 1966). Their small home ranges average 1.6 ha (Montgomery & Sunquist 1975, see also Chiarello 1998a). Furthermore, their outer fur harbors an alga, which grows in grooves in the surface of the hair (Alston 1879:183, Aiello 1985), giving the pelage a green tint and providing camouflage. Sloths move even more slowly on the ground than in trees, traveling on average 0.4 km per hour (Britton & Kline 1939). Surprisingly, they are known to swim well in rivers (Beebe 1926:7–9, Carvalho 1960), but we have found no reference to their swimming in salt water. Perhaps they have a behavioral aversion to salt water or to rough water and wave action. Their relatively large size, restricted diet, and low dispersal potential make sloths a model system for investigating the evolution of body size in large insular mammals.

*The islands of Bocas del Toro.*—The province of Bocas del Toro is located on the Caribbean coast of northwestern Panamá adjacent to Costa Rica (Fig. 1). Just off the coast lies a group of continental islands that were formed during the Holocene as a result of postglacial events, including rising sea level and continental submergence due to meltwater loading and redistribution of the Earth's magma. Rising sea levels isolated hilltops and ridges, first as peninsulae, and then eventually completely separated them as islands. The islands of Bocas del Toro have low elevations and occupy a Tropical Moist Forest life zone, *bosque húmedo tropical* (OEA 1959). They vary in

age, size, distance from the mainland, and depth of surrounding water. Mangrove swamps (primarily red mangroves, *Rhizophora mangle*) fringe parts of the shoreline of Bocas del Toro and the coasts of some of the islands, possibly acting as added barriers to the dispersal of some species.

Combining ocean floor topography with studies of pollen and coral cores from the western Caribbean allowed Handley and M. Varn (in litt.) to determine the sequence of island formation and to estimate the dates of separation events for the various islands of Bocas del Toro. We present their general conclusions as an introduction to this island system and to interpret the evolution of three-toed sloths in Bocas del Toro. Assuming that the present-day submarine topography of Bocas del Toro is not very different from that of the terrestrial topography 10,000 years ago (before flooding), then the depths of water at which land bridges to various present-day islands disappeared should be apparent from current sea-floor maps. Thus, given estimates of sea level at various time intervals in the past, it is possible to estimate the approximate date of isolation of each island. Handley and Varn obtained sea-floor data from maps of Bocas del Toro produced by the U.S. Army Map Service. Using geographic information systems (GIS) software, they digitized data points from isobars below present sea level. With a program produced by the Morphometrics Laboratory of the National Museum of Natural History, they converted the data points to a database transferable to Surfer 4 and then connected them to produce maps of bathymetric contours of Bocas del Toro for various depths below present sea level.

To estimate sea levels over the past 10,000 years, Handley and Varn utilized three models based on coral and pollen cores taken in the western Caribbean. Radioisotope dating of *Acropora palmata*, a coral restricted to the upper 5 m of water, formed the bases of the curves of depth-below-current-sea level vs. time produced by Lighty et al. (1982) and Fairbanks

(1989). Bartlett & Barghoorn (1973) used the pollen of *Rhizophora mangle* in deep-sea cores from the Gatún Basin in Panamá to produce a similar curve. *Rhizophora mangle* is an obligate saltwater species and represents the major component of Neotropical coastal mangrove swamps. Handley and Varn then created a composite curve with years-before-present and depth-below-current-sea-level as axes. Using this curve, they roughly dated each of the bathymetric maps and thus estimated island ages from dates of disappearance of land bridges between islands and the mainland. Even if their absolute dates err in one direction or the other, relative dates of island formation will be correct to the extent that sea-floor contours in this region have remained constant through the Holocene.

Isla Escudo de Veraguas (= Isla Escudo) occupies a position well outside the Laguna de Chiriquí (Fig. 1a), and was the first of the islands to be separated from the mainland of Bocas del Toro (ca. 8900 years B.P.). It fragmented from the eastern shore of the Península Valiente and is not directly related to the other islands (Fig. 1b). To the northwest of the Península Valiente and Isla Escudo, the islands of the Laguna de Chiriquí are much younger (Fig. 1a). They fragmented sequentially from the Península Tierra Oscura, which was once a long, J-shaped peninsula jutting out from the southwestern shore of the Laguna de Chiriquí. The peninsula was formed by the opening of the Boca del Drago Pass at the western end of the Laguna (Fig. 1b). These islands are related to each other, but not to Isla Escudo. The outermost, facing the ocean, are about 5000 years old: Isla Colón, which was the first to split off of the Península Tierra Oscura (ca. 5200 years B.P.), and Isla Bastimentos, which separated from the peninsula along with what now is Cayo Nancy (ca. 4700 years B.P.). Cayo Agua became isolated from the adjacent mainland (now part of Isla Popa) about 3400 years B.P. Cayo Nancy recently split from Isla Bastimentos proper (<1000 years B.P.), and

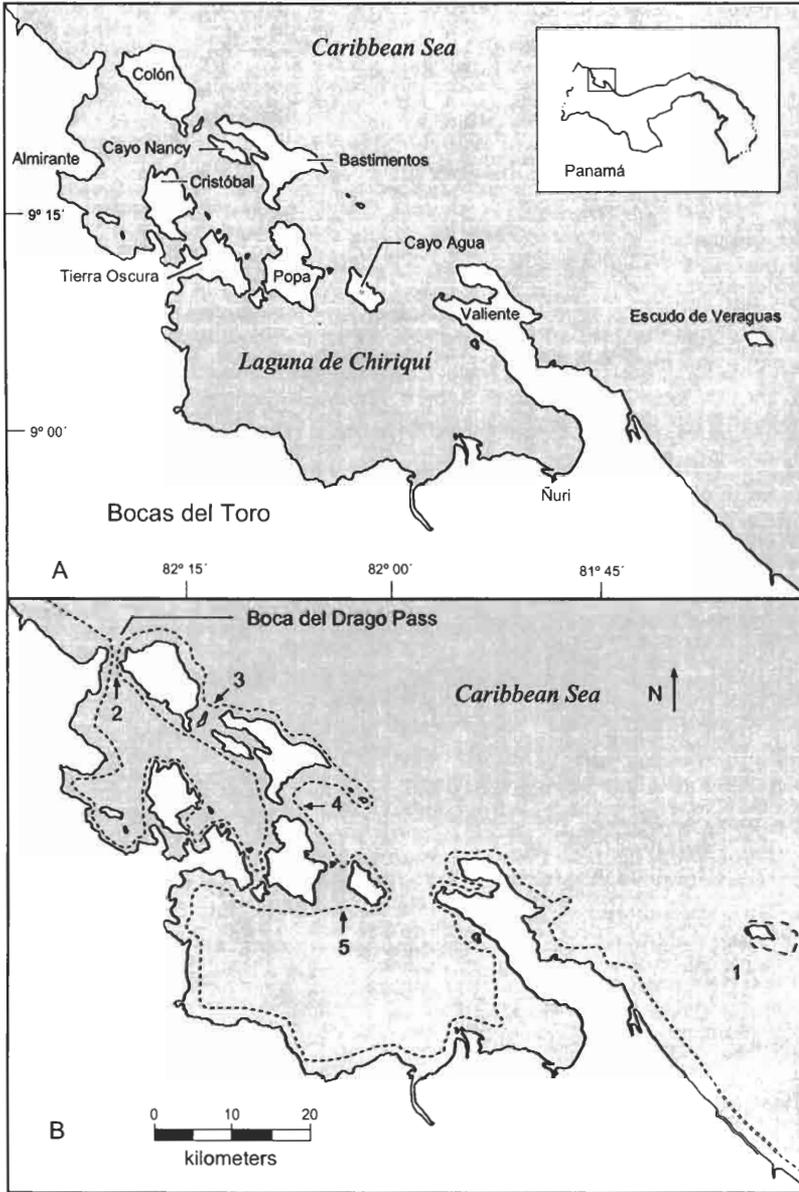


Fig. 1. Maps of Bocas del Toro showing major islands and place names on the mainland (A, upper) and reconstruction of the sequence of island formation (B, lower). In B, the dashed line approximates sea level at 10 m below present. Major events in the formation of the islands (Handley & Varn, in litt.) are as follows: 1) Isla Escudo separated from the southern coast of the province, ca. 8900 years B.P.; 2) the Boca del Drago pass opened, creating a J-shaped peninsula in the Laguna de Chiriquí, ca. 6300 years B.P.; 3) Isla Colón became isolated from the peninsula, ca. 5200 years B.P.; 4) the superisland Isla Bastimentos-Cayo Nancy became separated from what remained of the peninsula, ca. 4700 years B.P.; and 5) Cayo Agua was formed, ca. 3400 years B.P. More recently (in the past 1000 years), Isla Cristóbal and Isla Popa separated from the mainland, and Cayo Nancy split from Isla Bastimentos.

mangroves fringe the shallow channel between it and Isla Bastimentos. Isla Popa and Isla Cristóbal each separated from the mainland in the past 1000 years. They are isolated from the mainland only by narrow, shallow channels through mangroves. Island area and distance from the mainland follow, for each of the major islands: Cayo Agua—14.5 km<sup>2</sup>, 6.6 km; Cayo Nancy—6.8 km<sup>2</sup>, 9.5 km; Isla Bastimentos—51.5 km<sup>2</sup>, 6.3 km; Isla Colón—59.0 km<sup>2</sup>, 1.5 km; Isla Cristóbal—36.8 km<sup>2</sup>, 0.3 km; Isla Escudo—4.3 km<sup>2</sup>, 17.6 km; Isla Popa—53.0 km<sup>2</sup>, 1.8 km. Further discussion of the history of Bocas del Toro and surrounding regions can be found in Jackson et al. (1996).

Biological interest in the islands of Bocas del Toro emerged recently (summarized in Handley 1959, Olson 1993, Kalko & Handley 1994). Early collecting took place from 1958 to 1967 and intensified from 1987 to 1993, when scientists from the Smithsonian Institution sampled the biota on all of the islands and at several sites on the adjacent mainland. The major mainland collecting sites of sloths were Almirante and Tierra Oscura in the west, and Ñuri and the Península Valiente in the east (Fig. 1a). Smaller collections of *Bradypus* were made at Sibube and Changuinola in western Bocas del Toro. We assume that the fauna of the coastal plain of Bocas del Toro was relatively uniform as the islands sequentially became isolated from the mainland (Handley 1959, Olson 1993, Kalko & Handley 1994). Colinvaux (1997) has shown that despite significant climatological fluctuations, the vegetation of lowland tropical forests in Panamá remained intact during glacial times, lending support to this premise. Subsequent to their isolation, numerous species—including bats, rodents, cats, and weasels present on the nearby mainland—have been extirpated from some or all of the islands. Conversely, a few apparently relict species no longer found on the adjacent mainland are present on the islands. Many of the species that have survived on the islands exhibit marked morphological

differentiation from their mainland relatives. For example, a fruit-eating bat, *Artibeus incommittatus*, underwent rapid differentiation on Isla Escudo (Kalko & Handley 1994).

Collectors found three-toed sloths (*Bradypus*) on all of the major islands, as well as at the mainland sites. The *Bradypus* on several of the islands were notably small, and some lived in the red mangroves rather than in upland forest trees as elsewhere. On Isla Escudo, *Bradypus* was found only in mangroves. Except for one purchased at Tierra Oscura from a local boy who claimed to have caught it in a mangrove, no three-toed sloths were found in mangroves on the mainland of Bocas del Toro. The 1993 expedition searched in vain for sloths in extensive areas of mangroves near Ñuri. This ecological separation, coupled with the observed size differences, spawned the current study.

#### Materials and Methods

*Museum specimens.*—We examined a total of 531 specimens of the genus *Bradypus* in 13 natural history collections (see Specimens examined) identified as follows: American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BM, now Natural History Museum of London); Field Museum, Chicago (FMNH); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); Instituto del Desarrollo de Recursos Naturales Renovables, INDERENA, Bogotá (IND-M; specimens now part of the collection of the Instituto Alexander von Humboldt, Villa de Leiva); Michigan State University Museum, East Lansing (MSU); Museo del Instituto La Salle, Bogotá (MLS); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); United States National Museum of Natural History, Washington, DC (USNM; \* denotes specimens returned to Panamá-INRENARE); Universidad del Cauca, Popayán (UC); Universidad del Valle, Cali

(UV), University of Kansas Natural History Museum, Lawrence (KU); and University of Michigan Museum of Zoology, Ann Arbor (UMMZ). Information provided by any source other than the collector is placed in [brackets]. Numbers in (parentheses) after the country name indicate the total number of specimens examined for that country.

In the Specimens examined sections, latitude and longitude are given after the place name to which the coordinates belong. Coordinates provided by the collector appear in parentheses. We provide latitude and longitude in brackets for localities that appear in the following standard references: Brazil—Paynter & Traylor (1991); Bolivia—Paynter et al. (1975); Colombia—Paynter (1997), except where more exact coordinates are given by Hershkovitz (1947) or in original sources cited in Anderson (1999), as noted; Costa Rica—McPherson (1985); Ecuador—Paynter (1993); French Guiana, Guyana, and Suriname—Stephens & Traylor (1985); Nicaragua—USBGN (1956), except where more exact coordinates appear in Genoways (1973); Panamá—Fairchild & Handley (1966); Peru—Stephens & Traylor (1983); and Venezuela—Paynter (1982); additional coordinates for localities in several countries were taken from Hershkovitz (1977), and are so noted.

*Pelage analyses.*—We analyzed geographic variation in pelage characters in the *Bradypus* from Bocas del Toro and in *B. variegatus* from other regions, principally from Nicaragua, central Panamá, and Colombia. Pelage analyses were based on specimens in the ICN, IND-M, KU, MLS, USNM, UC, and UV collections. Because different methods of field preparation or tanning can affect the color of fur, we did not consider subtle color differences. We focused on striking differences in color and color pattern. We eliminated juvenal and immature animals from the pelage analyses by including only individuals whose skulls indicated them as adult (see Cranial analyses) if skull was available, or that had clearly reached adult size if only a skin was pre-

sent, based on the total length of specimens in that population verified as adult by their cranial characters.

We found seven pelage characters that varied among populations. Overall facial color is either tan (off-white to pale brown) or yellow (golden). Orange around the eyes is present to various degrees, or absent. Brow-color categories are: dark brow (a terminal band of 2–3 cm of dark brown or black hair), some dark hair on brow (a narrow terminal band of only about 1 cm of dark brown hair), or dark hair not present (in which case the brow is generally pale brown, with no dark terminal band). A distinct boundary line on the brow between the dark hair of the brow and the longer, paler hair of the crown is visible in some specimens, but in others the color of the brow hair blends in with that of the crown. Some individuals have a stripe down the midsagittal plane of the back. Dorsal underfur always appears blotchy, with pale and dark patches, but the surface coloration varies. Overall dorsal appearance is blotchy with brown and beige patches when the outer fur color corresponds to the color of the underfur in that particular area of the dorsum. In other animals, the surface color is uniformly pale, regardless of the color of the underfur. The color of the underfur can be observed by pushing aside the outer fur and examining the shorter underfur. In some specimens, the fur of the crown and the sides of the head is extremely long, overhanging the forehead and sides of the face and creating the aspect of a hood. In other specimens, the fur of the crown and sides of the head is shorter and not noticeably overhanging the face.

*Cranial analyses.*—For cranial analyses, we included only sloths that had reached adult size (Age classes 2 and 3, as defined below). Because no explicit standards exist for aging *Bradypus* skulls (but see Naples 1982:6–7), we developed the following system of age categories.

Age class 0, newborn and juvenile: all su-

tures open; size small; anterior skull elements small and poorly developed; masseter-temporal fossa smooth; postmastoid fossa not indicated; frontal sinuses little, if at all, swollen; lambdoidal crest not formed.

Age class 1, immature: all sutures open; size intermediate; anterior skull elements nearing adult proportions; masseter-temporal fossa usually smooth; postmastoid fossa may be indicated; frontal sinuses somewhat swollen; lambdoidal crest present (immatures may retain some juvenal characters).

Age class 2, young adult: all sutures open; size large; anterior skull elements at adult proportions. Young adults must also have some of the following: masseter-temporal fossa rugose to the touch; postmastoid fossa prominent; frontal sinuses swollen; lambdoidal crest sharp-edged.

Age class 3, full adult: some or all sutures closed; size large; anterior skull elements fully developed. Fully adult sloths have most or all of the following: masseter-temporal fossa visibly rugose; postmastoid fossa prominent; frontal sinuses swollen; lambdoidal crest sharp-edged.

Individuals reach adult size by Age class 2 in *Bradypus*. Skulls with all cranial sutures closed clearly represent adults, but closure of even one suture signifies full-adult status. The nasal (internasal) and interparietal sutures are usually the last to close. Closure of the basioccipital-basisphenoid suture represents a good indicator of maturity in bats and rodents, but this suture closes late in *Bradypus* after adult size is attained. Its lack of closure should not be used alone to judge adulthood.

*Measurements.*—We recorded external measurements—total length (TOTAL); tail length (TAIL); hind foot length (HF); and ear length (EAR)—in mm and body mass in kg from museum labels. Using dial calipers to the nearest 0.1 mm, we took 14 measurements on all adult-sized skulls of *Bradypus* (Age classes 2 and 3) from Bocas

del Toro (Fig. 2). To examine geographic variation in size in *B. variegatus* from other parts of its range, we measured only greatest length of skull (GLS) on series of *B. variegatus* of Age classes 2 and 3, using either dial or digital calipers to the nearest 0.1 mm. We chose GLS because preliminary morphometric analyses indicated that it was most highly correlated with general size in *Bradypus*. Specimens from the American Museum of Natural History were not included in the quantitative analyses, but we report them as additional confirmed distributional records. Cranial nomenclature follows Naples (1982). We here define and illustrate (Fig. 2) our measurements for *Bradypus*.

Greatest length of skull (GLS): Distance between the anteriormost point of the nasals and a line connecting the posteriormost surfaces of the occipital condyles.

Anterior zygomatic breadth (AZB): Greatest breadth across the jugal (anterior) zygomata.

Posterior zygomatic breadth (PZB): Greatest breadth across the squamosal (posterior) zygomata.

Postorbital breadth (POB): Least breadth across the constriction of the frontals, posterior to the postorbital processes.

Squamosal process length (SPL): Distance between anteriormost point of the squamosal process of temporal (posterior zygomata), and the notch formed by the junction of the posterior border of the bulla and the mastoid process.

Maxillary toothrow length (MTRL): Greatest alveolar length from the anteriormost edge of the anterior chisel-shaped tooth to the posteriormost edge of the last molariform tooth in a maxillary toothrow.

Postpalatal length (PPL): Distance between the anteriormost margin of the mesopterygoid fossa and the anteriormost margin of the foramen magnum.

Palatal breadth (PB): Greatest alveolar breadth across the lateral margins of the first molariform teeth.

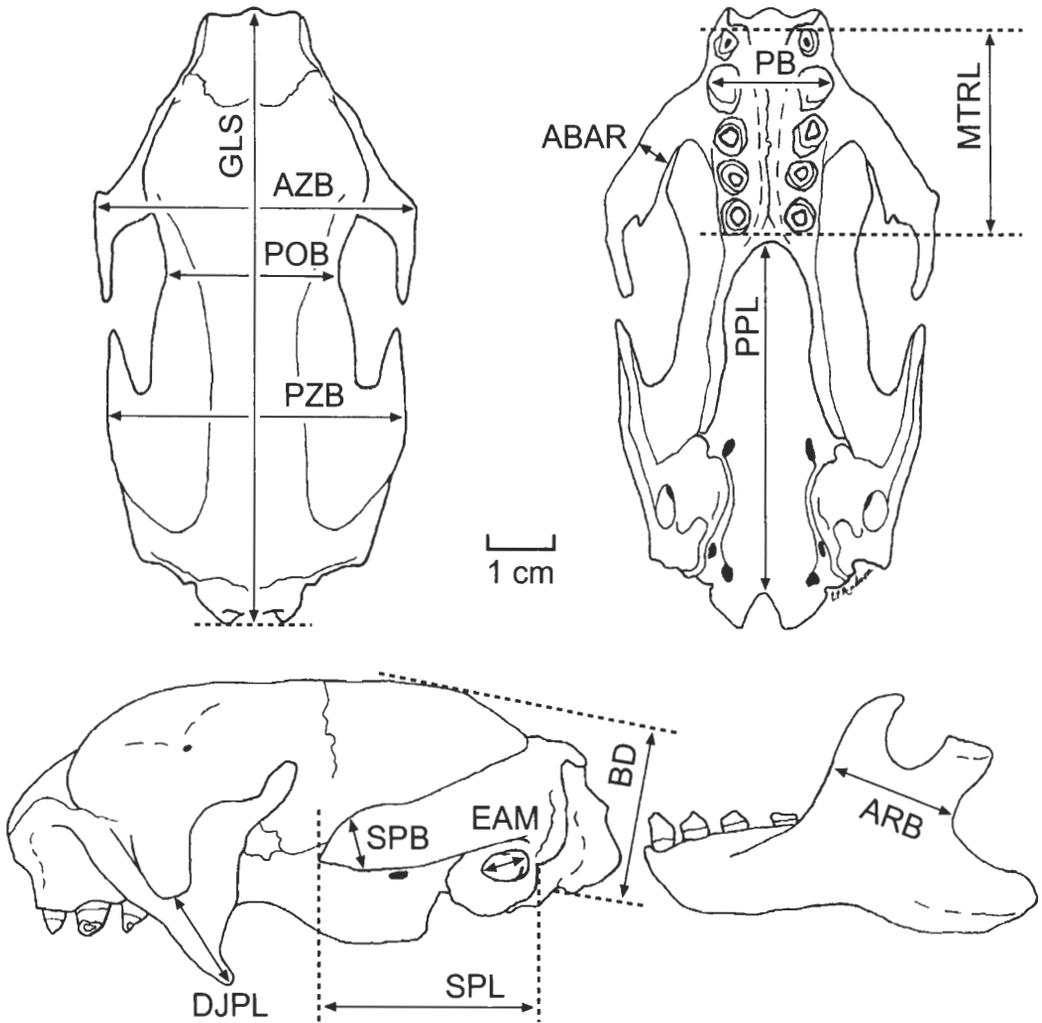


Fig. 2. Dorsal, ventral, and lateral views of a cranium and lateral view of a mandible of *Bradypus variegatus*, illustrating method of taking cranial measurements. Abbreviations and measurements are defined in the text.

**Braincase depth (BD):** Greatest distance between the medioventral surface of the basioccipital and the dorsalmost point of the braincase.

**Antorbital bar breadth (ABAR):** Least breadth across the flattened antorbital bar (jugal process of zygomata) anterior to its division into the ascending and descending jugal processes, taken in ventral view.

**Descending jugal process length (DJPL):** Distance between the ventralmost point of the descending jugal process and the

nearest point on the dorsal border of the jugal process.

**Greatest external auditory meatus diameter (EAM):** greatest internal diameter of the external auditory meatus.

**Squamosal process breadth (SPB):** Breadth of the squamosal process, taken 5 mm posterior to the anterior tip of the process.

**Ascending mandibular ramus breadth (ARB):** Least distance between the anteriormost point of the angular notch of the mandible, between the condylar and an-

gular processes, and the nearest point on the anterior margin of the ascending ramus below the coronoid process.

*Statistics.*—We calculated descriptive statistics and performed analyses of variance (ANOVAs) using MINITAB 11.12 software for personal computers (MINITAB 1996) and used SAS 6.12 for UNIX (SAS 1990) to examine the data using multivariate statistics. We used a Type-I error rate of  $\alpha = 0.05$  for all tests. The probability levels that we report should be considered approximate, however, because our sample sizes were too small to test adequately for departures from multivariate normality.

We conducted a multiple-group discriminant function analysis (DFA) on the *Bradypus* of Bocas del Toro using  $\log_{10}$ -transformed measurements. Collection locality denoted group membership. Ear length and body mass were excluded from the DFA because few individuals carried those measurements. We tested for multivariate differences among localities by *F*-statistics for Mahalanobis distances between pairs of group centroids using Holm's (1979) modification of the Bonferroni correction for multiple comparisons. We then conducted multiple unplanned comparisons between all pairs of localities for scores on the first two canonical axes, using Tukey's test with a family-wide error rate of  $\alpha = 0.05$ .

Additionally, we performed a principal components analysis on the same data matrix without regard to collection locality. The first principal component (PC I) of the covariance matrix of  $\log_{10}$ -transformed measurements was used as the best measure of overall sloth size in further analyses. For the two populations with several individuals of both Age classes 2 and 3 (Cayo Nancy and Isla Escudo), we tested for a difference in mean PC I scores between age classes while controlling for locality, using a general linear model. Likewise, for those localities with multiple individuals of each sex—Cayo Agua, Cayo Nancy, Isla Popa,

Península Valiente, and Tierra Oscura—we tested for a difference in mean PC I scores between sexes, again controlling for locality in a general linear model. Finally, we tested for differences between all pairs of localities on PC I, with the same protocols as in the comparisons of scores on the first two canonical axes.

We used measurements of greatest length of skull (GLS) to compare the small sloths from Bocas del Toro with *Bradypus variegatus* from mainland localities outside Bocas del Toro, as preliminary analyses indicated that GLS correlated highly with PC I, and thus represented a good measure of overall size. Series from Bonanza, El Recreo, and Tepeyac (Nicaragua); Bajo Calima-Río Raposo and Tumaco (Colombia); and Mojui dos Campos (Brazil) were our six mainland localities outside of Bocas del Toro, as few specimens were available from other sites. We conducted an ANOVA on GLS measurements of the six mainland samples outside Bocas del Toro and our samples from the five islands with small sloths in Bocas del Toro (Cayo Agua, Cayo Nancy, Isla Bastimentos, Isla Colón, and Isla Escudo), using a Tukey's test with a family-wide error rate of  $\alpha = 0.05$ .

## Results

*Pelage.*—Externally, the *Bradypus* of Bocas del Toro resemble specimens from central Panamá more closely than they do those of Nicaragua or South America (Table 1). All Central American specimens have tan faces, whereas faces of most South American sloths have a yellowish cast. In addition, while the sloths of Bocas del Toro, central Panamá, and many localities in Colombia have at least some orange coloring around their eyes, Nicaraguan specimens lack this trait. Most individuals from Bocas del Toro have either some (~1 cm) or much (2–3 cm) black or dark brown brow hair. Specimens from central Panamá and extreme NW Colombia match those from Bocas del Toro in this trait, but Nicaraguan

and most other South American sloths lack a dark brown brow. A distinct brow line is found in specimens from central Panamá, extreme NW Colombia, and in some localities in Bocas del Toro, but not in specimens from Nicaragua or elsewhere in Central America or western Colombia. Thus, the *Bradypus* from Bocas del Toro group with other Central American and western Colombian three-toed sloths, with closer affinity to those from central Panamá and extreme NW Colombia to the east rather than with sloths from Nicaragua to the northwest.

Within Bocas del Toro, geographically proximate populations share discrete pelage characters, often linking island populations with nearby populations on the mainland (Table 1; Fig. 1). For example, the only populations in Bocas del Toro with individuals lacking a dorsal stripe are found at Tierra Oscura and on the adjacent islands of Cristóbal, Popa, and Cayo Nancy. For dorsal appearance, there is a west-to-east cline from uniform to blotchy. The populations with the highest frequencies of individuals with a distinct brow line are two proximate localities in the west (Isla Colón and the adjacent mainland at Almirante) and two in the east (Isla Escudo and Ñuri, the nearest site on the mainland). Finally, while sloths from most localities in Bocas del Toro have orange eye patches, those of four central localities (Almirante, Isla Cristóbal, Isla Popa, and Península Valiente) have little if any orange. Overall, pelage of specimens from Isla Escudo closely matches pelage characters found at Ñuri. However, characters variable in the Ñuri population appear to be fixed on Isla Escudo. Sloths from Isla Escudo were unique in possessing long hair on the crown and sides of the head, giving the impression of a hood.

*Quantitative measurements.*—Both univariate and multivariate statistics documented the smaller overall size of *Bradypus* on the five outer islands (the older islands) of the archipelago of Bocas del Toro—Cayo Agua, Cayo Nancy, Isla Bastimentos, Isla

Table 1.—Discrete pelage characters for *Bradypus* from Bocas del Toro as well as from other selected regions throughout the range of *Bradypus variegatus*. Character abbreviations are as follows: face color, tan (T) or yellow (Y); orange on face, yes (Y), slight (sit), or no (N); dark on brow, yes (Y), some (S), or no (N); line on brow, yes (Y) or no (N); dorsal stripe, yes (Y) or no (N); dorsal appearance, uniform (U) or blotchy (B); and hood, yes (Y) or no (N). If samples are mixed for a character, both states are given with the most common state before the slash. Geographic groupings are arranged from NW to SE, with abbreviations as follows: NIC, Nicaragua; A, Almirante; CO, Isla Colón; N, Cayo Nancy; B, Isla Bastimentos; CR, Isla Cristóbal; TO, Tierra Oscura; P, Isla Popa; CA, Cayo Agua; V, Península Valiente; NU, Ñuri; E, Isla Escudo; CP, Central Panamá; SAW, South America west of the Andes; SAE, South America east of the Andes. Refer to Fig. 1 for geographic locations within Bocas del Toro.

Character	Locality																
	NIC	A	CO	N	B	CR	TO	P	CA	V	NU	E	CP	SAW	SAE		
Face color	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	Y/T	
Orange on face	N	Y	Y	Y	Y	Y	Y/slt	N	Y	slt/N	Y	Y	Y	Y	Y	Y/N	N/Y
Dark on brow	N	S/Y	Y/S	S/N	S	S	N	N	S/Y	S	S/Y	Y	Y	Y	N/Y	N/Y	N/Y
Line on brow	N	N/Y	Y	N	N	N	N	N	N/Y	N	N/Y	Y	Y	Y	N/Y	N/Y	N/Y
Dorsal stripe	Y	Y	Y	N/Y	Y	N	N	Y/N	Y	Y	Y	Y	Y	Y	Y	Y	Y
Dorsal appearance	B	U/B	U	U/B	U	U	B/U	B/U	U/B	B/U	B/U	B/U	U/B	B	B	B	B
Hood	N	N	N	N	N	N	N	N	N	N	N	Y	N	N	N	N	N

Table 2.—Descriptive statistics for external and cranial measurements (mm), mass (kg), and scores on multivariate axes of *Bradypus* of Age classes 2 and 3 from Bocas del Toro, Panamá, showing small body size of several insular populations. Each measurement or score is given as the mean  $\pm$  2 standard errors, minimum–maximum, and sample size. See text and Fig. 2 for methods of taking cranial measurements, Hall (1962) for external measurements, and Materials and Methods for details of the multivariate analyses (C 1 & PC I). Islands are arranged from outermost to innermost; mainland localities from west to east.

Locality	Total length	Tail length	Hind foot length	Ear length	Mass	Greatest length of skull	Anterior zygomatic breadth	Posterior zygomatic breadth
Isla Escudo	505.4 $\pm$ 11.42 485–530 (7)	49.7 $\pm$ 4.26 45–60 (7)	102.4 $\pm$ 3.92 94–110 (7)	10.0 $\pm$ — 10–10 (1)	2.9 $\pm$ 0.37 2.5–3.5 (7)	69.0 $\pm$ 1.34 67.5–72.2 (6)	41.5 $\pm$ 2.30 38.3–45.7 (6)	39.5 $\pm$ 2.04 36.5–42.9 (6)
Isla Bastimentos	513.2 $\pm$ 18.04 485–540 (6)	42.8 $\pm$ 4.72 37–50 (6)	114.0 $\pm$ 2.76 110–118 (5)	12.2 $\pm$ 0.95 11–14 (6)	3.2 $\pm$ 0.20 3.1–3.3 (2)	70.4 $\pm$ 1.53 68.3–73.4 (6)	42.6 $\pm$ 1.93 40.4–45.2 (5)	39.1 $\pm$ 1.23 37.0–41.6 (6)
Cayo Agua	547.8 $\pm$ 11.26 520–575 (12)	45.1 $\pm$ 1.25 40–47 (11)	114.5 $\pm$ 3.52 105–127 (12)	12.5 $\pm$ 0.58 11–14 (12)	3.8 $\pm$ 0.19 3.3–4.2 (10)	72.5 $\pm$ 1.18 68.7–74.9 (12)	45.3 $\pm$ 0.75 43.5–47.8 (12)	44.0 $\pm$ 0.68 42.1–45.9 (12)
Isla Colón	547.7 $\pm$ 14.44 535–560 (3)	49.7 $\pm$ 8.36 45–58 (3)	121.3 $\pm$ 8.52 113–127 (3)	11.0 $\pm$ 1.15 10–12 (3)	3.7 $\pm$ 0.48 3.2–4.0 (3)	73.4 $\pm$ 2.96 70.5–76.6 (4)	45.5 $\pm$ 2.42 42.6–48.5 (4)	42.8 $\pm$ 1.88 40.2–44.6 (4)
Cayo Nancy	565.4 $\pm$ 15.84 542–585 (5)	55.2 $\pm$ 3.76 49–60 (5)	117.4 $\pm$ 7.14 106–128 (5)	13.0 $\pm$ 2.60 11–18 (5)	3.6 $\pm$ 0.37 3.1–4.2 (5)	76.0 $\pm$ 2.60 73.2–80.0 (5)	44.2 $\pm$ 1.90 42.1–47.1 (5)	42.5 $\pm$ 2.26 39.3–45.2 (5)
Isla Cristóbal	582.4 $\pm$ 16.28 555–605 (5)	56.6 $\pm$ 2.42 53–60 (5)	124.5 $\pm$ 4.80 120–131 (4)	10.6 $\pm$ 1.96 8–14 (5)	4.1 $\pm$ 0.47 3.4–4.8 (5)	79.3 $\pm$ 2.00 76.5–82.1 (5)	47.6 $\pm$ 1.81 44.4–49.8 (5)	44.8 $\pm$ 1.93 41.3–47.0 (5)
Isla Popa	591.5 $\pm$ 18.28 562–618 (6)	57.7 $\pm$ 2.90 52–61 (6)	128.0 $\pm$ 6.04 116–138 (6)	11.5 $\pm$ 1.00 10–13 (6)	4.4 $\pm$ 0.31 3.9–5.0 (6)	80.0 $\pm$ 1.29 77.7–82.5 (6)	48.9 $\pm$ 1.76 46.3–52.3 (6)	45.6 $\pm$ 1.13 43.8–47.4 (6)
Almirante	581.5 $\pm$ 57.80 531–657 (4)	67.3 $\pm$ 5.46 62–71 (3)	135.0 $\pm$ 12.56 118–148 (4)	14.5 $\pm$ 1.00 14–16 (4)	— $\pm$ — — (0)	79.7 $\pm$ 2.88 75.9–82.5 (4)	48.6 $\pm$ 1.74 46.8–50.5 (4)	45.6 $\pm$ 1.41 44.2–47.4 (4)
Tierra Oscura	591.4 $\pm$ 28.20 538–645 (7)	48.7 $\pm$ 3.60 42–55 (7)	134.4 $\pm$ 4.40 126–140 (7)	13.3 $\pm$ 1.36 10–15 (7)	5.2 $\pm$ 0.56 4.5–6.3 (7)	80.5 $\pm$ 2.50 76.1–86.0 (7)	50.0 $\pm$ 1.60 47.5–53.7 (7)	47.2 $\pm$ 1.57 45.5–51.4 (7)
Valiente	585.7 $\pm$ 23.60 545–634 (6)	51.5 $\pm$ 4.70 47–62 (6)	128.7 $\pm$ 4.78 120–137 (6)	15.0 $\pm$ 0.89 13–16 (6)	4.6 $\pm$ 0.23 4.5–5.2 (6)	80.3 $\pm$ 1.99 77.7–83.5 (6)	49.9 $\pm$ 1.98 47.3–53.4 (6)	46.6 $\pm$ 1.28 44.9–49.1 (6)
Ñuri	608.4 $\pm$ 16.44 572–632 (7)	54.6 $\pm$ 4.54 45–64 (7)	130.4 $\pm$ 4.32 122–136 (7)	12.0 $\pm$ 1.31 10–14 (7)	4.7 $\pm$ 0.53 3.7–5.5 (7)	78.4 $\pm$ 1.13 77.0–80.6 (7)	48.3 $\pm$ 1.27 46.1–50.6 (7)	45.3 $\pm$ 1.19 43.8–47.9 (7)

Table 2.—Extended.

Locality	Postorbital breadth	Squamosal process length	Maxillary toothrow length	Postpalatal length	Palatal breadth	Braincase depth	Antorbital bar breadth	Descending jugal process length	External auditory meatus diameter
Isla Escudo	21.2 ± 0.79 20.2–22.4 (6)	21.5 ± 0.81 20.3–22.9 (7)	23.3 ± 0.76 22.3–24.7 (6)	34.8 ± 1.20 33.3–37.0 (6)	16.3 ± 0.49 15.5–17.2 (7)	24.5 ± 0.39 23.7–25.0 (6)	3.2 ± 0.27 2.8–3.7 (7)	16.2 ± 0.92 14.7–18.0 (7)	5.9 ± 0.45 5.3–6.7 (7)
Isla Bastimentos	21.9 ± 0.90 20.4–22.9 (5)	24.3 ± 1.25 22.4–27.0 (6)	23.9 ± 0.82 22.5–25.0 (6)	35.4 ± 0.99 34.0–36.9 (6)	16.6 ± 0.56 15.7–17.4 (6)	24.8 ± 0.48 23.8–25.6 (6)	3.1 ± 0.28 2.6–3.5 (6)	13.2 ± 1.83 10.3–17.1 (6)	5.2 ± 0.29 4.6–5.5 (6)
Cayo Agua	22.3 ± 0.66 19.8–24.2 (12)	26.4 ± 0.75 23.2–28.0 (12)	23.9 ± 0.71 22.0–26.8 (12)	36.0 ± 0.81 33.2–38.0 (12)	16.6 ± 0.41 15.6–18.0 (12)	26.1 ± 0.27 25.0–26.8 (12)	3.9 ± 0.24 3.2–4.6 (12)	16.0 ± 0.96 13.4–18.4 (12)	5.2 ± 0.20 4.7–5.8 (12)
Isla Colón	23.0 ± 1.17 21.7–24.2 (4)	25.3 ± 1.55 23.2–26.6 (4)	25.3 ± 1.33 23.5–26.7 (4)	36.4 ± 2.96 33.7–39.8 (4)	17.0 ± 0.74 16.2–17.9 (4)	25.2 ± 1.15 23.8–26.6 (4)	3.9 ± 0.57 3.2–4.6 (4)	15.7 ± 1.25 14.2–16.9 (4)	5.7 ± 0.34 5.3–6.1 (4)
Cayo Nancy	24.2 ± 0.60 23.6–25.3 (5)	26.2 ± 1.13 24.3–27.8 (5)	25.2 ± 0.91 24.0–26.5 (5)	38.0 ± 2.08 35.1–40.3 (5)	17.2 ± 0.82 16.6–18.8 (5)	26.0 ± 0.85 24.9–26.8 (5)	3.4 ± 0.22 3.2–3.8 (5)	15.3 ± 1.46 13.1–17.4 (5)	5.7 ± 0.43 4.9–6.1 (5)
Isla Cristóbal	24.9 ± 1.01 23.8–26.5 (5)	27.2 ± 1.41 25.2–29.5 (5)	25.5 ± 0.92 23.7–26.2 (5)	40.0 ± 0.93 38.9–41.7 (5)	18.3 ± 0.59 17.6–19.1 (5)	27.3 ± 0.89 26.2–28.7 (5)	4.0 ± 0.45 3.2–4.4 (5)	15.9 ± 0.94 14.1–16.9 (5)	5.1 ± 0.19 4.9–5.4 (5)
Isla Popa	23.8 ± 1.09 21.3–25.1 (6)	28.4 ± 1.05 26.4–30.0 (6)	24.6 ± 0.35 23.9–25.1 (6)	41.0 ± 1.79 37.1–42.7 (6)	17.4 ± 0.48 16.6–17.9 (6)	27.6 ± 0.59 26.4–28.2 (6)	4.5 ± 0.35 4.0–5.2 (6)	16.3 ± 1.58 14.1–19.9 (6)	5.1 ± 0.36 4.5–5.5 (5)
Almirante	24.6 ± 1.12 23.2–25.8 (4)	28.1 ± 1.66 26.7–30.5 (4)	25.5 ± 1.41 23.8–26.8 (4)	40.7 ± 1.62 39.3–43.0 (4)	18.3 ± 0.54 17.8–19.0 (4)	27.0 ± 0.46 26.7–27.7 (4)	4.4 ± 0.21 4.2–4.6 (4)	17.1 ± 2.22 14.3–19.4 (4)	5.6 ± 0.26 5.3–5.8 (4)
Tierra Oscura	25.0 ± 1.20 22.0–26.4 (7)	28.6 ± 1.15 26.7–30.6 (7)	25.1 ± 0.86 23.9–27.4 (7)	41.4 ± 1.33 38.9–43.9 (7)	18.7 ± 0.77 17.7–20.7 (7)	27.9 ± 0.72 26.3–28.7 (7)	4.8 ± 0.35 4.0–5.3 (7)	16.5 ± 1.11 14.6–19.0 (7)	5.6 ± 0.28 5.1–6.1 (7)
Valiente	25.0 ± 1.02 23.9–26.6 (6)	27.7 ± 0.64 27.0–28.8 (6)	25.1 ± 0.77 23.7–26.0 (6)	41.9 ± 1.77 39.8–45.3 (6)	18.3 ± 0.81 16.8–19.6 (6)	28.5 ± 0.33 28.0–29.0 (6)	4.6 ± 0.36 4.1–5.3 (6)	16.3 ± 1.35 13.2–17.9 (6)	5.5 ± 0.27 5.1–6.0 (6)
Ñuri	25.1 ± 0.44 24.4–26.0 (6)	27.4 ± 1.02 25.6–29.1 (7)	25.3 ± 0.69 24.3–26.7 (6)	40.1 ± 0.86 38.9–41.8 (7)	18.4 ± 0.71 16.5–19.3 (7)	28.2 ± 0.55 27.3–29.3 (7)	4.3 ± 0.29 3.8–4.7 (7)	15.4 ± 1.79 12.3–18.8 (7)	5.6 ± 0.16 5.2–5.8 (7)

Table 2.—Extended.

Locality	Squamosal process breadth	Ascending mandibular ramus breadth	First canonical axis (C 1)	First principal component (PC I)
Isla Escudo	4.3 ± 0.47	13.2 ± 0.92	-7.32 ± 0.71	-0.28 ± 0.05
	3.5-5.0 (7)	11.9-14.9 (7)	-8.03--6.34 (5)	-0.35--0.22 (5)
Isla Bastimentos	5.4 ± 0.64	16.4 ± 0.62	-4.70 ± 0.63	-0.14 ± 0.07
	4.9-7.0 (6)	15.3-17.4 (6)	-5.33--4.36 (3)	-0.18--0.07 (3)
Cayo Agua	6.3 ± 0.39	15.9 ± 0.60	-2.41 ± 0.72	-0.04 ± 0.03
	5.5-7.5 (12)	14.0-17.5 (12)	-4.46--0.43 (11)	-0.14-0.02 (11)
Isla Colón	5.3 ± 0.60	15.8 ± 1.22	-4.34 ± 1.79	-0.08 ± 0.12
	4.5-5.9 (4)	14.7-16.8 (3)	-6.14--3.39 (3)	0.20-0.00 (3)
Cayo Nancy	6.0 ± 1.02	16.0 ± 1.50	-2.05 ± 0.46	-0.05 ± 0.07
	4.9-7.9 (5)	13.4-17.7 (5)	-2.78--1.39 (5)	-0.15-0.05 (5)
Isla Cristóbal	6.4 ± 0.73	17.2 ± 1.39	3.38 ± 0.75	0.06 ± 0.08
	5.0-7.0 (5)	15.5-18.8 (5)	2.66-4.18 (4)	-0.06-0.13 (4)
Isla Popa	6.6 ± 0.23	16.8 ± 0.65	4.26 ± 0.37	0.11 ± 0.03
	6.3-6.9 (5)	15.6-17.5 (5)	3.67-4.68 (5)	0.09-0.16 (5)
Almirante	6.0 ± 0.76	16.9 ± 0.26	3.16 ± 1.01	0.09 ± 0.07
	4.9-6.7 (4)	16.6-17.2 (4)	2.57-4.17 (3)	0.04-0.15 (3)
Tierra Oscura	5.9 ± 0.39	17.6 ± 0.83	3.06 ± 0.91	0.12 ± 0.05
	5.0-6.5 (7)	16.3-19.5 (7)	1.41-4.76 (7)	0.02-0.19 (7)
Valiente	5.7 ± 0.64	16.7 ± 0.87	3.36 ± 1.09	0.09 ± 0.04
	5.0-7.1 (6)	15.7-18.0 (6)	1.49-5.55 (6)	0.04-0.17 (6)
Ñuri	5.8 ± 0.47	16.1 ± 0.49	2.91 ± 0.49	0.06 ± 0.03
	5.0-6.9 (7)	15.1-17.0 (7)	2.27-3.76 (5)	0.01-0.10 (5)

Table 3.—Approximate statistics for morphometric separation among populations of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá. *F*-statistics with 17 and 30 degrees of freedom are given for Mahalanobis distances between pairs of group centroids, with an asterisk (\*) signifying significant differences, using Holm's (1979) correction for multiple tests. Below the *F*-statistic, pairs are marked by PC I (Principal component I), C 1 (Canonical axis 1), or C 2 (Canonical axis 2) if their mean scores on those respective axes were significantly different by Tukey's tests of multiple comparisons with family-wide error rates of  $\alpha = 0.05$ . Note that the sloth of Isla Escudo is morphometrically distinct from all other samples in Bocas del Toro, and that the samples from Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón are significantly smaller than most or all mainland localities (*F*-statistics, PC I, and C 1). Significance levels attached to all tests must be regarded as approximate due to small sample sizes. Locality abbreviations are given in Table 1.

	E	B	CA	CO	N	CR	P	TO	V	A
B	5.18*									
	C 1, 2									
CA	7.65*	3.22								
	PC I, C 1, 2	C 1								
CO	3.49*	2.00	1.96							
	PC I, C 1, 2									
N	4.41*	3.00	2.15	1.54						
	PC I, C 1, 2	C 1, 2	C 2							
CR	11.55*	6.74*	5.37*	5.41*	3.32*					
	PC I, C 1, 2	PC I, C 1, 2	C 1, 2	C 1	C 1					
P	14.68*	8.46*	7.44*	7.19*	5.29*	0.84				
	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1	PC I, C 1					
TO	14.94*	6.92*	6.55*	5.39*	4.46*	2.12	2.69			
	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1	PC I, C 1	PC I, C 1					
V	13.23*	7.17*	7.19*	6.04*	4.19*	1.51	1.72	0.70		
	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1	PC I, C 1					
A	9.08*	6.13*	4.90*	4.39*	2.62	1.05	1.30	1.74	1.41	
	PC I, C 1	PC I, C 1, 2	PC I, C 1, 2	PC I, C 1, 2	C 1			C 2		
NU	11.67*	6.67*	5.99*	5.00*	3.03	1.67	2.29	1.09	0.91	0.80
	PC I, C 1, 2	PC I, C 1, 2	C 1, 2	C 1	C 1					

Colón, and Isla Escudo—in comparisons with those from the younger islands (Isla Popa and Isla Cristóbal) and sites on the adjacent mainland (Tables 2 and 3). The discriminant function analysis showed differences in both size and shape. In the DFA, 32 of 55 comparisons between pairs of group centroids were significantly different and followed a clear pattern (Table 3, Fig. 3). The sloths on Isla Escudo were morphometrically distinct from all other populations. Furthermore, sloths on the outer islands were generally distinct from those of Isla Popa and Isla Cristóbal as well as from those from all mainland sites in Bocas del Toro. The first canonical axis accounted for most (63%) of the variation among groups, and the first and second together encompassed 76% of the variation (Table 4). The first canonical axis may be interpreted as general size, with smaller sloths having lower scores. Most measurements loaded strongly and positively on this axis; external auditory meatus diameter (EAM) had a negative loading, but its magnitude was small enough to be negligible, indicating that EAM diameter did not correlate with general size. The second canonical axis contrasted tail length and EAM diameter to squamosal process breadth and ascending mandibular ramus breadth (Table 4). Sloths with relatively long tails, large EAMs, narrow squamosal processes, and narrow rami scored high on this axis.

In the principal components analysis of overall variation in the sloths of Bocas del Toro, the first component (PC I) accounted for 51% of the variation among individuals, without regard to locality (Table 5). Specimens from Isla Escudo again plotted far from all other specimens from Bocas del Toro (Fig. 4). The loadings on PC I indicate that it represents overall size, with EAM loading so slightly as to be immaterial. No difference between Age classes 2 and 3 or age-locality interaction was detected for PC I scores in a general linear model ( $F_{\text{age } 1,6} = 0.23$ ,  $P = 0.650$ ;  $F_{\text{age}*\text{locality } 1,6} = 0.00$ ,  $P = 0.981$ ). Similarly, the difference between

the sexes and the sex-locality interaction also were nonsignificant ( $F_{\text{sex } 1,23} = 1.32$ ,  $P = 0.262$ ;  $F_{\text{sex}*\text{locality } 4,23} = 1.04$ ,  $P = 0.408$ ). These tests suggest that our pooling of the sexes and Age classes 2 and 3 was justified. Scores on PC I, however, were significantly different among localities in a one-way ANOVA ( $F_{10,46} = 21.79$ ,  $P < 0.001$ ). Patterns of localities differing significantly on PC I paralleled the results for the first canonical axis (Table 3). PC II and PC III represent shape differences, but given the multiple groups involved they probably do not represent the most appropriate way to examine shape.

In comparing the small sloths from Bocas del Toro with six series of *Bradypus variegatus* from its range outside Bocas del Toro, only the population on Isla Escudo is significantly smaller than all mainland samples (Table 6) in the greatest length of skull. Sloths from the other differentiating populations in Bocas del Toro—Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón—fall within the size variation in *B. variegatus* from Colombia and Brazil.

## Discussion

The three-toed sloths of the outer islands of Bocas del Toro—Isla Colón, Isla Bastimentos, Cayo Nancy, Cayo Agua, and Isla Escudo—are significantly smaller than the *Bradypus* of the adjacent mainland of Bocas del Toro, as evidenced by Canonical axis 1, Principal component I, and univariate statistics. Furthermore, sloths on those five islands themselves vary in mean size, with those from Isla Escudo being the smallest (Tables 2 and 3). The samples from Isla Popa and Isla Cristóbal, which are young islands close to shore, are not significantly different in size from sloths on the mainland of Bocas del Toro (Table 3).

Sloths on Isla Escudo display differences in cranial shape when compared with other populations of *Bradypus* from Bocas del Toro. The position of specimens from Isla Escudo on the second canonical axis (Fig.

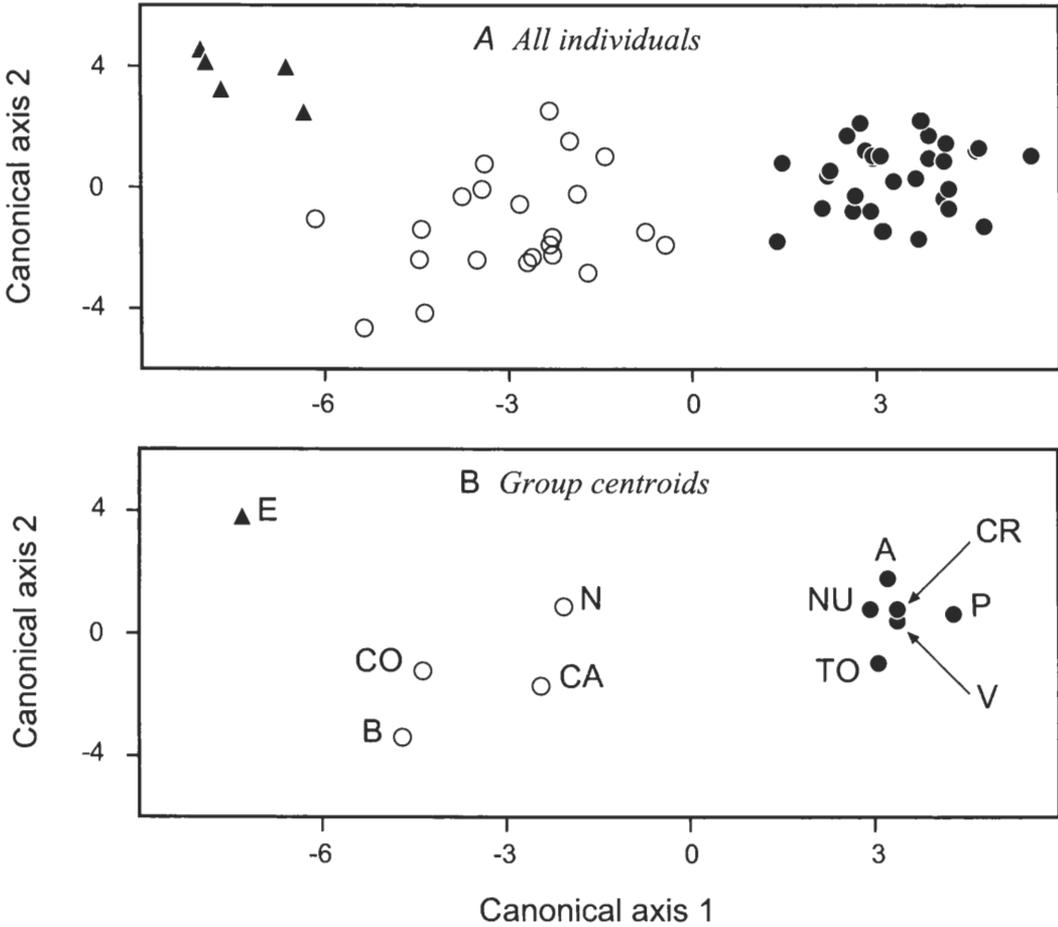


Fig. 3. Plot of specimen scores (A, upper) and locality centroids (B, lower) on the first two canonical axes from a multiple-group discriminant function analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, showing morphometric distinctiveness of sloths of Isla Escudo and moderate dwarfing on four other islands. In A, specimens from Isla Escudo are marked with solid triangles; specimens from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. Abbreviations for locality centroids in B follow, with symbols following the same scheme as in A: A, Almirante; B, Isla Bastimentos; CA, Cayo Agua; CR, Isla Cristóbal; CO, Isla Colón; E, Isla Escudo; N, Cayo Nancy; NU, Ñuri; P, Isla Popa; TO, Tierra Oscura; V, Península Valiente.

3) is due primarily to their large external auditory meatus, narrow squamosal process, and narrow ascending mandibular ramus (Table 2, Table 4). For the other island and mainland populations in Bocas del Toro, variation in shape is minimal as compared with differences in size.

Although the sloths from the outer islands share small size, our examinations of pelage show similarities between island and

mainland populations that were once contiguous (Table 1, Fig. 1). These analyses show that the small sloths on the outer islands share no discrete pelage characters. The pelage traits are independent of body size, which is notably predisposed to convergence (Roth 1992). The few cranial characters common to the small sloths on various islands are all gracile traits associated with size reduction and ontogenetic

Table 4.—Loadings (correlation coefficients) of three external and 14 cranial measurements ( $\log_{10}$ -transformed) on the first three canonical axes of a multiple-group discriminant function analysis of three-toed sloths (*Bradypus*) from 11 localities in Bocas del Toro, Panamá. Eigenvalues and the corresponding cumulative percent of total dispersion explained are given for each axis. For the analysis, specimens were grouped by collection locality. See Materials and Methods for variable abbreviations. The first canonical axis represents a measure of general size.

	C 1	C 2	C 3
TOTAL	0.804	0.026	0.081
TAIL	0.423	0.620	-0.136
HF	0.822	-0.158	0.252
GLS	0.895	0.046	0.132
AZB	0.856	-0.141	0.096
PZB	0.797	-0.178	-0.004
POB	0.742	0.027	0.268
SPL	0.795	-0.324	-0.058
MTRL	0.452	0.009	0.202
PPL	0.862	0.124	0.202
PB	0.716	0.027	0.398
BD	0.885	-0.027	0.136
ABAR	0.760	-0.258	0.107
DJPL	0.236	0.160	-0.199
EAM	-0.152	0.437	0.515
SPB	0.477	-0.467	-0.355
ARB	0.681	-0.481	0.070
Eigenvalue & (cumulative % of total dispersion)	17.7800 (63.3%)	3.6367 (76.3%)	2.2703 (84.4%)

truncation (e.g., thin zygomatic arches, weakly developed temporal crests). The geographic distribution of the pelage traits apparently represents the relictual manifestation of previously continuous geographic variation that was subdivided into isolated populations when the islands formed. Movement of sloths between islands or to or from the mainland probably has been insignificant. We propose that those populations independently underwent selection for smaller size when separated from the mainland, under a vicariant model consistent with the patterns of island formation elucidated by Handley & Varn (see Introduction). This hypothesis of strict vicariance is currently being tested by Anderson and L. Olson by comparing a population-level phylogeny produced from DNA sequence

data, with an area cladogram based on the sequence of island formation derived from sea level mapping (Brooks & McLennan 1991:197–198, Avise 1994).

Thus, we suggest that the evolution of smaller body sizes occurred at least four times in Bocas del Toro: independently on Isla Escudo, Isla Colón, and Cayo Agua—each of which formed separately—and once on Cayo Nancy and Isla Bastimentos together (they became isolated from the mainland as a unit and only recently have become separated from each other). The sloths from the outer islands are not linked by a common ancestry as might be presumed because of their small size, but rather they adapted separately as isolated populations while experiencing similar environmental changes following insularization, in an instance of parallel evolution. The sloth of Isla Escudo has clearly reached the species level, but we consider that the populations on Cayo Agua, Cayo Nancy, Isla Bastimentos, and Isla Colón remain conspecific with *Bradypus variegatus*. Future work will evaluate the factors that may have led to these instances of dwarfism.

We have documented the extremely small size of the three-toed sloth on Isla Escudo, as well as its unique cranial and pelage characters relative to other known species of the genus. For these reasons, we here formally describe this endemic insular population as:

*Bradypus pygmaeus*, new species  
Fig. 5

*Holotype*.—USNM 579179, adult female, skin and skull (Fig. 5), collected on 27 Mar 1991 by Charles Handley and Penny Nelson, from Panamá: Bocas del Toro: Isla Escudo de Veraguas, West Point. Original number EPN 166. Also examined: nine paratypes from Isla Escudo: USNM 578413, 579171–579175, 579176 (returned to Panamá-INRENARE), 579177–579178.

*Etymology*.—From the Latin *pygmaeus*,

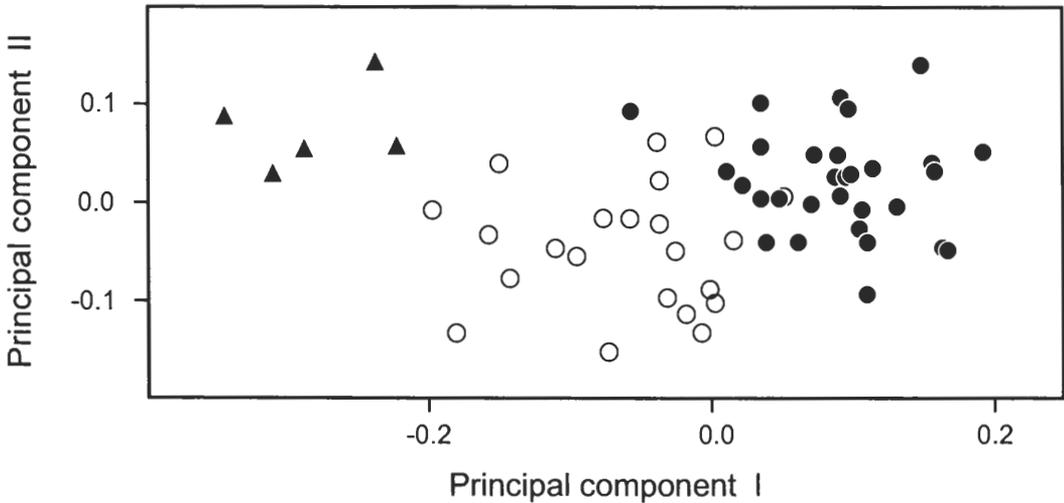


Fig. 4. Plot of specimen scores on the first two axes of a principal components analysis of three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, showing dwarfing of sloths on Isla Escudo and four other islands. Specimens from Isla Escudo are marked with solid triangles; specimens from the four islands of intermediate age (Cayo Agua, Cayo Nancy, Isla Colón, and Isla Bastimentos) are represented by open circles; and specimens from the mainland and from the two youngest islands (Isla Cristóbal and Isla Popa) are denoted by solid circles. The first principal component represents general size.

meaning dwarf or pygmy. Suitable vernacular name is pygmy three-toed sloth.

**Distribution.**—Known only from Isla Escudo de Veraguas, Province of Bocas del Toro, Republic of Panamá, where it is found exclusively in red mangroves at sea level (Fig. 6).

**Diagnosis.**—A species of *Bradypus* characterized by the following combination of characters: size small (Table 2); orange speculum on dorsum of adult males; nape without black mane; face tan with distinctive dark band across forehead; long hair of forehead hanging over face, giving the impression of a hood; pterygoids not inflated; no foramina in anterodorsal nasopharynx; frontal sinuses swollen; stylomastoid foramen miniscule, external carotid foramen usually absent or minuscule; external auditory meatus large; ventral surface of hyoid (stylohyal) smoothly concave; descending process of jugal long and thin; coronoid process of mandible thin and strongly falcate.

**Description.**—Size small ( $n = 7$  adults: total length,  $\bar{X} = 505.4$  mm, range 485–530

mm; tail,  $\bar{X} = 49.7$  mm, range 45–60 mm; hind foot,  $\bar{X} = 102.4$  mm, range 94–110 mm; mass,  $\bar{X} = 2.9$  kg, range 2.5–3.5 kg); dorsal coloration usually blotchy and always with a midsagittal stripe; adult males with orange speculum, woolly around anterior margin; fur of crown long and shaggy, hanging over short hair of face to give a hooded appearance; brow very dark with abrupt posterior termination (line on brow present); face buff with orange wash around dark eye stripe; throat grizzled gray-brown.

Skull small ( $n = 6$  adults: greatest length,  $\bar{X} = 69.1$  mm, range 67.5–72.2 mm; anterior zygomatic breadth,  $\bar{X} = 41.5$  mm, range 38.3–45.7 mm; maxillary toothrow length,  $\bar{X} = 23.3$  mm, range 22.3–24.7 mm; see also Table 2) and gracile (Fig. 5); parietal ridges weak and usually convex (hourglass-shaped when viewed dorsally); masseter-temporal fossa rather smooth; pterygoids thin, not inflated; no foramina present in anterodorsal nasopharynx; premaxillae minute, barely if at all articulated with maxillary; zygomatic arch incomplete, anterior and posterior roots slender; de-

Table 5.—Loadings, eigenvalues, and cumulative percent of variance explained for the first three axes of a principal components analysis undertaken on three-toed sloths (*Bradypus*) from Bocas del Toro, Panamá, using the covariance matrix of  $\log_{10}$ -transformed values of 14 cranial measurements and three external measurements for each of 57 individuals. See Materials and Methods for abbreviations. The first principal component represents general size, which is uncorrelated with external auditory meatus diameter (EAM).

	PC I	PC II	PC III
TOTAL	0.786	0.302	0.103
TAIL	0.331	0.788	0.456
HF	0.801	0.141	-0.057
GLS	0.878	0.221	0.075
AZB	0.905	0.049	-0.218
PZB	0.895	-0.010	-0.214
POB	0.682	0.129	0.044
SPL	0.874	-0.062	0.073
MTRL	0.610	0.164	0.214
PPL	0.839	0.269	0.017
PB	0.712	0.236	-0.042
BD	0.794	0.054	-0.187
ABAR	0.866	-0.092	-0.419
DJPL	0.354	0.348	-0.251
EAM	-0.044	0.481	-0.252
SPB	0.689	-0.477	0.455
ARB	0.842	-0.191	0.200
Eigenvalue & (cumulative % variance explained)	0.0164 (51.2%)	0.0046 (65.5%)	0.0033 (75.9%)

scending process of jugal long and thin; lambdoidal crest continuous across posterior margin of occiput, lateral margins of crest straight in lateral view; occipital region barely projecting posterior to lambdoidal crest; hyoid (stylohyal) smoothly arched on ventral surface to point of articulation with epihyal on anterior limb; posterior limb of hyoid usually wider than anterior limb; external auditory meatus large; stylomastoid foramen minute; external carotid foramen usually closed or miniscule; ventral mandibular surface strongly concave; coronoid process of mandible thin and strongly falcate.

Tooth formula: (anterior chisel-shaped teeth 1/1, molariform teeth 4/3)  $\times 2 = 18$  (terminology of Naples 1982). Upper anterior chisel-shaped tooth tiny or absent; lower anterior chisel-shaped tooth anteroposteriorly compressed.

*Measurements of the holotype.*—Total length, 510 mm; tail length, 54 mm; hind foot length, 94 mm; mass, 3.5 kg. Cranial measurements (in mm): GLS, 68.8; AZB, 43.6; PZB, 40.7; POB, 20.5; SPL, 21.3; MTRL, 22.8; PPL, 33.3; PB, 16.3; BD, 24.7; ABAR, 3.2; DJPL, 16.2; EAM, 6.7; SPB, 5.0; ARB, 12.8.

Table 6.—Results of ANOVA of greatest length of skull (GLS) measurements. All possible pairwise comparisons were made among samples of *Bradypus* from the five outer islands of Bocas del Toro, Panamá and six samples of *B. variegatus* from mainland localities outside Bocas del Toro using Tukey's procedure with a family-wide error rate of  $\alpha = 0.05$ . Results for comparisons of island populations vs. mainland populations outside Bocas del Toro are presented here. Significant comparisons are marked with an asterisk (\*), whereas nonsignificant ones are denoted "n.s." Bonanza, El Recreo, and Tepeyak are localities in Nicaragua; Bajo Calima-Río Raposo and Tumaco lie along the southern Pacific coast of Colombia; and Mojui dos Campos is located in the lower Amazon of Brazil. Note that sloths from Isla Escudo are significantly smaller than those of all mainland localities outside Bocas del Toro, whereas the *Bradypus* from the four other outer islands of Bocas del Toro fall within the range of variation of *B. variegatus* in South America. Descriptive statistics (mean  $\pm$  2 standard errors, minimum-maximum, and sample size) are given here in mm for mainland localities outside Bocas del Toro; see Table 2 for descriptive statistics of localities in Bocas del Toro.

	Bonanza 78.9 $\pm$ 1.12 75.3–82.3 (12)	El Recreo 78.5 $\pm$ 1.15 76.1–80.7 (7)	Tepeyak 83.2 $\pm$ 3.08 80.0–86.5 (4)	Bajo Calima- Río Raposo 73.7 $\pm$ 2.18 68.9–76.8 (6)	Tumaco 76.9 $\pm$ 4.18 70.6–79.3 (4)	Mojui dos Campos 72.8 $\pm$ 1.15 67.0–78.3 (21)
Isla Colón	*	*	*	n.s.	n.s.	n.s.
Isla Bastimentos	*	*	*	n.s.	*	n.s.
Cayo Nancy	n.s.	n.s.	*	n.s.	n.s.	n.s.
Cayo Agua	*	*	*	n.s.	n.s.	n.s.
Isla Escudo	*	*	*	*	*	*

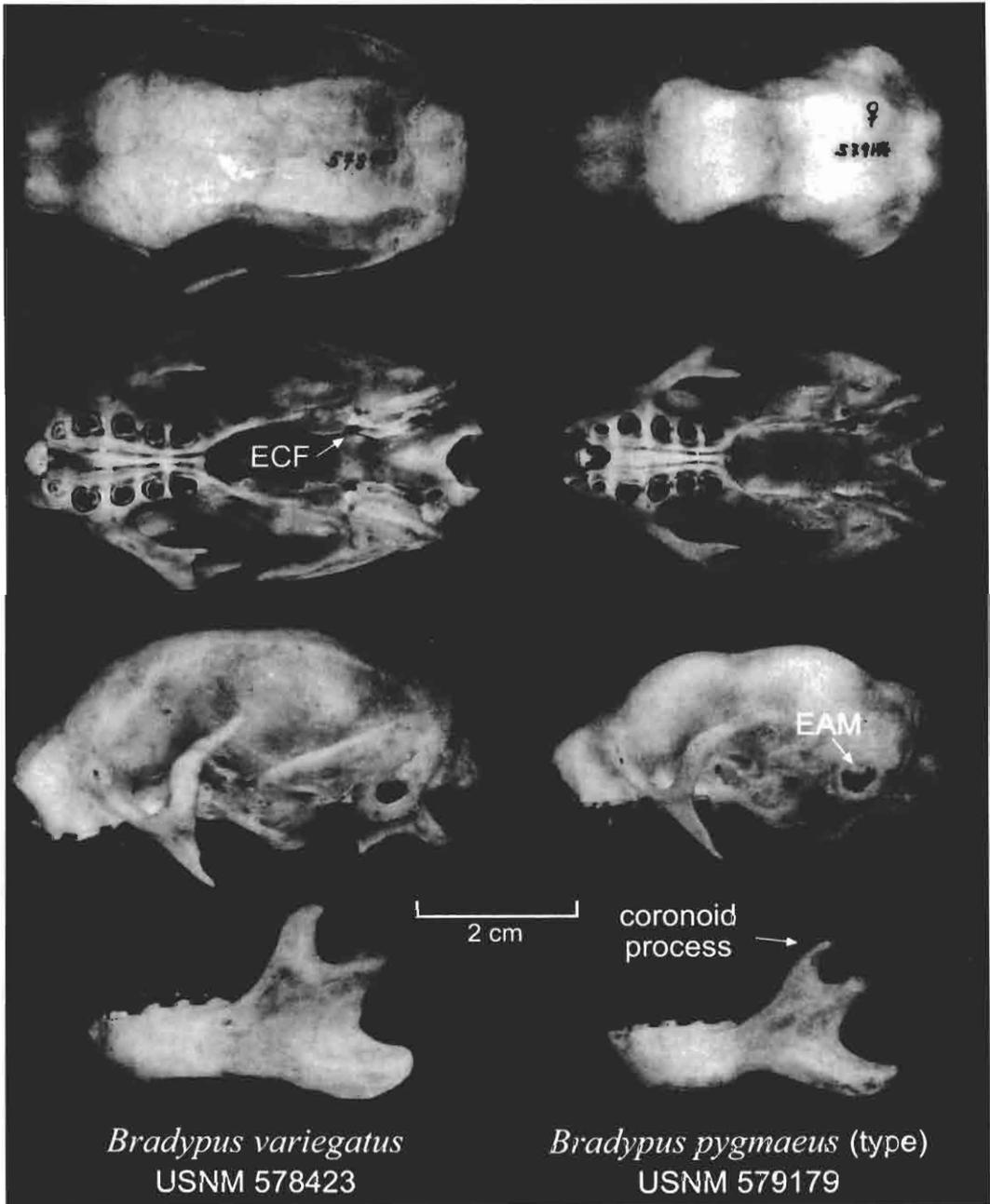


Fig. 5. Dorsal, ventral, and lateral views of the crania and lateral view of the mandibles of the holotype of *Bradypus pygmaeus* (USNM 579179, right) from Isla Escudo and a specimen of *B. variegatus* from the adjacent mainland on the Península Valiente (USNM 578423, left). Note the diminutive size and gracile qualities of *B. pygmaeus* and the open external carotid foramen (ECF) of USNM 578423, which is closed in USNM 579179. Also note the strongly falcate coronoid process on the mandible of *B. pygmaeus* and the large external auditory meatus (EAM) characteristic of that species, despite its overall small size.

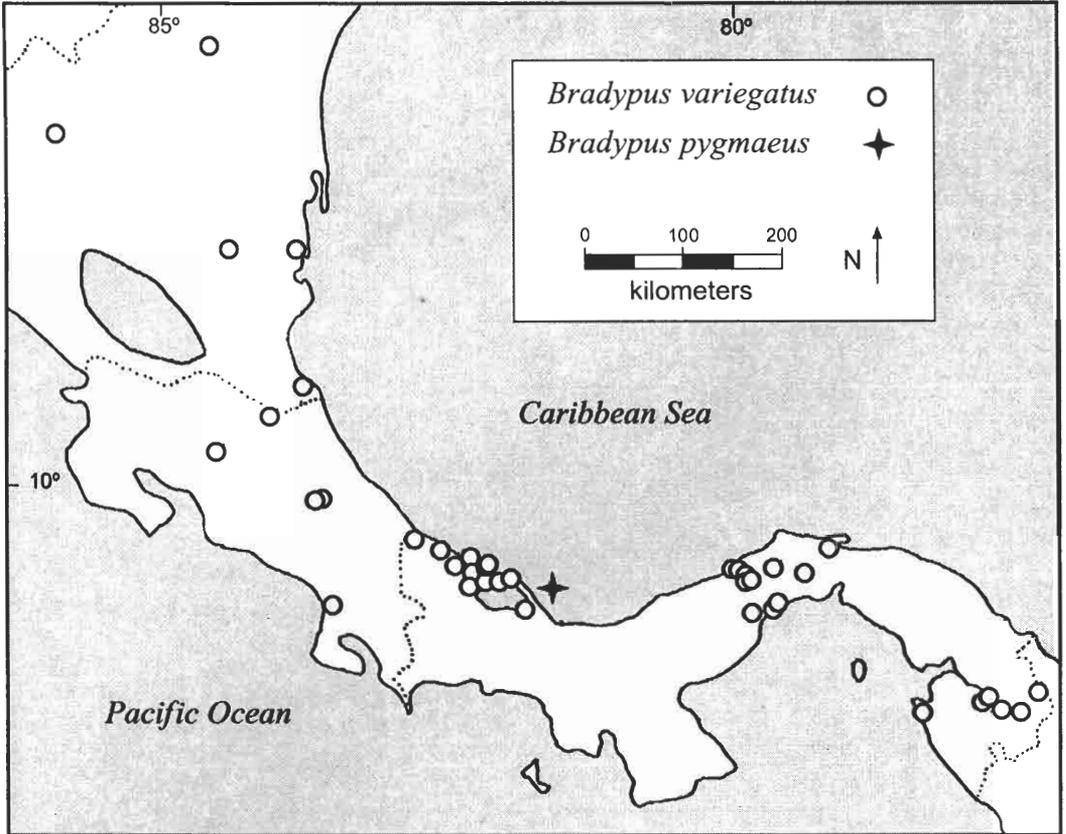


Fig. 6. Verified Central American distribution of *Bradypus*. Georeferenced collection localities reported here are plotted for *B. variegatus* (open circles) and *B. pygmaeus* (star). The distribution of *Bradypus variegatus* continues northward into Honduras (voucher specimens from the Río Patuca region [see Specimens examined] and additional sight records reported in Marineros & Martínez-Gallegos 1998) and south into South America (see Fig. 7). *Bradypus pygmaeus* is endemic to Isla Escudo de Veraguas in western Panamá. See Specimens examined sections for full provenience and museum catalogue numbers.

*Comparisons.*—Compared with populations of *Bradypus variegatus* on the adjacent mainland, *B. pygmaeus* averages approximately 40% smaller in mass, 15% smaller in total length, and 12–16% smaller in most cranial dimensions. It is smaller than any studied population of *Bradypus variegatus* in Central or South America (Tables 2, 3, and 6). Additionally, its external auditory meatus is conspicuously large for a sloth of overall small size. The diameter of the EAM decreases as the bulla ossifies; the development of this region of the skull is especially truncated in *B. pygmaeus* (Fig. 5).

Discrete cranial characters separate *Bradypus pygmaeus* from all other species of the genus. It lacks the distinctly inflated pterygoid sinuses and the two or three roughly circular foramina in each side of the anterodorsal nasopharynx of *B. torquatus* (Wetzel & Avila-Pires 1980, Wetzel 1985). It lacks the pair of oblong foramina present in the medial roof of the anterodorsal nasopharynx of *B. tridactylus* (Wetzel 1985). From populations of the closely related *B. variegatus*—including both mainland sloths and the moderately dwarfed sloths of other islands in Bocas del Toro—the pygmy sloth differs in having (Fig. 5):

external carotid foramen, through which the carotid artery normally passes, absent or minute in most specimens (the homologous foramen is markedly larger in *B. variegatus*, suggesting a different pattern of cranial circulation); stylomastoid foramen at the posterior external base of the auditory bulla tiny (the facial nerve exits this foramen in *B. variegatus*, in which the foramen is markedly larger and almost always visible to the naked eye); external auditory meatus large (usually smaller in *B. variegatus* and all other three-toed sloths); ventral edge of stylohyoid usually smoothly concave (angular or undulating in *B. variegatus*); coronoid process of the mandible slender and strongly falcate (usually thick and straight-edged or only moderately curved in *B. variegatus*). No other insular population of three-toed sloth in Bocas del Toro shows autapomorphic cranial characters.

Externally, *Bradypus pygmaeus* may be separated from *B. torquatus* of both sexes by the lack of a black dorsal mane originating at the nape and by the presence of short, tan facial pelage with a black stripe lateral to the eye; and in adult males by possessing a dorsal speculum. From *B. tridactylus*, the pygmy sloth is distinguished by its tan facial and gular pelage and dark stripe lateral to the eye. In contrast, *B. tridactylus* has brilliant golden hair on the brow, face, and throat. The pygmy sloth differs externally from *B. variegatus* by long hair projecting over the brow, creating the aspect of a hood (Table 1). This character provoked Handley to refer to this sloth in the field as the "monk sloth." No other sloth of the Bocas islands is hooded, and the "ruff" on the brow (hair projecting over the forehead) mentioned for other Central American *Bradypus* by Goldman (1920:57), Goodwin (1946:352), Hall (1981:279), and others is not so long and distinctive.

*Specimens examined.*—*Bradypus pygmaeus*, total 10. Panamá (10). Bocas del Toro: Isla Escudo de Veraguas (9°06'N, 81°33'W), 1 (USNM 578413); Isla Escudo

de Veraguas (9°06'N, 81°33'W), West Point, 9 (USNM 579171–579175, 579176\*, 579177–579179).

*Bradypus torquatus* Illiger, 1811

*Distribution.*—Restricted to the Atlantic forests of southeastern Brazil (Fig. 7; Wetzel & Avila-Pires 1980).

*Diagnosis.*—Size large; no speculum on dorsum (contra Eisenberg & Redford 1999: 94); nape with distinct black plume or mane; facial and body pelage grizzled; hair of forehead short; pterygoids distinctly inflated; two or three small, circular foramina present on each side of anterodorsal nasopharynx.

*Comparisons.*—This species is easily separated from all other species of the genus by its black dorsal mane and inflated pterygoids.

*Comments.*—Extremely rare in museum collections. Endangered due to deforestation in its restricted range (Emmons & Feer 1997). Considered the most basal species of *Bradypus* (Wetzel & Avila-Pires 1980) and placed in its own subgenus, *Scaeopus*.

*Specimens examined.*—*Bradypus torquatus*, total 4. Brazil (4). Bahia. Itabuna, near Ilhéus [14°48'S, 39°16'W], 1 (USNM 259473); Tres Bracos, Fazenda Piabanha (13°32'S, 39°45'W), 37 km N, 34 km E Jequeie, 2 (USNM uncatalogued, field numbers MTB 1706–1707). State unknown: no specific locality, 1 (MCZ 1024).

*Bradypus tridactylus* Linnaeus, 1758

*Distribution.*—The Guianas and adjacent regions of eastcentral Venezuela (Estado Bolívar) and northcentral Brazil, principally north of the Amazon (Fig. 7). Distribution probably does not extend southwest of the Rio Negro or as far south of the Amazon as indicated in Eisenberg & Redford (1999), where it is replaced by *Bradypus variegatus*.

*Diagnosis.*—Size average for genus; orange speculum present on dorsum of adult males; nape without black mane; face and

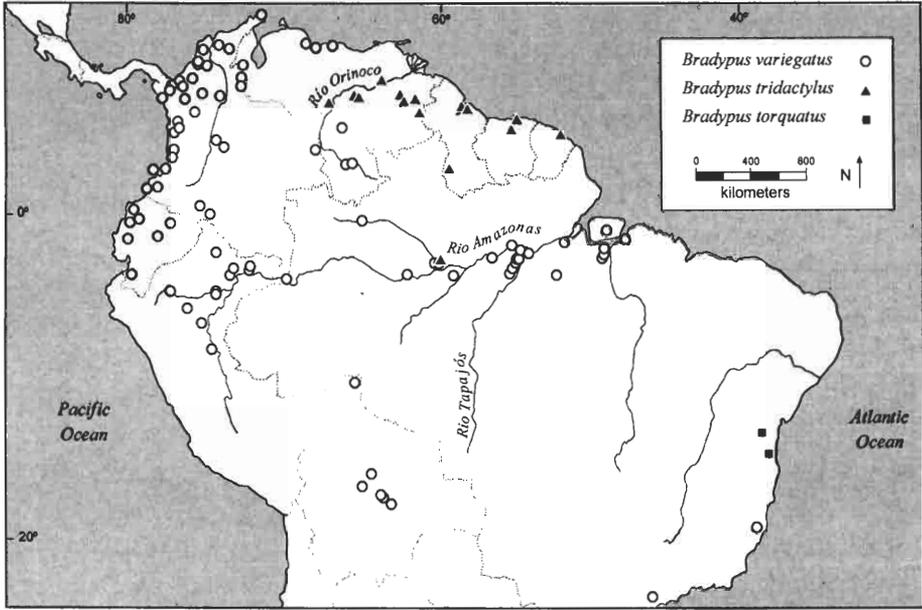


Fig. 7. Verified South American distribution of *Bradypus*. Georeferenced collection localities are mapped for *B. variegatus* (open circles), *B. tridactylus* (solid triangles), and *B. torquatus* (solid squares). The distribution of *Bradypus variegatus* continues northwest into Central America (see Fig. 6) and south to Argentina (voucher specimen from Jujuy province, see Specimens examined). Wetzel and Avila-Pires (1980) reported additional distributional records for *B. torquatus*, which ranges southward from the localities of that species confirmed and plotted here. See Specimens examined sections for full provenience and museum catalogue numbers.

forehead golden with no dark stripe at level of eyes (contra Emmons & Feer 1997:43); throat golden to the base of the hairs, or predominantly golden with bases of hairs smoky gray; hair of forehead short and stiff; pterygoids not inflated; a single pair of oblong foramina present in the anterodorsal nasopharynx; frontal sinuses seldom swollen.

*Comparisons.*—*Bradypus tridactylus* may be easily separated from *B. torquatus* by the lack of a black dorsal mane or inflated pterygoid sinuses. It is most similar to *B. variegatus*, whose range it probably contacts in Venezuela and Brazil. It differs from that species by possessing a pair of oblong foramina in the anterodorsal nasopharynx, and by its golden throat. All *B. tridactylus* have golden faces and throats, either golden to the base of the hair or with a slight smoky gray color at the base of the hairs. In contrast, most *B. variegatus* have tan faces. Many specimens of *B. variegatus*

in South America possess golden faces, however, and a few Brazilian populations even have throats frosted with golden-tipped fur (e.g., localities on the lower Rio Tapajós), but the base of the gular hairs is characteristically brown for most of the length of the hair in those populations. The golden facial and gular hair of *B. tridactylus* is generally shorter and stiffer than in *B. variegatus*. See Comments in *B. variegatus*. No *B. pygmaeus* have golden throats or faces. The dorsum of *B. tridactylus* is often speckled or blotchy, but this character does not serve to distinguish it from *B. variegatus* (contra Eisenberg 1989, Eisenberg & Redford 1999), which often displays this trait as well.

*Comments.*—In the older literature, individuals of *Bradypus variegatus* were often incorrectly reported as *B. tridactylus*.

*Specimens examined.*—*Bradypus tridactylus*, total 50. Brazil (6). Amazonas: Manaus [3°08'S, 60°01'W], 1 (AMNH 143012);

Rio Amazonas, bought in Manaus [3°08'S, 60°01'W], 4 (FMNH 165441–165444); Rio Amazonas, Manaus [3°08'S, 60°01'W], Hacienda Rio Negro, 1 (AMNH 78968). French Guiana (1). Cayenne [4°56'N, 52°20'W], 1 (AMNH 77891). Guyana (20). Cuyuni-Mazaruni: Essequibo, Kartabo Point [6°23'N, 58°41'W], 12 (AMNH 42454, 42871–42872, 42888, 48369, 74134–74137, 142932, 142934, 142992); Kalacoon [= Kalakun, 6°24'N, 58°39'W], 2 (AMNH 48103, 269846); Kartabo [6°23'N, 58°41'W], 1 (AMNH 48180); Kartabo River, 1 (AMNH 74131); Kyk-over-al [island in Mazaruni River facing Karatabu Point (= Kartabo Point), AMS 1944], 1 (AMNH 48104). Demerara-Mahaica: Dunoon [6°25'N, 58°18'W, Hershkovitz 1977], 1 (UMMZ 46410). Upper Takutu-Upper Essequibo: Dadanawa [2°50'N, 59°30'W], 20 mi E, 1 (USNM 362241); no specific locality [in former Rupununi], 1 (USNM 395070). Suriname (7). Brokopondo: Saramacca Rivier, Loksie Hattie [5°10'N, 55°28'W, Hershkovitz 1977], 1 (FMNH 95443). Paramaribo: near Paramaribo [5°50'N, 55°10'W], 1 (MCZ 19570); Paramaribo [5°50'N, 55°10'W], 900 ft, 2 (FMNH 93297, 95446); Paramaribo [5°50'N, 55°10'W], brush land, 900 ft, 1 (FMNH 93296). Saramacca: La Poule, 2 (FMNH 95444–95455). Venezuela (16). Bolívar: Camarata Valley, 450 m, 1 (AMNH 135474); Ciudad Bolívar [8°08'N, 63°33'W], 3 (AMNH 16134–16136); El Manaco (6°17'N, 61°19'W), 59 km SE El Dorado, 150 m, 1 (USNM 374821); La Bomba [7°02'N, 61°33'W], 1 (AMNH 30738); Los Patos (7°11'N, 62°22'W), 25 km SE El Manteco, 350 m, 2 (USNM 374822, 387803); Maripa [7°26'N, 65°09'W], 2 (AMNH 21305–21306); Río Suapure [6°48'N, 67°01'W], 4 (AMNH 16932–16934, 17560); Río Supamo (7°00'N, 62°15'W), 50 km SE El Manteco, 150 m, 1 (USNM 374818); Ríos Mato [7°09'N, 65°07'W] and Caura, 1 (AMNH 30201).

*Bradypus variegatus* Schinz, 1825

*Distribution.*—From eastern Honduras to northern Argentina (Wetzel & Avila-Pires 1980, McCarthy et al. 1999). Widespread in forested areas at low-to-middle elevations of eastern Central America (Fig. 6); South America west of the Andes to southern Ecuador; east of the Andes in South America throughout Amazonian forests (but not in the Guianan region, where replaced by *B. tridactylus*); and in some areas of southeastern Brazil and northern Argentina (Fig. 7). Absent from the open *llanos* of Colombia and Venezuela, the Brazilian *cerrado*, and other savanna habitats—contrary to distributional maps provided by Emmons & Feer (1997) and Eisenberg & Redford (1999).

*Diagnosis.*—Size variable but most populations averaging at least 72 mm in GLS; orange speculum present on dorsum of adult males; nape without black mane; face tan or golden—if golden, hairs usually with dark brown bases; face usually with dark band lateral to eye; throat brown or occasionally brown frosted with golden; hair of forehead variable in length but never hanging over face giving the appearance of a hood; pterygoids not inflated; no foramina present in anterodorsal nasopharynx; frontal sinuses often but not always well-swollen; stylomastoid foramen large; external carotid foramen large; external auditory meatus medium in size; ventral surface of hyoid (stylohyal) distinctly bent or undulating, not smoothly concave; descending process of jugal variable, but usually relatively short and robust; coronoid process of mandible thick.

*Comparisons.*—This species lacks the black dorsal mane and inflated pterygoid sinuses characteristic of *B. torquatus*. *Bradypus tridactylus* has a pair of oblong foramina in the anterodorsal nasopharynx lacking in *B. variegatus* (although in young of Age class 1, the roof of the nasopharynx is poorly ossified, complicating the identification of newborn and juvenal individuals

of *B. variegatus* and *B. tridactylus*). Also, *B. variegatus* has a brown throat (rarely frosted with golden), in contrast to *B. tridactylus*, which has a brilliant golden throat with hairs golden to the base of the hairs, or with only a slight smoky gray tint to the bases. See account of *B. pygmaeus* for comparisons with that closely related species.

*Comments.*—*Bradypus variegatus* is the only species of the genus that displays notable geographic variation. In Central America, it almost always has a tan face. Many specimens from South America—especially from southwestern Colombia, western Ecuador, and northcentral Brazil—possess strikingly golden faces, although the bases of the facial hairs are usually dark brown. A few populations in northern Brazil (e.g., on the lower Rio Tapajós) also show a strong golden frosting on the throat. This species also varies widely in the blotchiness of its dorsal coloration. Cranially, specimens from west of the Andes tend to have more elongated, strongly hourglass-shaped skulls, whereas many populations east of the Andes possess proportionately shorter, wider skulls. All populations agree with the diagnoses of Wetzel (1985) in lacking foramina in the anterodorsal nasopharynx.

Some populations show moderate dwarfing in size. The series from Mojui dos Campos represents one of the few such South American populations. In Central America, populations of *Bradypus variegatus* on several islands of the Laguna de Chiriquí in Bocas del Toro, Panamá average smaller than most but not all populations of the species that we examined from the mainland (Tables 2 and 6). If similar series were available from throughout the species' range, a detailed study of geographic variation might show that these populations deserve subspecific status. Given the present state of understanding of geographic variation within *B. variegatus*, however, it is premature to recognize subspecies of this wide-ranging and highly variable species.

*Bradypus gorgon* Thomas, 1926 (the

only named insular form of the genus prior to this study) does not show dwarfing similar to that of *B. pygmaeus*, and it is conspecific with *B. variegatus*. *Bradypus gorgon* is from Isla Gorgona, an island with an area of 15.6 km<sup>2</sup> (Aguirre-C. & Rangel-Ch. 1990) approximately 30 km off the southwestern coast of Colombia. Isla Gorgona is located on the continental shelf of South America (von Prael 1986) and has strong biological affinities with the lowlands of western Colombia and Ecuador (Alberico 1986, Rangel-Ch. 1990b). Although its geological history remains controversial (Aguirre-C. & Rangel-Ch. 1990), it may represent the tip of a sunken volcanic peak belonging to a fourth (coastal) Colombian cordillera (Haffer 1970, Alberico 1986). This coastal cordillera, or at least an arc of volcanic islands, was formed at the end of the middle Eocene, including the Serranía del Baudó, Serranía de los Saltos, and Alto de Nique, in western Colombia and extreme eastern Panamá (Haffer 1970, see also Hershkovitz 1969, Coates & Obando 1996). In the late Pliocene, the Atrato-San Juan sea corridor (= Bolívar Geosyncline) closed, uniting these volcanic blocks with the main body of South America (Alberico 1990, Coates & Obando 1996). Subsequently, glacial cycles alternately raised and lowered sea level; during one or more of these episodes, Isla Gorgona presumably became isolated from the adjacent Chocoan lowlands.

Thomas justified naming *Bradypus gorgon* partly on the basis of size: "Size small, about as in *tridactylus*, *infuscatus*, and *ephippiger*, the skull markedly smaller than in the Ecuadorean *macrodon*" (Thomas 1926:309–310). *Bradypus infuscatus*, *B. ephippiger*, and *B. macrodon* are currently considered junior synonyms of *B. variegatus* (see Gardner 1993). Three of the four taxa that Thomas compared with the sloth from Isla Gorgona occur only east of the Andes, making them poor comparisons. Thomas (1917) restricted the fourth one, *B. ephippiger*, to NW Colombia, and Cabrera

(1957) further restricted it to the Río Atrato region. Thus, a better comparison for the *Bradypus* from Isla Gorgona would have been with *B. epihippiger* rather than with *B. macrodon*, as the occurrence of *B. epihippiger* west of the Andes in Colombia places it in the biogeographic region from which the sloth on Isla Gorgona almost certainly was derived.

Contrary to Thomas' conclusions, in the two specimens from Isla Gorgona for which we have measurements (both adults), the greatest length of the skull averages near that of adults from the closest available mainland populations in southwestern Colombia (Isla Gorgona: GLS,  $\bar{X} = 76.7$ , standard error of the mean (SEM) = 1.20,  $n = 2$ ; Río Raposo & Bajo Calima: GLS,  $\bar{X} = 73.7$ , SEM = 1.09,  $n = 6$ ; Tumaco: GLS,  $\bar{X} = 76.3$ , SEM = 2.85,  $n = 3$ ). We agree with Wetzel & Avila-Pires (1980) and Gardner (1993) in considering *Bradypus gorgon* to be conspecific with *B. variegatus*.

Isla Gorgona is twice as far from the mainland as any of the islands of Bocas del Toro, falls within the size range of those islands, and surely has been isolated longer, since it is separated from the mainland by water about 70 m deep (Alberico 1986), whereas the greatest depth of water separating Isla Escudo from the adjacent mainland is ca. 29 m (Kalko & Handley 1994). This raises the question of why the three-toed sloth on Isla Gorgona has not undergone a decrease in size similar to that of *Bradypus pygmaeus* on Isla Escudo. We speculate that dwarfism in *B. pygmaeus* may be related to foraging in mangroves, which are absent from Isla Gorgona (Rangel-Ch. 1990a). Another scenario that should not be dismissed is the possibility that three-toed sloths could have been recently introduced to Isla Gorgona from the mainland by humans (Alberico 1986).

*Specimens examined.*—*Bradypus variegatus*, total 467. Argentina (1). Jujuy: no specific locality, 1 (FMNH 21672). Bolivia (13). Beni: Beni River [10°23'S, 65°24'W], 1

(USNM 238668); Río Mamoré [10°23'S, 65°23'W], 5 km S Guayaramerin, 1 (AMNH 209940); Río Mamoré [10°23'S, 65°23'W], 8 km N Exaltación, 1 (AMNH 211663). Cochabamba: Todos Santos [16°48'S, 65°08'W], 1 (AMNH 38784). Santa Cruz: Buena Vista [17°27'S, 63°40'W], 4 (AMNH 61792; FMNH 21393–21394, 21430); Buena Vista [17°27'S, 63°40'W], 450 m, 1 (FMNH 51871); Río Surutú [17°24'S, 63°51'W], 400 m, 1 (AMNH 61791); Río Yapacaní [16°00'S, 64°25'W], 1 (FMNH 51870); Santa Cruz de la Sierra [17°48'S, 63°10'W], 1 (AMNH 133435); 5 km E Río Palometillas, 300 m, 1 (AMNH 261304). Brazil (130). Amazonas: Rio Amazonas, Santo Antonio de Amatary, 1 (AMNH 93103); Rio Amazonas, south bank, Villa Bella Imperatriz [= Parintins, 2°36'S, 56°44'W], 12 (AMNH 93104–93115); Rio Madeira, Rosarinho [3°42'S, 59°08'W], 4 (AMNH 92335, 92828–92829, 92845); Rio Madeira, Rosarinho, Santo Antonio de Uayará, 3 (AMNH 92332–92334); Rio Negro, Cacao Pereira [3°08'S, 60°05'W], Igarapé, 2 (AMNH 80447–80448); Rio Negro, Iauari [0°31'S, 64°50'W], 1 (AMNH 79396); Rio Negro, Manaus [3°08'S, 60°01'W], 1 (AMNH 91353); Rio Solimões, Codajás [3°50'S, 62°05'W], 1 (FMNH 50906); Solimões, 1 (AMNH 37155). Espírito Santo: Lagoa Juparana [19°20'S, 40°04'W, Hershkovitz 1977], 4000 ft, 1 (AMNH 78844). Pará: Altamira, 85 km SW, east bank Rio Iriri (3°50'S, 52°40'W), 1 (USNM 549523); Belém [1°27'S, 48°29'W], 2 (MCZ 31001; USNM 393816); Belém [1°27'S, 48°29'W], Utinga, 2 (USNM 339631–339632); Currealinho, 2 (AMNH 133438, 133457); Currealinho, Ilha de Marajó [1°00'S, 49°30'W], 8 (AMNH 133406, 133415, 133419, 133421, 133426, 133432–133433, 133455); Ilha de Marajó [1°00'S, 49°30'W], 4 (FMNH 34401, 34712–34714); Patagonia, 12 mi, 2 (AMNH 75140–75141); Rio Amazonas, Igarapé Piaba [1°55'S, 55°33'W], 3 (MCZ 30993, 30995, 31002); Rio Majary, Recreio [1°42'S, 52°12'W], 1 (AMNH 95841); Rio Tapajós, Aramanay [2°45'S, 54°59'W, Hershkovitz 1977], 3

(AMNH 95101–95103); Rio Tapajós, Caxiricatuba [2°50'S, 55°08'W], 1 (AMNH 95104); Rio Tapajós, east bank, Fordlandia [3°40'S, 55°30'W], 1 (FMNH 94551); Rio Tapajós, Igarapé Amarin [2°26'S, 55°00'W, Hershkovitz 1977], 1 (AMNH 95329); Rio Tapajós, Igarapé Bravo [2°26'S, 55°00'W, Hershkovitz 1977], 2 (AMNH 95105–95106); Rio Tapajós, Inajatuba, 4, (AMNH 95325–95328); Rio Tapajós, Santarem [2°26'S, 54°42'W], nearby, 1 (FMNH 21551); Rio Tapajós, Tauary [3°05'S, 55°06'W], 3 (MCZ 30996–30997, 31731); Rio Tapajós, west bank, São Raimundo [3°27'S, 55°17'W], 1 (FMNH 92079); Rio Tocantins, Baião [2°41'S, 49°41'W], 1 (AMNH 96255); Rio Tocantins, Cameté [2°15'S, 49°30'W], 1 (MCZ 30998); Rio Tocantins, Ilha do Taiuna [2°15'S, 49°30'W], 14 (AMNH 96241–96251, 96256, 97315); Rio Tocantins, Mocajuba [2°35'S, 49°30'W], 2 (AMNH 96253–96254); Santarém [2°26'S, 54°42'W], 5 (USNM 111636/49590, 111637/49591, 239454–239455, skin number 49592); Santarém, Cuiaba, km 35, 1 (USNM 461731); Santarém [2°26'S, 54°42'W], near, 2 (AMNH 40829–40830); Santarém, Mojui dos Campos (2°26'S, 54°42'W), 27 (USNM 545911–545937); no specific locality, 7 (FMNH 25315–25319, 34402; UMMZ 53929). São Paulo: Jaraguá [23°27'S, 46°44'W] 1 (FMNH 94296). Colombia (83). Amazonas: Leticia [4°09'S, 69°57'W], Río Amazonas, 1 (MLS 2213); no specific locality, 1 (IND-M 387). Antioquia: Dabeiba [7°01'N, 76°16'W], Río Sucio, 2000 ft, 2 (AMNH 37792–37793); Medellín [6°15'N, 75°35'W], 1 (MCZ 5015); Turbo [8°06'N, 76°43'W], 1 (ICN 800); Zaragoza, 23 km S, 22 km W, at Providencia [7°21'N, 75°03'W], 400 m, 1 (USNM 449524). Bolívar: San Juan Nepomuceno, 167 m [9°58'N, 75°04'W, Hershkovitz 1977], 2 (FMNH 68916–68917). Caquetá: no specific locality, 1 (FMNH 140254). Cauca: Isla Gorgona [2°59'N, 78°12'W], 2 (BM skin 24.12.6.17/skull 24.16.6.17 [holotype of *Bradypus gorgon* Thomas, examined by E. Kalko and N. Simmons]; IND-M 2613); Río Saija [2°52'N, 77°41'W], 100 m, 1 (FMNH 90060). Cesar: Colonia Agrícola de Caracolicito [10°18'N, 74°00'W, Hershkovitz 1947], 2 (USNM 281352–281353); Valledupar, Río Cesar, El Orinoco [10°09'N, 73°26'W, Hershkovitz 1947], 1 (USNM 281354). Chocó: Andagoya [5°06'N, 76°41'W], 1 (FMNH 86760); Juradó [7°07'N, 77°46'W], 100 m, 1 (UC 3909); Quibdó [5°42'N, 76°40'W], 1 (AMNH 42838); Río Baudó, Río Sandó [5°03'N, 76°57'W], 160 m, 2 (FMNH 90061, 90314); Riosucio, corregimiento de Cacarcas, Río Peranchó [7°40'N, 77°10'W], Parque Nacional Natural Los Katíos, 1 (IND-M 3907); Unguía [8°01'N, 77°07'W, Hershkovitz 1977], Golfo de Urabá, 4 (FMNH 69587–69590). Córdoba: Arboletes, 1 (ICN 12978); Catival [8°17'N, 75°41'W], upper Río San Jorge, 1 (FMNH 68921); Río San Jorge [9°07'N, 74°44'W], 2 (AMNH 32699–32700); Upper Río Sinú [7°51'N, 76°17'W, Hershkovitz 1977], 2 (FMNH 68919–68920). Cundinamarca: Salto del Tequendama [4°35'N, 74°18'W], 1 (IND-M 3906). Guainía: Caño Carbón, Puerto Inírida [3°52'N, 67°56'W], 1 (IND-M 3964). La Guajira: Puerto Estrella [12°21'N, 71°19'W], 1 (USNM 216665). Meta: Villavicencio [4°09'N, 73°37'W], 1 (ICN 801). Nariño: Barbacoas [1°41'N, 78°09'W], 1 (AMNH 34153); Tumaco [1°49'N, 78°46'W], 1 (IND-M 4112); Tumaco, Inguapí del Guadual, Río Mira, 2 (UV 8131, 10920); Tumaco, 15 km E, Inguapí del Guadual, 4 (UV 4657, 4658, 8132, 8133). Norte de Santander: Catatumbo, Petrólea [8°30'N, 72°35'W], 1 (MLS 576); Cúcuta [7°54'N, 72°31'W], “comprado en Cúcuta,” 1 (MLS 578). Putumayo: Puerto Leguizamo [0°12'S, 74°46'W], Caño Cauayá, Finca Velásquez, entrando por Limonconcho NW de Leguizamo, 1 (IND-M 590); Río Mecaya [0°28'N, 75°20'W], 185 m, 2 (FMNH 70812–70813). Santander: Barrancabermeja, Peroles, Caño Muerto [7°10'N, 73°55'W], 150–200 m, 1 (ICN 2952). Sucre: Chochó, Sincelejo [9°18'N, 75°24'W], 1 (IND-M 4133); Colosó [9°30'N, 75°21'W], Las Campanas, 1 (FMNH 68918). Valle del Cauca: Bajo Calima [4°00'N, 76°56'W, González-M.

& Alberico 1993], Quebrada La Brea, parte alta, ca. 250 m, 2 (UV 4078, 10919), Buenaventura, Bajo Calima [4°00'N, 76°56'W, González-M. & Alberico 1993], 35 m, 3 (UV 4079–4081); Buenaventura, Río Raposo [3°41'N, 77°05'W, Alberico 1983], ca. sea level, 17 (UV 4843–4859); Calima, 300 m, 1 (MSU 2077); Rockefeller Research Station, 5 mi up Río Raposo from the Pacific, 20 mi. SE Buenaventura, 1 (UMMZ 115803); Sabaletas, 500 m, 4 (MSU 2078–2081); Zabaletas, 500 m, 3 (FMNH 86761–86762, 86879). Costa Rica (8). Alajuela: Jabillo, San Carlos [= Vijagual and La Vieja de San Carlos, 10°20'N, 84°30'W, see also Goodwin 1946], 1 (AMNH 139833). Cartago: Angostura [9°53'N, 83°38'W], 1 (USNM 12871/14104). Heredia: Río Sarapiquí, Puerto Viejo [10°38'N, 84°01'W], 300 ft, 2 (UMMZ 112319–112320). Limón: Pacuare [9°55'N, 83°34'W], 1 (USNM 12870/15961); Talamanca, 2 (USNM 11381, 12103/14215). Puntarenas: Palmar [8°57'N, 83°28'W], 1 (AMNH 139313). Ecuador (20). El Oro: Portovelo [3°43'S, 79°39'W]; Cuatro Lomas, 1 (AMNH 46552). Esmeraldas: Achote, 1 (MSU 9339); Dogola, 1 (MSU 9338); Hacienda de Tinbre, near Quinindé [= Rosa Zárate, 0°20'N, 79°28'W], 1 (MSU 8675); Montaña de Cole, near Quinindé [= Rosa Zárate, 0°20'N, 79°28'W], 1 (MSU 8676); Montañas de Chancamita, 1 (MSU 8664). Los Ríos: Vinces [1°32'S, 79°45'W], 8 (AMNH 62877, 62879–62885); Vinces [1°32'S, 79°45'W], Hacienda Pijigal, 2 (AMNH 62876, 62878). Manabí: Río de Oro [0°28'S, 79°36'W], 1 (AMNH 34270). Napo: Río Suno [0°42'S, 77°08'W], below Loreto, 1 (FMNH 31119). Pastaza: Puyo, east of (1°29'S, 77°57'W), 2000 ft, 1 (MSU 3724). Pichincha: Santo Domingo de los Colorados [0°15'S, 79°09'W], bypass road, 1 (USNM 528706). Honduras (2). Gracias a Dios: Patuca River, 2 (USNM 21010/36058, 21011/36059). Nicaragua (44). Boaco: Chontales, 2 (AMNH 28477–28478). Jinotega/Nueva Segovia: Río Coco, 1 (AMNH 29441). Matagalpa: Finca Tepeyac [13°11'N, 85°56'W, Genoways 1973], 10.5 km N, 9 km E Matagalpa, 960 m, 5 (KU 97876–97880); Hacienda Tepeyac [13°11'N, 85°56'W, Genoways 1973], 3 (KU 104581; USNM 337556–337557). Río San Juan: Greytown [= San Juan del Norte, 10°56'N, 83°42'W], 2 (USNM 59010, 16352/23251); La Esperanza, 2 (KU 108389; USNM 361231). Zelaya: Bonanza [13°57'N, 84°32'W], 16 (KU 99451–99458; USNM 338773–338780); Bonanza [13°57'N, 84°32'W], 3.5 mi SW of, 780 ft, 1 (KU 96356); Bonanza [13°57'N, 84°32'W], 4 mi NE of, 800 ft, 1 (KU 96357); El Recreo [12°09'N, 84°26'W], 71 km ENE Bluefields, 5 (KU 104368–104369; USNM 337713–337715); El Recreo [12°09'N, 84°26'W], north side Río Mico, 25 m, 2 (KU 115212–115213); El Recreo [12°09'N, 84°26'W], south side Río Mico, 25 m, 3 (KU 106317, 111343–111344); Escondido River [12°09'N, 83°46'W], 1 (USNM 51273). Panamá (127; specimens collected in the former “Canal Zone” are now placed in Colón or Panamá provinces, as listed here) Bocas del Toro: Almirante (9°18'N, 82°24'W), 9 (USNM 315847–315852, 315855–315856, 399052); Cayo Agua (9°10'N, 82°02'W), 18 (USNM 324249–324260, 578414\*, 578415–578419); Cayo Nancy (9°19'N, 82°11'W), 7.3 km ESE Bocas del Toro (town), 6 (USNM 464853–464855, 464856\*, 464857–464858); Changuinola (9°27'N, 82°31'W), 2 (USNM 315853–315854); Elena Farm, 1 (USNM 291179); Isla Bastimentos (9°19'N, 82°08'W), 2 (USNM 324248, 324261); Isla Bastimentos, Cedar Creek (9°19'N, 82°08'W), 6 (USNM 335267–335172); Isla Colón (9°24'N, 82°16'W), La Gruta, 5 (USNM 464849\*, 464850–464852, 464859); Isla Popa, south shore (9°10'N, 82°08'W), 1 km E Sumwood Channel, 7 (USNM 579164\*, 579165–579170); Isla San Cristóbal, Bocatorito (9°15'N, 82°16'W), 7 (USNM 449525–449530, 449531\*); Ñuri (8°56'N, 81°48'W), 10 (USNM 575379–575381, 575382\*, 575383–575388); Península Valiente, Punta Alegre (9°10'N, 81°54'W), 8 (USNM 578412, 578420–578424, 578425\*, 578426); Sibube (9°36'N, 82°47'W), 1 (USNM 335466); Tierra Oscura (9°11'N,

82°15'W), 3.5 km S Tiger Key, 8 (USNM 449542\*, 449543–449549). Colón: Brujo Point, 3 (UMMZ 64942, 64950; USNM 256182); Frijoles [9°10'N, 79°49'W], 3 (UMMZ 56659, 58926, 59971); Fort Davis [9°15'N, 79°56'W], 3 (USNM 296408–296409, 298712); Gatún [9°15'N, 79°56'W], 2 (AMNH 36816; USNM 170889); Gatún, near, Río Indio [9°15'N, 79°59'W], 2 (USNM 170950–170951); Lion Hill [9°13'N, 79°54'W], 1 (USNM 172729); Loma de León [= Lion Hill, 9°13'N, 79°54'W], 1 (MCZ B8427), Monte Lirio, 1 (USNM 256178); Río Pequeni, Salamanca Hydrographic Station [9°17'N, 79°36'W], 1 (MCZ 34334). Darién: Cerro Tacarcuna (8°10'N, 77°18'W), 4600 ft, 2 (USNM 338124–338125); Cituro [8°00'N, 77°36'W], 1 (AMNH 38191); El Real [8°06'N, 77°45'W], 3 (AMNH 37619–37621); Marragantí [8°08'N, 77°44'W], about 2 mi above Real de Santa María, on the Río Tuyra, ca. sea level, 1 (USNM 179551 [holotype of *Bradypus ignavus* Goldman]); Mount Sapo [7°58'N, 78°22'W], 1 (MCZ 19844); Tapalisa [7°59'N, 77°26'W], 400 ft., 1 (AMNH 38102). Panamá: Balboa [8°57'N, 79°35'W], 1 (USNM 296410); Barro Colorado Island [9°09'N, 79°51'W], 2 (FMNH 30738; UMMZ 64943); Cerro Azul [= La Zumbadora], (9°14'N, 79°21'W), 1 (USNM 306856); La Chorrera [8°52'N, 79°48'W], 2 (AMNH 31427; USNM 324956); Fort Kobbe [8°54'N, 79°36'W], 2 (USNM 296293, 318366). San Blas: Mandinga (9°29'N, 79°05'W), 2 (USNM 305593–305594). Perú (31). Loreto: Alto Amazonas, Río Morona, boca Río Amaya [4°39'S, 77°07'W], 200 m, 1 (FMNH 88893); Boca Río Curarray [2°22'S, 74°05'W], 1 (AMNH 71822); Iquitos [3°46'S, 73°15'W], 6 (AMNH 98532–98533, 98536, 98542, 98545–98546); Nauta, Río Samiria, Santa Elena [4°50'S, 74°13'W], 130 m, 1 (FMNH 86896); Río Amazonas, Apayacu [3°19'S, 72°06'W], 1 (AMNH 74429); Río Amazonas, Orosa [3°26'S, 72°08'W], 2 (AMNH 73758–73759); Río Amazonas, Puerto Indiana [3°28'S, 73°03'W], 6 (AMNH 73571–73575, 73757);

Río Samiria [4°42'S, 74°13'W], 4 (AMNH 188193–188196); Río Ucayali, Sarayacu [6°44'S, 75°06'W], 7 (AMNH 76402–76403, 76408, 76423, 76495–76497); Yurimaguas, Puerto Arturo [5°50'S, 76°03'W], 1 (FMNH 20132). Ucayali: Pucallpa [8°23'S, 74°32'W], 200 m, 1 (AMNH 147462). Venezuela (8). Amazonas: Mount Duida, Esmeralda [3°10'N, 65°33'W], left bank Río Orinoco, 1 (AMNH 76904); Río Casiquiare, orilla izquierda, El Mery [3°05'N, 65°55'W], 1 (AMNH 78515); San Juan (5°18'N, 66°13'W), Río Manapiare, 163 km ESE Puerto Ayacucho, 155 m, 1 (USNM 406693). Aragua: Rancho Grande [10°22'N, 67°41'W], 1 (AMNH 144824); Carabobo/Yaracuy: 10 km NW Urama (10°32'N, 68°23'W), 25 m, 1 (USNM 374817). Miranda: San Andrés (10°22'N, 66°50'W), 16 km SSE Caracas, 1144 m, 2 (USNM 372832–372833). Zulia: El Rosario (9°09'N, 72°36'W), 42 km WNW Encontrados, 24 m, 1 (USNM 443760).

#### Key to three-toed sloths (*Bradypus*)

1. Distinctive black mane originating at nape and extending halfway down the back; pterygoids inflated; two or three foramina present on each side of the anterodorsal nasopharynx; dorsal speculum never present; no differentiation between color or length of facial and dorsal pelage. Known only from the Atlantic forests of southeastern Brazil. . . . . subgenus *Scaeopus*, *Bradypus* (*S.*) *torquatus*
- 1'. No black mane on nape; pterygoids not inflated; no foramina present on lateral walls of the anterodorsal nasopharynx; orange speculum present on the dorsum of adult males; facial hair shorter than dorsal hair and of a different color. . . . . subgenus *Bradypus*, 2
2. Single pair of large oval foramina present on the dorsal roof of the anterodorsal nasopharynx; throat with stiff hairs golden-yellow to the base or with a slight smoky gray tint to the base, no dark stripe extending laterally from eye; face and forehead covered with golden-yellow hairs to the base; hair of fore-

- head short. Known only from the Guianas and adjacent regions of Venezuela and Brazil. . . . . *Bradypus (B.) tridactylus*
- 2'. No foramina in any part of the anterodorsal nasopharynx; throat with soft hairs, typically brown or cream-colored, but occasionally dark brown frosted with golden; dark stripe usually present lateral to eye; face variable in color, with either tan or yellowish hair; long brownish hair of dorsum usually extending to forehead. . . . . *B. variegatus*-group, 3
3. Size small; skull small and gracile; external carotid foramen usually closed or minute; stylomastoid foramen minute; external auditory meatus both absolutely and relatively large; coronoid process of mandible strikingly falcate; long hair of forehead and shoulders forming an obvious hood around short facial hair. Known only from Isla Escudo de Veraguas, Panamá. . . . . *Bradypus (B.) pygmaeus*
- 3'. Size variable but usually large; skull robust; external carotid foramen large; stylomastoid foramen larger, usually visible to naked eye; external auditory meatus both absolutely and relatively smaller; posterior border of coronoid process of mandible straight or only moderately curved; hair of forehead not especially long, never giving the appearance of a hood. Wide-ranging in both Central and South America. . . . . *Bradypus (B.) variegatus*

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