
MAMMALIAN DIVERSITY AND MATSES
ETHNOMAMMALOLOGY IN AMAZONIAN PERU
PART 2. XENARTHRA, CARNIVORA, PERISSODACTYLA,
ARTIODACTYLA, AND SIRENIA

ROBERT S. VOSS AND DAVID W. FLECK



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AND SIRENIA

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ABSTRACT

This report continues our monographic analysis of mammalian diversity and Matses ethnomammalogy in the Yavari-Ucayali interfluvial region of northeastern Peru. Based primarily on specimens collected in the region from 1926 to 2003, interviews with Matses hunters, and published sight surveys of large mammals, we document the local occurrence of 33 species of xenarthrans, carnivores, perissodactyls, artiodactyls (including cetaceans), and sirenians. All of the species in these groups, with the exception of the Amazonian manatee (*Trichechus inunguis*), are recognized and named by the Matses, from whom we recorded extensive accounts of mammalian natural history.

The local xenarthran fauna consists of nine species (*Cabassous unicinctus*, *Priodontes maximus*, *Dasyurus novemcinctus*, *D. pastasae*, *Bradypus variegatus*, *Choloepus hoffmanni*, *Cyclopes didactylus*, *Myrmecophaga tridactyla*, *Tamandua tetradactyla*), all of which are represented by examined specimens. Only two xenarthrans (*D. pastasae* and *C. hoffmanni*) are primary game species for the Matses, who are familiar with many aspects of their biology that were previously unrecorded in the scientific literature. However, Matses interviews also provide important new information about the behavior of *D. novemcinctus* (a secondary game species) and *M. tridactyla*, neither of which has previously been studied in rainforested environments.

The local carnivore fauna consists of 16 species (*Atelocynus microtis*, *Speothos venaticus*, *Leopardus pardalis*, *L. wiedii*, *Panthera onca*, *Puma concolor*, *Pu. yagouaroundi*, *Eira barbara*, *Galictis vittata*, *Mustela africana*, *Lontra longicaudis*, *Pteronura brasiliensis*, *Bassaricyon alleni*, *Nasua nasua*, *Potos flavus*, *Procyon cancrivorus*), most of which are represented by examined specimens; six species without preserved voucher material are known from camera-trap photographs and/or unambiguous sightings by Matses hunters and field biologists. Although the coati (*N. nasua*) is the only carnivore occasionally hunted by the Matses for food, Matses interviews are richly informative about the natural history of other species, notably including *S. venaticus*, *Leopardus* spp., *Pa. onca*, *Puma* spp., and *E. barbara*.

All of the local ungulates (*Tapirus terrestris*, *Pecari tajacu*, *Tayassu pecari*, *Mazama americana*, *M. nemorivaga*) are hunted by the Matses for food, and the hunters we interviewed are correspondingly well informed about the natural history of most of these species, with the exception of the seldom-encountered gray brocket (*M. nemorivaga*). Both species of local cetaceans (*Inia geoffroyi*, *Sotalia fluviatilis*) are familiar to the Matses, although neither is eaten.

The xenarthrans, carnivores, ungulates, and aquatic mammals that inhabit the Yavari-Ucayali interfluvium are all widespread species, so this component of the regional fauna, as currently understood, is not biogeographically distinctive, nor is it extraordinarily diverse (by western Amazonian standards). Although we discuss several noteworthy taxonomic and nomenclatural issues relevant to these taxa, the principal contribution of this report consists in the natural history information compiled from our Matses informants and the resulting overview of local community structure as defined by diurnal activity, locomotion, social behavior, and trophic relationships.

INTRODUCTION

This report is the second installment of a monographic series on mammalian diversity and ethnomammalogy in a sparsely inhabited rainforest region between the Yavari and Ucayali rivers in northeastern Peru. Our study is based on several large collections of mammals made at various localities in this region between 1926 and 2003, and on our long-term ethnobiological

and linguistic fieldwork with the Matses, a Panoan-speaking group of indigenous Amazonians who still obtain most of their dietary protein by hunting mammals. Our primary objectives are to document the species richness of the regional fauna through taxonomic analysis of collected specimens, and to assess the extent of Matses knowledge of mammalian natural history based on linguistic analysis of recorded interviews.

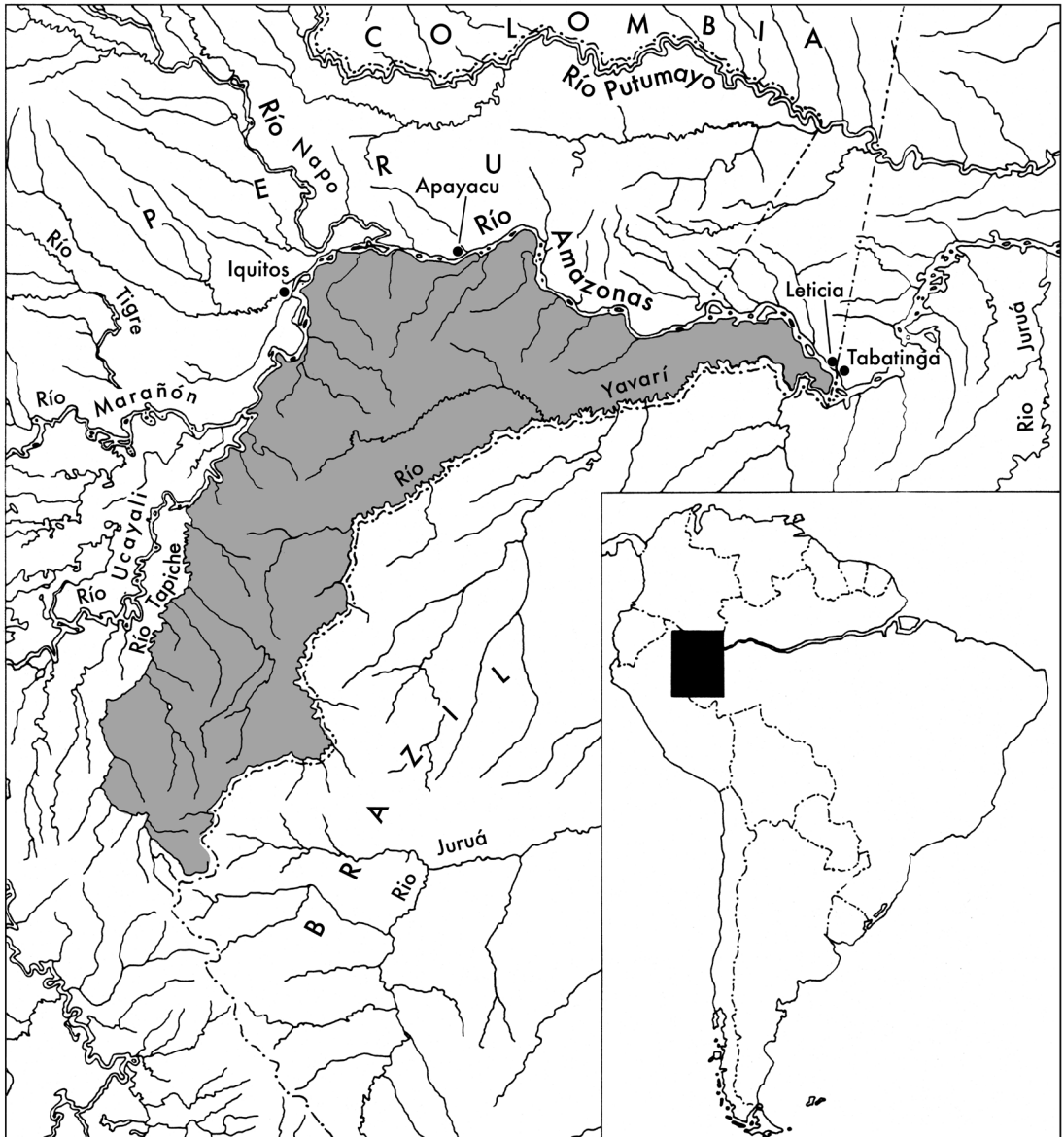


FIG. 1. The Yavari-Ucayali interfluvium (shaded) in relation to surrounding geographical features of western Amazonia.

The first report in this series (Voss and Fleck, 2011) introduced our materials and methods, summarized current knowledge about the physical geography and floristics of the Yavari-Ucayali interfluvium (figs. 1, 2), and analyzed taxonomic and ethnographic information about the local primate fauna. In this report we provide equiva-

lent treatment of the large nonprimate fauna, comprising local species of xenarthrans, carnivores, ungulates, cetaceans, and manatees. Together with primates and a few large rodents (Voss and Fleck, in prep.), the species treated in this report include all of the important mammalian game that occurs in Matses territory.

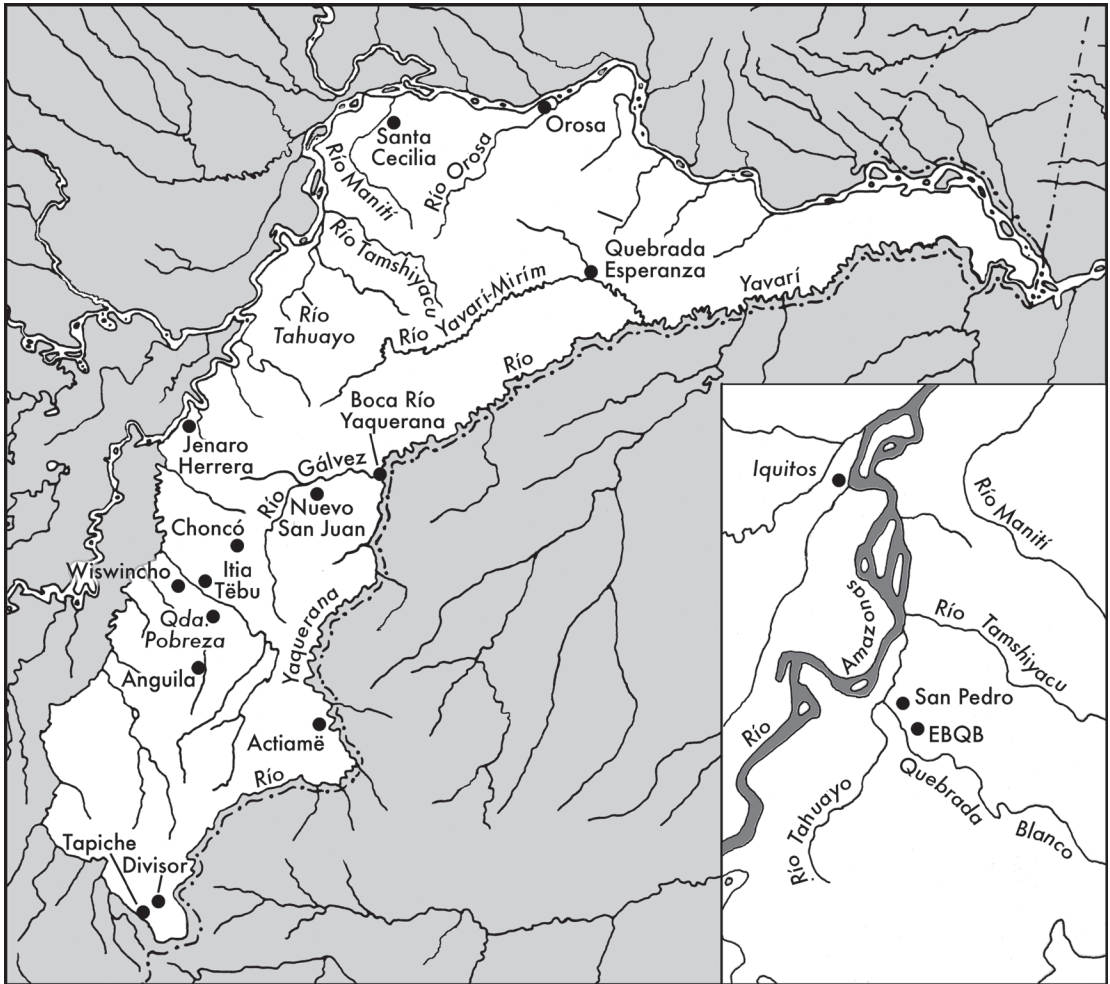


FIG. 2. Faunal inventory sites and collecting localities within the Yavari-Ucayali interfluvium (see appendix 2 for geographic coordinates and other information). Inset: Faunal inventory sites in or near the Tamshiyacu-Tahuayo watersheds (EBQB = Estación Biológica Quebrada Blanco).

MATERIALS AND METHODS

Ethnobiological Methods

RECORDED MONOLOGS: From May to July of 1998 we elicited monologs about the natural history of local mammals from Matses men from four different Peruvian Matses villages, and we recorded these interviews on digital minidisk. All monologs were recorded in the Matses language. To elicit these texts, informants were asked to talk about a single mammalian taxon (e.g., a species of armadillo), which was men-

tioned only once by the interviewer (Fleck). Informants were asked to say as much as they liked about any topic relating to the taxon in question (see appendix 1 for a free English translation of one of these recorded monologs). Each informant's monologs were recorded with no other adults present in order to achieve independence of response. For each taxon, the interview was replicated a total of seven or eight times with different informants. These recordings were subsequently transcribed and translated by Fleck and literate Matses assistants and checked for

linguistic accuracy with several other Matses speakers. The texts were then checked with speakers other than the narrators to obtain second opinions on the validity of some of the less commonly asserted natural history details. Using similar methodology, additional natural history monologs were recorded from 2010 to 2013 from a single Matses speaker as part of a language documentation project.

Sentences in the translated texts were sorted by topic (physical appearance and anatomy, habitat preference, social behavior, vocalizations, daily activities, and food), and then combined to obtain composite essays for each taxon. These essays, which are presented under the heading "Matses natural history" in the accounts that follow, are supplemented by parenthetical editorial comments only as necessary to interpret otherwise obscure passages or to identify botanical taxa corresponding to Matses plant names. To provide a more complete ethnographic picture, topics concerning Matses nomenclature, classification, hunting strategies, and cultural significance (summarized under the heading "Ethnobiology" in each species account) were elaborated using data from additional sources, including interview-style question-and-answer sessions and participant observation (e.g., more than 600 hours that Fleck spent hunting with the Matses).

PLANT IDENTIFICATIONS: Most of the plants mentioned by the Matses in their monologs were identified by various means. Palms were collected by Fleck in 1998 and 1999 from the area surrounding Nuevo San Juan with the help of Matses assistants, who named the palms while in the forest, prior to being collected. Palm specimens were identified in the field using published identification guides (Henderson, 1994; Henderson et al., 1995), and voucher material was subsequently deposited at the herbarium at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima) and in the New York Botanical Garden (Bronx, New York). Other plants, particularly dicotyledonous trees, were identified by Fleck and two Matses assistants at the arboretum of the Instituto de

Investigaciones de la Amazonia Peruana. This arboretum is maintained at the Centro de Investigaciones Jenaro Herrera, a forestry research station located about 80 km west of Nuevo San Juan, where Swiss botanists have identified all trees >10 cm at breast height (Spichiger et al., 1989, 1990). Plants and trees in the proximity of Nuevo San Juan were also identified by Fleck using identification keys in Gentry (1993).

Botanical taxa corresponding to Matses plant names are provided using the following conventions: (1) Only the generic name is given if the Matses plant name corresponds to all the species in a locally polytypic genus (e.g., bin, which refers to all of the local species of the genus *Castilla* [Moraceae]). (2) The generic name is followed by "sp." if the Matses plant name corresponds to just one unidentified local species in a genus (e.g., ichibin, which refers to an unidentified species of *Matisia* and another of *Eriotheca* [Bombacaceae]). (3) The generic name is followed by "spp." if the Matses plant name corresponds to two or more unidentified species, but not to all the local species of that genus (e.g., shankuin, which refers to multiple unidentified local species of *Pourouma* [Moraceae]). Where alternative technical names for plant families are current in the literature (e.g., Palmae vs. Arecaeae, Clusiaceae vs. Guttiferae), the nomenclature used here follows Gentry (1993).

Faunal Sampling and Bibliographic Methods

Most of the xenarthran, carnivoran, and ungulate specimens that serve as voucher material for systematic accounts in this report were obtained by commercial collectors at various localities in the Yavarí-Ucayali interfluvium from 1926 to 1957 (Voss and Fleck, 2011: 9–10), others were obtained by Matses hunters working with D.W.F. at Nuevo San Juan from 1995 to 1999, and additional material was obtained haphazardly by other investigators. In addition to these vouchered records, we include unvouchered observations made by us or by our Matses colleagues at Nuevo San Juan, and we reviewed

the literature for sightings made in the course of other faunal surveys carried out in the Yavarí-Ucayali interfluvium.

BIBLIOGRAPHIC REVIEW: In assessing faunal studies carried out in the Yavarí-Ucayali interfluvium by other investigators (e.g., Salovaara et al., 2003; Amanzo, 2006) we counted only unambiguous observations as records of local occurrence, discounting reports of tracks, burrows, and unspecified “sign” as insufficient indications, and we treated these records as unvouchered even if specimens were said to have been collected. Not having examined such specimens ourselves, we are unable to confirm the accuracy of reported identifications. However, most of the taxa treated in this report are easily distinguished from one another by obvious external characters (Emmons, 1997), so sight records by competent observers provide generally reliable evidence of local occurrence.

Taxonomic Methods

SOURCE OF SPECIMENS: Specimens that we examined in the course of this study and others mentioned in our text are preserved in the American Museum of Natural History (AMNH, New York), the Field Museum of Natural History (FMNH, Chicago), the Museum of Natural Science of Louisiana State University (LSUMZ, Baton Rouge), the Museum of Michigan State University (MSU, East Lansing), the Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos (MUSM, Lima), the Museum of Vertebrate Zoology (MVZ, Berkeley), the Senckenberg Naturmuseum Frankfurt (SMF, Frankfurt), the National Museum of Natural History (USNM, Washington), and the Zoologische Staatssammlung München (ZSM, Munich).

MEASUREMENTS: We recorded external measurements (in millimeters, mm) of fresh specimens in the field following the standard American protocol: total length (nose to fleshy tip of tail), length of tail (basal flexure to fleshy tip), hind foot (length from heel to tip of longest claw or hoof), and ear (length from notch to the

distalmost edge of the pinna). We computed head-and-body length by subtracting length of tail from total length. Weights are reported below in either grams (g) or kilograms (kg). Unfortunately, field measurements of large mammals were sometimes recorded in haste under difficult circumstances, and obvious errors were subsequently detected in compiling the results for these accounts.

We took craniodental measurements to supplement other kinds of character data and document our identifications. Only a subset of the measurements listed below were taken for any particular species because anatomical endpoints that are present in some taxa are absent in others. “Condylbasal length,” for example, cannot be measured on three-toed sloths (whose skulls almost always lack attached premaxillae) nor can “nasal length” be measured on adult procyonids (which do not retain nasal sutures). In general, we selected traditional cranial measurements to maximize overlap with comparative morphometric data in the literature, but we also defined new ones to quantify dimensional differences observed between skulls of closely related taxa. A few measurements (e.g., Breadth of M1) are self-explanatory, and so are not defined below).

Condylalveolar length: distance from the posteriormost point on the occipital condyles to the anteriormost surface of alveolar bone sheathing the first maxillary tooth (pseudoincisor). This is the cranial length measure we used for *Bradypus* (in which nasal bones are often seamlessly fused with the maxillae, and which lack attached premaxillae).

Condylbasal length: distance from the posteriormost point on the occipital condyles to the anteriormost point of the premaxillae. This is the cranial length measure we used for *Choloepus* (in which the nasal bones are often seamlessly fused with the maxillae, but which have firmly attached premaxillae) and for all non-xenarthran species treated in this report.

Condylonasal length: distance from the posteriormost point on the occipital condyles to the

tips of the nasals. This is the cranial length measure we used for armadillos and anteaters following Wetzel (1980, 1985b), Wetzel and Mondolfi (1979), and Wetzel et al. (2008).

Condyloincisive length: distance from the posteriormost point on the occipital condyles to the anteriormost surface of the incisor crowns. Measured for peccaries to compare with data tabulated by Roosmalen et al. (2007), who called this dimension “length of cranium.”

Nasal length: the greatest length of one nasal bone (the longest if the right and left nasals are of unequal length).

Rostral breadth: the greatest transverse distance across the maxillae lateral to the caniniform teeth (the first maxillary teeth in *Choloepus*, but the second maxillary teeth in *Bradypus*). We measured this dimension only for sloths.

Least interorbital breadth: least distance across the frontals between the orbital fossae (anterior to the postorbital processes or postorbital swellings, if any).

Least postorbital breadth: least distance across the frontals between the temporal fossae (behind the postorbital processes or postorbital swellings, if any).

Anterior zygomatic breadth: for sloths, the greatest transverse distance across the left and right jugals (equivalent to zygomatic breadth in *Dasybus*, but not in chlamyphorid armadillos).

Posterior zygomatic breadth: for sloths, the greatest transverse distance across the left and right squamosal zygomatic processes (equivalent to zygomatic breadth in chlamyphorid armadillos).

Zygomatic breadth: the greatest transverse dimension across the zygomatic arches for species in which the anatomical locus of this maximum is homologous from specimen to specimen.

Breadth of braincase: the greatest transverse dimension across the braincase dorsal to the squamosal zygomatic processes. This dimension is impossible to measure in taxa with no unique maximal breadth above the zygomatic processes.

Length of diastema: measured from the posterior aspect of the crown of C1 to the crown of P2. This dimension was only measured for peccaries.

Maxillary tooththrow: in xenarthrans, this dimension was taken as the greatest alveolar length from the anteriormost paired maxillary tooth to the posteriormost paired maxillary tooth (i.e., ignoring unilateral supernumerary teeth, if any); for carnivores, this dimension was measured as the crown length from C1 to the posteriormost molar (M1 or M2).

Cheektooth row: crown length of ungulate postdiastemal maxillary teeth (P1–M3 in tapirs, P2–M3 in peccaries and deer).

Greatest diameter of pseudoincisor: the greatest dimension across the crown of the first maxillary tooth (*Bradypus* only).

Anterior “pterygoid” breadth: greatest distance across the mesopterygoid fossa anterior to the swollen pterygoid processes (*Choloepus* only). This dimension is actually measured between the right and left palatines, which form the lateral margins of the “inter-ptyergoid space” (sensu Wetzel, 1985a) at this point.

Posterior pterygoid breadth: least distance across the mesopterygoid fossa between the swollen pterygoid processes (*Choloepus* only).

SYSTEMATIC ACCOUNTS

The taxonomic sequence of these accounts roughly follows Wilson and Reeder (2005), although we do not consistently recognize the same higher taxa that they do, nor do we necessarily use the same taxon names in the same sense as theirs (our use of Artiodactyla, for example, includes cetaceans). We use higher-taxonomic headings to summarize information about interfluvial diversity (e.g., of orders and families), to list English names associated with Latin binomina, and to summarize aspects of Matses folk nomenclature associated with supra-specific categories.

Several headings are used to organize information for each species. Under “Voucher Material” we

TABLE 1
Niche Separation among Nine Sympatric Xenarthrans of the Yavari-Ucayali Interfluve according to Matses Informants

	Activity	Locomotion	Diet	Social behavior
CHLAMYPHORIDAE				
<i>Cabassous unicinctus</i>	nocturnal	terrestrial & fossorial	soil invertebrates	?
<i>Priodontes maximus</i>	nocturnal	terrestrial	invertebrates & some fruit	solitary
DASYPODIDAE				
<i>Dasypus novemcinctus</i>	nocturnal	terrestrial	omnivorous	solitary
<i>Dasypus pastasae</i>	nocturnal	terrestrial	omnivorous	solitary
BRADYPODIDAE				
<i>Bradypus variegatus</i>	diurnal & nocturnal	arboreal	mostly folivorous	solitary
MEGALONYCHIDAE				
<i>Choloepus hoffmanni</i>	nocturnal	arboreal	folivorous & frugivorous	solitary
MYRMECOPHAGIDAE				
<i>Cyclopes didactylus</i>	nocturnal	arboreal	?	solitary
<i>Myrmecophaga tridactylus</i>	diurnal & nocturnal	terrestrial	social insects	solitary
<i>Tamandua tetradactyla</i>	diurnal & nocturnal	terrestrial & arboreal	social insects	solitary

list the cataloged museum specimens (if any) collected within the limits of the Yavari-Ucayali interfluve as defined above. Under “Other Interfluvial Records” we list unvouchered regional sightings made by us or by authors of published reports. Under “Identification” we discuss the taxonomic criteria we used to assign a Latin binomen to the species in question; entries under this heading can be extensive when current taxonomic usage is problematic. Under “Ethnobiology” we describe Matses names associated with each species, explain the cultural importance (if any) of the species, and describe any relevant folk beliefs. Under “Matses Natural History” we summarize allegedly factual information about each species obtained from the interview methods described above.

We provide external and craniodental measurements to document our identifications of voucher material from the Yavari-Ucayali interfluve, and we sometimes provide measurements of extralimital specimens if no relevant vouchers are available (e.g., for canids and large cats). The latter provide a basis for identifying cranial material discovered by future researchers in our region. Cra-

nial photographs of most taxa treated herein are available elsewhere (e.g., in Husson, 1978; Feijó and Langguth, 2013), but we take this opportunity to illustrate several speciose local assemblages with crania drawn to the same scale. Although these are of limited taxonomic value, they provide visually compelling perspectives of size and form among closely related sympatric species.

Xenarthra

Nine species of xenarthrans in five families are definitely known to occur in the Yavari-Ucayali interfluve, and all are represented by examined voucher material. Following McKenna and Bell (1997) xenarthrans are now classified in the orders Cingulata (armadillos) and Pilosa (sloths and anteaters), but we treat armadillos (Chlamyphoridae and Dasypodidae), sloths (Bradypodidae and Megalonychidae), and anteaters (Myrmecophagidae) under separate headings below. Of the nine xenarthran species in our region, only two (one armadillo and one sloth) are primary game species for the Matses. Eco-

TABLE 2
Morphological Characters of Four Armadillo Species from the Yavari-Ucayali Interfluve^a

	<i>Cabassous unicinctus</i>	<i>Priodontes maximus</i>	<i>Dasypus novemcinctus</i>	<i>Dasypus pastasae</i>
Adult weight	2–4 kg	to ca. 35 kg	3–6 kg	8–11 kg
Movable bands ^b	>10	>10	7–10	7 or 8
Manual digits	5	5	4	4 or 5 ^c
Enlarged scutes on knee	absent	absent	absent	present ^d
Tail (integument)	naked	armored	armored	armored
Tail (length)	< ½ head-and-body	> ½ head-and-body ^e	> ½ head-and-body	> ½ head-and-body
Maxillary teeth	7–10	16–20	7 or 8	7 or 8
Lateral palatine margins ^f	rounded	rounded	rounded	keeled
Height condyloid process ^g	> coronoid process	≥ coronoid process	< coronoid process	< coronoid process

^a Character data from Wetzel and Mondolfi (1979), Wetzel (1980, 1985b), and Wetzel et al. (2008).

^b Of carapace (between scapular and pelvic shields).

^c A fifth digit, when present in *D. pastasae*, is vestigial and very small.

^d See Wetzel (1985b: fig. 13).

^e The key to armadillo genera in Wetzel et al. (2008: 129) implies that *Priodontes* has a short tail, but our voucher specimen and those measured by Wetzel (1985b) have tails that are >50% of head-and-body length.

^f See figure 4.

^g Of the mandible.

logical niche separation among members of this local fauna based on information obtained from Matses informants is summarized in table 1.

Armadillos (Cingulata)

Living armadillos have traditionally been placed in a single family (e.g., by Wilson and Reeder, 2005; Gardner, 2008), but recent phylogenetic results, including the astonishing discovery that glyptodonts are nested within the radiation of Recent armadillos, suggest that Dasypodidae and Chlamyphoridae be recognized as distinct clades of commensurate rank (Gibb et al., 2015; Mitchell et al., 2016). Four armadillo species—two dasypodids and two chlamyphorids—all easily distinguished by salient external and cranial characters (table 2; fig. 3), are known to occur in the Yavari-Ucayali interfluve.

For the purpose of these accounts, we consider armadillos to be adults if the basioccipital-basisphenoid suture is fused, and if the permanent dentition is fully erupted. In dasypodids (which include the only xenarthrans known

to have two functional generations of teeth; Ciancio et al., 2012) some specimens that we consider to be adult by these criteria retain vestiges of the deciduous dentition.

Chlamyphoridae

Two species of chlamyphorid armadillos, the naked-tailed armadillo (*Cabassous unicinctus*) and the giant armadillo (*Priodontes maximus*), are known to occur in the Yavari-Ucayali interfluve, and no others could be expected to occur here on the basis of geographic range data. The two local chlamyphorid species are infrequently encountered by the Matses and neither is hunted for food. Although strikingly similar in certain aspects of external appearance, they differ greatly in size and behavior.

Cabassous unicinctus (Linnaeus, 1758)

Figure 3C

VOUCHER MATERIAL (TOTAL = 2): Orosa (AMNH 74113), Río Manití (FMNH 112563).

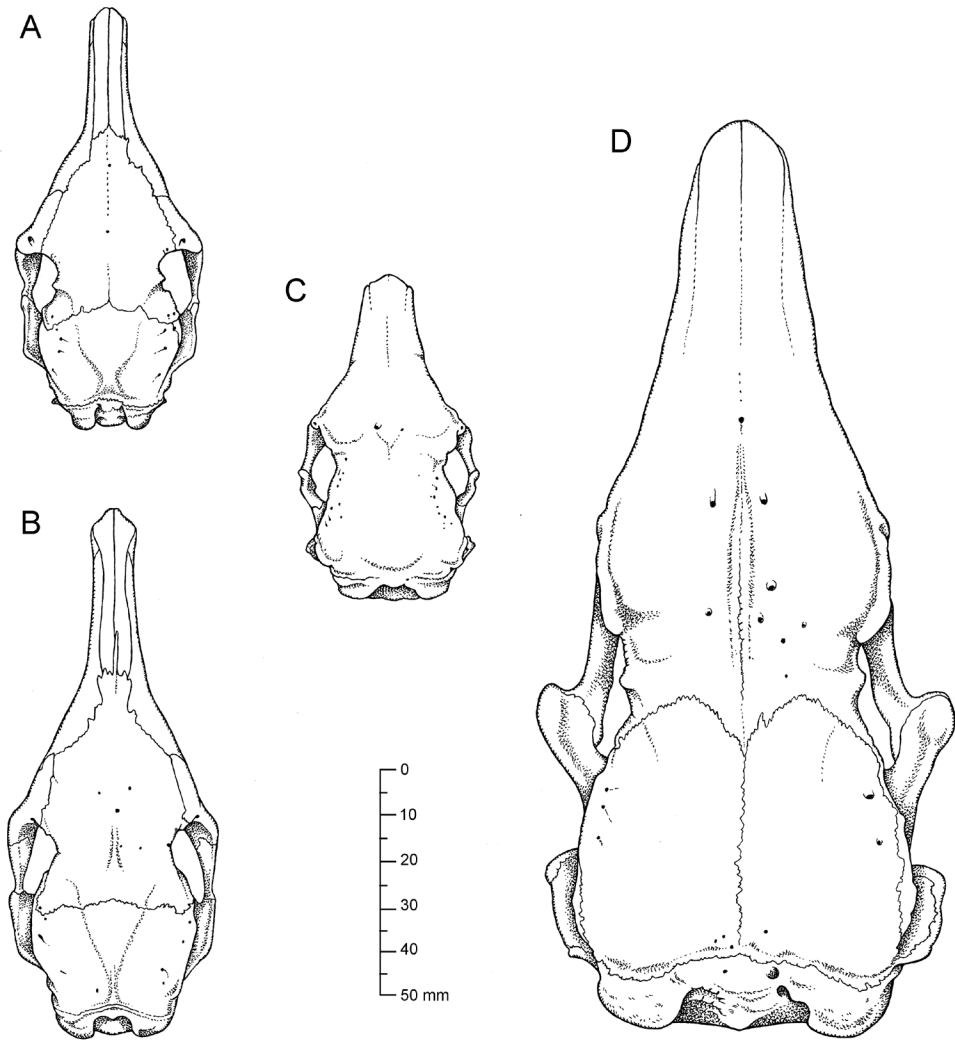


FIG. 3. Crania of four armadillo species that occur in the Yavari-Ucayali interfluvium, illustrating taxonomic differences in size and shape: *Dasyurus novemcinctus* (A, AMNH 268229); *D. pastasae* (B, AMNH 268228); *Cabassous unicinctus* (C, AMNH 74113); *Priodontes maximus* (D, AMNH 93418). All illustrated specimens are adults, but AMNH 93418 is not from the Yavari-Ucayali interfluvium.

OTHER INTERFLUVIAL RECORDS: Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Both specimens of naked-tailed armadillos that we examined from the Yavari-Ucayali interfluvium conform to the diagnosis of *Cabassous unicinctus* in Wetzel's (1980) revision of *Cabassous*. The Orosa specimen (AMNH

74113) was among those that Wetzel (1980) examined and assigned to the nominotypical subspecies (with type locality "Surinam"). According to this authority, *C. u. unicinctus* intergrades with the smaller subspecies, *C. u. squamicaudis* (Lund, 1843; type locality Minas Gerais, Brazil) in "the Amazon-Solimões River area in Brazil and Peru." The material at hand is entirely inadequate to

TABLE 3

Measurements (mm) and weights (g) of Adult Armadillo Specimens from the Yavari-Ucayali Interfluve

	<i>Cabassous</i>	<i>Priodontes</i>	<i>Dasypus novemcinctus</i>		<i>Dasypus pastasae</i>	
	<i>unicinctus</i>	<i>maximus</i>	AMNH	MUSM	AMNH	MUSM
	AMNH 74113	MUSM 11091	268229	11089	268228	11083
Sex	female	male	female	female	female	male
Head-and-body length	480 ^b	733	429	— ^a	532	481
Length of tail	145 ^b	541	361	385	431	373
Hind foot	66 ^b	190	— ^a	103	106	107
Ear	—	61	40	45	50	51
Condylonasal length	76.0	188.7	97.6	102.7	113.8	112.8
Zygomatic breadth	40.2	81.1	45.0	43.4	45.3	44.5
Least interorbital breadth	25.3	47.8	24.0	22.2	25.3	25.8
Breadth of braincase	32.0	64.7	33.7	32.4	34.6	35.0
Maxillary toothrow	26.0	69.8	24.0	26.5	30.2	29.5
Weight	—	35000	5300	5400	7700	5900

^a Collector's measurement is not plausible.

^b Estimated from skin (no collector's measurements).

assess geographic variation in this species, but it is noteworthy that cranial measurements of AMNH 74113 (table 3) are much smaller than the mean values for *C. u. unicinctus* tabulated by Wetzel (1980: table 1), but they are close to the corresponding means for *C. u. squamicaudis*. However, the number of scutes on the cephalic shield of this specimen ($N = 36$) is much closer to the mean value tabulated for *C. u. unicinctus* (34.6 ± 2.2 SD; Wetzel, 1980: table 4) than it is to the mean value for *C. u. squamicaudis* (54.0 ± 5.5). The taxonomic significance of these conflicting indications is unclear, but the mean differences between Wetzel's (1980) subspecies are substantial, and a fresh assessment of the material he allocated to these nominal taxa would seem to be appropriate in any future taxonomic study of *Cabassous*.

The second known specimen of *Cabassous unicinctus* from the Yavari-Ucayali interfluve (FMNH 112563) consists only of a live-mounted skin of a specimen "caught swimming in the river" (P. Soini's notation on skin tag); this specimen has 33 scutes on the cephalic shield. The skull, apparently, is lost.

ETHNOBIOLOGY: The naked-tailed armadillo has only one name, *menkudu*, which is not analyzable and has no cognate in other Panoan languages, but which may contain the adjective *kudu* ("grayish" or "light-colored"). No subtypes are named by the Matses, although some informants claim that there is more than one kind.

This species is not eaten by the Matses, and is of no economic importance. Very rarely a hunter will kill one out of curiosity.

If a hunter encounters a naked-tailed armadillo, it may cause his children to fall ill, in which case a medicine man will try several different medicinal plants, some of which are said to be specific to contagions caused by this species (other plants are said to be general remedies for contagions caused by any type of armadillo). Adults can become constipated due to exposure to a naked-tailed armadillo, in which case there is a specific plant to cure this. As is generally the case with rarely encountered animals, coming across a naked-tailed armadillo is interpreted as an omen that someone in the (extended) family of the person who sees it will fall ill and die soon thereafter.

MATSES NATURAL HISTORY: The naked-tailed armadillo is like a small giant armadillo. It is small, the size of a nine-banded long-nosed armadillo (*Dasybus novemcinctus*). It is lighter in color than other armadillos. Its front claws are large, the central ones as large as table-spoons (an obvious exaggeration). Its back feet are like those of a long-nosed armadillo. They are hairier than other armadillos. The tail is hard, but not ringed.

Naked-tailed armadillos are seldom seen and apparently very rare. Many Matses have never seen one, but burrows are somewhat frequently found. Their burrows are usually found in primary forest.

Naked-tailed armadillos sleep in burrows. The burrow has a small diameter, barely wide enough for the animal to fit. The burrow is deep and points straight down, unlike those of other armadillos, and one can recognize unquestionably that a burrow belongs to a naked-tailed armadillo. One informant found a naked-tailed armadillo sleeping in a hollow log. No leaf beds have been found in burrows of this species.

The naked-tailed armadillo is nocturnal. It roots at the bases of trees and digs into rotten logs. It walks around on the surface of the ground but also travels underground. It is very strong and can dig very quickly and very deep. It escapes by digging a deep hole in the ground, covering itself with excavated soil as it digs. It expels the dirt when it surfaces, as if it had dug up to the surface from another location. It does not make or use paths (as dasypodid armadillos are said to do; see below).

One informant saw three individuals of this species traveling together.

There are no flies at the entrances to burrows of this species (as there are at the burrow entrances of other sympatric armadillos; see below).

Naked-tailed armadillos are said to grunt by some informants, but others say they make no sounds.

The naked-tailed armadillo eats earthworms, millipedes, grubs that live in the ground, and other invertebrates. (Most informants had no idea what it eats, but they assumed it eats the same foods as long-nosed armadillos.)

REMARKS: Although sparse, Matses information about *Cabassous unicinctus* includes a few novel observations, notably that this species travels underground as well as on the surface.¹ The nocturnal activity reported by the Matses agrees with other rainforest observations (Emmons, 1997), but not with the diurnal activity reported from Brazilian savanna habitats (Bonato et al., 2008). The perpendicular orientation of burrows attributed to this species by the Matses is consistent with quantitative data on burrow characteristics summarized by Trovati (2015).

Priodontes maximus (Kerr, 1792)

Figure 3D

VOUCHER MATERIAL (TOTAL = 1): Nuevo San Juan (MUSM 11091).

OTHER INTERFLUVIAL RECORDS: Nuevo San Juan (camera-trap photograph), Río Yavarí-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Adult giant armadillos cannot be confused with any other mammal, although juveniles might be mistaken for *Cabassous unicinctus*, which they superficially resemble. Our single voucher, of which only the skull is preserved, is a young adult male with a completely co-ossified occiput but unfused preoccipital sutures.

The only traits in which our specimen differs from the diagnosis of *Priodontes maximus* provided by Wetzel (1985b: 31) concerns the dentition, which he reports as consisting of “18/19 pairs [of teeth], which are very flattened transversely.” In MUSM 11091, by contrast, there are alveoli for only 16 upper teeth (T) on the left side, of which the first (T1) seems to have been a tiny cylindrical peg; T2–T10 are sharp, flat blades; and T11–T16 are worn, peglike elements. There are alveoli for 17 upper teeth on the right side of this specimen, of which T1 and T17 are

¹ Pine (1973) previously suggested that this species might be fossorial based on its clumsy above-ground locomotion. The only specimen encountered by a longtime resident naturalist at Paracou, French Guiana, was unearthed by a bulldozer (Voss et al., 2001).

missing but were obviously tiny pegs; T2–T10 are sharp, flat blades like their counterparts on the left side; and T11–T16 are worn and peglike. Therefore, the symmetrical dental complement of this specimen includes 16 paired teeth, of which only nine on each side conform to the flattened morphology described by Wetzel.

ETHNOBIOLOGY: The principal name for the giant armadillo is *tsawesamë*, a term that can be analyzed as a compound of *tsawes* (“armadillo”) and *amë* (“father” or “large”). The archaic synonym is *panu*, the pan-Panoan term for “giant armadillo.” No subtypes are recognized by the Matses.

The giant armadillo is not eaten or killed by the Matses, and it is of no economic importance. However, members of the Mayú tribe (whom the Matses exterminated and from whom they captured many women) formerly ate giant armadillos.

The Matses believe that it is a death omen to encounter a giant armadillo as it is foraging during the day, or to find giant armadillo diggings in a swidden; such omens are interpreted to mean that someone (other than the observer) will soon die. Additionally, if one steps on dirt that an armadillo has dug up, one may become weak and thin. If a hunter sees or touches a giant armadillo, his children may fall ill. To cure the child's illness, a medicine man will try several different medicinal plants, some of which are specific to contagion by giant armadillos and others are general for contagion caused by any type of armadillo. A baby that suffers from giant armadillo sickness will dig its nails into its mother's flesh, and it may die from this condition.

MATSES NATURAL HISTORY: The giant armadillo is similar to other armadillos, but it is huge. It has very large claws on its front feet, like spoons. It bends its claws inward when it walks. The tracks of its hind feet look like the footprints of a (small) tapir. It has a large head similar to that of an armadillo. It has a very hard carapace. Its carapace has round bumps on the neck portion. It has less distinct bands and has lightly haired undersides.

Giant armadillos prefer primary upland forest, especially the area of headwater gullies, but their tracks can also be found in floodplain forest. (Not every Matses has seen one, though their diggings and tracks are commonly encountered.)

They make many very large holes. They do not make dens with leaf nests, but simply sleep in the large holes they have dug, usually in a stream headwater gully. They may fix up an old hole to sleep in for a night.

The giant armadillo is almost exclusively nocturnal. It does not make or use paths, although it may follow the same route occasionally. It travels far, visiting different streams. When it forages, it digs large holes, toppling saplings and removing roots. It leaves behind large piles of dirt and clay where it forages. It also forages by digging into rotten logs and at the base of swamp palms (*Mauritia flexuosa* [Arecaceae]), where there is black soil. Giant armadillos escape by digging into the ground, so that they are difficult to kill with a club.

Giant armadillos are solitary.

There are many white flies (probably phlebotomine psychodids) in the holes where a giant armadillo has slept.

The giant armadillo grunts when one touches it with a stick when it is in its burrow.

The giant armadillo roots in the ground to eat earthworms and grubs that live in the ground. It digs up rotten logs and stumps to eat armored millipedes (*Barydesmus* sp. [Platyrrhacidae]) and termite larvae. It digs up termite nests to eat the larvae. It digs out beehives in hollow trees to eat their larvae and drink their honey. It digs out the pith of fallen rotting swamp-palms to eat beetle grubs. It takes apart the crowns of fallen *isan* palms (*Oenocarpus bataua* [Arecaceae]) to eat the beetle grubs that eat the heart of the palm. Giant armadillos eat *isan* palm fruits and swamp palm fruits, chewing up the whole fruit, including the seed.

REMARKS: Matses observations about this species are not very extensive—understandably so, since giant armadillos are not hunted for food and are seldom encountered while active at night—but they include some information that

does not appear in the scientific literature (reviewed by Carter et al., 2016), notably about foraging behavior and diet. By comparison with Matses accounts of sympatric dasypodid armadillos (see below), their remarks that *Priodontes maximus* does not follow paths or make leaf nests seem noteworthy.

Dasypodidae

Living dasypodids are all placed in the genus *Dasypus*, of which two species are known from our region: the nine-banded long-nosed armadillo (*D. novemcinctus*) and the greater long-nosed armadillo (*D. pastasae*). Although similar in appearance and habits, the latter is a primary game species of the Matses, whereas the former is partially tabooed.

Dasypus novemcinctus Linnaeus, 1758

Figures 3A, 4A

VOUCHER MATERIAL (TOTAL = 6): Nuevo San Juan (AMNH 268229, 268230, 268231; MUSM 11088, 11089, 11090).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Pavlinov, 1994), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Our voucher material conforms to the qualitative descriptions of *Dasypus novemcinctus* provided by Wetzel and Mondolfi (1979) and Wetzel (1985b). Additionally, measurements of our voucher material (table 3) fall within the observed range of variation among Amazonian specimens of *D. novemcinctus* tabulated by Wetzel and Mondolfi (1979: table 1). Our single preserved skin (MUSM 11088) has eight moveable bands, of which the fourth has 56 scutes; both counts are well within the range of meristic variation for the species (Wetzel and Mondolfi, 1979).

Wetzel et al. (2008) recognized several subspecies of *Dasypus novemcinctus* but provided no phenotypic criteria for distinguishing them. In

the absence of any critical revision of this implausibly widespread taxon (which ranges from the southern United States to Uruguay), it seems pointless to use trinomial nomenclature or to speculate about the validity of any nominal forms currently treated as subspecies or synonyms. However, it is noteworthy that (1) Amazonian specimens seem to be substantially larger than specimens from other South American landscapes (e.g., the Brazilian highlands and northern Venezuela; Wetzel and Mondolfi, 1979: table 1), (2) sequence variation at the mitochondrial ND1 locus among specimens identified as *D. novemcinctus* appears to be highly structured geographically (Loughry and McDonough, 2013: fig. 7.2), and (3) phylogenetic analyses of mitogenomes do not recover *D. novemcinctus* as a monophyletic taxon (Gibb et al., 2015; Mitchell et al., 2016). Unfortunately, western Amazonian populations of *D. novemcinctus* are not represented in any published molecular analysis.

Dasypus novemcinctus is easily distinguished from its sympatric congener *D. pastasae* by its smaller adult size (typically <6 kg, versus >8 kg in *D. pastasae*); by lacking a vestigial fifth digit on the forefoot (a tiny fifth digit is almost always present in *D. pastasae*); by the absence of enlarged, spurlike scales on the knee (present in *D. pastasae*); and by having rounded lateral palatine margins (fig. 4A).

ETHNOBIOLOGY: The only general name for the nine-banded long-nosed armadillo is sedudj (an unanalyzable term with no other meaning), a word that is not found in other Panoan languages and which has no archaic or ceremonial synonyms. Three subtypes of the nine-banded long-nosed armadillo are recognized by Matses hunters: sedudimpi (“small nine-banded long-nosed armadillo”), sedudidapa (“large nine-banded long-nosed armadillo”), and akte tsawes (“water/stream/river armadillo”). It is notable that the term for the third subtype contains the term tsawes, which is also the name for the great long-nosed armadillo (*D. pastasae*), but in this case the term tsawes can be interpreted as a general term for “armadillo” (the Matses are steadfast in their

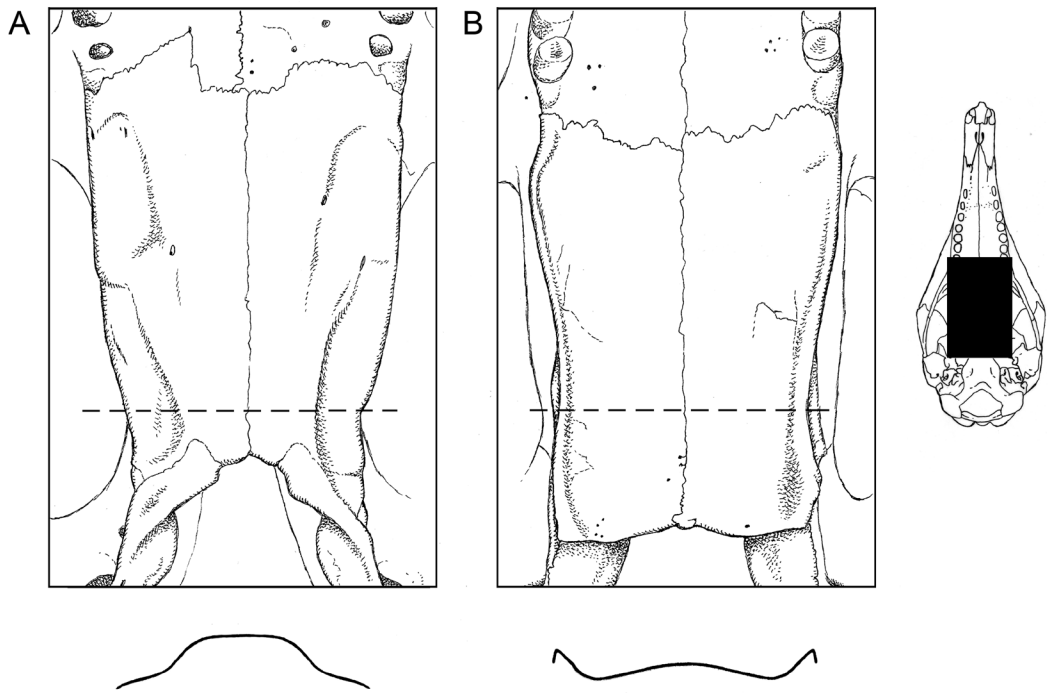


FIG. 4. Ventral view of posterior palate of *Dasyus novemcinctus* (A, AMNH 268229) and *D. pastasae* (B, AMNH 268228). In *D. novemcinctus* the lateral margins of the palatines are rounded, whereas the lateral palatine margins are keeled in *D. pastasae*.

classification of this variety as a type of *sedudi*). In addition to being smaller, *sedudimpi* is said differ from the other varieties by having a darker back, a grayish yellow underside, and a tail with stripes along the edges of the bands. *Sedudidapa*, in addition to being larger, is said to be lighter in color than other varieties. *Akte tsawes* is said to be characterized by living in or adjacent to floodplain forest along large streams and rivers.

The only economic importance of nine-banded long-nosed armadillos for the Matses is as food, but unlike the greater long-nosed armadillo it is not a preferred game species and, due to the dietary taboo limiting its consumption to old people, it is not frequently hunted.

When a nine-banded long-nosed armadillo is encountered in a burrow it may be flooded out in the same manner as described below for the great long-nosed armadillo, but this species often nests on the surface under piled-up leaves,

typically in floodplain forest and on levee islands. A hunter may come upon armadillo spoor and follow it, or he may simply happen upon such a leaf nest. When he finds the leaf nest, he lightly introduces a palm frond into the entrance of the nest to see if it is inhabited. If the armadillo growls, he cuts saplings into stakes and makes a circular fence around the nest. Then he enters the circle, takes apart the nest, and kills the trapped armadillo with a machete.

Now that the Matses have flashlights, they hunt at night by walking along forest paths. The primary motivation for night-hunting is to kill pacas, which are common in secondary forest near villages, especially when peach palm (*Bactris gasipaes*) fruits are ripe (from January to March), but nine-banded long-tailed armadillos also frequent secondary forest and are sometimes shot if encountered on a night hunt.

Young people do not eat the nine-banded long-nosed armadillo lest they become weak and thin or begin to eat clay. This armadillo is also believed to make children ill, causing a high fever. Therefore, it is primarily eaten by the elderly.

MATSES NATURAL HISTORY: The nine-banded long-nosed armadillo is similar to the greater long-nosed armadillo, but it is smaller, has a thinner tail and head, has a bump on its head, has a yellower underside, narrower bands on its carapace, and a stronger and fouler smell. Both species have a “branched” penis.

Nine-banded long-nosed armadillos are found in upland forest, in the floodplains of large streams and rivers, and in both primary and secondary forest. They are frequently found in abandoned swiddens and old blowdowns. They are also common in fresh blowdowns and on levee islands along rivers. (Thus, nine-banded long-nosed armadillos use a wider range of habitats than greater long-nosed armadillos.) They are common and, unlike greater long-nosed armadillos, do not tend to get hunted out (at least in part because they are not a preferred game species).

Nine-banded long-nosed armadillos make their nests in underground burrows, on the surface under leaf piles, and inside hollow logs. Burrows are especially common in blowdowns. These armadillos have more than one nest and typically sleep in a different one each night. Burrows may be on hilltops or hillsides, in floodplain forest, or in secondary forest, but not in stream headwater gullies (the preferred site of great long-nosed armadillo burrows). The typical burrow entrance is angled straight down. If the burrow is in floodplain forest or on a levee island it goes straight down for about 30 cm and then becomes horizontal and extends only a short distance (in which case the armadillo can be easily dug out). If the burrow is in a hillside in upland forest, it will become horizontal for a short distance and then angle upward (in which case it cannot be flooded out). The burrows have a bed made of dead leaves. Nests in hollow logs also have a leaf bed. Leaf-pile nests are usually made

next to a log or a buttress root. The leaf litter is piled very high and the armadillo sleeps under the leaves, not on them. Leaf-pile nests are made in floodplain forest.

The nine-banded long-nosed armadillo is nocturnal. It forages all night long. It has clear and wide paths that it follows as it forages. It leaves its path to root for earthworms at the base of hills and other places. Sometimes it returns to the same place to forage, and at other times it does not. It follows streams, rooting in the soft soil for earthworms. It roots in places that are close to each other, leaving areas clear of leaf litter where it roots. It makes a lot of noise as it travels quickly along its path, with its tail up in the air. It runs very quickly along its path to escape from humans, smacking its tail on the ground as it runs. Where there is no path it cannot run as quickly, having to jump over or go around obstacles. It can be grabbed when it is not on its path. Armadillos are safer from predation when they are on their paths, but they must leave their paths to forage. (One could infer the same for greater long-nosed armadillos, but because those are more rarely encountered at night, Matses informants did not comment on this.)

Nine-banded long-nosed armadillos are solitary. The female gives birth to two or three offspring. Larger females give birth to three. The young follow the mother when they are little.

White flies (small biting flies that look like light-colored mosquitoes; probably phlebotomine psychodids) live with and follow nine-banded long-nosed armadillos. Jaguars, pumas, bush dogs, and caimans eat nine-banded long-nosed armadillos.

They make a low grunting growl when disturbed.

Nine-banded long-nosed armadillos dig into rotten logs to eat armored millipedes (*Barydesmus* spp. [Platyrrhacidae]) and other invertebrates. They root in the ground to eat earthworms and grubs that live in the ground. They also eat mole crickets and other insects.

They eat the mesocarp of isan palms (*Oenocarpus bataua* [Arecaceae]), kuëbun isan palms (*O. mapora*) and swamp palms (*Mauritia flexuosa* [Arecaceae]). They also eat some dicot tree fruits and the seeds of tonnad trees (an unidentified species of Myristicaceae). They eat maggots that they find in rotten meat, but do not eat the meat itself.

REMARKS: The nine-banded long-nosed armadillo has been the subject of numerous field studies at temperate latitudes, especially as an invasive species in the United States, but little has been published about its ecology or habits in tropical rainforest. Information about this species (or species complex; see above) obtained from Matses interviews is notable for observations about several behaviors not or seldom mentioned in the literature, including use of well-worn pathways (mentioned only by Neck [1976] and Emmons [1997] among the references we consulted), tail-slapping when pursued by predators, the use of surface nests rather than burrows as diurnal refugia in floodplain habitats (Layne and Waggener, 1984; Platt and Rainwater, 2003), and frugivory (Emmons, 1997). Also of interest is the alleged association of this species with small biting flies (?*Brumptomyia* spp. [Psychodidae]; Lainson et al., 1979), and observations about predators (*Dasypus novemcinctus* leads an almost predation-free existence in the partially defaunated habitats of temperate North America; Loughry and McDonough, 2013). By contrast, Matses observations about litter size are anomalous. Whereas the Matses report litters of only two to three offspring in this species, 95% of *D. novemcinctus* litters in North America consist of genetically identical quadruplets (Newman, 1913; Prodöhl et al., 1996), and similar observations have been reported from South America (e.g., Noss et al., 2003: table 3). Although we could offer several ad hoc explanations for this discrepancy, none are supported by actual evidence, so we cannot discount the probability that the Matses are simply wrong.

Dasypus pastasae (Thomas, 1901)

Figures 3B, 4B

VOUCHER MATERIAL (TOTAL = 4): Nuevo San Juan (AMNH 268227, 268228; MUSM 11081, 11083).

OTHER INTERFLUVIAL RECORDS: Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: We follow Feijó and Cordeiro-Estrela (2016) in recognizing three distinct species among the nominal taxa formerly synonymized with *Dasypus kappleri* Krauss, 1862. Of these, *D. kappleri* (sensu stricto) is restricted to the Guiana Region (north of the Amazon and east of the Rio Negro/Orinoco), whereas *D. beniensis* Lönnberg, 1942, occurs in southeast Amazonia (south of the Amazon and east of the Rio Madeira), and *D. pastasae* is widespread in western Amazonia (on both banks of the upper Amazon west of the Negro and Madeira rivers). Together, these three taxa belong to the subgenus *Hyperoambon* Peters, 1864, whereas the nine-banded species is referred to the nominotypical subgenus (Wetzel and Mondolfi, 1979).

Our voucher material exhibits most of the distinguishing features attributed to *Dasypus pastasae* by Feijó and Cordeiro-Estrela (2016), of which the most consistently useful seem to be (1) the high relief of the central scale of each scale-rossette on the pelvic shield (giving this part of the carapace a diagnostically bumpy texture), and (2) the relatively low and uninflated lateral palatine keels (fig. 6B). Measurements of our two adult vouchers (table 3) are within the range of morphometric variation for *D. pastasae* as quantified in their study.

ETHNOBIOLOGY: The principal Matses name for the greater long-nosed armadillo, tsawes, is not analyzable and has no other meaning, except that it can be used a general term for all armadillos. It has one archaic synonym, yosh, also not analyzable but cognate with the term for “armadillo” in many other Panoan languages. In the language formerly used in the Matses’ komok ceremony (Romanoff et al., 2004), the greater long-nosed



FIG. 5. Matses woman butchering a long-nosed armadillo (*Dasyus* sp.) on the upper Quebrada Chobayacu, ca. 1975 (photo by Steven Romanoff).

armadillo is called *shēdēk-shēdēk*, a term that refers to its many bands (literally “wrinkles”).

Three subtypes of the greater long-nosed armadillo are recognized by Matses hunters: *tsawes chēshe* (“black/dark-colored armadillo”), *tsawes ushu* (“white/light-colored armadillo”), and *tsawes piu* (“yellowish armadillo”) or *tsawes takpiu* (“yellow-bellied armadillo”). The latter type is said to be characterized by a yellow-gray venter, and the dark variety is said to be smaller than the others. While there is some consensus with respect to these color and size distinctions, there is much variation among speakers—who often directly contradict one another—with respect to the habitat preferences of these subtypes.

The only economic importance of greater long-nosed armadillos for the Matses is as food (fig. 5). It is one of the most appreciated game species, and it is the most favored meat for some Matses. Occasionally, when a female with young is killed, the young are kept as pets.

Armadillos are hunted principally by flooding them out of their burrows. A hunter may decide to hunt greater long-nosed armadillos after having seen fresh armadillo spoor the day before, or he may come across fresh tracks when it is still early in the day. When his wife or children request it, or during the period when armadillos have much fat (in April and May), a hunter may decide to search primarily for armadillos, even without having found any tracks (in which case much more search time is invested). This species, along with two-toed sloths and caimans, were formerly the most important species to be hunted during the *komok* ceremony (which is no longer practiced; Romanoff et al., 2004).

When a hunter finds armadillo tracks he inspects them and then searches for burrows in the vicinity. Generally the hunter does not attempt to follow armadillo tracks, because armadillo trackways are not continuously visible, and because armadillos tend to forage going in

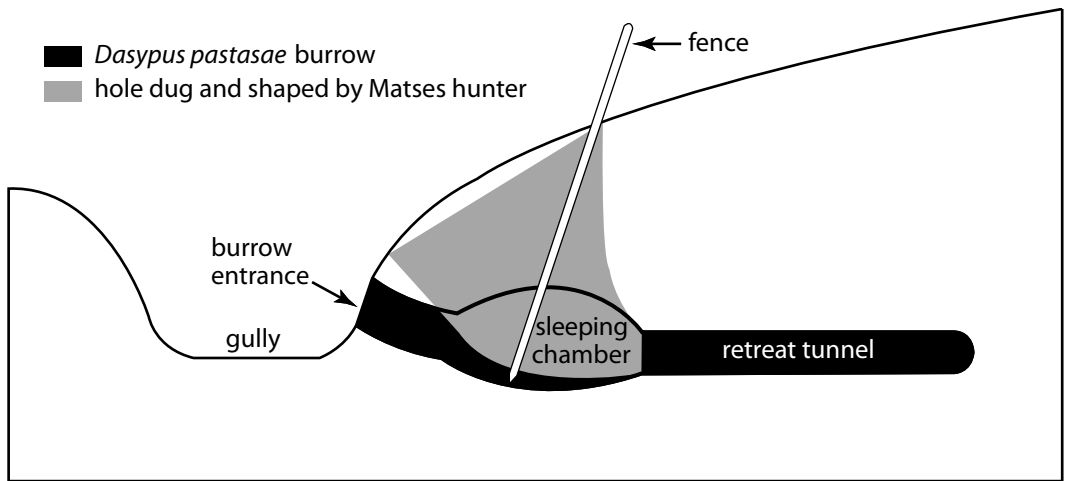


FIG. 6. Cut-away diagram illustrating how *Dasybus pastasae* is captured by Matses hunters (see text for explanation).

circles. Rather, the hunter searches nearby places that might be suitable for burrows; specifically, stream headwater gullies and stream banks. When he finds a fresh burrow, he looks for fresh tracks and white flies at the burrow entrance and sniffs the burrow for the armadillo's scent. If these signs are present, he cuts a palm frond, knots the leaflets at the tip of the frond into a ball, and removes the rest of the leaflets. He then introduces the frond into the burrow and listens. The armadillo generally growls if disturbed in this manner.

If the armadillo growls or rustles around in its leaf bed, the hunter will stop up the hole with dry or rotting pieces of logs to keep the armadillo from running out while he goes to cut a digging stick and stakes to make a fence. Once he has gathered these materials, he begins to dig inward toward the sleeping chamber, either by enlarging the burrow entrance or by opening a new hole from above; meanwhile, the armadillo goes into its retreat tunnel (a blind, narrow, horizontal tunnel adjacent to its sleeping chamber; fig. 6). The hunter continues to dig until he reaches the sleeping chamber and has room enough to stand upright in it. After removing the bed of dry leaves, the hunter blocks the entrance

tunnel with excavated clay, forming a funnel so that water poured into the excavation will fill the retreat tunnel. To keep the armadillo from escaping, a fence is made of stakes to block the exit from the retreat tunnel.

The next step is to make a watertight basket by weaving a palm frond, lining it with wild banana leaves, and reinforcing it with a vine. The hunter will then make several trips back and forth to a nearby stream, fetching water to flood the hole. The hunter's wife often accompanies her husband on the hunt, in which case she will help dig, make the basket, and haul water. It may take 10 or more baskets of water to fill the retreat tunnel. Once it is flooded, the hunter waits quietly beside the excavation. If properly flooded, the armadillo will not be able to breathe and will try to exit the retreat tunnel. The first sign of the armadillo's exit is bubbles of air, then churning water; finally, the armadillo bumps into the fence. When the armadillo emerges, the hunter quickly introduces several sticks through the fence to block the armadillo from going back into the retreat tunnel. Once he has blocked its retreat, the armadillo is helplessly trapped. The hunter simply waits for the armadillo to eventually stick its head between

the sticks that form the fence and clubs it, breaking its skull or neck. With particularly deep holes, it may take several hours to flood the burrow to obtain this highly prized game. Sometimes water leaks into the ground, and the burrow will not flood. In such cases, the armadillo cannot be killed.

A less frequently used method for extracting an armadillo from its burrow is to smoke it out. This is done simply by lighting a fire at the entrance and fanning the smoke into the burrow. The armadillo comes out with its eyes closed and the hunter kills it with a machete or a stick. Although this method requires much less work than flooding, it is less effective, and hunters seldom carry matches, fire drills, or other means of starting a fire.

Nowadays the Matses hunt at night by walking along forest paths with a flashlight and shotgun. Because greater long-nosed armadillos do not live in the secondary forest near villages and are usually hunted out from adjacent primary forest, it is rare for one to be killed in this manner. (By contrast, nine-banded long-nosed armadillos are more commonly killed by hunting at night; see above.)

The Matses formerly hung the pelvic shields of armadillo carapaces on the horizontal poles of their longhouses as hunting trophies and to keep track of how many armadillos had been killed locally. Today this is still done by a few old men.

Although all Matses eat greater long-nosed armadillos, there are several partial dietary taboos. Young people do not eat greater long-nosed armadillo fat lest their teeth rot. Young men also do not eat young armadillos lest they become cowards. Young men don't eat the tail, lest they grow thin. Old people can eat the young, and the fat, and the tail. No one eats the lungs. Greater long-nosed armadillos can make children ill, causing a high fever. When several people are flooding out an armadillo, they cannot say out loud "the armadillo is coming out of its burrow," lest it not come out; instead, they whistle softly to announce that it is starting to exit its burrow. Additionally, one should not throw around pieces of clay that are dug out of the bur-

row (as small boys are often tempted to do), lest the armadillo not come out.

The tail is sometimes burned, letting the smoke enter the hunter's eyes, which is believed to help him find armadillos in the future.

MATSES NATURAL HISTORY: Greater long-nosed armadillos prefer primary upland forest. They make their burrows in the headwaters of streams and along small streams. They forage in the dry floodplains of streams and in palm swamps, where the earth is softer, but they also root around on hilltops and hillsides. They are common in upland forest where they have not been hunted out.

Greater long-nosed armadillos always nest in burrows that they dig in the ground. Each armadillo has several active burrows and sleeps in a different one each night. There are also abandoned burrows in the vicinity of active burrows. Burrows in stream headwater gullies are deeper than burrows in stream floodplains. Each burrow has a large sleeping chamber, where the armadillo has its leaf bed. The leaf bed smells like armadillo urine. The burrow also has a long, narrow, blind retreat tunnel adjacent to the sleeping chamber. The retreat tunnel is generally somewhat horizontal and has a few centimeters of water on the floor. Greater long-nosed armadillo burrows have only one entrance.

The greater long-nosed armadillo is nocturnal. During the day it sleeps in its burrow. Before dusk it is awake in its burrow, rustling the dry leaves in its leaf bed, waiting for it to get dark. Right at dusk it rushes out of its burrow and then begins to travel noisily along one of its paths, which are primarily along hilltops. It stops along its path to forage, rooting for worms and grubs in soft dirt and digging into rotten logs for armored millipedes and other invertebrates. It leaves its path to root in lower ground, in the floodplains of streams or in palm swamps. If these are flooded, it roots at the edges of the flooded area. It sniffs the ground as it roots for earthworms. It follows streams as it forages, often crossing one or more streams, and then circles back to its path. It swims across deep streams. It

bathes in mud holes, where collared peccaries may also bathe (during the day). It may come across one of its other burrows and check it out, but it will not sleep there if it is not yet late. When it is near dawn (between 05:00 and 05:30 in northeastern Peru) it finds its path and follows it to its nearest burrow. Once it finds its burrow, it collects fresh leaf litter to add to its bed. It leaves an area clear of leaf litter near its burrow where it does this. It rolls in its leaf bed to pack it down and may be awake in its burrow rustling the leaves in its bed for a short time after the day dawns. It sometimes walks around during the day in a heavy rain.

Greater long-nosed armadillos are solitary. Males do not sleep with females in their burrows. They copulate when they find each other while foraging at night. The female gives birth to two offspring inside its burrow. The female eats the placenta. The young follow the mother when they are little.

White flies (small biting flies that look like light-colored mosquitoes; probably phlebotomine psychodids) live with greater long-nosed armadillos. They are always present at the entrance of active burrows. When the armadillo leaves its burrow, some follow it while others remain at the burrow. A burrow that is inhabited will have more white flies during the day than other, uninhabited but active burrows.

Jaguars eat greater long-nosed armadillos while hunting at night. They may pounce on an armadillo from above as the armadillo passes by. They remove the carapace, and often stash a portion of the armadillo to eat later. Pumas also kill armadillos. Bush dogs kill armadillos by entering the burrow and following them into the (blind) retreat burrow. They pull the armadillo out and eat it at the entrance of the burrow. Tayras that hunt in trios can also kill an armadillo. Black caimans and anacondas catch armadillos as they swim across large streams.

Greater long-nosed armadillos make a low rumbling growl when disturbed. They growl loudly when a predator grabs them. Newborns whine inside the burrow.

Greater long-nosed armadillos find armored millipedes (*Barydesmus* sp. [Platyrrhacidae]), round millipedes (*Neocricus* sp. [Rhinocricidae]), centipedes, beetles, and beetle grubs in rotten logs. They root in the ground for earthworms and grubs that live in the ground. They eat any invertebrate they find. They are also very fond of isan palm (*Oenocarpus bataua* [Arecaceae]) fruits. They eat the mesocarp of ripe isan palm fruits that fall to the ground. They also eat chukē ants that feed on the isan fruits. While eating isan palm fruit they also root in the vicinity for earthworms. They also eat the mesocarp of fallen swamp palm (*Mauritia flexuosa* [Arecaceae]) fruits. They eat insect larvae that they find in rotten echo tree (*Jacaratia* sp. [Caricaceae]) fruits.

REMARKS: In a recent publication (Fleck and Voss, 2016), we compared Matses natural history information about *Dasybus pastasae* item by item with the scientific literature on *D. kappleri* (the name by which this species was formerly known; see above). Briefly, almost 80% of what the Matses have to say about *D. pastasae* is new information, and most of the rest essentially agrees with the literature. The single point of disagreement between our interview results and the literature concerns burrow construction, for which it seems likely that the Matses account is correct.

Matses observations about *Dasybus pastasae*, a primary game species, are more detailed than those about *D. novemcinctus*, which is much less often hunted and consumed. To the extent that information about the two species overlaps, it would seem that these sympatric congeners are ecologically and behaviorally similar, with the noteworthy exception that *D. pastasae* seems invariably to dig its burrows in the sides of streams and stream headwater gullies, whereas *D. novemcinctus* digs burrows in different places and sometimes also uses surface nests. In the absence of other evidence for niche divergence, this difference in use of diurnal refugia is perhaps significant for species coexistence.

Sloths (Bradypodidae and Megalonychidae)

The taxonomy of Recent sloths remains unrevised, and the current application of names is based on decades-old conventions that are now being challenged by molecular analyses. Morphological examination of available specimens from the Yavari-Ucayali interfluvium suggest that only a single species each of *Bradypus* (three-toed sloths, Bradypodidae) and *Choloepus* (two-toed sloths, Megalonychidae) occur here, although a second species of *Choloepus* might also be expected.

Bradypus variegatus Schinz, 1825

Figures 7–9

VOUCHER MATERIAL (TOTAL = 4): Nuevo San Juan (MUSM 11075, 23811), Orosa (AMNH 73758, 73759).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Jenaro Herrera (Pavlinov, 1994), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Four living species of bradypodid sloths are currently recognized, of which one (*B. pygmaeus* Anderson and Handley, 2001) is an insular endemic, another (*B. tridactylus* Linnaeus, 1758) is restricted to northeastern Amazonia (east of the Rio Negro and north of the lower Amazon), a third (*B. torquatus* Illiger, 1811) is endemic to the Atlantic forest of southeastern Brazil, and the fourth (*B. variegatus*) is thought to range throughout most of Central America and tropical South America (Anderson and Handley, 2001; Gardner, 2008).

Although *Bradypus variegatus* (the “brown-throated three-toed sloth” of English usage) and *B. tridactylus* (the “pale-throated three-toed sloth”) are the only currently recognized species of Amazonian bradypodids (Wetzel, 1985a; Anderson and Handley, 2001; Gardner, 2008), Amazonian three-toed sloths have received no modern revisionary attention, and there is little compelling evidence to support current taxonomic usage. In particular, the extensive distribution of *B. variegatus* (from Hon-

duras to northern Argentina), substantial geographic variation in morphology (see below), and preliminary genetic evidence from gene-sequencing studies (e.g., Moraes-Barros and Arteaga, 2015; Ruiz-García et al., 2017) all suggest that brown-throated three-toed sloths include several distinct taxa. Seven South American subspecies of *B. variegatus* were recognized by Gardner (2008), but no explicit justification for sloth trinomial nomenclature has yet been provided by any author.

The type locality of *Bradypus variegatus* is assumed to be somewhere in the Atlantic Forest of southeastern Brazil (Wetzel and Kock, 1973), and specimens that are morphologically similar to Atlantic Forest material have been collected throughout southeastern Amazonia, from the vicinity of Belém westward to the left (west) bank of the Tapajos. Sequence data analyzed by Moraes-Barros and Arteaga (2015) and Ruiz-García et al. (2017) likewise suggest that southeastern Amazonian and Atlantic Forest populations of brown-throated three-toed sloths are closely related. Additionally, photographs of the holotype skull (SMF 4313; available online from the Senckenberg Naturmuseum database) closely match the craniodental morphology of southeastern Amazonian specimens that we examined. In the paragraphs that follow, we assume that southeastern Amazonian three-toed sloths represent the nominotypical form, *B. variegatus variegatus*.

Three-toed sloths from the Yavari-Ucayali interfluvium and others that we examined from western Amazonia fit the description of *Bradypus variegatus* in the inclusive sense that this binomen is currently applied (e.g., by Wetzel and Avila-Pires, 1980; Wetzel, 1985a; Anderson and Handley, 2001; Gardner, 2008). Traits that support the identification of western Amazonian three-toed sloths as belonging to the *B. variegatus* complex include (1) the presence of a speculum in adult males (a speculum is absent in *B. torquatus*); (2) absence of a mane of long black hair (present in *B. torquatus*); (3) the consistently brownish coloration of the throat (the gular fur is whitish or yellowish in *B. tridactylus*); (4) the absence of large foramina in

TABLE 4
Craniodental Measurements (mm) of Three-toed Sloths (*Bradypus variegatus* ssp.)

	<i>B. v. infuscatus</i> ^a	<i>B. v. variegatus</i> ^b
Condyloalveolar length	74.3 ± 3.1 (69.6–80.9) 24	66.8 ± 2.4 (61.3–71.5) 25
Rostral breadth	21.1 ± 1.3 (18.6–25.1) 24	16.5 ± 0.8 (14.7–17.9) 26
Least interorbital breadth	23.8 ± 1.0 (21.8–25.6) 24	21.6 ± 1.7 (18.0–24.9) 25
Least postorbital breadth	24.3 ± 1.8 (21.1–28.6) 24	21.8 ± 1.6 (18.0–24.9) 26
Anterior zygomatic breadth	48.7 ± 2.0 (44.9–53.3) 19	42.6 ± 2.1 (37.0–46.3) 25
Posterior zygomatic breadth	48.2 ± 2.5 (43.0–54.9) 24	42.8 ± 2.1 (38.5–46.7) 26
Maxillary toothrow	26.8 ± 1.1 (25.1–29.1) 24	23.8 ± 0.9 (22.7–25.7) 26
Greatest diameter of pseudoincisor	4.0 ± 0.4 (3.2–5.0) 24	2.5 ± 0.4 (1.9–3.4) 24

^a The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series from western Amazonia: AMNH 71822, 73572, 73574, 73758, 73759, 74429, 76408, 76495, 76497, 78515, 188196; BMNH 80.5.6.56, 80.5.6.58; FMNH 20132, 70812, 86896; LSUMZ 12304; MUSM 8301, 8302, 11075, 33610; MVZ 155186, 157796, 157797.

^b The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for measurements of the following series from southeastern Amazonia: AMNH 75140, 95101, 95102, 95104–95106, 95325, 95326, 95328, 96244–96246, 96250, 96252, 96253, 96255, 133415, 133419, 133426, 133432, 133438; BMNH 4.7.4.92, 4.7.4.110, 4.7.4.111; FMNH 92079, 94551.

the anterior part of the mesopterygoid fossa (present in *B. tridactylus* and *B. torquatus*); and (5) large size (*B. pygmaeus* is much smaller). However, other phenotypic characters distinguish western Amazonian material from southeastern Amazonian specimens of *B. variegatus*.

In western Amazonian specimens of brown-throated three-toed sloths, the anteriormost maxillary teeth (the “pseudo-incisors” of Thomas, 1917) are large and procumbent; the rostrum is correspondingly broad; the nasal bones are short, often exposing the nasal orifice and the projecting pseudoincisors in dorsal view; and the postorbital process of the jugal is well developed (figs. 7A, 7B, 8A). The co-ossified mandibles are likewise distinctive, entirely lacking any trace of the median anterior process (symphyseal spout) seen in other sloths, but with a deep symphysis that often extends posteriorly between the third pair of teeth (fig. 9A). By contrast, the pseudoincisors of southeastern Amazonian specimens are much smaller and nonprocumbent; the rostrum is narrower; longer nasal bones conceal the nasal orifice from dorsal view but extend the orifice such that it is visible

from below; and a postorbital process of the jugal is absent or indistinct in most examined specimens (figs. 7C, 7D, 8B). Additionally, the mandibles of all examined specimens from southeastern Amazonia have a small but distinct symphyseal spout, and the symphysis only extends posteriorly between or just beyond the second pair of teeth (fig. 9B). On average, skulls from western Amazonia are substantially larger than those from southeastern Amazonian in all measured dimensions (table 4), but most measurements exhibit overlapping variation; an exception is rostral breadth, which is diagnostically greater in western Amazonian material than in specimens from southeastern Amazonia. We have not been able to discover any pelage or other external differences between three-toed sloths from western and southeastern Amazonia, which both seem to be highly variable (e.g., in pelage coloration).

Western Amazonian three-toed sloths are usually associated with the epithet *infuscatus* (e.g., by Thomas, 1928; Gardner, 2008), a convention that we follow despite misgivings about the application of this name. According to

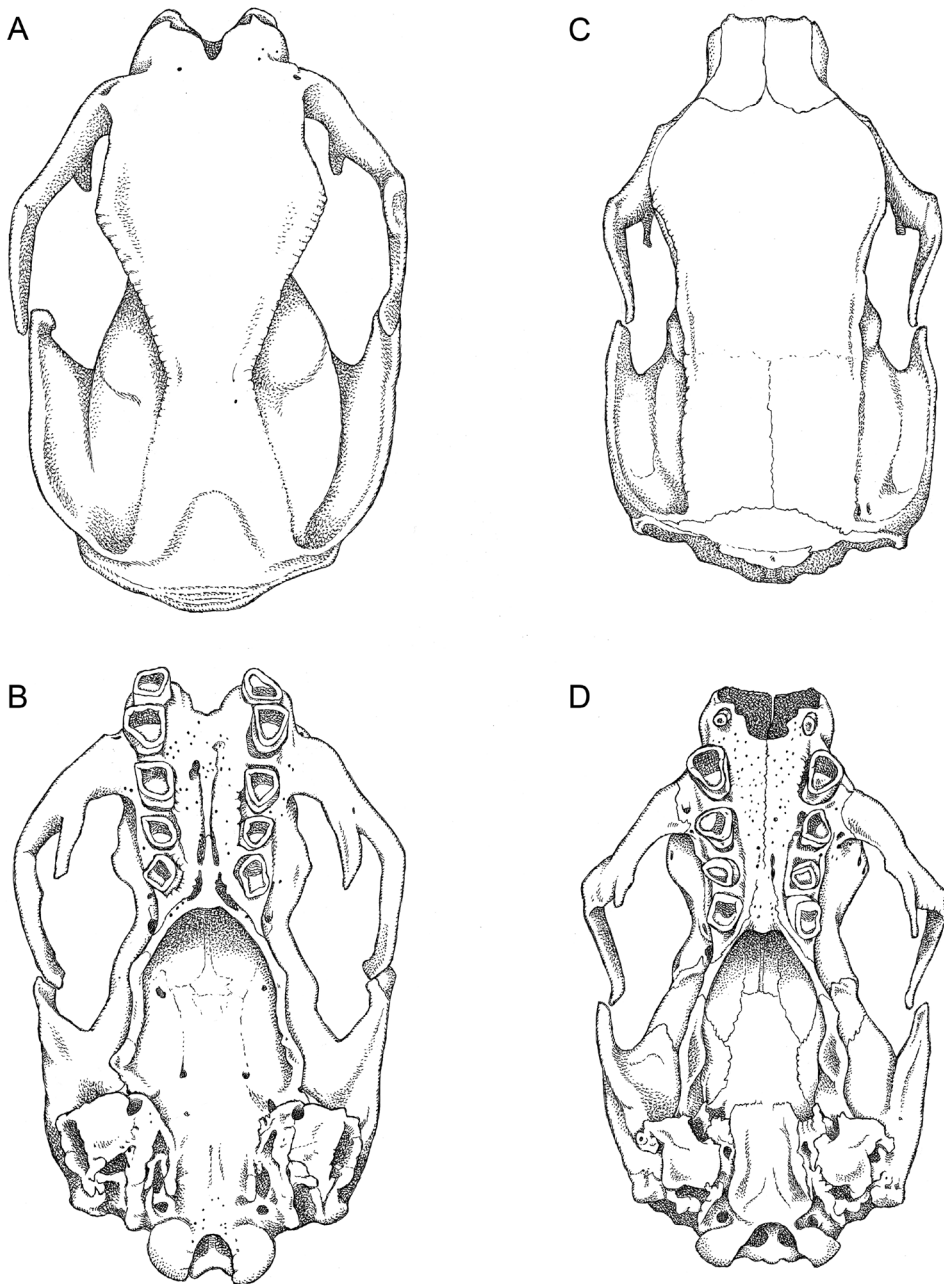


FIG. 7. Dorsal and ventral cranial views of *Bradypus variegatus infuscatus* (A, B, AMNH 76497) and *B. v. variegatus* (C, D, AMNH 95105). Both skulls lack the premaxillae, which are only loosely attached in brady-podid sloths and are often lost in specimen preparation. Cranial sutures are fused in AMNH 76497, whereas most sutures persist in AMNH 95105 (a younger adult); the conspicuous shape differences between these specimens, however, are not age dependent.

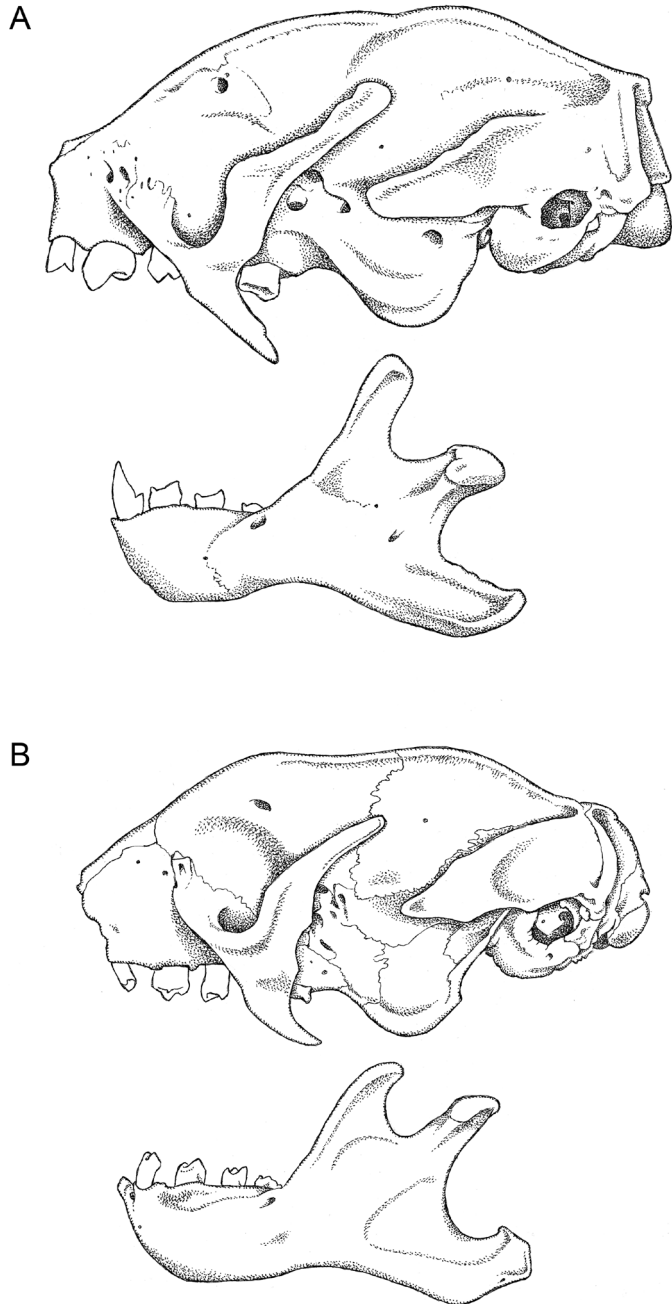


FIG. 8. Lateral views of skulls and mandibles of *Bradypus variegatus infuscatus* (A, AMNH 76497) and *B. v. variegatus* (B, AMNH 95105).

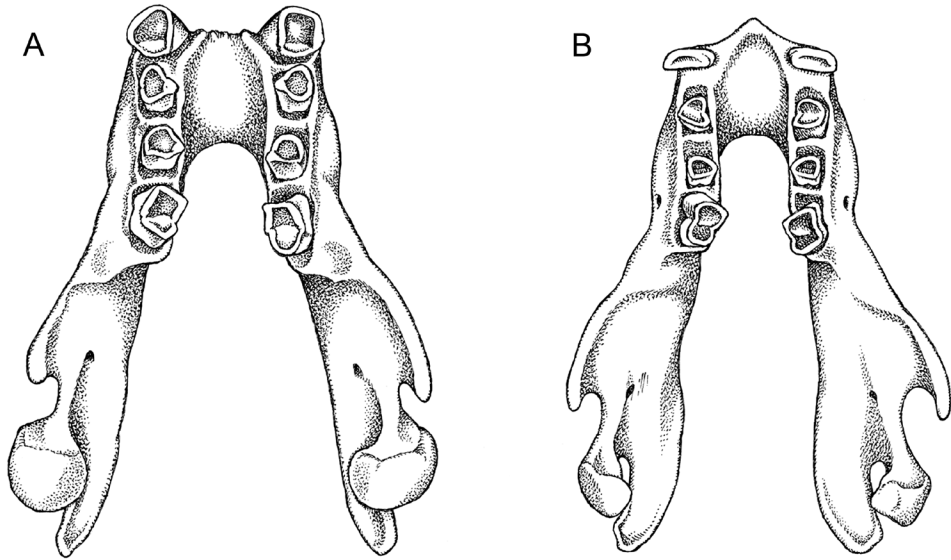


FIG. 9. Dorsal views of mandibles of *Bradypus variegatus infuscatus* (A, AMNH 76497) and *B. v. variegatus* (B, AMNH 95105).

Wagler (1831: 611), *Bradypus infuscatus* was based on a single specimen collected by “Herr von Spix” (= Johann Baptist Ritter von Spix) on the border between Brazil and Peru (“*Brasilia versus Peru*”). Based on Spix’s known itinerary (Vanzolini, 1981; Hershkovitz, 1987), it seems reasonably certain that the holotype (by monotypy, a specimen in the Zoologische Staatssammlung München, ZSM 1162; Wetzel and Kock, 1973) was collected at or near Tabatinga, on the left (north) bank of the upper Amazon, just across the river from Peru and the mouth of the Yavari (fig. 1).² We have not examined this specimen, which consists only of a mounted skin (A. van Heteren, personal commun., 2016); the skull was said to be missing in the original description (Wagler, 1831) and has not been recovered.

² No original locality datum accompanies ZSM 1162, but Spix is known to have arrived at Tabatinga on 9 January 1820, and the holotype was collected on 14 January (A. van Heteren, personal commun., 2016). Cabrera (1958) “restricted” the type locality of *Bradypus infuscatus* to the confluence of the Solimões (upper Amazon) and the Iça (Putumayo), but the confluence of the Solimões with the Iça is >200 km from the Peruvian frontier, and there seems to be no evidence that ZSM 1162 was actually collected there; Kraft (1995: 56) apparently repeated Cabrera’s error without attribution.

Based on the geographic distribution of examined material with the morphological traits described above, it is plausible that *B. v. infuscatus* is the proper trinomen for this form, but without confirmatory evidence (e.g., DNA sequence data obtained from the holotype skin) it is hard to be sure. Possible junior synonyms include *brachydactylus* Wagner, 1855; *macrodon* Thomas, 1917; *codajazensis* Lönnberg, 1942; and *subjuruanus* Lönnberg, 1942 (for type localities, see Gardner, 2008). Of these nominal taxa, we have only examined the holotype of *macrodon* (BMNH 80.5.6.56), which exhibits all the diagnostic craniodental traits of the western Amazonian phenotype as described above.

Given the distinct morphologies associated with western Amazonian specimens on the one hand and southeastern Amazonian specimens on the other, we would be inclined to call these distinct species. However, we are provisionally using trinomial nomenclature because there are intermediate phenotypes, suggestive of intergradation, in central Amazonia. Based on specimens we examined with the morphological distinctions described and illustrated above, *Bradypus*

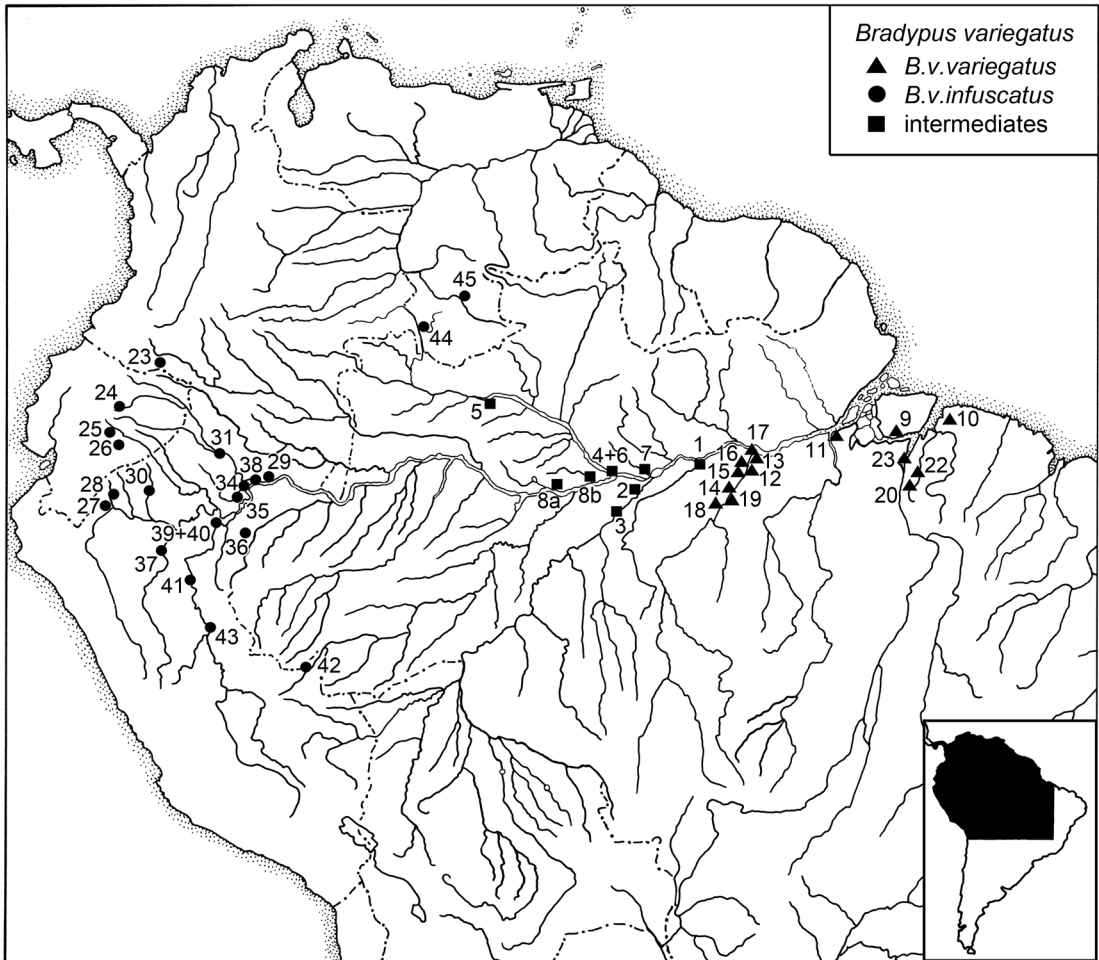


FIG. 10. Collecting localities of specimens of *Bradypus variegatus* examined for this report. See appendix 3 for geographic coordinates.

variegatus variegatus occurs along the right (south) bank of the Amazon from the vicinity of Belém westward to the left (west) bank of the Tapajós, whereas *B. v. infuscatus* occurs in eastern Ecuador, eastern Peru, and southern Venezuela (fig. 10). Only a few specimens are available from the wide (ca. 1300 km) central-Amazonian gap between these morphologically diagnosed taxa, but those we examined are difficult to assign with certainty to either form. For example, three BMNH specimens from Codajás (on the north bank of the upper Amazon west of Manaus; fig. 10: locality 8a) have small pseudoincisors,

long nasals, narrow rostrums, and short mandibular symphyses (like *B. v. variegatus*), but they have well-developed postorbital jugal processes and lack symphyseal spouts (like *B. v. infuscatus*). Pending a much-needed revision of the brown-throated three-toed sloth complex, trinomial nomenclature seems like the appropriately conservative option.

ETHNOBIOLOGY: The three-toed sloth has only one name, *mëinkanchush*. It is not analyzable and there are no cognates in other Panoan languages. No subtypes are recognized by the Matses. The Matses do not hunt three-toed sloths, eat them, or

keep them as pets. The Matses generally will not even look directly at them, because if a hunter looks at a three-toed sloth it can make his children ill. Therefore, the Matses know very little about the natural history of this species.

MATSES NATURAL HISTORY: The three-toed sloth is similar to the two-toed sloth, but it has three claws on its front feet, a short tail, a smaller head, a striped face, and a spotted back. Its face looks like that of a little person.

Three-toed sloths are found mostly beside rivers in stands of cecropia trees (*Cecropia* spp. [Moraceae]). They are rarely encountered in Matses territory (where large stands of cecropia trees are absent).

It makes no nest. It is nocturnal and diurnal. It swims slowly but effectively across rivers. It climbs along lianas and branches upside-down. It sits in thickets. It is solitary. It eats mostly cecropia tree leaves and also eats fig-tree (*Ficus* sp. [Moraceae]) fruits.

REMARKS: The Matses do not have a lot to say about three-toed sloths—doubtless because this species is seldom seen and never hunted for food—and their few observations seem intended primarily to distinguish this species from the superficially similar two-toed sloth (a primary game species). This intent is explicit in the comparative phrasing of their morphological descriptions, but diagnostic comparisons are also implied by their remarks that three-toed sloths are both nocturnal and diurnal (two-toed sloths are exclusively nocturnal), and that three-toed sloths swim (whereas two-toed sloths do not, at least according to the Matses; see below).

The widespread notion that three-toed sloths have a close relationship with trees of the genus *Cecropia* has been called a myth by Montgomery (1983), who averred that *Bradypus* are simply easier to see in the relatively open, sunlit crowns of cecropia trees than in the denser crowns of other tree species. However, it should be noted that Montgomery's research on sloths (e.g., Montgomery and Sunquist, 1978) was carried out on an island with very little early-successional vegetation (the preferred seral stage of *Cecropia* spp.), where

an essentially captive population of sloths may have had no choice but to forage in habitats that would have been avoided by unconstrained animals. Subsequent studies from mainland habitats seem to agree with earlier reports that young cecropia leaves are a preferred forage for *Bradypus*, perhaps due to their low fiber content, high nutrient value, and lack of defensive secondary compounds (Urbani and Bosque, 2007). Therefore, the Matses observation that riparian stands of cecropia trees are the primary habitat of three-toed sloths merits credibility despite Montgomery's (1983) dismissal of essentially similar observations in the older literature.

Choloepus hoffmanni Peters, 1858

VOUCHER MATERIAL (TOTAL = 10): Nuevo San Juan (AMNH 268225, 268226, 273184; MUSM 5072, 11077, 11079, 11080, 15346), Orosa (AMNH 73760, 73761).

OTHER INTERFLUVIAL RECORDS³: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Estación Biológica Quebrada Blanco (Heymann et al., 2011), Itia Tëbu (Amanzo, 2006), Jenaro Herrera (Pavlinov, 1994), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: The genus *Choloepus* has received no modern revisionary attention. The current recognition of two valid species and the application of their names are largely based on diagnoses provided by Wetzel and Avila-Pires (1980) that were subsequently incorporated in dichotomous keys by Wetzel (1985a) and Gardner and Naples (2008). According to these sources, *C. didactylus* (with type locality in Surinam) is a widespread Amazonian species, whereas *C. hoffmanni* (with type locality in Costa Rica) occurs in Central America, trans-Andean South America, and western Amazonia. Mapped

³ Unvouchered records of two-toed sloths are sometimes identified as "*Choloepus* sp." (e.g., by Salovaara et al., 2003), but sometimes as *C. didactylus* (e.g., by Heymann et al., 2011). In the absence of evidence for the presence of a second species of *Choloepus* in the Yavari-Ucayali interfluvium, we assume that all of these sightings were of *C. hoffmanni*.

TABLE 5
Diagnostic Cranial Traits of *Choloepus didactylus* and *C. hoffmanni*^a

	<i>C. didactylus</i>	<i>C. hoffmanni</i>
Preorbital osteology	maxilla contacts frontal	lacrimal contacts nasal
Posterior mesopterygoid foramen ^b	absent	present
Mesopterygoid ratio (AMB/PMB) ^c	>2.0	<2.0

^a After Wetzel and Avila Pires (1980), Wetzel (1985a), and Gardner and Naples (2008); see illustrations in Wetzel (1985a).

^b Opening into pterygoid sinus (see text).

^c Ratio of anterior mesopterygoid breadth (AMB) to posterior mesopterygoid breadth (PMB).

geographic ranges (in Wetzel, 1985a; Gardner and Naples, 2008) suggest that both species occur in northeastern Peru, so either *C. didactylus* or *C. hoffmanni* might occur in the Yavarí-Ucayali interfluve; alternatively, the two species might be sympatric in our region.

According to the literature cited above, *Choloepus didactylus* and *C. hoffmanni* can be distinguished by several cranial characters (table 5): (1) On the dorsal surface of the rostrum, just anterior to the orbit, either the maxillary bones contact the frontals, or the lacrimals contact the nasals; because most cranial sutures are fused in fully adult sloths, this is a character that can only be scored from immature specimens. (2) In the rear of the mesopterygoid (“interpterygoid”) fossa, a pair of large foramina—one on each side—that communicate with the pterygoid sinuses is either present or absent; unlike the preceding character, this feature can be scored from both immature and adult specimens. (3) The ratio between the anterior (widest) and posterior (narrowest) transverse dimensions of the mesopterygoid fossa is said to be taxonomically diagnostic. Additionally, pelage differences are said to distinguish *C. didactylus* from *C. hoffmanni*, but we experienced considerable difficulty in evaluating pelage traits, none of which appear to offer an unambiguous basis for character scoring, so we do not consider them further here.

In order to evaluate the allegedly diagnostic cranial traits of *Choloepus didactylus* and *C. hoffmanni*, we examined series of specimens from regions where these species occur allopatrically (table 6). Of the three characters described above, only the presence/absence of posterior

mesopterygoid foramina consistently distinguishes eastern Amazonian specimens (*C. didactylus*) from Central American material (*C. hoffmanni*). Although the mean difference in computed mesopterygoid ratios between these samples is obviously significant, the observed ranges overlap, so specimens cannot be sorted consistently by this criterion. Similarly, although most eastern Amazonian specimens exhibit maxillary-frontal contact, over 20% exhibit lacrimal-nasal contact (which appears to be a fixed trait in Central American material). Nevertheless, these results provide compelling evidence of phenotypic divergence, and they are consistent with the current recognition of two species of two-toed sloths, albeit with somewhat less distinct recognition criteria than suggested by the literature cited above.

The ten voucher specimens we examined from the Yavarí-Ucayali interfluve are all referable to *Choloepus hoffmanni* as that species is currently recognized by these criteria. All the immature specimens (juveniles and subadults: AMNH 73761, 268225, 273184; MUSM 11077, 11080) exhibit lacrimal-nasal contact, and all the specimens that preserve an intact mesopterygoid region ($N = 9$) have paired posterior foramina that open into the pterygoid sinuses. All of the four adults we measured (table 7) have mesopterygoid ratios <2.0.

Interestingly, almost all the two-toed sloths we examined from the north bank of the Amazon (directly opposite the Yavarí-Ucayali interfluve) are referable to *Choloepus didactylus* by the criteria discussed above, as are all the specimens

TABLE 6

Morphological Trait Frequencies in Allopatric Populations of *Choloepus didactylus* and *C. hoffmanni*

	Preorbital osteology ^c			Posterior mesopterygoid foramen ^c			Mesopterygoid ratio ^d
	LN contact ^e	MF contact ^f	both ^g	present	absent	both ^g	
<i>C. didactylus</i> ^a	3 (23%)	9 (69%)	1 (8%)		29 (97%)	1 (3%)	2.09 ± 0.16 (1.85–2.50) 15
<i>C. hoffmanni</i> ^b	27 (100%)			53 (100%)			1.57 ± 0.19 (1.26–1.96) 25

^a From the Guianas and southeastern Pará: AMNH 133405, 133410, 133414, 133416, 133417, 133427, 133439, 133444, 133446, 133447, 133449, 133452, 133453, 265952; BMNH 1904.7.4.94–1904.7.4.98, 1910.5.4.42, 1952.1175, 1952.1176; FMNH 21730, 34326, 34711, 41208, 93177, 95447–95450.

^b From Nicaragua, Costa Rica, and Panama: AMNH 2857/3780, 10274, 18895, 18896, 18897, 22703, 24441, 26900, 26901, 26905, 26907, 26908, 26912, 26913–26916, 26918–26922, 26925, 26934, 28475, 29440, 29608, 29643–29652, 29829, 30765, 131821–131823, 135331, 135332, 135490, 135524, 135925, 137280, 137281, 139772, 139773, 140333, 141856, 141857.

^c Table entries are numbers of specimens scored (percentage in parentheses).

^d Computed from adult measurements; table entries are the sample mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size. Descriptive statistics for the *C. hoffmanni* sample excludes one outlier (AMNH 26915) with a mesopterygoid ratio of 2.59 (>5 standard deviations from the mean).

^e Bilateral lacrimal-nasal contact.

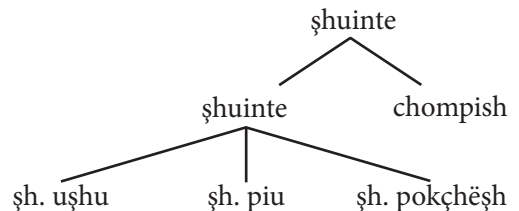
^f Bilateral maxillary-frontal contact.

^g Asymmetrical trait expression.

we examined from eastern Ecuador. By contrast, both *C. didactylus* and *C. hoffmanni* occur south of the Amazon in Peru, but they occur at different localities. Therefore, although the ranges of these species overlap, we have yet to find any place where they are actually sympatric. Possibly they occur in different forest types, a hypothesis that merits testing in the field.

ETHNOBIOLOGY: The principal name for the two-toed sloth is shuinte, which is not analyzable or found in other Panoan languages. It has three archaic synonyms: nai, posën, and tabidiate. The first two are not analyzable but, unlike the principal term, they do occur as sloth names in other Panoan languages; the third term is a nominalization meaning “one for tying up its feet” (when the Matses bring a sloth back to the village alive, they tie their claws to their hand so that they cannot harm the person carrying it; this was the standard way of bringing back sloths during the komok ceremony, and is still done sometimes today). In the language used in the komok ceremony, the two-toed sloth is called uštud kudu; the first word seems to include the verb uṣh ‘sleep’ (the Matses associate two-toed sloths with sleepiness and laziness)

and the second term is an archaic adjective meaning “grayish” or “light-colored.” Four subtypes of two-toed sloth are recognized by Matses hunters: shuinte uṣhu (“white/light-colored two-toed sloth”), shuinte piu (“red/reddish-brown two-toed sloth”), shuinte poçhëṣh (“black-/dark-bellied two-toed sloth”), and chompish. The last name is not analyzable, but it is also the name of a small bird that purportedly reveals the presence of two-toed sloths. Chompish and the other three subtypes seem to occupy different levels in the Matses classification, in the sense that chompish is considered more distinct from the other three types. This could be represented as follows:



The chompish variety is said to be much rarer than the others and to be the size of a young two-toed sloth, but to have head, claws, and teeth the

TABLE 7
Measurements (mm) and Weights (g) of Adult *Choloepus hoffmanni*
from the Yavari-Ucayali Interfluve

	AMNH 73760	MUSM 11079	MUSM 15346	AMNH 268226	MUSM 5072
Sex	female	female	female	male	unknown
Head-and-body length	—	650	647	614	—
Length of tail	—	28	18	27	—
Hind foot	—	148	155	144	—
Ear	—	28	22	27	—
Weight	—	—	7700	8100	—
Condylobasal length	—	118.6	121.2	120.2	126.2
Rostral breadth	40.8	39.3	37.0	43.1	39.1
Least interorbital breadth	34.9	37.6	35.6	39.2	40.1
Least postorbital breadth	40.0	41.1	35.9	41.9	39.9
Posterior zygomatic breadth	71.9	71.4	71.8	78.4	75.4
Maxillary toothrow	42.2	44.4	43.9	43.5	44.7
Mesopterygoid ratio	1.92	—	1.63	1.77	1.76

size of a full-grown adult. It has a short back, rostrum, and limbs. Its body is reddish, while its head is light colored. Informants never fail to mention that its meat is very hard and takes a long time to cook. The other three varieties are generally associated with different sizes and habitat preferences, but there is much inconsistency and even direct contradictions among informants.

This is a primary game species that is much appreciated by the Matses. Informants emphasize that every part of the sloth is eaten, including its vulva, bladder, and viscera. This species, along with the greater long-nosed armadillo and the spectacled caiman, were the most important species to be hunted during the Matses *komok* ceremony. Two-toed sloths are considered very desirable and hardy pets. When a hunter kills a mother that is carrying its young, the hunter brings it home for his children to raise (fig. 11).

Two-toed sloths are usually hunted by climbing trees and clubbing or strangling them.⁴ A

hunter may be tipped off as to the presence of two-toed sloth by hearing its urine drip from the treetops or by hearing the call of a bird called *chompish* (a type of flycatcher). Otherwise the hunter simply scans the canopy as he walks down a path. The sloth is typically curled up asleep in the crotch of a branch, in the crown of a bottle palm (*Iriartea deltoidea* [Arecaceae]) or in a vine tangle. When he spots a sleeping sloth, the hunter makes a climbing ring (a loop of epiphyte stems or a palm frond, to loop between his feet as he shinnies up the trunk) and judges whether he can get within arm's reach of the sloth. If he can get close to it, he cuts a hard stick to use as a club, climbs up next to the sloth, wakes it, and then clubs it on the head until it dies or falls out of the tree. Two-toed sloths are very resistant, and do not succumb quickly when they are clubbed. While the hunter is clubbing a sloth, it will become fierce and try to bite the hunter. If he cannot get close to it (for example, if it is in the crown of a bottle palm), he prepares a noose from epiphyte stems and attaches it to a stick 1.5 to 2 m long. He

⁴ Occasionally a hunter may shoot a sloth out of a tree with a shotgun, but this is uncommon since hunters prefer not to waste ammunition on game that can be taken by other means.

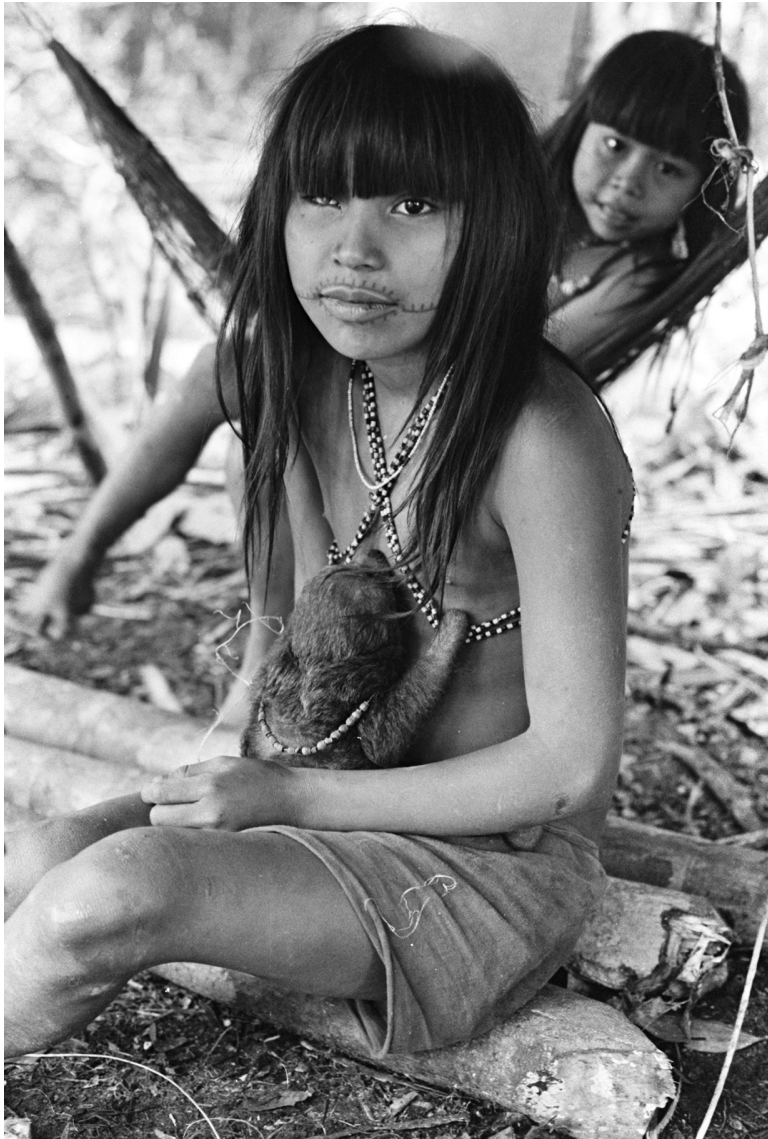


FIG. 11. Matsigenka girl with pet two-toed sloth on the upper Quebrada Chobayacu, ca. 1975 (photo by Steven Romanoff).

then climbs an adjacent tree, taps the sloth lightly with the stick (so that it wakes up and sticks out its head), snares it around the neck, and then pulls hard to yank it off its perch. Next, he throws down the sloth with the noose still attached. He may then club it to death on the ground or decide to take it back home alive. The latter option is preferred if the hunter is far from home, to keep the meat from spoiling.

There is a particular way to pack up a sloth for carrying it home. First, the hunter presses on its abdomen to make it defecate and urinate. Then, he breaks all of its limb bones with a club, ties the hind feet together, tucks the tied-up legs together, and lashes all in place to make a roughly spherical bundle. If the sloth is still alive, its front and back claws are tied tightly to its arms and feet, so that it cannot grab the carrier. Then a

tumpline (a carrying strap worn across the forehead, made from the bark of certain trees) is attached to the sloth and the hunter carries it home on his back.

Hunters typically leave hunting signs where they kill certain game, usually next to the path that is closest to the kill site. Sloth kills are marked with a meter-long stick jammed into the ground; a slot is cut in the top of the stick, and a tuft of the sloth's fur is wedged in the slot. If the sloth was captured by noosing, the noose stick is jammed in the ground next to the stick with fur; if the sloth was captured by clubbing, the club and the climbing ring are placed next to the trophy stick.

The Matses used to hang two-toed sloth mandibles on one the horizontal poles of their long-houses, as hunting trophies and to keep track of how many sloths had been killed at that locality. Today this is still done by a few old men.

The Matses believe that a certain type of owl hoots at night near a Matses house to announce human visitors or the presence of game species, including two-toed sloths. After killing a sloth, a hunter may remove the sloth's anal scent gland and rub it across his eyes. This is believed to improve his ability to find two-toed sloths in the future. A similar effect is thought to be achieved by burning a sloth forearm bone and letting the smoke enter one's eyes.

Children do not eat the jaw meat, lest their jaws swell up. Young men do not eat young sloths, lest they not wake up early. Young men do not eat the ball of fat that is found in the two-toed sloth's abdominal cavity, lest they become unable to spot sloths. The hunter who killed the sloth does not eat the intestines, lest he not find more sloths. Young men and the hunter who killed the sloth do not eat the liver, lest they do not find more sloths.

When a sloth is killed, the hunter's children (or any other child that looks upon the dead sloth) may be made ill by the sloth's spirit. The symptoms of contagion by sloths include oversleeping and fever.

MATSSES NATURAL HISTORY: Two-toed sloths are very hairy. They have no tail. They have

sharp black teeth, small ears, and hairless noses. They have two long claws on their front feet and three on their hind feet. Their backs are lighter-colored than their undersides. Their meat is hard and takes a long time to cook. They have the most fat during the rainy season (December to April), especially in February.

Two-toed sloths are found in any type of primary forest, including upland forest, and flooded or dry floodplain forest. They are also found in very old (>25 years old) abandoned swiddens. They are relatively common, especially in areas that have not been hunted.

Two-toed sloths do not make nests. They sleep during the day in vine tangles, under the cover of large-leaved epiphytes, in crotches of trees high in the canopy, or in the crown of bottle palms (*Iriartea deltoidea* [Arecaceae]). They sleep curled up, with their head tucked in. They usually perch high up to sleep, but they perch lower when they are at the edge of a river or when it is raining.

The two-toed sloth is nocturnal. After sleeping all day, it wakes up at dusk and stays in its perch looking around until it is fully dark. It sets out traveling along the undersides of branches and horizontal lianas looking for leaves and fruits to eat. It avoids dead branches. It drinks water from holes in trees in the canopy, where frogs have laid eggs, or water trapped in palm-tree crowns. It also licks rainwater from leaves. It climbs down to the ground to drink water when there is none in the treetops. It also climbs down to the ground to eat clay that has been dug out by an armadillo, to eat rotten meat, and to defecate. It climbs back up quickly after having defecated, drunk water, or eaten clay or rotten meat. After eating a lot it stops to sleep for a while before setting out to forage again. Unlike three-toed sloths, two-toed sloths do not swim.

Two-toed sloths are usually solitary but are sometimes found in male-female pairs perched near each other. They give birth to a single young, which clings to its mother's venter.

Two-toed sloths are followed by a small swarm of little black flies and sweat bees (tabanid flies that have black-and-yellow striped abdomens). A bird called chompish (a type of fly-catcher) follows sloths (perhaps to feed on its flies?). Large eagles and hawks kill and eat two-toed sloths, even fully grown adults. Jaguars also occasionally kill them.

Two-toed sloths do not make any noise while perched or while feeding. They huff when they are being killed or when they are defending themselves.

Two-toed sloths eat the young leaves of almost any tree. They are particularly fond of the leaves of tote trees (*Eschweilera* spp., *Lecythis* spp., or *Cariniana* spp. [Lecythidaceae]). Other favored foods are the ripe fruits and leaves of trees in the cacao (Sterculiaceae) family, particularly tonkodo (*Theobroma* sp.) and senad dēbiate (*Theobroma subincanum*). They eat the ripe fruits of a few other types of dicot trees, including mamuin (*Garcinia longifolia* [Guttiferae]), which they eat after splitting open the rind; piuṣh bēchi (*Helicostylis tomentosa* [Moraceae]); tonnad (a general term for trees in the Myristicaceae); and mannan tsipuis (*Inga* spp. [Leguminosae]). They also eat the fruits of some epiphytes and the heart and young leaves of okodonte epiphytes (*Philodendron* [Araceae]). They feed much more on leaves than on fruits, and they do not eat old/mature leaves. They descend to the ground to eat rotten meat.

REMARKS: Matses interviews include many original observations about the behavior and diet of two-toed sloths, notably including their use of water sources in the canopy, geophagy, occasional carrion eating, food plants, and a possibly mutualistic interaction with an unidentified species of bird. To the extent that Matses observations overlap with previously published results of scientific research on *Choloepus*, there is good agreement (e.g., about nocturnality, reproduction, and predation), but one discrepancy merits comment. Two literature reviews—one about *C. didactylus* and the other about *C. hoffmanni*—both claim that two-toed sloths can swim (Adam, 1999; Hayssen, 2011a), but none of the refer-

ences cited in either review explicitly report swimming behavior in these species.⁵ Most mammals, of course, can swim when necessary, but the absence of any published observation of swimming by *Choloepus* spp. tends to support the Matses' claim that two-toed sloths do not often do so, by contrast with three-toed sloths, which are frequently found swimming across rivers and lakes.

Myrmecophagidae

Three species of anteaters, the usual complement in intact Amazonian habitats, are found in the Yavari-Ucayali interfluvium: the pygmy anteater (*Cyclopes didactylus*), the giant anteater (*Myrmecophaga tridactyla*), and the tamandua (*Tamandua tetradactyla*). All are readily distinguished by obvious external characters (Emmons, 1997), and their edentulous skulls are easily identified by nonoverlapping measurements and ratio variables (Wetzel, 1985a). *Myrmecophaga* and *Tamandua* are not currently known to be associated with any taxonomic problems, but molecular sequencing has revealed unexpectedly deep (Miocene) divergence within *Cyclopes*, which is currently thought to be monotypic. The genus *Cyclopes* is sometimes placed in its own family (Cyclopedidae; e.g., by Gardner, 2008), but the distinction seems phylogenetically pointless.

Cyclopes didactylus (Linnaeus, 1758)

VOUCHER MATERIAL (TOTAL = 2): Nuevo San Juan (AMNH 268232; MUSM 11093).

OTHER RECORDS: None.

IDENTIFICATION: The pygmy (or “silky”) anteaters currently recognized as *Cyclopes didactylus* cannot be confused with any other mammal, although it seems highly probable that they comprise a species complex rather than a single species (Coimbra et al., 2017). Among the numerous

⁵ Both references cited by Adam (1999) refer to swimming by “sloths” or “the sloth” in contexts that do not distinguish behaviors attributed to *Bradypus* from those attributed to *Choloepus*.

epithets currently treated as synonyms or subspecies of *C. didactylus* (see Gardner, 2008) are several that might apply to the population that occurs in the Yavari-Ucayali interfluve, but available museum specimens are too few and widely scattered to attempt a revision for this report.

Our two voucher specimens have co-ossified occiputs but unfused braincase and facial sutures. AMNH 268232 consists only of a skull, but MUSM 11093 includes a skin. The pelage of the latter specimen is silvery grayish-brown dorsally and lacks any distinct markings, although the fur is noticeably browner over the head, shoulders, and upper back, whereas the lower back and rump are grayer; the ventral fur is abruptly self-beige over the chest and abdomen, but brownish on the throat. Measurements of MUSM 11093 are: head-and-body length, 182 mm; length of tail, 229 mm; hind foot, 43 mm; ear, 16 mm; condylonasal length, 50.1 mm; nasal length, 14.0 mm; least interorbital breadth, 9.4 mm (measured just anterior to small postorbital processes); anterior zygomatic breadth, 14.2 mm; posterior zygomatic breadth, 22.5 mm; breadth of braincase, 22.9 mm. This specimen weighed 286 g.

ETHNOBIOLOGY: The pygmy anteater is generally called tsipud, which is not analyzable and has no cognates in other Panoan languages. In some villages the term tsekeded is used instead. Tsekeded is an onomatopoeic representation of the “purr” that the pygmy anteater makes when disturbed. A few Matses consider tsekeded to be a synonym of tsipud. No subtypes are recognized. Some Matses consider it to be a type of sloth, while others consider it to be more closely related to tamanduas.

The pygmy anteater is not hunted, eaten, or kept as a pet.

It is a death omen to come across a pygmy anteater. If a person comes in contact with one, his children are very likely to fall ill with excessive sleepiness and fever (symptoms similar to those caused by two-toed sloths). Men with children will not even look at them.

MATSES NATURAL HISTORY: The pygmy anteater is like a baby two-toed sloth, but has a tail.

Its tail has a hairless patch (the ventral prehensile surface). The soles of its feet are hairless and reddish. Its eyes are small and its nose is pink. It is pretty and its fur is like cotton.

Pygmy anteaters are usually found perched on thin vines in open forest. They can be found high or low in the canopy. They sit on branches that hang over large streams.

Pygmy anteaters are nocturnal. During the day they forage along vines and thin trees. They stop to rest frequently, perching in the same position as two-toed sloths.

Pygmy anteaters are generally solitary, but occasionally two are found near each other.

A pygmy anteater may curl up and cover its face with its front paws when it is scared.

When knocked off its perch or poked with a stick, a pygmy anteater purrs loudly, saying “tsekededededed.”

Its diet is not known by the Matses.

REMARKS: Most of what little the Matses have to say about the pygmy anteater agrees with the sparse natural history literature on this species (reviewed by Hayssen et al., 2012), although no vocalizations seem to have been reported previously.

Myrmecophaga tridactyla Linnaeus, 1758

VOUCHER MATERIAL (TOTAL = 3): Boca Rio Yaquerana (FMNH 88890), Nuevo San Juan (MUSM 11094), Quebrada Esperanza (FMNH 88891).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Only three specimens of the giant anteater seem to have been collected in the Yavarí-Ucayali interfluve. Two of them, both females, are preserved as skins and skulls. Of these, FMNH 88890 is obviously the younger animal, with a co-ossified occiput but otherwise unfused cranial sutures; the skull is lightly built, and partially disarticulated. The second, FMNH 88891, is much larger and has a more heavily

ossified skull, but all of the cranial sutures (except those of the occiput) are still visible. Although the latter specimen is seemingly immature according to the age classification that Wetzel (1975) proposed for tamanduas, measurements of FMNH 88891 are within the range of variation that Wetzel (1985a) subsequently reported for adult *Myrmecophaga*. Both skins exhibit all of the usual diagnostic external traits of *M. tridactyla* (e.g., those described by Husson, 1978; Emmons, 1997), with no apparent pigmental or other pelage difference between the younger and older individual. Selected measurements of FMNH 88891 are: head-and-body length, 1202 mm; length of tail, 687 mm; hind foot, 157 mm; ear, 51 mm; condylonal length, 330.7 mm; nasal length, 151.3 mm; least interorbital breadth, 45.5 mm; posterior zygomatic breadth, 65.6 mm; breadth of braincase, 63.0 mm.

Our specimen from Nuevo San Juan (MUSM 11094) was killed by a Matses hunter to protect his dogs, which were fighting with it. This is a fully adult female (braincase elements are co-ossified) with the following measurements: head-and-body length, 1150 mm; length of tail, 710 mm; hind foot, 153 mm; ear, 49 mm; condylonal length, 353.0 mm; nasal length, 178.4 mm; least interorbital breadth, 45.9 mm; anterior zygomatic breadth, 61.2 mm; posterior zygomatic breadth, 68.5 mm; breadth of braincase, 63.5 mm. This specimen weighed 32 kg.

ETHNOBIOLOGY: The giant anteater has only one name, *shaë*. It is not analyzable, but it is a common term for this species in other Panoan languages. A few informants suggested that there is a large and a small subtype, but most Matses do not recognize any subtypes.

Giant anteaters are not eaten or kept as pets. Although giant anteaters are not hunted, the Matses sometimes club them to death when they fight with dogs. Giant anteaters sometimes kill dogs if a hunter does not arrive at the scene quickly enough. The Matses are quite careful in approaching giant anteaters, knowing that they could kill a person with their claws.

People don't look at giant anteaters, lest their children fall ill.

MATSES NATURAL HISTORY: Giant anteaters are very large and have a big, bushy tail with long hairs, reminiscent of the flowers of arrow cane (*Gynerium sagittatum* [Gramineae]). They wag their tails back and forth as they walk. They have large claws on their front feet, which they tuck in when they walk around. Their hind footprints look like a human child's. They have a very elongated snout and a very long and thin tongue. They have a stripe around their neck. Their eyes and ears are small.

Giant anteaters use all habitats: floodplain forest, upland forest, primary forest, and secondary forest (including abandoned swiddens).

Giant anteaters do not make a nest. Instead, they sleep lying in hollows in the ground, all curled up. They also sleep between buttress roots.

Giant anteaters are diurnal and nocturnal. They are strictly terrestrial.

Giant anteaters are solitary. The young ride on the mother's neck.

Giant anteaters are a favorite food of jaguars.

Giant anteaters can roar loudly, like a jaguar.

Giant anteaters eat bullet ants (*Dinoponera* spp., *Ectatomma* [Formicidae]). They eat bullet ants by sticking their nose in the nest to make many come out, and then lick them up with their tongue. They dig into leaf-cutter ant (*Atta* sp.) nests and feed there for a long time. They also eat other ants, including army ants (*Eciton* spp.), *ëu* ants (tiny biting ants), and *masioko* ants (small biting ants). They dig into hives of stingless bees (Apidae: Meliponini) that are at the base of trees and stick their snouts in to eat bee larvae and lick up the honey. They do not eat *isan* palm (*Oenocarpus bataua* [Arecaceae]) fruits or other fruits.

REMARKS: Matses interviews about giant anteaters are of particular interest because most of what is known about the natural history of this magnificent species is based on fieldwork in savanna habitats (e.g., Redford, 1985; Shaw et al., 1987; Medri et al., 2003). Although Matses information is sparse and generally agrees with the scientific literature, their observation that giant

anteaters are a preferred prey of jaguars is noteworthy because the high frequency of jaguar attacks on *Myrmecophaga* has only recently been documented (Cavalcanti and Gese, 2010; Sollmann et al., 2013).

Giant anteaters are predators of social insects, and they are widely believed to feed almost exclusively on termites and ants (Redford, 1985, 1986). However, Matses observations suggest that stingless bees might be an important alternative food resource in Amazonia. In upland savannas (e.g., the Cerrado; Redford, 1985), giant anteaters are said to feed mostly on termites, whereas populations in seasonally inundated grasslands (e.g., the Llanos and Pantanal; Medri et al., 2003) appear to eat mostly ants. Judging from Matses observations, Amazonian populations of *Myrmecophaga* feed primarily on ants, perhaps because most rainforest termitaria are arboreal (Constantino, 1992). The feeding bouts of giant anteaters are said to be very brief (usually less than a minute; Redford, 1985), so it is interesting that the Matses say they feed for a long time at leaf-cutter ant nests.

Tamandua tetradactyla (Linnaeus, 1758)

VOUCHER MATERIAL (TOTAL = 7): Nuevo San Juan (AMNH 268233; MUSM 11095, 11096), Orosa (AMNH 73752, 74114, 74115), Santa Cecilia (FMNH 86892).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: The seven tamandua specimens we examined from the Yavarí-Ucayali interfluvial exhibit all the pelage color variants that Wetzel (1975) reported for the species, from entirely blond (FMNH 86892, MUSM 11095) to completely blackish (AMNH 74115, 268233) and vested (with dark-brownish mid-body, shoulders and nape but pale legs, face,

and tail; FMNH 74115, MUSM 11096). As noted by Wetzel (1975), these phenotypes appear to be uncorrelated with age or sex and seem to represent genuine coat-color polymorphisms. All of our specimens are females, of which four could be called subadults (Wetzel's age class 1; with co-ossified occiputs but otherwise unfused cranial sutures) and three are young adults (with fused midfrontal sutures). Measurements of the latter specimens (AMNH 74114, FMNH 86892, MUSM 11095) are all within the range of variation for homologous dimensions of *Tamandua tetradactyla* provided by Wetzel (1985b). All of our specimens have three foramina in the back of the orbital fossa, a trait that is said to reliably distinguish *T. tetradactyla* from its trans-Andean congener *T. mexicana* (see Wetzel, 1975: fig. 3). Selected measurements of FMNH 86892 and MUSM 11095 (the specimens with the most complete data in our series) are, respectively: head-and-body length, 605 and 538 mm; length of tail, 515 and 497 mm; hind foot, 102 and 111 mm; ear, 51 and 56 mm; condylo-nasal length, 129.3 and 121.7 mm; nasal length, 45.9 and 38.2 mm; least interorbital breadth, 22.7 and 24.0 mm; posterior zygomatic breadth, 39.6 and 44.2 mm; breadth of braincase, 40.1 and 44.9 mm. The weight of MUSM 11095 (our only adult specimen accompanied by this datum) was 5.3 kg.

ETHNOBIOLOGY: The collared tamandua has only one name, *bëwî*. It is not analyzable but it is a common term for this species in other Panoan languages. The Matses are aware of different color morphs (black, blond, and vested), but these are not named or considered subtypes. Some informants describe the coat variation as analogous to that found among domestic dogs. Informants agree that it is similar and closely related to the giant anteater.

The tamandua is not hunted, eaten, or kept as a pet by the Matses. Tamanduas sometimes injure dogs, when dogs attack them. When such a fight is in progress, a hunter will try to kill the tamandua with a stick. Tamanduas may try to claw people if approached too closely.

TABLE 8
Niche Separation among 16 Carnivores of the Yavari-Ucayali Interfluve
according to Matses Informants

	Activity	Locomotion	Diet	Social behavior
CANIDAE				
<i>Atelocynus microtis</i>	diurnal	terrestrial ^a	mostly carnivorous	pairs, trios, or solitary
<i>Speothos venaticus</i>	diurnal	terrestrial ^a	carnivorous	group-living
FELIDAE				
<i>Leopardus pardalis</i>	diurnal & nocturnal	terrestrial ^a	carnivorous	solitary
<i>Leopardus wiedii</i>	diurnal & nocturnal	arboreal & terrestrial	carnivorous	solitary
<i>Panthera onca</i>	diurnal & nocturnal	usually terrestrial	mostly carnivorous	solitary
<i>Puma concolor</i>	diurnal & nocturnal	usually terrestrial ^a	mostly carnivorous	solitary
<i>Puma yagouaroundi</i>	diurnal	terrestrial ^a	mostly carnivorous	[ambiguous]
MUSTELIDAE				
<i>Eira barbara</i>	diurnal	arboreal & terrestrial	omnivorous	usually solitary
<i>Galictis vittata</i>	?	terrestrial ^a	carnivorous	?
<i>Mustela africana</i>	?	terrestrial ^a	?	?
<i>Lontra longicauda</i>	diurnal	semiaquatic	piscivorous	usually solitary
<i>Pteronura brasiliensis</i>	diurnal	semiaquatic	piscivorous	group-living
PROCYONIDAE				
<i>Bassaricyon alleni</i>	nocturnal	arboreal	mostly frugivorous	solitary
<i>Nasua nasua</i>	diurnal	usually terrestrial	omnivorous	group-living
<i>Potos flavus</i>	nocturnal	arboreal	mostly frugivorous	solitary
<i>Procyon cancrivorus</i>	?	?	?	?

^a Implied rather than stated explicitly.

People don't look at tamanduas, lest their children become ill.

MATSES NATURAL HISTORY: Tamanduas have a tail with a bare patch (the ventral prehensile surface), an elongated snout, a long thin tongue, small eyes, small ears, and very strong forelegs. The claws of its forefeet are similar to those of a two-toed sloth. Some tamanduas are black, others are tan, and other have a black body with light-colored head and limbs. They have a strong, bad smell, like a termite nest.

Tamanduas are found in all habitats: upland forest, floodplain forest, and along rivers and streams, in primary forest, and in abandoned swiddens.

Tamanduas sleep in holes in trees and also in abandoned paca and armadillo burrows.

Tamanduas are diurnal and nocturnal. They forage up in trees and on the ground. They travel long distances while foraging. They rest curled up on branches.

Tamanduas are usually solitary, although sometimes more than one are found travelling together.

When dogs bark at a tamandua, it rears up on its haunches and spreads its arms. Tamanduas are preyed upon by jaguars, pumas, and large raptors.

Tamanduas dig into rotten logs and arboreal termite nests to eat termites. They also dig into binsan (black arboreal ants) nests and eat the ants and their larvae. (Some informants say tamanduas dig into stingless-bee hives to lick up the honey, but other informants deny this.)

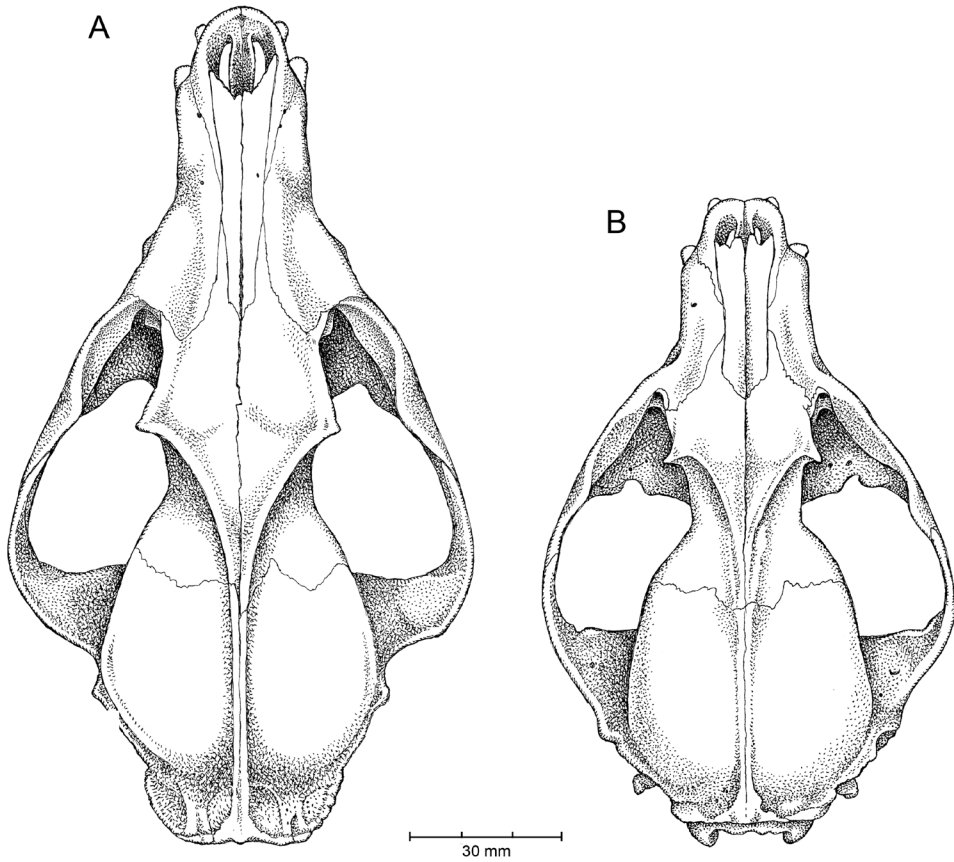


FIG. 12. Dorsal views of adult skulls of *Atelocynus microtis* (A, AMNH 98639) and *Speothos venaticus* (B, AMNH 98560). Both specimens are from northeastern Peru, but neither is from the Yavari-Ucayali interfluvium.

REMARKS: Matses observations are completely consistent with published natural history information about tamanduas (Emmons, 1997; Haysen, 2011b; Navarrete and Ortega, 2011). Among the few novel items mentioned by our interviewees, the Matses add pumas (*Puma concolor*) to the very short list of predators known to attack this species.

Our three specimens from Nuevo San Juan were all killed by Matses hunters in primary floodplain forest.

Carnivora

The known carnivore fauna of the Yavari-Ucayali interfluvium includes 16 species in five

families—Canidae, Felidae, Mustelidae, and Procyonidae—and it seems unlikely that any additional species will be found in the region. The Matses recognize and name all of the local carnivores, and experienced hunters are familiar with the principal ecobehavioral traits of most species (table 8).

Canidae

Two species of wild canids are known to occur in the Yavari-Ucayali interfluvium, the small-eared dog (*Atelocynus microtis*) and the bush dog (*Speothos venaticus*); both are easily recognized by external characters (Hershkovitz, 1957, 1961; Emmons, 1997). Although canid

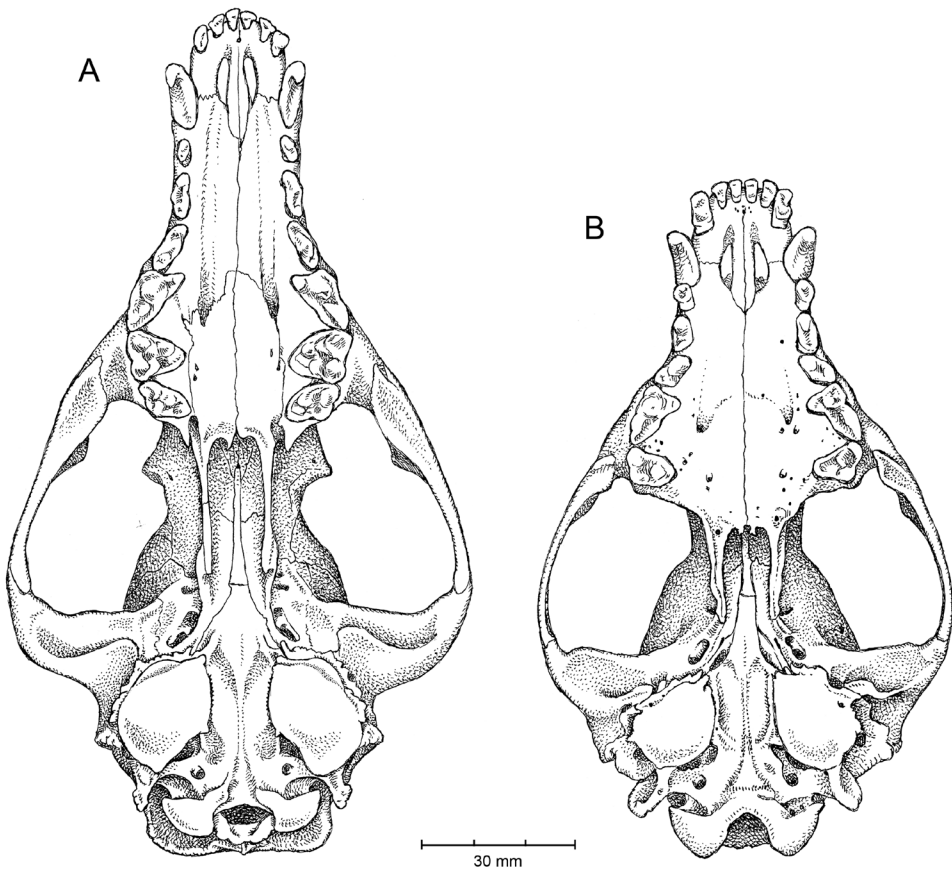


FIG. 13. Ventral views of adult skulls of *Atelocynus microtis* (A, AMNH 98639) and *Speothos venaticus* (B, AMNH 98560). Note the absence of M2 in *Speothos*.

voucher material is lacking from our region, we provide cranial illustrations and measurements of extralimital specimens to help identify skeletal material that might eventually be found there (figs. 12, 13; tables 9, 10).

The Matses have raised domestic dogs (*Canis lupus familiaris*) for many generations, primarily for hunting, but a Matses myth implies that they did not always have dogs. The principal name for the domestic dog is *opa* (unanalyzable, but cognate with names for dogs in several other Panoan languages). There is also one archaic synonym for the domestic dog, *mēntsis*, which also means “fingernail” or “claw of forefoot.” The term *opa* is also a general term that includes wild canids.

Atelocynus microtis (Sclater, 1883)

Figures 12A, 13A

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Quebrada Pobreza (Escobedo-Torres, 2015), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: The short-eared dog is unmistakable in external appearance (Emmons, 1997), so sight records from competent observers are reliable evidence for local occurrence. There is, additionally, a published camera-trap photograph of this species from Quebrada Pobreza (Pitman et al., 2015: fig. 10S).

TABLE 9
Cranial Measurements (mm) of Adult Specimens of *Atelocynus microtis*
from Eastern Peru^a

	AMNH 98639	AMNH 76031	AMNH 76579
Sex	female	male	male
Condylobasal length	158.9	157.8	158.6
Nasal length	55.8	51.2	56.4
Least interorbital breadth	29.5	29.3	32.1
Least postorbital breadth	24.2	22.9	24.8
Zygomatic breadth	89.1	87.5	94.2
Maxillary tooththrow ^b	68.0	67.0	68.0
Length P4	15.5	15.1	16.7 ^c
Width P4	8.1	7.7	8.9

^a Loreto, Iquitos (AMNH 98639); Ucayali, Boca Río Urubamba (AMNH 76031); Ucayali, Lagarto (AMNH 76579).

^b C1 to M2.

^c Hershkovitz (1961: table 1) reported a value of 13.5 mm for this dimension, an obvious lapsus.

ETHNOBIOLOGY: Few Matses have ever seen the short-eared dog, which is either called mayanën opa (“demon’s dog”) or nimëduk opa (“jungle dog”). These are never considered synonyms; rather, there is intervillage variation whereby one of the names is used and the other is considered incorrect. Short-eared dogs are sometimes confused with jaguarundis, some informants believing them to be the same species. Some Matses comment that they would seem to make nice pets, but they are never raised as such.

Touching or even looking at a short-eared dog is likely to make one’s children ill with high fever and intense thirst. As with most very rare animals, an encounter with a short-eared dog is interpreted as an omen that someone in the person’s village or a close relative will soon die.

MATSES NATURAL HISTORY: Short-eared dogs look very much like domestic dogs, but with small ears. One can easily mistake one for a domestic dog. Their footprints are like a dog’s footprints.

Short-eared dogs are found in all habitats. They frequent mineral licks to look for prey, and frequent palm swamps to eat swamp-palm (*Mau-*

ritia flexuosa [Arecaceae]) fruits, and to look for game. They den in hollow logs, holes in the ground, or undercut banks of streams. They are diurnal and are most commonly encountered in pairs or groups of three, but they are also frequently solitary. They give birth to as many as three pups, which may be found abandoned in their dens (in hollow logs or holes in the ground), presumably while the mother is out hunting. (According to one informant, the inside of the hollow log in which pups were found was scraped smooth.) They whine and snarl. They do not bark like domestic dogs.

Short-eared dogs eat pacas, agoutis, acouchies, and spiny rats, which they chase down or dig out of their burrows or nests. They also eat ground-dwelling birds like white-throated tinamous, wood-quails, and trumpeters. They dig jungle frogs out of their burrows. They eat bata tree (*Pseudolmedia* spp. and ?*Maquira* spp. [Moraceae]) fruits and the mesocarp of swamp-palm (*Mauritia flexuosa*) fruits.

REMARKS: Short-eared dogs are among the least known of all canid species, and even the Matses have little to say about them. Most of the natural history observations in the interviews we

TABLE 10
Cranial Measurements (mm) of Adult Specimens of *Speothos venaticus*
from Eastern Peru^a

	AMNH 76806	AMNH 98559	AMNH 98560	AMNH 76035	AMNH 98558
Sex	female	female	female	male	male
Condylobasal length	136.1	125.8	129.8	136.6	131.8
Nasal length	37.6	35.9	34.7	42.3	36.4
Least interorbital breadth	28.7	26.4	27.8	29.0	26.3
Least postorbital breadth	24.4	23.9	23.9	22.7	22.3
Zygomatic breadth	79.4	74.0	79.8	80.3	73.7
Maxillary tooththrow ^b	50.3	46.6	49.0	50.8	48.9
Length P4	14.4	14.0	13.6	14.8	14.9
Width P4	8.0	7.4	7.8	8.4	7.6

^a Loreto, Iquitos (AMNH 98558, 98559, 98560); Ucayali, Boca Río Urubamba (AMNH 76035); Ucayali, Lagarto (AMNH 76806).

^b C1 to M1.

compiled about this species agree with the literature reviewed by Pitman and Williams (2004), notably with respect to diurnality, denning sites, and diet. However, whereas those authors reported fish to be the most frequent item found in short-eared dog scat from their study site in southern Peru, the Matses do not mention fish among the items consumed by *Atelocynus* in the Yavari-Ucayali interfluvium, where only terrestrial prey and fruit are said to be eaten. The Matses observation that short-eared dogs eat the fruit of *Mauritia flexuosa* (not mentioned as a food plant by Pitman and Williams, 2004) is corroborated by a recent report based on a camera-trap survey at a Colombian locality by Acevedo-Quintero and Zamora-Abrego (2016).

Speothos venaticus (Lund, 1842)

Figures 12B, 13B

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Chonco (Amanzo, 2006), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Bush dogs are unmistakable in external appearance (Emmons, 1997), so sight

records from competent observers are reliable evidence for local occurrence.

ETHNOBIOLOGY: The bush dog has only one name, achu kamun. The term achu (“red howler monkey”) is used as a modifier of the term kamun (“feline/canine”) based on the similarity in pelage coloration of bush dogs and howler monkeys.

Bush dogs are not eaten. The Matses often comment that they would seem to make nice pets, but they almost never raise them due to the belief that they will make children fall ill. One informant knew of a single case in which a woman found a bush dog pup and raised it; when it became an adult it hunted together with Matses hunting dogs.

The spirits of bush dogs can make children ill when a Matses looks at a bush dog or kills one. If a hunter does so, he will collect medicinal plants to bathe his children with, to prevent them from becoming ill. Among the symptoms of being made ill by a bush dog (or a feline or other wild canine) are a high fever and intense thirst.

MATSES NATURAL HISTORY: The head and forequarters of bush dogs are orangeish. Their tails and hindquarters are black or blackish. Bush dogs are smaller and fatter than domestic dogs.

Bush dogs are more commonly encountered than short-eared dogs (but there are many Matses who have never seen one). They are found in all types of habitats.

They den together in hollow logs or in large holes in hillsides. Sometimes they dig depressions in the ground to sleep there one night.

Bush dogs are diurnal. They hunt as a group searching for the spoor of their prey. They search for pacas, sniffing for their scent along large or small streams. When they find paca spoor, all the members of the pack begin to follow it. When one dog finds the paca's burrow, it calls the other dogs. A large male dog enters the burrow. The paca then dashes out of one of the other exits of its burrow, and all the dogs chase it down, barking. The paca typically goes to a stream, follows it to a deep bend, plunges in, and holds its breath underwater. The bush dogs arrive and the leader barks out orders for the others in the pack to surround the deep stream bend ready to pounce on the paca when it comes out. While some wait upstream, others downstream, and some on the bank above the stream bend, one or two of the bush dogs plunge into the water and feel around for the paca underwater. When one of the dogs touches it underwater, the paca emerges and flees to a shallow section of the stream, where the waiting dogs pounce on it. They kill it together, biting its neck and other vital parts, and they eat it together after pulling it to the bank. They eat every part of it.

When bush dogs find a greater long-nosed armadillo in its burrow, one of them enters the burrow, follows the armadillo into its retreat tunnel, kills it, and drags it out of the burrow to eat it with the other bush dogs. When they find a nine-banded long-nosed armadillo in a leaf nest on the ground, they surround the nest, and one of the bush dogs jumps on it (to make the armadillo come out). The other dogs then pounce on the armadillo and kill it, or they may have to chase it down to kill it.

When bush dogs find an agouti, they chase it down barking until it seeks refuge in a hollow log or a hole in the ground. Then, one of the dogs

goes into the hole while the others wait at the opening. If the log or the hole in the ground has more than one opening, one dog goes into each hole. Then they kill the agouti in the log or hole, or they kill it as it exits. Bush dogs rest after eating, lying in a dry spot for a while, before hunting again. Or they may first drink water at a stream.

Bush dogs travel in packs of three to eight individuals; five is the typical size of a pack. The pack has a male leader. Both males and females hunt.

(The Matses do not know of any animal that eats bush dogs, although they imagine a jaguar would do so.)

Bush dog barks are more high-pitched than those of domestic dogs.

Bush dogs eat pacas, long-nosed armadillos, agoutis, acouchies, and spiny rats. They do not eat larger mammals like peccaries. They also eat white-throated tinamous, smaller species of tinamous, wood-quails, and other terrestrial birds. They dig jungle frogs out of their burrows to eat them.

REMARKS: Bush dogs have long been something of a zoological enigma, with their small size, highly developed social behavior, hypercarnivorous dentition, absurdly short legs, partially webbed feet, diurnal activity, and a remarkable ability to swim underwater (Sheldon, 1992; Beisiegel and Zuercher, 2005). This odd combination of traits seems all the more extraordinary by comparison with those of closely related *Chrysocyon brachyurus* (the maned wolf; Perini et al., 2010), a much larger, solitary, omnivorous, long-legged, crepuscular/nocturnal, and strictly nonaquatic species. Attempts to explain bush dog morpho-behavioral traits have included seemingly implausible suggestions that packs of these diminutive, dachshundlike animals can run down and kill much larger prey (e.g., peccaries, deer, and even tapirs; Zuercher et al., 2004); that their short legs and hypercarnivorous dentition are the nonadaptive consequence of phyletic dwarfing (Wayne and O'Brien, 1987); that their partially webbed feet are somehow useful for walking on soft soil near streams (Beisiegel and Zuercher, 2005); and that they might cache their food underwater (Kleiman, 1972). A defining aspect of the literature on this

species is that most information about diet and behavior is derived from captive studies; few biologists have seen bush dogs alive in the wild for more than a few minutes at a time (e.g., Deutsch, 1983; Peres, 1991; Strahl et al., 1992; Aquino and Puertas, 1997).

Matses observations about bush dogs—which agree strikingly with reports by Tate (1931) and Cabrera and Yepes (1940) that were also derived from indigenous sources—convincingly account for many unusual aspects of the bush dog phenotype. In particular, their dachshundlike morphology⁶ is clearly adaptive for entering burrows or hollow logs to drag or flush their inhabitants (armadillos, pacas, agoutis) to the surface. Their cooperative social behavior and swimming abilities may be especially important for hunting pacas, whose streamside burrows have multiple exits, and whose evasive behavior often includes hiding underwater (Tate, 1931; Cabrera and Yepes, 1940; personal obs.). Although Matses accounts of bush dog hunting behavior include obvious anthropomorphisms, the ambush tactics they describe are plausible in the context of hunting behavior previously reported for other social canids (e.g., wolves and African hunting dogs). From these accounts, and from previously published anecdotes and captive observations, *Speothos venaticus* seems best characterized as a pack-hunting diurnal predator anatomically and behaviorally specialized to extract medium-sized (ca. 3–12 kg) mammalian prey from burrows, and to pursue escaped prey (especially pacas) into water.

Felidae

Five species of felids are definitely known to occur in the Yavari-Ucayali interfluve, including the ocelot (*Leopardus pardalis*), the margay (*L. wiedii*), the jaguar (*Panthera onca*), the puma (*Puma concolor*), and the jaguarundi (*Pu. yagouaroundi*). Most Matses hunters recognize and name

all five of these confirmed local species of wild felids, which they include in the folk-taxonomic category bēdi. The term bēdi is polysemous: it can refer to the jaguar by default, to all felids (as a group name, or folk genus), or to any of the five local species of cats. However, wild dogs are also included in the bēdi group, and some Matses likewise include the tayra (*Eira barbara*). Bēdi also means “spotted” (or having a diamond pattern of spots), and seems to be a relatively new coinage (as it does not occur with the meaning of “jaguar” in other Panoan languages). Note that, despite this implication of spotting, bēdi can refer to animals with uniform coloration, like the jaguarundi, the short-eared dog, etc. Domestic cats, introduced to the Matses by American evangelical missionaries sometime after 1969, are called kidi kidi (an obvious corruption of “kitty kitty”), and they are also considered to be a type of bēdi.

Some Matses hunters claim that there is a sixth local wild felid species that they call cachu bēdi (the meaning of the word cachu is unknown), which is described as a very small ocelot. The Matses description suggests the oncilla (*Leopardus tigrinus*), but other hunters consider the cachu bēdi to be a synonym for the margay. Although *L. tigrinus* was reported from Jenaro Herrera by Pavlinov (1994), we have not examined the voucher specimen (in Moscow), and in the absence of other records of this species from northeastern Peru (Nascimento and Feijó, 2017), we are reluctant to include it here.

Matses interviews provide a unique source of information about the diets of sympatric Amazonian felids, which we have extracted from their accounts of both prey and predator taxa and tabulated for ease of interspecific comparisons (table 11).

Leopardus pardalis (Linnaeus, 1758)

Figure 14D

VOUCHER MATERIAL (TOTAL = 5): Boca Río Yaquerana (FMNH 88887), Nuevo San Juan (MUSM 11170, 13150), Orosa (AMNH 73762), Quebrada Esperanza (FMNH 88888).

⁶ Dachshunds (from German *Dachs* [badger] + *Hund* [dog]) were originally bred and trained to enter the subterranean burrow systems of badgers.

TABLE 11

Prey Eaten by Sympatric Felids according to Matses Informants^a

	<i>Leopardus pardalis</i>	<i>Leopardus wiedii</i>	<i>Panthera onca</i>	<i>Puma concolor</i>	<i>Puma yagouaroundi</i>
Opossums	X	X	X		X
<i>Priodontes</i>			X		
<i>Dasypus</i> spp.			X	(X)	
Sloths			X		
<i>Tamandua</i>			X	(X)	
<i>Myrmecophaga</i>			X		
Primates			X	(X)	
<i>Eira</i>			(X)	(X)	
<i>Nasua</i>			X	(X)	
<i>Tapirus</i>			X	no	
<i>Pecari tajacu</i>			X	X	
<i>Tayassu pecari</i>			X	X ^b	
<i>Mazama</i> spp.			X	X	
<i>Hydrochoerus</i>			X		
<i>Cuniculus</i>	X	X	X	X	no
<i>Dasyprocta</i>	X	X	X	X	X
<i>Myoprocta</i>	X	X			X
Other large rodents			X ^c		
<i>Proechimys</i> spp.	X	X			X
Squirrels		X			
Other small rodents		X			
Tinamous	X	X	X		X ^d
Other birds	X	X			X ^e
Bird eggs					X
Caimans			X	X	
Tortoises			X		
River turtles			X	X	
River turtle eggs			X		
Lizards	X	X			X ^f
Frogs	X	X		X	
Fish			X		
Carrion					X
Fruit			X	X	X

^a Table entries: X, mentioned as prey in interviews about cat species; (X), mentioned as prey in interviews about prey species (Voss and Fleck, 2011, in preparation); "no," explicitly stated not to be prey.

^b Only juvenile white-lipped peccaries are said to be eaten by pumas.

^c *Coendou* and *Dinomys*.

^d Several species of tinamous are mentioned.

^e Several species of nontinamid birds are mentioned.

^f Several lizard species are mentioned.

TABLE 12

Measurements (mm) and Weights (g) of Adult Specimens of *Leopardus pardalis* and *L. wiedii* from the Yavari-Ucayali Interfluve

	<i>L. pardalis</i>					<i>L. wiedii</i>
	AMNH 73762	FMNH 88888	MUSM 11170	FMNH 88887	MUSM 13150	FMNH 88889
Sex	female	female	female	male	male	male
Head-and-body length	—	730	608	755	687	543
Length of tail	—	323	362	330	331	355
Hind foot	—	155	163	166	150	134
Ear	—	55	51	57	62	47
Weight	—	—	9200	—	9150	—
Condylobasal length	124.1	123.3	122.7	127.6	125.2	91.8
Nasal length	35.4	34.5	32.9	32.3	33.5	22.8
Least interorbital breadth	26.8	23.2	23.9	25.0	22.8	16.8
Least postorbital breadth	35.4	27.9	32.7	26.8	27.5	34.3
Zygomatic breadth	88.1	85.0	88.0	88.6	87.0	64.7
Maxillary tooththrow ^a	41.3	41.7	41.6	41.0	42.9	28.9
Length P4	15.1	16.6	16.2	15.6	17.0	11.6
Width P4	7.4	8.6	7.8	8.3	9.2	6.3

^a From C1 to M1.

OTHER INTERFLUVIAL RECORDS: Jenaro Herrera (Pavlinov, 1994), Quebrada Pobreza (Escobedo-Torres, 2015), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: The ocelot (*Leopardus pardalis*) and the margay (*L. wiedii*) are gaudily streaked-and-spotted small cats with reversed nuchal fur (the hairs of the nape pointing forward rather than backward; Pocock, 1941).⁷ Ocelot specimens from northeastern Peru are consistently larger than margays in most measured dimensions (table 12), and these species can also be distinguished by external and cranial proportions (see the account for *L. wiedii*, below).

Numerous subspecies of the ocelot are currently recognized as valid (e.g., by Wozencraft, 2005), but it is not known whether any represent taxonomically meaningful subdivisions. The last specimen-

based revision was Pocock's (1941), who assigned all the Peruvian material he examined to the subspecies *L. p. aequatorialis* (Mearns, 1902), the type locality of which is in the Pacific lowlands of northern Ecuador. Although Eizirik et al. (1998) suggested that several phylogeographic partitions are present within *L. pardalis*, their study did not include any western Amazonian sequence data, so the assignment of our material to any of the phylogroups they recognized is problematic. In the absence of any compelling reason for trinomial nomenclature, it seems pointless to speculate about the subspecific assignment of our material.

ETHNOBIOLOGY: The Matses name for the ocelot is bēdimpi, the term for jaguar/feline with the diminutive suffix mpi. It has no other names and no varieties are distinguished by the Matses. The term bēdimpi can also be a more general term that includes the ocelot, the margay, the jaguarundi, and the house cat.

The ocelot is of no economic importance to the Matses. It is not eaten or kept as a pet. The

⁷ The oncilla (*Leopardus tigrinus*), if it really does occur in our region (see above), has unreversed nuchal fur (Nascimento and Feijó, 2017).

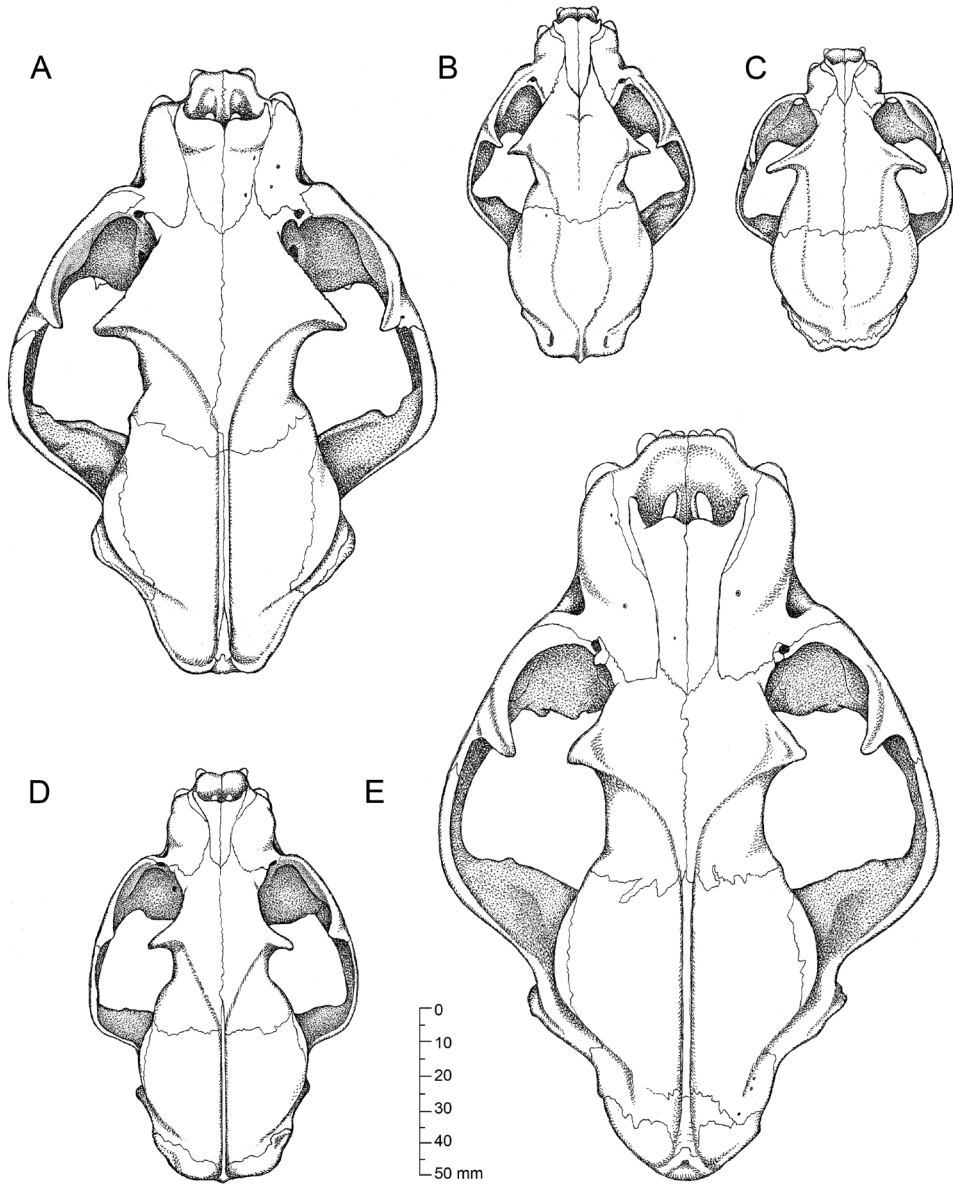


FIG. 14. Adult skulls of five sympatric felid species, illustrating taxonomic differences in size and shape: *Puma concolor* (A, AMNH 73221), *Pu. yagouaroundi* (B, AMNH 215137), *Leopardus wiedii* (C, AMNH 74428), *L. pardalis* (D, MUSM 13150), *Panthera onca* (E, AMNH 98683). All illustrated specimens are from western South America, but only MUSM 13150 is from the Yavarí-Ucayali interfluve. Old adult male skulls of *Pa. onca* and *L. pardalis* can be substantially larger and proportionately wider than the young adults illustrated here.

Matses are not afraid of ocelots, because they are too small to attack humans. However, ocelots enter villages to eat chickens in their coops at night, and they prowl around near villages in the daytime to attack free-ranging chickens on the outskirts of clearings. Once an ocelot kills and eats a chicken, it keeps coming back to get more. When an ocelot becomes a pest in this way, the Matses hunt it down with dogs.

Matses with young children avoid having any contact with or even looking at ocelots, lest the ocelot's spirit make their children ill (see the ethnobiology entry for *Puma concolor* for details on symptoms and treatment of contagion by felids).

MATSES NATURAL HISTORY: The ocelot is small and spotted.

The ocelot is found in any type of habitat, including upland and floodplain forest, and primary and secondary forest. It mainly walks on the ground, but also often climbs trees.

The ocelot is diurnal and nocturnal. It walks following streams, sniffing as it hunts. Or it lies in wait for prey on the ground or sitting up in a tree. It lies on fallen trees in blowdowns to warm itself in the sun. It sleeps on trees that lean somewhat horizontally. It defecates in habitats called "demon's swiddens" that have an open understory.⁸

The ocelot is solitary. Sometimes two are seen together, perhaps male and female. The ocelot gives birth to two kittens in a hollow log or in a hole in the ground.

During the day ocelots kill agoutis and acouchies, and at night they kill pacas. As an ocelot walks along a small stream at night it may find and catch a paca that is eating aquatic snails. Then it drags the paca to dry land to eat it. It may dig into an acouchy burrow when it chases one into its burrow. The ocelot stalks its prey crouching, as it slowly advances, and then pounces on

the quarry, grabs it with its claws, and bites its head. Ocelots go to drink water repeatedly while eating. An ocelot will stash part of the kill, if it is a large animal.

The ocelot growls when it is taking prey.

Ocelots eat pacas, agoutis, acouchies, spiny rats, opossums, tinamous, other terrestrial birds, lizards, and jungle frogs (*Leptodactylus* spp. [Leptodactylidae]).

REMARKS: Matses observations about ocelots largely overlap with the scientific literature on this common and widespread species, notably agreeing with the results of radio-tracking studies in rainforest habitats (Emmons, 1988; Aliaga-Rossel et al., 2006) with respect to diel activity pattern, killing behavior, and caching of large prey. Curiously, Matses observations suggest that twinning is common for ocelots, whereas most captive litters consist of a single young (Havlanová and Gardiánová, 2013).

The Matses list of ocelot prey closely resembles that obtained by analyzing scat at another Peruvian rainforest site (Emmons, 1987), but not with known ocelot diets from other rainforested regions. In particular, the Matses list omits sloths, which are said to be commonly eaten by Central American ocelots (e.g., by Moreno et al., 2006), and primates, which are often eaten by ocelots in southeastern Brazil (Bianchi and Mendes, 2007). To the best of our knowledge, no previous dietary study has reported that ocelots eat frogs. The omission of any mention of ocelot frugivory by our informants seems noteworthy by contrast with lists of fruits eaten by jaguars, pumas, and jaguarundis in Matses accounts of those species (see below).

Leopardus wiedii (Schinz, 1821)

Figure 14C

VOUCHER MATERIAL (TOTAL = 1): Boca Río Yaquerana (FMNH 88889).

OTHER INTERFLUVIAL RECORDS: Nuevo San Juan (this report), Río Yavarí-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

⁸ "Demon's swiddens" (*mayanën sebad*; Fleck, 1997) are habitats dominated by the myrmecophilous subcanopy tree *Duroia hirsuta* (Rubiaceae) whose roots secrete an apparently allelopathic compound (Page et al., 1994), and whose ant mutualists attack the foliage of other plant species with formic acid (Frederickson, 2005).

IDENTIFICATION: The only available margay specimen from the Yavari-Ucayali interfluvium consists of the skin and skull of a young adult male (FMNH 88889). Although margays are much smaller than ocelots on average, large specimens of margays are sometimes confused with small specimens of ocelots; fortunately, these species are readily distinguished by tail length and cranial proportions (Pocock, 1941). Based on collectors' measurements (table 12), the ratio $LT/HBL \times 100$ equals 65% for our margay voucher versus 44%–48% for three adult ocelot vouchers.⁹ Additionally, the tanned skin of FMNH 88889 can be folded to show that the tail is substantially longer than the hind leg (a useful field character mentioned by Emmons, 1997), whereas the tail is substantially shorter than the hind leg on the ocelot skins that we examined.

The postorbital constriction is much wider than the interorbital constriction in *Leopardus wiedii* by contrast with *L. pardalis*, whose postorbital and interorbital constrictions are more nearly equal (Pocock, 1941). For FMNH 88889, the postorbital constriction is approximately twice as wide as the interorbital constriction ($LPB/LIB \times 100 = 204\%$), whereas this ratio ranges from 118% to 137% among our four adult ocelots. In dorsal view, margay skulls have larger orbital fossae than temporal fossae, whereas ocelots have larger temporal than orbital fossae. Lastly, margay skulls usually lack a sagittal crest, whereas most fully adult ocelots have well-developed sagittal crests. These cranial differences are visually conspicuous (fig. 14).

The last comprehensive revision of *Leopardus wiedii* was Pocock's (1941), which restricted the nominotypical form to southeastern Brazil, Argentina, and Paraguay; in his classification, western Amazonian margays were referred to *L. w. pirrensis* (Goldman, 1920), with type locality in eastern Panama. However, *amazonicus* Cabrera, 1917, based on a specimen from Tabatinga, Brazil, would appear to be the appropriate

name if western Amazonian populations were judged to be taxonomically distinct from other margays (Oliveira, 1998b).

ETHNOBIOLOGY: The margay is called *těstuk mawekid*, which literally means "one that lays under epiphytes" owing to its habit of lying on tree limbs under the cover of large-leaved arboreal plants. The margay is sometimes called *bëdimpi* (ocelot) by observers unfamiliar with the species, but more knowledgeable Matsigenka hunters say that this usage is incorrect.

The margay is of no economic importance to the Matsigenka. Only rarely does one approach the outskirts of a Matsigenka village to stalk chickens in the daytime. Unlike ocelots, margays do not raid chicken coops at night.

Matsigenka with young children avoid having any contact with or even looking at margays, lest the margay's spirit make their children ill (see the ethnobiology entry for the puma for details on symptoms and treatment of contagion by felids).

MATSIGENKA NATURAL HISTORY: The margay is small and spotted. It has a long tail.

The margay is found in any habitat, including floodplain and upland forest. It is more frequently found in primary forest than in secondary forest (e.g., sites of abandoned swiddens). It is more rarely encountered than the ocelot.

The margay spends much of its time lying up in the trees, on tree branches or on upward-spiraling lianas. It walks up inclined trees and lies on the inclined trunk waiting for prey to pass by underneath. As it lies on a branch, tree, or liana, it hides under epiphytes or thick vegetation. It also lies in the open on branches or inclined tree trunks to rest after eating and to sleep. It also hunts by searching for prey on the ground, but it does not lie down on the ground.

The margay is solitary. It gives birth to two kittens in a hollow log on the ground or in a burrow, not up in the trees.

A margay may pounce on a tinamou that passes under the tree where the cat is waiting. Margays walking on the ground also kill tinamous, pouncing on them from far away. At night margays find tinamous sleeping on low perches.

⁹ A fourth voucher (MUSM 11170), with an improbably longer tail, may have been mismeasured in the field.

Margays pluck the feathers from tinamous before eating them. Margays kill other animals in the same ways (from ambush and by active diurnal and nocturnal hunting).

The margay growls when it is taking prey.

The margay eats pacas, agoutis, acouchies, spiny rats, other rats and mice, squirrels, common opossums, four-eyed opossums, and mouse opossums. It also eats white-throated tinamous (*Tinamus guttatus*), great tinamous (*T. major*), smaller tinamous (*Crypterellus* spp.), other terrestrial birds, and small arboreal birds. It also eats lizards, tree frogs, and jungle frogs (*Leptodactylus* spp.).

REMARKS: Matses observations broadly agree with the scattered scientific literature on this small cat (reviewed by Oliveira, 1998b), notably with respect to its arboreal habits, denning behavior, and the wide range of prey taken. Matses accounts of arboreal ambushing versus active terrestrial searching, however, suggest a characteristic foraging strategy that is not described as such in the literature, nor does the literature describe several other details of margay predatory and feeding behaviors (e.g., feather-plucking) mentioned by our informants.

Panthera onca (Linnaeus, 1758)

Figure 14E

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Nuevo San Juan (this report), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Jaguars are unmistakable externally (Emmons, 1997), and their skulls can be distinguished cranially from those of pumas (the only other large Amazonian cat) by non-overlapping measurements (e.g., condylobasal length, zygomatic width; Husson, 1978); therefore, identification is not problematic. Rumors have long existed, however, of large Amazonian

cats thought (by some) to represent one or more undescribed species of *Panthera*. Recent morphometric analyses of two skulls from eastern Peru alleged to represent such cryptic taxa suggest that they are simply jaguars, albeit perhaps with unusual coat-color phenotypes (Naish et al., 2014). Size variation among the eastern Peruvian material we examined is bracketed by a small female from the Río Cenepa (AMNH 98679) and a large individual (sex unrecorded but probably male) from the Río Aguaytía (AMNH 147513): condylobasal length, 190.5–240.5 mm; least interorbital breadth, 39.8–50.3 mm; least postorbital breadth, 42.4–50.4 mm; zygomatic breadth, 148.9–174.1 mm; length P4, 25.6–30.2 mm.

Numerous subspecies of the jaguar have long been recognized (e.g., by Wozencraft, 2005). The western Amazonian population was referred to the nominotypical form in the last specimen-based revision (Pocock, 1939), but jaguar “subspecies” seem not to correspond either to mtDNA phylogeographic units (Eizirik et al., 2001) nor to geographic variation in cranial measurements (Hoogesteijn and Mondolfi, 1996), so it is not clear that any purpose is served by a trinomial nomenclature of these cats.

ETHNOBIOLOGY: In addition to the term *bëdi*, the Matses have three archaic synonyms that refer to the jaguar. The first, *kamun* (an unanalyzable term commonly encountered among other Panoan languages), like *bëdi*, can also refer collectively to members of the category that includes all felids, wild canids, and the tayra. A second archaic synonym, *winsad*, specific to the jaguar, also means “frightening.” The third archaic synonym, *chuisad*, also specific to the jaguar, is not analyzable and has no other current meaning. In the language used in the Matses’ *komok* ceremony, the jaguar is called *mëndu*, a monomorphemic term that also designates the domestic dog.

Because *bëdi* can refer to any felid, or can be used generically, the term *bëdidapa* (literally “large jaguar/felid”) is used to specify the jaguar, although it can also refer to a Matses-recognized variety of the jaguar. In fact, there are two over-

differentiated varieties: bēdidapa and wispan kamun ("jaguar of the stars," in reference to its particular spotted pattern). The wispan kamun variety is said to be fiercer and to have a larger head and a smaller body than the typical variety. Interestingly, melanistic jaguars seem to be absent in Matses territory. Men who have travelled outside Matses territory have heard of them, but the Matses have no names for them.

Jaguars are not currently of any economic importance to the Matses. They are not eaten, nor are they kept as pets. Several decades ago some Matses hunters participated in the illegal fur trade, trapping jaguars and other cats in box traps made from split palm logs and baited with capuchin monkey meat.

All Matses (especially women and children) fear jaguars, which often stalk people without attacking them. Although jaguars usually run away when they are encountered, occasionally a jaguar will bound toward a person. When they do so, the animal can sometimes be scared off by yelling loudly or by pounding on a buttress root. However, these tactics do not always work, and many Matses hunters tell of having to defend themselves with shotguns, arrows, or sticks. There have been a few isolated cases of jaguars killing men, women, and children in the forest, and there have been two instances within the last 40 years of a jaguar entering a Matses village and attacking people. Jaguars often kill Matses hunting dogs.

The Matses believe that if one kills, touches, or even looks at a jaguar, the spirit of the jaguar can make their child ill. The principal symptoms of jaguar-induced illness are a fever and constant thirst for water (jaguars are characterized by the Matses as drinking water constantly while eating meat). Several plants known as "jaguar/felid" medicine can be used to cure jaguar sickness. The child is bathed with an infusion of their leaves. If hunter has had contact with or seen a jaguar, he will collect these medicinal plants to treat his children prophylactically.

The Matses have two clans, the jaguar clan and caterpillar clan. If a jaguar whines within hearing range of a Matses household, the Matses

say that it is announcing that someone of the jaguar clan will soon die.

MATSES NATURAL HISTORY: Jaguars are large, spotted, and have large feet and large canines.

Jaguars are mostly terrestrial, but they also climb trees. Although jaguars can be found in any habitat, including upland forest and floodplain forest, they are most often encountered along rivers and streams. Another favorite habitat is forest whose understory is dominated by the stemless palm *Attalea racemosa* (according to one informant, the palms provide cover, and this habitat is otherwise free of obstructive undergrowth). Jaguars are rarely encountered, but their tracks on river beaches and claw marks on trees are seen frequently. They are especially common on the banks of the Yaquerana (upper Río Yavará).

Jaguars are nocturnal and diurnal. They travel very far, to other large streams. They spend much of their time walking slowly, searching for prey, or waiting to ambush prey. They sleep in hollow logs, hollow trees, cavities in the banks of stream headwater gullies, or between buttress roots, but not in the open. A jaguar does not sleep in the same place on consecutive nights, unless it is a female that has just given birth to cubs. However, a jaguar may return to a sleeping place after several days or more. Jaguars rest up in trees, in a sunny spot, or in or beside a treefall. Jaguars scratch trees and fallen logs, leaving claw marks that the Matses often find. Tonnad trees (species of Myristicaceae) are those most frequently found with jaguar claw marks.

Jaguars are solitary. The female gives birth to two cubs in a hole in a stream headwater gully or in a hollow log. At the entrance of the hollow log where it gives birth, the ground is swept clear. The female brings meat back to the den for the cubs to eat.

Jaguars wait beside tapir trails and follow tapir paths. When the tapir comes walking by, the jaguar pounces on it, grabs it with its claws, bites the back of its head and eats it. If the tapir runs, the jaguar chases it and grabs it. The pursued tapir may plunge into a stream, but the jaguar

can kill it while it is still submerged, and will eat it right in the streambed. Jaguars also wait for tapirs and other prey at mineral licks. The jaguar also walks where there are no paths. It stalks collared peccaries without rustling the leaves as it walks. It captures the peccary by grabbing it with its claws and biting its head. It does likewise with deer. It ambushes monkeys up in trees. It kills most of its prey by biting the head.

After killing an animal, the jaguar begins to eat it right away. It eats the intestines first and laps up the blood. If the prey is not a small animal, the jaguar will hide part of the kill, covering it with leaf litter at the base of a tree. It may hide the meat in more than one stash. It drinks a lot of water after eating its fill of meat. After drinking, it lies down to rest near its stash. After resting it eats some more. Before it is all done, it hunts again. If it does not kill anything else, it comes back to eat more. It may return to eat the bones last.

The jaguar growls when it attacks. It has a very loud whining roar that can be heard from far away, day or night.

The jaguar eats tapirs, deer, collared and white-lipped peccaries, giant anteaters, tamanduas, giant armadillos, long-nosed armadillos, sloths, capybaras, pacas, pacaranas, agoutis, porcupines, coatis, monkeys, common opossums, tinamous, tortoises, river turtles, river turtle eggs, caimans, and fish. It commonly eats the mesocarp of isan palm (*Oenocarpus bataua* [Arecaceae]) fruits, but it does not eat most dicot tree fruits. Two types of dicot tree fruit that it does eat are those of the bata tree (*Pseudolmedia* spp. [Moraceae]) and the dadain tree (*Clarisa racemosa* [Moraceae]).

REMARKS: Matses observations about jaguars are consistent with an emerging consensus about the distinctive trophic role of these top predators in Amazonian ecosystems. Whereas jaguar diets in subtropical and semiarid landscapes broadly overlap those of sympatric pumas (Taber et al., 1997; Núñez et al., 2000), Amazonian jaguars often eat armored reptiles and large mammals that are seldom taken by pumas. Such prey are thought to be uniquely vulnerable to jaguars

because these cats have adaptations for durophagy that allow them to bite through reptilian armor and heavily ossified mammalian skulls (Schaller and Vasconcelos, 1978; Emmons, 1989; Miranda et al., 2016). Other prey commonly taken by Amazonian jaguars, but not (or less often) by other sympatric cats, include aquatic and semiaquatic taxa that jaguars hunt by patrolling river beaches and lakeshores (Emmons, 1987; Silveira et al., 2010).

The prey species that Matses interviewees report to be eaten by jaguars but not by pumas—notably giant armadillos, giant anteaters, tapirs, adult white-lipped peccaries, capybaras, tortoises, river-turtle eggs, and fish (table 11)—exemplify both aspects of this hypothetically distinctive niche (defined by durophagy and riparian/aquatic foraging). However, Matses descriptions of jaguar behavior also extend our knowledge of the remarkable predatory abilities of this species, which has not previously been reported to kill tapirs under water. That jaguars routinely patrol trails is well known, but the Matses say that jaguars also hunt in trailless parts of the forest (contra Weckel et al., 2006). An apparently novel observation is occasional frugivory, which seems not to have been reported in any previous analysis of jaguar diets.

Puma concolor (Linnaeus, 1771)

Figure 14A

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Pumas are externally distinctive (Emmons, 1997), so sightings by competent observers are not problematic; cranial measurements of Amazonian specimens are provided in Husson (1978: table 51). Although the nominal taxon *borbensis* Nelson and Goldman, 1933, is based on a western Amazonian type, all tropical South American pumas are now referred to the nominotypical subspecies (*Puma concolor*

concolor) following Culver et al.'s (2000) analysis of mtDNA sequence data.

ETHNOBIOLOGY: The Matses name for the puma, *bēdi piu*, literally means “red(dish) jaguar/feline” (the color term *piu* can refer to red, orange, pink, yellow, or reddish brown). All Matses hunters recognize at least two subtypes of puma, one of which is known by the same term as the superordinate category, *bēdi piu* (an example of multilevel polysemy). The second subtype of puma is called *sipidin*. The *sipidin* subtype is characterized principally by having a white muzzle. Although the term *sipidin* is not completely analyzable, it appears to contain the term *sipi* (“tamarin”), perhaps because tamarins have white muzzles. The *sipidin* variety is said to be fierce and to attack people, whereas the *bēdi piu* variety runs away when it sees people. Some speakers recognize a third variety they call *bēdi piudapa* (“large puma”), which they say is the most rarely encountered variety.

Pumas are of no economic importance to the Matses. They are not eaten or kept as pets. Despite the purported aggression of the *sipidin* variety, in the last 40 years there has been only one instance of a Matses being attacked by a puma; although the victim was able to fight the cat off with a stick, he suffered serious wounds. Pumas often kill Matses hunting dogs.

The Matses believe that if one kills, touches, or even looks at a puma, the spirit of the puma can make one's child ill. A child can also be made ill by seeing or touching a puma. The principal symptoms of puma sickness are identical to those of jaguar sickness: a high fever and constant thirst for water. The cure for such illness is several plants known as “puma medicine,” and along with these plants, others known as “jaguar/felid” medicine are also collected. The child is bathed with an infusion of the leaves. If a hunter has had contact with or seen a puma, he will collect these medicinal plants to treat his children prophylactically. Contagion and symptoms are the same for all the wild felids and wild canines, with the exception that jaguars and pumas are more likely to make children ill, and the illness

is more likely to result in death. In any case, the spirits of the smaller wild felids and canids are more likely to make children ill (when the animal is touched or seen) than are the spirits of game animals. Their propensity to cause illness is the main reason why wild felids and canids are not kept as pets. Treatment for contagion by smaller felids and the canids is the same as for the puma: one collects medicinal plants specific to species suspected to have caused the illness along with “jaguar/felid” medicinal plants.

MATSSES NATURAL HISTORY: The puma is reddish, the color of a red brocket deer. Its undersides are light colored. It is smaller than a jaguar and has a large tail. Its spoor can be distinguished from that of the jaguar because the marks made by the toes are further from the impression of the central paw pad in puma tracks than in jaguar tracks.

The puma uses all rainforest habitats, including upland forest and floodplain forest. It is rarely seen.

The puma is nocturnal and diurnal. It walks slowly looking for prey with its tail hanging down close to the ground. It also sits up in trees, on large spiraling lianas, or on the ground waiting for prey to pass by. It waits at mineral licks for deer and peccaries. The puma sleeps day or night in cavities in the ground or in hollow trees or other sheltered places. It does not sleep in same place every night. If hunting dogs chase it, the puma may climb up a tree. Or, especially if there is only one dog, the puma may kill a dog. It does not kill a dog quickly, but rather keeps it alive for a while, making it whine.

The puma is solitary. Occasionally two are seen together. It gives birth to two cubs in holes in stream headwater gullies and in hollow logs. It goes out to hunt and eat and then comes back to the den to suckle its young. When they get older, it brings meat back to the den for them. Once they get strong, it walks around with the cubs. Before they are fully grown they leave the mother, one by one, and begin to hunt for themselves.

The puma stalks and pounces on deer, collared peccaries, or agoutis from a distance, grabs

the prey with its claws, and bites the back of its head. It eats the liver and the rest of the viscera first. It continually goes to drink water while it eats. When it gets full, it stashes part of its prey, covering it with leaves, and lies down to rest nearby. It hunts again while there is still stashed meat left. Sometimes vultures find its stashed prey and finish it off. If the puma does not kill another animal, it comes back and eats the bones.

The puma vocalizes differently than the jaguar. Its roar/whine sounds a bit like the way one Matses calls out to another Matses in the forest, saying “ooo.”

The puma eats deer, pacas, agoutis, collared peccaries, young white-lipped peccaries, river turtles, caimans, and tree frogs. It does not eat tapirs. It eats the mesocarp of isan palms (*Oenocarpus bataua* [Arecaceae]) and a very few types of dicot tree fruits, such as those of the bata tree (*Pseudolmedia* spp. [Moraceae]).

REMARKS: Although pumas are very widely distributed (from Canada to Chile) and have often been studied by wildlife biologists at high latitudes and in open habitats, the biology of this species in lowland tropical rainforest is not well documented. Matses observations are largely consistent with known aspects of puma behavior reported in previous studies, but their description of frugivory is apparently unique. Additionally, Matses assertions that pumas eat caimans and turtles are noteworthy given the absence of these taxa from previous accounts of rainforest puma diets (e.g., Emmons, 1987; Novack et al., 2005; Moreno et al., 2006).

Puma yagouaroundi
(Geoffroy Saint-Hilaire, 1803)

Figure 14B

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Jaguarundis are externally distinctive (Emmons, 1997), although inexperi-

enced observers sometimes confuse them with tayras. Several subspecies are currently recognized (Wozencraft, 2005), of which the local form is *melantho* Thomas, 1914, with type locality at 800 m in the upper Ucayali drainage (Pasco department, Peru). Recent phylogeographic analyses of mtDNA sequence data, however, do not support the taxonomic recognition of any geographic subdivisions of this widespread species (Ruiz-Garía and Pinedo Castro, 2013). Thomas's (1914) measurements of an adult male and an adult female appear to be the only published morphometric data from western Amazonian specimens of *Puma yagouaroundi*.

ETHNOBIOLOGY: The most common name for the jaguarundi is bēdi chēshē (“black feline/canine”). A variant of this term is bēdi wisu, in which the archaic term for “black” (wisu) is substituted for the regular term for “black” (chēshē). In some villages it is called shododon, which is an onomatopoeic form imitating the jaguarundi's loud whining call. Some speakers who use shododon for the jaguarundi use the term bēdi chēshē or bēdi wisu to refer to the short-eared dog. Others consider bēdi chēshē, bēdi wisu, and shododon to be synonyms. A minority consider the short-eared dog and the jaguarundi to be the same animal.

The jaguarundi is of no economic importance. Is not eaten by the Matses, and there only is only one known case of one being kept as a pet.

When the jaguarundi whines loudly at night near a village or longhouse, saying “shon shon shon,” it is interpreted as a death omen, that is, that someone in the village will soon die.

Matses with young children avoid having any contact with or even looking at a jaguarundi, lest its spirit make their children ill (see the ethnobiology entry for *Puma concolor* for details on symptoms and treatment of contagion by felids).

MATSES NATURAL HISTORY: The jaguarundi is black or grayish black. It has a very long tail.

Jaguarundis can be found in any rainforest habitat, including upland and floodplain forest. They sometimes hunt along the margins of Matses swiddens where rodents (spiny rats, agoutis,

and acouchis) that feed on Matses crops (especially manioc) are abundant.

Jaguarundis hunt during the day. At *bata* trees (*Pseudolmedia* spp. [Moraceae]), where ripe fruits have fallen to the ground, the jaguarundi waits for animals that come to eat the fruits, and it also eats the fallen fruits. It waits for prey sitting on or under fallen trees.

Jaguarundis do not travel in large groups. The female gives birth to two young in a hollow log or a hole in the ground. When the young are very small and still have their eyes closed, the mother hunts and brings back meat for them. When their eyes open and they are a bit stronger, they travel with the mother and the mother kills prey and gives them some to eat. Eventually they leave the mother and begin to hunt for themselves.

The jaguarundi chases down lizards that are sunning themselves. It does not eat the tails of lizards. It kills geckos by jumping up on a tree trunk as they are climbing up. It covers its kill with dry leaves after eating a part and then goes to drink water. It walks on logs to catch tinamous.

The jaguarundi makes a whining sound (the Matses imitate the whine as “sho-do-doon”).

The jaguarundi has a very varied diet. It eats terrestrial birds, including white-throated tinamous (*Tinamus guttatus*), great tinamous (*T. major*), smaller species of tinamous (*Crypterellus* spp.), wood quails (*Odontophorus* spp.), ground doves (multiple species) and striated antthrushes (*Chamaeza nobilis*). It also eats agoutis, acouchies, spiny rats, and other small rodents, but not pacas or other large animals. It also eats short-tailed opossums (*Monodelphis* spp.), iguanas, golden tegus, other large lizards, and geckos. It also eats *bata* tree fruits, ripe plantains, and fallen *echo* tree (*Jacaratia* sp. [Caricaceae]) fruits. It eats the eggs of Spix’s guan (*Penelope jacquacu*) and those of other birds that nest close to the ground. It eats meat that a jaguar has stashed and the guts of armadillos that Matses have butchered, dragging the guts into the forest from the edge of the village.

REMARKS: Most Matses observations about jaguarundis agree with the literature reviewed by

Oliveira (1998a) and Giordano (2016), especially with respect to diurnal activity and terrestrial habits (the latter is implied rather than stated directly in Matses interviews). Their observation that “jaguarundis do not travel in large groups” contrasts with unambiguous statements that other felids are solitary (see Matses accounts for ocelots, margays, jaguars, and pumas; above) and is probably explained by the fact that these small cats are sometimes observed travelling in pairs (Giordano, 2016). The repeated mention of lizards and birds as prey by Matses interviewees contrasts with an emphasis on mammals (especially rodents) in much of the jaguarundi dietary literature; because the latter is mostly based on observations from Central America and southeastern Brazil, it is possible that Amazonian populations are distinctive in this respect. Frugivory—not previously mentioned in the jaguarundi literature—is another dietary trait described by the Matses that may also be distinctively Amazonian. Alternatively, if jaguarundis consume only fruit pulp (without swallowing seeds), this dietary component may have been missed in published studies based on analyses of scat. Jaguarundis are the only cats that the Matses report to eat birds’ eggs and carrion.

Mustelidae

Five mustelid species are definitely known to occur in the Yavari-Ucayali interfluvium, including three terrestrial species and two otters. The terrestrial species—tayra (*Eira barbara*), grison (*Galictis vittata*), and Amazonian weasel (*Mustela africana*)—were formerly classified in the subfamily Mustelinae, but Mustelinae (sensu lato) is now known to be paraphyletic (Koepfli et al., 2008; Sato et al., 2012). In the alternative subfamilial classification suggested by Nascimento (2014), the tayra would be referred to the subfamily Guloninae, the grison to the subfamily Ictonychinae, and the Amazonian weasel to the subfamily Mustelinae (sensu stricto). Otters remain in their traditional subfamily, Lutrinae (below).

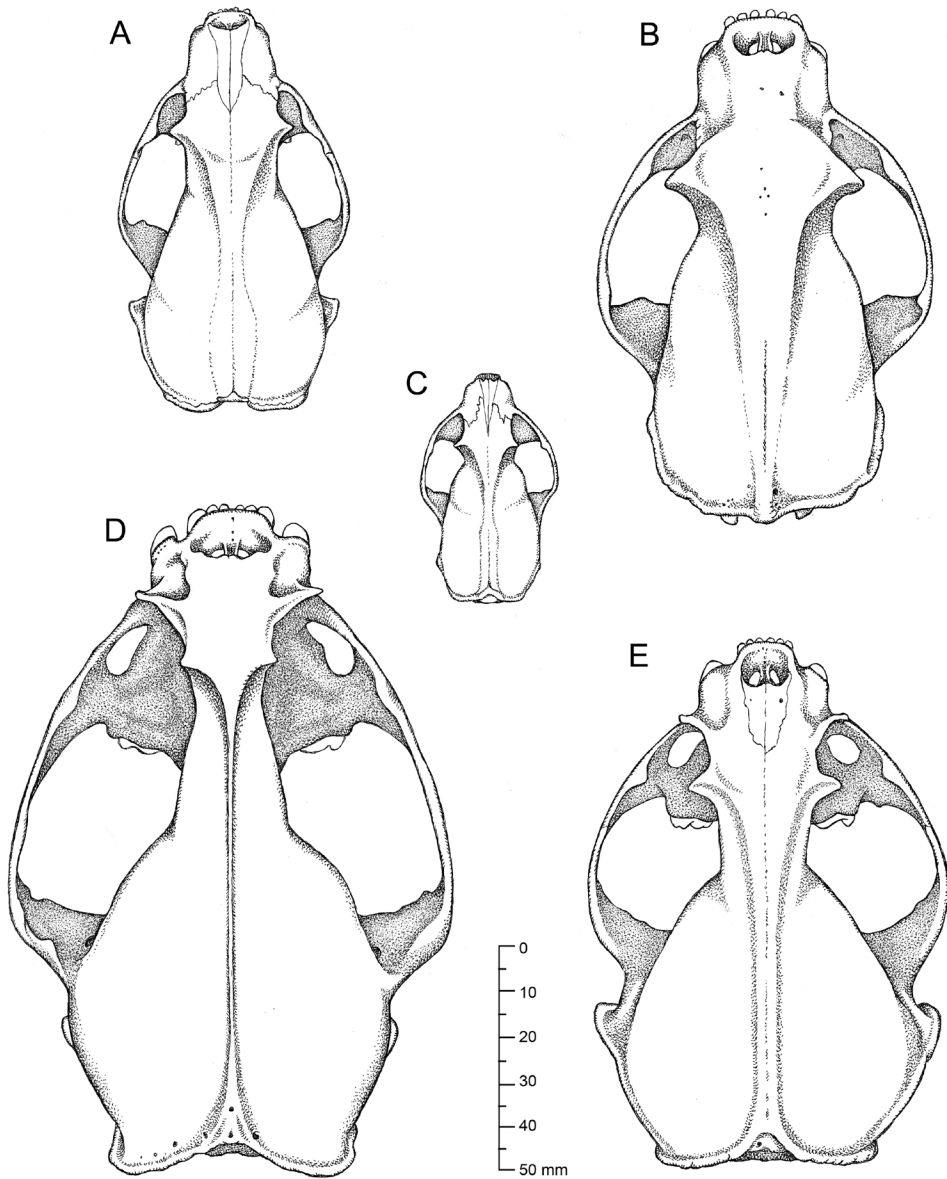


FIG. 15. Adult skulls of five sympatric mustelid species illustrating taxonomic differences in size and shape: *Galictis vittata* (A, MUSM 15157), *Eira barbara* (B, MUSM 13149), *Mustela africana* (C, AMNH 61813), *Pteronura brasiliensis* (D, AMNH 74431), *Lontra longicaudis* (E, AMNH 98589). All illustrated specimens are from eastern Peru, but only MUSM 13149 and MUSM 15157 are from the Yavari-Ucayali interfluve.

Eira barbara (Linnaeus, 1758)

Figure 15B

VOUCHER MATERIAL (TOTAL = 3): Nuevo San Juan (MUSM 11171, 13149), Orosa (AMNH

74116).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Jenaro Herrera (Pavlinov, 1994), Quebrada Pobreza (Escobedo-Torres,

TABLE 13

Measurements (mm) and Weights (g) of Adult Mustelid Specimens from the Yavari-Ucayali Interfluve

	<i>Eira barbara</i> MUSM 13149	<i>Galictis vittata</i> MUSM 15157	<i>Lontra longicaudis</i> MUSM 11172 ^a	<i>Pteronura brasiliensis</i> MUSM 11173 ^b
Sex	female	female	unknown	female
Head-and-body length	641	523	—	1015
Length of tail	398	150	—	592
Hind foot	115	83	—	174
Ear	40	31	—	28
Weight	4900	2260	—	—
Condylobasal length	111.4	88.8	104.4	146.5
Nasal length	—	20.9	—	—
Least interorbital breadth	27.9	19.6	19.3	17.6
Least postorbital breadth	26.3	20.8	14.4	15.9
Zygomatic breadth	70.9	49.5	63.2	92.5
Breadth of braincase	50.2	41.0	51.5	73.7
Maxillary toothrow ^c	30.9	25.8	34.6	48.6
Breadth of M1	8.1	7.6	12.4	15.8

^a Shot by a Matses hunter; sex unrecorded and no external measurements taken.

^b Found dead; not sufficiently intact to weigh.

^c From C1 to M1.

2015), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Of the three tayra specimens known to have been collected in the Yavari-Ucayali interfluve, one (AMNH 74116) is a juvenile, and another (MUSM 11171) cannot now be located. Fortunately, the remaining specimen (MUSM 13149) consists of the well-preserved skin and skull of a fully adult individual that exhibits all the diagnostic external and craniodental traits attributed to the species by authors (e.g., Husson, 1978). Like many other tayra skins from northeastern Peru, MUSM 13149 has a grizzled-brownish head that does not contrast abruptly in coloration with the fur of the shoulders and middle back, the brownish tones of these regions darkening posteriorly and laterally to merge with the blackish pigmentation of the limbs, flanks, hindquarters, and tail. There is a small self-cream marking on the throat.

Tayras exhibit geographic variation in pelage color that is reflected in the description of numerous subspecies; Wozencraft (2005), for example, recognized eight, some of which have multiple synonyms. Our material perhaps represents the nominal form that Lönnberg (1913) called *Eira barbara peruana* Tschudi, 1844, but analyses of mtDNA sequence data (Ruiz-Garcia et al., 2013) suggest an almost complete lack of phylogeographic structure in this species. Although a trinomial nomenclature of tayras seems pointless at the present time, we note that genetic data are currently lacking from Central American and Atlantic Forest populations, which might yet be shown to be taxonomically distinct. Morphometric data from our adult female voucher (table 13) compare closely with homologous dimensions of Surinamese specimens (Husson, 1978: table 45) and reinforce our impression that Amazonian tayras comprise a single, genetically cohesive, undifferentiated species.

ETHNOBIOLOGY: The Matses name for the tayra, batachued (“one that likes sweet food”), derives from their observation that tayras eat sweet wild tree fruits and ripe plantains and papayas from Matses swiddens. There are no archaic synonyms or overdifferentiated varieties, and the Matses term differs from the name for tayra in other Panoan languages. Some Matses include the tayra in the category bēdi, which otherwise designates felids and wild canids.

The tayra is not eaten by the Matses, who consider it a pest and often call it “thief” because it frequently feeds on plantains and papayas in Matses swiddens. Tayras also eat chickens that are ranging at the edge of the village during the day, but they do not raid coops. When dogs pursue a tayra, the tayra sometimes bites the dogs. Tayras are not kept as pets.

Matses with young children avoid having any contact with or even looking at tayras, lest the tayra’s spirit make their children ill. Symptoms of tayra sickness include a high fever (but not constant thirst, as is case with contagions induced by felids). To treat this ailment, certain medicinal plants (“tayra medicine”) are collected, and the sick child is bathed with an infusion of their leaves. It is noteworthy that, unlike felid-induced contagions, tayra sickness is not treated with jaguar medicine, suggesting that the folk-taxonomic association of tayras with other members of the bēdi category is not strong.

MATSSES NATURAL HISTORY: The tayra has a dark body and a light-colored head and neck. It has the shape of a dog with long neck. It has a furry tail. It has a distinctive but not strong smell.

Tayras are found in all habitat types, including upland and floodplain forest, and in primary and secondary forest. They are frequently encountered in secondary forest while walking to swiddens, in primary forest while hunting, and on the banks of rivers and streams while traveling by canoe or motorized boat.

The tayra is diurnal. It walks on the ground and also climbs high up in trees. It comes to swiddens to eat ripe plantains, bananas, and papayas. It stashes plantains at the base of a tree

and covers them with leaves. It eats fallen fruits on the ground and up in trees. It can be heard rustling branches as it climbs through trees. It often walks on the trunks of fallen trees and defecates on the fallen trees. Its feces often have many seeds of fruits. It climbs high up in trees when it sees people. It sleeps in the same hole in a tree every night.

Tayras are usually solitary, but they also travel in pairs, trios, or sometimes larger groups. They give birth to two young in a den in a hole in a tree.

Jaguars and pumas eat tayras.

The tayra snarls.

Tayras eat all types of sweet things, including ripe bananas, plantains, papayas, and wild dicot tree fruits, such as those of diden kēku (*Couma macrocarpa* [Apocynaceae]), bata (*Pseudolmedia* spp. and/or *Maquira* spp. [Moraceae]), and kēku (*Parahancornia peruviana* [Apocynaceae]). They also eat the fruits of cecropia trees (*Cecropia* spp. [Moraceae]). They drink honey from beehives. They also eat meat, particularly agoutis, acouchies, spiny rats, lizards, tinamous, bird eggs, and hatchlings. (One informant said he saw a large group of tayras chase a gray brocket deer, kill it, and start eating it.)

REMARKS: Matses interviews about tayras include many of the salient facts about this versatile diurnal omnivore mentioned in the literature reviewed by Presley (2000), including its use of every forest stratum from ground level to canopy. Additionally, Matses observations confirm the tayra’s curious habit of caching fruit stolen from gardens (Soley and Alvaro-Díaz, 2011), and they provide novel information about predation on this species by jaguars and pumas. However, perhaps the most interesting aspect of tayra biology contained in these accounts and in Matses interviews about *Dasypus pastasae* (see above) are the suggestions that tayras hunting in groups can kill larger prey than solitary tayras can subdue. Although the notion of tayras attacking ungulates seems implausible, this behavior was previously reported by Villa (1948), who witnessed a solitary individual chasing a deer;

if one of our informants is to be believed, tayras hunting deer cooperatively are sometimes successful.

Galictis vittata (Schreber, 1776)

Figure 15A

VOUCHER MATERIAL (TOTAL = 1): Nuevo San Juan (MUSM 15157).

OTHER INTERFLUVIAL RECORDS: Río Yavarí-Mirím (Salovaara et al., 2003).

IDENTIFICATION: Our single grison specimen from the Yavarí-Ucayali interfluve consists of the skin and skull of a young adult female. The pelage markings of this specimen correspond exactly with those of topotypical (Surinamese) material described by Husson (1978: 291–292), and most of its measurements (table 13) fall within the range of morphometric variation reported for females of the species by Bornholdt et al. (2013: table 4).¹⁰ Among other (nonmetrical) traits that distinguish *Galictis vittata* from its southern congener (*G. cuja*), MUSM 15157 has a well-developed metaconid on the lower first molar. Several subspecies of *G. vittata* are recognized as valid by some authors (e.g., Yensen and Tarifa, 2003; Wozencraft, 2005), but no compelling empirical basis for a trinomial nomenclature seems to have been published.

ETHNOBIOLOGY: Although the grison's Matses name is bosen uşhu (literally, “white otter”), the Matses do not consider grisons to be a type of otter. There are no archaic synonyms or overdifferentiated varieties. Many Matses have never seen a grison, and only a limited number of Matses are familiar with its name. Some know of it through the accounts of those who have seen it.

The grison is of no economic importance to the Matses.

Because grisons are so rarely encountered, the Matses have no specific beliefs regarding them

and no special medicinal plants for contagions by a grison spirit. However, Matses medicine men say that grisons could make a child ill if touched or looked upon and that “Neotropical otter medicine” would probably be effective.

MATSES NATURAL HISTORY: The grison is black with a light-colored back. Its teeth are small. They are found near streams, but they are not aquatic like otters. They can swim. (One interviewed Matses hunter said that he saw one catch and eat an agouti).

REMARKS: Matses informants had little to say about this seldom-encountered species, but its pursuit of agoutis is corroborated by the literature cited in Yensen and Tarifa's (2003) review.

Our voucher was shot by a Matses hunter, who encountered a group of three individuals fighting over a dead spiny rat (*Proechimys* sp.) in upland primary forest near a muddy mineral lick during the day.

Mustela africana Desmarest, 1818

Figure 15C

VOUCHER MATERIAL: None.

OTHER RECORDS: This report (Matses observations).

IDENTIFICATION: No other Amazonian mammal resembles this species, which we judge to be present in the Yavarí-Ucayali interfluve on the basis of unambiguous Matses observations. The local form is *Mustela africana stolzmanni* Taczanowski, 1881, which was described from a specimen collected at Yurimaguas, a lowland site about 200 km west of our region. Technical descriptions and measurements of the holotype and other referred material were provided by Hall (1951).

ETHNOBIOLOGY: Only three Matses men whom we interviewed have seen an Amazon weasel, and each had encountered them only once. As such, the name we give here, mayanën opampi (“demon's little dog”) is far from established. However, it has some currency among people who had heard of it from those who have

¹⁰ Male grisons are substantially larger than females (Bornholdt et al., 2013).

seen it. One informant called it *bosenēmpi*, the term for the Neotropical otter with the diminutive suffix *-mpi* (i.e., “little otter”).

The Amazon weasel is of no economic or cultural importance to the Matses. Since most Matses are not familiar with the species, they have no established beliefs about it.

NATURAL HISTORY: Amazon weasels are small, the size of an acouchy. They are brown, the color of an otter. They have an extremely strong and foul smell. They run very fast. One informant said that his hunting dogs were not able to catch one. Another informant said he found three together in a burrow at the base of a tree.

REMARKS: This exceptionally rare (or elusive) species is seldom encountered, even by field researchers with many years of Amazonian experience, so it is not surprising that only a few Matses have seen one.

Otters (Lutrinae)

Two species of otters occur sympatrically throughout most of Amazonia. Whereas the Neotropical otter (*Lontra longicaudis*) is unremarkable in morphology and habits, the giant otter (*Pteronura brasiliensis*) is strikingly unlike any other freshwater lutrine species in size and social behavior. Oddly, the Matses lack a generic term for otters, although their ethnomedical lore suggests that they do recognize otters as a covert folk-taxonomic category (see below).

Lontra longicaudis (Olfers, 1818)

Figure 15D

VOUCHER MATERIAL (TOTAL = 1): Nuevo San Juan (MUSM 11172).

OTHER INTERFLUVIAL RECORDS: Anguila (Escobedo-Torres, 2015), Choncó (Amanzo, 2006), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Following van Zyll de Jong's (1972) revision of the Nearctic and Neotropical

river otters (previously treated as congeneric with Old World *Lutra*), three subspecies of *Lontra longicaudis* have been consistently recognized: *L. l. annectans* (Major, 1897) from Central America and trans-Andean South America, *L. l. enudris* (Cuvier, 1823) from Amazonia, and *L. l. longicaudis* (Olfers, 1818) from southeastern Brazil and the La Plata drainage. Analyses of mtDNA sequence data (Trinca et al., 2012) suggest that *annectans* should perhaps be recognized as a distinct species, but there is evidence of genetic exchange between Amazonian populations (referred to *enudris*) and La Platan populations (referred to *longicaudis*). Although Feijó and Langguth (2013) recently suggested that all the South American subspecies of *L. longicaudis* (sensu van Zyll de Jong, 1972) be recognized as full species, we prefer to maintain current usage until the reproductive isolation and/or diagnosability of these nominal taxa can be more convincingly established. Cranial measurements of our voucher specimen (table 13) compare closely with those of almost-topotypical specimens of *L. l. enudris* (from Surinam; Husson, 1978: table 46).

ETHNOBIOLOGY: The name for the Neotropical otter is *bosen*, which is monomorphemic and widespread in other Panoan languages. There are no archaic synonyms or overdifferentiated varieties.

Otters are not eaten by the Matses, nor are they usually kept as pets.

The spirit of a Neotropical otter can make children ill if their parent looks at one. Contagion by an otter spirit causes high fever, which is treated with certain medicinal plants (“Neotropical otter medicine”). Other medicinal plants effective against sickness caused by giant otters (“giant otter medicine”) are also said to cure contagion by Neotropical otters, suggesting that, despite the lack of any linguistically labeled category for otters and the complete dissimilarity between the Matses names for *Lontra longicaudis* and *Pteronura brasiliensis*, the Matses recognize an association between these taxa at some level.

MATSES NATURAL HISTORY: The Neotropical otter has a smooth, slick body, with a somewhat

flat tail and a head like a dog's. Its fur is shiny and gray when wet. The underside of its neck is light-colored. It has thick whiskers. It has short legs and webbed feet with which it cannot run quickly on land.

The Neotropical otter lives along rivers, large and small streams, streams with muddy bottoms or sandy bottoms, and in lakes and flooded forest.

The Neotropical otter is diurnal. It spends much of the day swimming along streams looking for fish. It travels short distances overland to search for fish at other streams. It makes the water in small streams turbid as it chases fish and looks for wolffishes (*Hoplias* spp. [Erythrinidae]) lying in the streambed. It feels inside submerged hollow logs and under submerged logs for armored catfishes and têpush fish (*Erythrinus erythrinus* [Erythrinidae]). When it catches a fish, it eats it sitting on a log that is in the water, or on the bank. It makes a loud gnawing sound as it eats. The otter sleeps in the undercut banks of streams, in holes made in the bank by motmots (birds in the family Momotidae), or other sheltered places along the bank. It does not sleep in the same place every night, and it does not make burrows to sleep in (as it does to give birth). When it sees people it flees quickly, swimming underwater.

Neotropical otters are usually solitary, but they are also found in groups of two or three. When two or three are together, they play by chasing each other and taking fish from each other. The female gives birth to two young in a shallow burrow dug into the bank of a stream or river. She continually goes to catch fish, eats them, and then comes back to suckle her young. When the young get older, she brings fish to the den for them to eat.

No predators eat Neotropical otters.

The Neotropical otter whines, saying "weee weee weee." It barks saying "kuesak kuesak kuesak."

The Neotropical otter eats all kinds of fish, including armored catfish, large pimelodid catfishes, têpush (*Erythrinus erythrinus* [Erythri-

dae]), pone (*Hoplias* spp. [Erythrinidae]), and bédichued (*Leporinus* spp. and/or *Schizodon* spp. [Anostomidae]). It also eats crabs and shrimp.

REMARKS: Matses interviews about Neotropical otters are consistent with the results of most published studies of this widespread taxon (e.g., Kasper et al., 2008; Silva, 2010), notably with respect to its fondness for slow-moving benthic prey (such as armored catfish and erythrinids), but Amazonian field studies are almost nonexistent, so these observations also provide novel details of habitat use and behavior that may be peculiar to the local subspecies (*Lontra longicaudis enudris*; see above). Matses accounts that Neotropical otters make transient and opportunistic use of makeshift shelters (including burrows made by other species) is interesting by comparison with the fixed den sites of sympatric giant otters (see below). Another noteworthy point of comparison based on Matses observations of these species is that female Neotropical otters with newborn young in nursery burrows are said to forage for themselves, whereas female giant otters with nursing young are said to be provisioned by the male.

A published range map (Larivière, 1999: fig. 3) that shows *Lontra longicaudis* as absent throughout most of western Amazonia is inconsistent with the documented presence of this species in the Yavari-Ucayali interfluvium and at many other western Amazonian inventory sites (e.g., Balta, Cocha Cashu/Pakitza; Voss and Emmons, 1996). An accompanying statement that "*Lontra longicaudis* favors clear, fast-flowing rivers and streams and may be absent or rare from sluggish, silt-laden lowland rivers," (Larivière, 1999: 2) is likewise impossible to reconcile with the presence of Neotropical river otters throughout the flat, sedimentary landscapes of western Amazonia where clear, fast-flowing rivers and streams are virtually nonexistent, and where this species is known to forage in lentic habitats (e.g., oxbow lakes and flooded forest).

Pteronura brasiliensis (Gmelin, 1788)

Figure 15D

VOUCHER MATERIAL (TOTAL = 1): Nuevo San Juan (MUSM 11173).

OTHER INTERFLUVIAL RECORDS: Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999).

IDENTIFICATION: Giant otters are externally and cranially unmistakable (Husson, 1978; Emmons, 1997) and no conspicuous morphological differences have been reported among the Amazonian populations traditionally referred to *Pteronura brasiliensis brasiliensis*. Apparently, the same mtDNA phylogroup—the “Amazon/Orinoco/Guianas” clade of Pickles et al. (2011)—extends from western Amazonia to French Guiana (the type locality; Husson, 1978), and craniodental measurements of our single voucher specimen (table 13) compare closely to those of nearly topotypic material from Surinam (Husson, 1978: table 47).

ETHNOBIOLOGY: The Matses name for the giant otter is *onina*. It is probably onomatopoeic and does not occur in other Panoan languages. There are no archaic synonyms or overdifferentiated varieties.

The giant otter is of no economic importance to the Matses. They are never kept as pets.

The spirit of a giant otter can make children ill if their parent looks at one. Matses with children formerly made great efforts to avoid seeing giant otters, but now that the Matses frequently travel by boat, it is almost impossible to avoid seeing them. Giant otter sickness causes high fever (as does contagion by Neotropical otters), which can be treated with particular medicinal plants (“giant otter medicine”). Other plants used to treat illness caused by Neotropical otters are also used to treat contagion by giant otters.

MATSES NATURAL HISTORY: The giant otter has a head like a paca’s and teeth like a jaguar’s. It has a light-colored patch on the front of its neck. It has thick whiskers, a flat tail, short legs, and webbed feet. It is much larger than the Neotropical otter.

Giant otters are always near water, in ox-bow lakes, rivers, and large streams, but not in small streams, except near their mouths. They also catch fish in flooded forest.

Giant otters are diurnal. They sleep at night in an undercut bank or some other sheltered place along a river, stream, or lake. They spend much of the day chasing fish, swimming very quickly. They travel far, swimming along rivers and streams. They can swim underwater and are always poking their heads out of the water. They fish for a long time in deep river curves. They play in the water chasing each other.

They make clearings on riverbanks and lake-shores where they eat the fish they have caught. Such clearings are free of all vegetation and look as if they had been swept. Giant otters come back to the same clearings to eat. One clearing is close to their den, and others are further off, often on the bank of a deep curve of a river, or at the mouth of a stream. Such clearings are littered with fish bones and scales and smell of rotting fish.

When giant otters see people, they dive and swim away underwater. If they have young, they become fierce when they see people, baring their teeth and growling. When one imitates their call, they come calling.

Giant otters live in packs of five to 20 individuals. The females give birth to two young in a burrow, the entrance of which is in the undercut bank of a stream. Males catch fish and take them to feed the young while the female stays with the young. The den stinks like rotten fish and has many flies. Only the female with young sleeps in the den. When the young are strong enough to swim, they abandon the den and sleep in other places (not burrows).

Giant otters fish in the presence of dolphins. No predators kill giant otters.

Giant otters have a loud squealing call that the Matses imitate as “waa waa waa.”

Giant otters eat mostly fish, all types of fish including *inchishchued* (*Brycon* spp. [Characidae]), *bédichued* (*Leporinus* spp., *Schizodon* spp. [Anostomidae]), wolffishes (*Hoplias* spp. [Ery-

TABLE 14
 Measurements (mm) and Weights (g) of Adult Specimens of *Bassaricyon alleni*
 and *Potos flavus* from the Yavari-Ucayali Interfluve

	<i>Bassaricyon alleni</i>		<i>Potos flavus</i>	
	AMNH 268247	MUSM 11174	AMNH 268249	AMNH 73765
Sex	female	male	female	male
Head-and-body length	399	391	425 ^a	—
Length of tail	456	458	430	—
Hind foot	92	88	93	—
Ear	40	42	36	—
Weight	1170	1350	2110	—
Condylobasal length	77.8	80.0	77.1	79.6
Least interorbital breadth	16.9	17.4	18.9	19.2
Least postorbital breadth	21.6	21.4	21.9	22.9
Zygomatic breadth	51.8	52.9	56.4	57.7
Breadth of braincase	35.0	35.5	38.7	40.0
Maxillary tooththrow ^b	28.2	28.8	24.1	25.3
Breadth of M1	5.9	5.7	4.8	5.3

^a Collector's value for total length (655 mm) is an obvious lapsus; this value for head-and-body length is based on the assumption that total length was 855 mm.

^b From C1 to M3.

thrinidae]), armored catfish, and large pimelodid catfishes. They also eat crabs.

REMARKS: Matses interviews about giant otters include most of the essential natural history facts about this remarkable species, including its diurnal activity, piscivorous diet, highly social behavior, almost predator-free existence, construction of vegetation-free campsites on river banks, exclusive use of a birthing den by females and newborn young, and aggressive defense of family groups against human intruders (Duplaix, 1980; Carter and Rosas, 1997; Duplaix et al., 2015). The Matses observation that males provision females with nursing young is not reported in the literature we consulted. Their interesting observation that giant otters fish in the presence of dolphins hints at, but does not explicitly confirm, the possibly cooperative association between *Pteronura* and *Inia* suggested by Defler (1983).

Procyonidae

Four procyonid species are known to inhabit the Yavari-Ucayali interfluve, including the olingo (*Bassaricyon alleni*), the coati (*Nasua nasua*), the kinkajou (*Potos flavus*), and the crab-eating raccoon (*Procyon cancrivorus*). All have Matses proper names, although not all Matses are aware that olingos and kinkajous are distinct species. Because olingos and kinkajous are nocturnal canopy species and the crab-eating raccoon is seldom observed, the Matses are only well informed about the natural history of the commonly encountered, diurnal, terrestrial coati.

Bassaricyon alleni Thomas, 1880

Figure 16B

VOUCHER MATERIAL (TOTAL = 2): Nuevo San Juan (AMNH 268247; MUSM 11174).

OTHER INTERFLUVIAL RECORDS: *Anguila* (Escobedo-Torres, 2015).

IDENTIFICATION: Our two voucher specimens conform qualitatively to Helgen et al.'s (2013) diagnosis of *Bassaricyon alleni*, the only olingo species known to occur in Amazonia. Additionally, the external and craniodental measurements of our specimens (table 14) fall within the range of morphometric variation in *B. alleni* tabulated in that study. No subspecies of *B. alleni* are currently recognized, and the trivial genetic distance between sequenced specimens from Guyana and Peru (ca. 1.3% at the cytochrome-*b* locus; Helgen et al., 2013) suggests that even widely separated Amazonian populations are not significantly differentiated.

ETHNOBIOLOGY: The Matses name for the olingo is *shēmēn*, a monomorphemic term that is common in other Panoan languages as a name for the olingo and/or the kinkajou. Only a small number of Matses are aware that olingos and kinkajous are different animals. Those who recognize them as distinct note the nonprehensile, ringed tail of the olingo and its slightly different vocalization. Those who are not aware that these are two species consider the name for the kinkajou, *kuichikkekid*, to be a synonym of *shēmēn*.

The olingo is of no economic importance to the Matses.

Contagion by an olingo spirit causes a very high fever in children (like the illness caused by a kinkajou spirit).

MATSES NATURAL HISTORY: The olingo is like a kinkajou, but has a nonprehensile and ringed tail and a smaller head. Its call is very similar to but softer than that of the kinkajou. The olingo's call is heard less frequently than the kinkajou's, and is seldom heard in secondary forest. (The remaining natural history information that Matses interviewees provided for the olingo is essentially the same as that provided for the kinkajou.)

REMARKS: Both of our specimens were shot at night in trees (at estimated heights of 15 and 35 m above the ground) in primary upland forest.

Nasua nasua (Linnaeus, 1766)

Figure 16C

VOUCHER MATERIAL (TOTAL = 8): Boca Río Yaquerana (FMNH 88877, 88878), Nuevo San Juan (AMNH 268248; MUSM 11176, 11178), Quebrada Esperanza (FMNH 88879–88881).

OTHER INTERFLUVIAL RECORDS: Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Quebrada Pobreza (Escobedo-Torres, 2015), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: Measurements of our voucher material (table 15) fall within the range of variation for *Nasua nasua* tabulated by Decker (1991), at least to the extent that her unexplained measurement abbreviations can be deciphered,¹¹ but morphometric variation in this species broadly overlaps with that of the somewhat larger white-nosed species (*N. narica*), so quantitative comparisons are of limited diagnostic value. Of the qualitative characters said to distinguish *N. nasua* from *N. narica* in Decker's revision, our material lacks a whitish patch of postrhinial fur (present in *N. narica*), the anterior alveolar foramen is visible anterior to the infraorbital foramen (the anterior alveolar foramen is concealed inside the infraorbital canal of *N. narica*), and a well-developed post-orbital process of the jugal is present (this process is absent or indistinct in *N. narica*). By contrast, we were not consistently able to distinguish our material from *N. narica* using the other craniodental and pelage characters alleged to diagnose these species.

Although 41 nominal taxa are currently regarded as synonyms or subspecies of *Nasua nasua* (see Wozencraft, 2005), the empirical basis for a subspecies classification has never

¹¹ For example, we assume that her "CBL," "ZYB," and "MAX" correspond to condylobasal length, zygomatic breadth, and maxillary toothrow length, respectively, but the meaning and/or endpoints of other abbreviated dimensions (e.g., PPL, ROS, PMX, ABL, COR) are unclear.

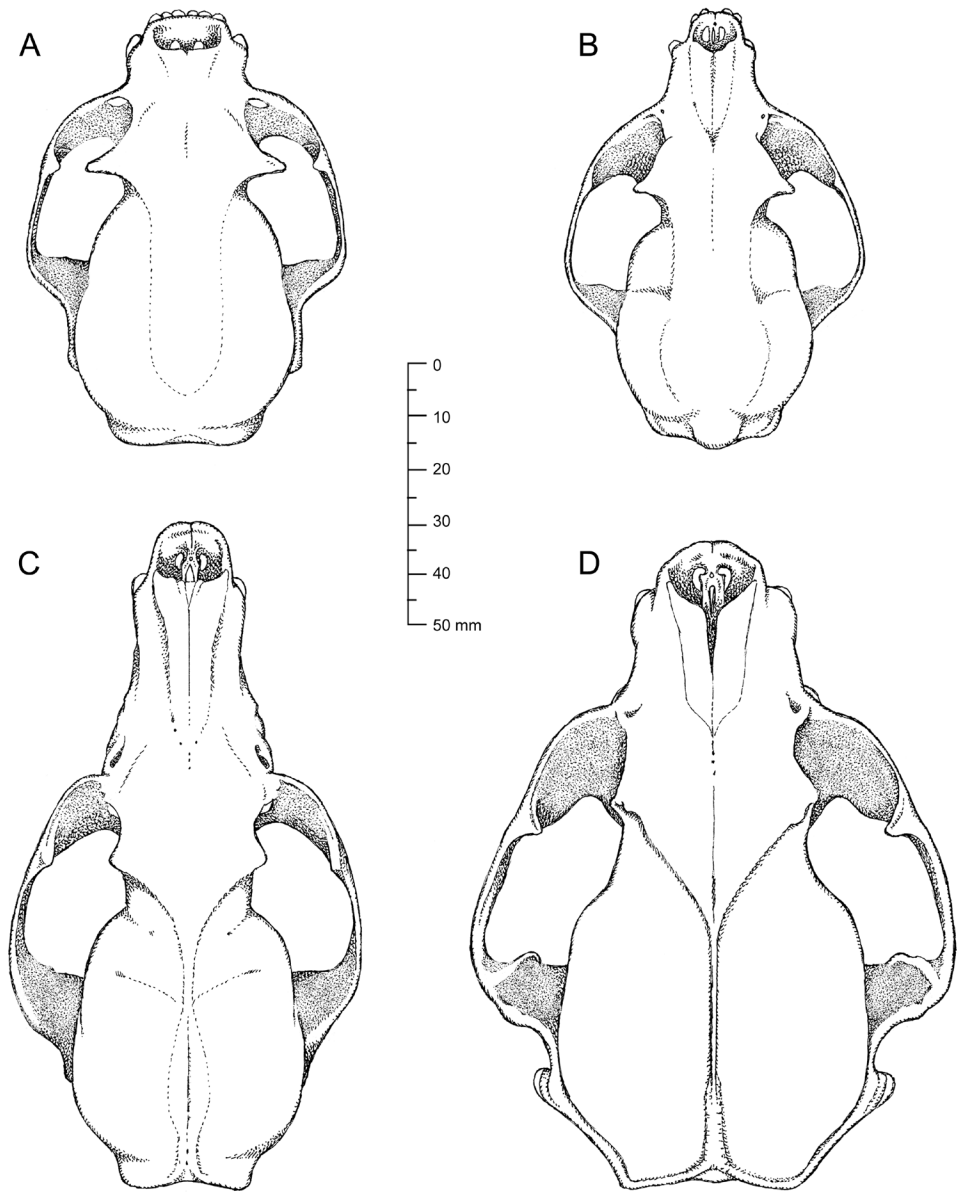


FIG. 16. Adult skulls of four sympatric procyonid species, illustrating taxonomic differences in size and shape: *Potos flavus* (A, AMNH 268249), *Bassaricyon alleni* (B, AMNH 98709), *Nasua nasua* (C, AMNH 76642), *Procyon cancrivorus* (D, AMNH 94247). All illustrated crania are from western South America, but only AMNH 268249 is from the Yavari-Ucayali interfluve.

TABLE 15

Measurements (mm) and Weights (g) of Adult Specimens of *Nasua nasua* from the Yavari-Ucayali Interfluve

	AMNH 268248	FMNH 88878	FMNH 88880	FMNH 888877	FMNH 88881	MUSM 11176	MUSM 11178
Sex	female	female	female	male	male	male	male
Head-and-body length	483	521	524	565	536	535 ^a	516
Length of tail	428	413	420	465	422	438	414
Hind foot	96	87	90	98	88	90	95
Ear	40	36	37	38	38	40	42
Weight	3700	—	—	—	—	3480	3780
Condylobasal length	110.7	113.9	113.5	118.3	115.3	117.2	115.0
Nasal length	38.1	—	—	—	—	39.6	—
Least interorbital breadth	23.8	23.5	24.0	26.8	24.1	23.8	25.4
Least postorbital breadth	25.2	23.9	24.4	24.1	20.2	22.1	21.1
Zygomatic breadth	59.7	61.1	61.5	77.6	—	63.4	70.4
Breadth of braincase	43.7	42.9	43.1	45.3	42.9	44.3	44.0
Maxillary toothrow	42.5	44.1	45.5	47.1	45.5	45.2	47.4
Breadth of M1	6.9	7.2	7.1	7.8	7.5	7.2	8.0

^a Collector's measurement of total length (1073 mm) is an obvious lapsus; computed value for head-and-body length is based on the assumption that total length was 973 mm.

been established. Following Cabrera (1958), western Amazonian coatis (which tend to have very dark pelage) are usually referred to *Nasua nasua dorsalis* Gray, 1866, but the type locality of *dorsalis* is effectively unknown; among the nominal taxa commonly listed as synonyms of *dorsalis*, the oldest that might apply to any population from western Amazonia is *juruaana* Ihering, 1911. In the absence of any assessment of geographic variation in phenotypic or molecular traits, however, we are not persuaded of the need for a trinomial classification of *N. nasua*. A comparison of our measurement data (table 15) with measurements of Surinamese specimens identified as *N. nasua vittata* (in Husson, 1978: tables 41, 42), for example, does not suggest any substantial morphometric divergence between populations from opposite sides of Amazonia.

Most coati skins from the Yavari-Ucayali interfluve are rich reddish brown lined with black, but the pelt of FMNH 88881 (an old adult male) is predominantly blackish, the black

almost obscuring the banding pattern on the tail. As usual for this species, old male skulls have tall sagittal crests, widely flaring zygomatic arches, and huge canines by comparison with female skulls (which lack sagittal crests and have narrower zygomatic arches and much smaller canines; fig. 16C).

ETHNOBIOLOGY: The coati is called *tsise*, a monomorphemic term common in the Panoan family. The Matses recognize two named varieties: *tsisedapa* ("big coati") and *tsisempi* ("small coati"). The large variety occurs in smaller packs (up to about 10) and the small variety is darker and runs in larger packs (up to about 15). The Matses have no archaic synonyms for the coati.

The coati is a game animal of secondary importance. Traditionally only old people ate coatis. Today, after having seen that non-Indians eat them, some younger Matses eat them, but only roasted and if they have a lot of fat. Sometimes coatis injure dogs by biting them when chased. Coatis are considered very good

pets to keep, not only because young animals readily become tame and are fun to play with, but because pet coatis warn people about pitvipers (e.g., *Bothrops* spp.) near the village. Coatis give a warning call (“tsa tsa tsa”) when they find a venomous snake, and then someone goes and kills it.

Young people do not eat coatis lest they become lethargic. Coati spirits sometimes make children ill, causing them to have a high fever, which is treated by bathing the sick child with certain medicinal plants (“coati medicine”).

MATSES NATURAL HISTORY: The coati has a ringed tail that it carries raised up vertically as it walks on the ground. It has a dark-colored body and a light-colored face. It has a long snout, small ears, and big claws. Seasonally it has a lot of fat. It has a very strong smell, such that one can easily know that coatis have recently passed by.

Coatis are found in all types of habitats, including upland and floodplain forest, and in primary and secondary forest. They are encountered frequently while hunting.

Coatis are strictly diurnal. They sleep together up in trees at night. They lie together in trees to rest when it is dry. They eat fruits up in the trees and also forage for fallen fruits on the ground. They search the ground for earthworms, and when they find a place with many earthworms they root there for a long time. They eat beetle grubs that feed on the rotting pith of fallen palm trees. They dig into rotten logs with their noses to search for invertebrates.

When they see people from far off, they yell, saying “kosh,” drop to the ground, and flee running on the ground. If they are on the ground when they see or hear people, they climb part-way up a tree to get a good look at the person(s), yelling “kosh, kosh, kosh,” and then drop to the ground and flee running on the ground.

Coatis live in packs of up to about 15 individuals. Sometimes only two or three are seen traveling together. To give birth, coatis make big nests by breaking off many small branches with the leaves still attached and weaving them together in the crotch of a tree branch. Each

female that is going to give birth makes a separate nest in the same tree. They give birth and suckle their young in the nest. Once they get stronger, the females take their young down to the ground to forage with the rest of the pack, and then at dusk they carry them back up to the nest. Once the young are strong enough to grasp tightly, they begin to come down to the ground on their own, and eventually the nests are abandoned. The nests are often made in a fruiting tree.

Jaguars and pumas eat coatis.

Coatis bark saying “tsat tsat tsat tsat,” and hiss saying, “tse, tse, tse.”

Coatis eat all sorts of things. They eat dicot tree fruits, including those of *bata* (*Pseudolmedia* spp. [Moraceae]). They eat the mesocarp of the fruits of *isan* palms (*Oenocarpus bataua* [Arecaceae]) and swamp palms (*Mauritia flexuosa*) that have ripened and fallen to the ground. They eat earthworms, armored millipedes, round millipedes, scorpions, beetle grubs that feed on palm pith, and grubs that live in the soil.

REMARKS: Matses observations about *Nasua nasua* agree in most essential details (e.g., diurnal activity, sociality, omnivory, construction of arboreal nursery nests, escape behavior) with Kaufmann’s (1962) classic study of the Central American species (*N. narica*), and with the scattered natural history literature on *N. nasua* (reviewed by Gompper and Decker, 1998). A significant omission from our interviews is any mention of solitary males.¹² Additionally, these accounts describe nursery-nesting behavior in greater detail than in any previous report about *Nasua* spp. (including Olifiers et al., 2009), and they provide new information about fruit species and invertebrate taxa consumed in Amazonia, where the foraging habits of coatis have not previously been studied.

¹² Except during the breeding season, social groups of *Nasua narica* are composed only of adult females and their immature offspring (Kauffman, 1962; Gompper, 1997), but male *N. nasua* sometimes associate in bachelor groups (Hirsch, 2011) and might do so more consistently in predator-rich Amazonian habitats than elsewhere.

Potos flavus (Schreber, 1774)

Figure 16A

VOUCHER MATERIAL (TOTAL = 3): Nuevo San Juan (AMNH 268249; MUSM 11179) Orosa (AMNH 73765).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Itia Tëbu (Amanzo, 2006), Quebrada Pobreza (Escobedo-Torres, 2015), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Kinkajou specimens collected in the Yavarí-Ucayali interfluve conform closely to Husson's (1978: 285–287) description of topotypical material from Surinam, and measurements of our vouchers (table 14) broadly overlap the range of variation in homologous dimensions reported from kinkajous collected in the Guianas (Husson, 1978; Voss et al., 2001). Side-by-side comparisons of crania from eastern Peru and French Guiana suggest that the former have somewhat larger auditory bullae, but no other consistent differences are apparent. Therefore, based on the phenotypic evidence at hand, we are quite confident of this identification and would even assign our vouchers to the nominotypical subspecies if a trinomial identification were deemed necessary. Remarkably, however, DNA sequence data suggest that western Amazonian and Guianan kinkajous differ by as much as 7%–9% at the mitochondrial cytochrome-*b* locus according to Nascimento et al. (2016). Those authors correctly point out that such high levels of sequence divergence are often found between full species, and they reasonably suggest that additional studies based on other genetic loci are needed to assess the possibility that several valid taxa are represented among the nominal forms currently treated as synonyms or subspecies of *P. flavus*. In this context, our morphological comparisons of Peruvian and Guianan specimens are inconclusive, but if a different name were eventually needed for our material, the geographically closest nominal

taxon is *chapidensis* Allen, 1885, based on a type from Mato Grosso, Brazil.

ETHNOBIOLOGY: The Matses name for the kinkajou is kuichikkekid, which can be analyzed as meaning “one that says ‘kuichik” (“kuichik” is the Matses rendition of the vocalization that kinkajous are often heard to make from the treetops at night). The name is often shortened to kuichik. It has no archaic synonyms or named overdifferentiated varieties (but see the Ethnobiology entry for olingos, above).

The Matses do not kill or eat kinkajous, they do not raise them as pets, and they have no other interest in them. Although most Matses have never seen a kinkajou, most have heard kinkajous vocalizing in the treetops at night. One of the few occasions when the Matses get a close look at a kinkajou is when they find one when felling trees for a swidden.

Contagion by a kinkajou spirit causes a very high fever in children.

MATSES NATURAL HISTORY: The kinkajou is like a small dog, but with a prehensile tail and larger eyes. It has a short rostrum, large eyes, and ears like a jaguar's. Its body is reddish gray.

Kinkajous are arboreal. They almost never come down to the ground. They can be found in all types of habitat, including floodplain and upland forest, and primary and secondary forest.

Kinkajous sleep in dicot tree holes and holes in the trunks of bottle palms (*Iriartea deltoidea* [Arecaceae]).

The kinkajou is nocturnal. It is almost never active in the daytime. It climbs around on the branches of trees looking for fruits, calling out “kuichik.” As it moves around up in the trees it rustles the branches lightly. Kinkajous come out of their holes during the day when a hunter climbs up a tree (to kill a sloth, retrieve an arrow, recover a killed monkey, etc.) and may try to bite him.

Kinkajous are solitary.

Kinkajous call out at night repeatedly saying “kuichik.”

Kinkajous eat mostly dicot tree fruits, especially those of këku (*Parahancornia peruviana* [Apocynaceae]) and bata (*Pseudolmedia* spp.

[Moraceae]). They also eat bottle palm (*Iriartea deltoidea*) fruits. They also eat the eggs of toucanets (*Selenidera* sp. [Rhamphastidae]) and other birds, baby birds, and adult passerines. They also eat katydids.

REMARKS: Matses observations about kinkajous are mostly consistent with published field studies of this species (e.g., Julien-Laferrière, 1993; Kays, 1999; Kays and Gittleman, 2001)—notably with respect to its exclusively nocturnal-arboreal activity and predominantly solitary lifestyle—but they are notably discrepant in one respect. Whereas published dietary studies suggest that *Potos flavus* is entirely frugivorous (Julien-Laferrière, 1999; Kays, 1999) or partially insectivorous (Bisbal, 1986; Redford et al., 1989), the Matses claim that it also eats bird eggs, nestlings, and adult birds. Given that captive kinkajous are known to eat meat and eggs (Ford and Hoffmann, 1988), Matses observations are not implausible, but the discrepancy is of interest. Although Matses hunters could have mistaken olingos for kinkajous, olingos are also thought to be frugivorous (Kays, 2000), so either the Matses are wrong, or there is still more to be learned about the diets of arboreal procyonids.

Procyon cancrivorus (Cuvier, 1798)

Figure 16D

VOUCHER MATERIAL (TOTAL = 1): Boca Río Yaquerana (FMNH 88876).

OTHER INTERFLUVIAL RECORDS: San Pedro (Valqui, 1999)

IDENTIFICATION: The single specimen of *Procyon* that we examined from the Yavari-Ucayali interfluvium (FMNH 88876) consists of the well-preserved skin and skull of a young adult female (with fully erupted permanent dentition but unworn molars). These elements exhibit all of the diagnostic qualitative traits of the subgenus *Euprocyon* and its single referred species, *P. cancrivorus*, including reversed fur on the nape of the neck, lack of a distinct lingual accessory cusp on I3, the isolated hypcone of P4, and massively developed molars

with robust cingula and rounded-coniform cusps (Hollister, 1915).

The external and craniodental dimensions of FMNH 88876 compare closely to those of almost-typotypical (Surinamese) specimens of *Procyon cancrivorus* tabulated by Husson (1978) but are slightly smaller for least interorbital breadth and zygomatic breadth and slightly larger for breadth of M1. The differences are not large enough, however, to suggest any substantial geographic variation among Amazonian populations of this species, all of which could be referred to the nominotypical race if a trinomial nomenclature were adopted. Selected measurements of FMNH 88876 are: head-and-body length, 494 mm; length of tail, 307 mm; hind foot, 143 mm; ear, 55 mm; condylobasal length, 127.0 mm; nasal length, 36.0 mm; least interorbital breadth, 25.2 mm; least postorbital breadth, 27.0 mm; zygomatic breadth, 81.8 mm; breadth of braincase, 56.8 mm; maxillary tooththrow (C1–M2), 52.2 mm; breadth of M1, 13.8 mm.

ETHNOBIOLOGY: The crab-eating raccoon is called *tsisebiekkid* (“one that is like the coati”). Although the name indicates a perceived similarity to the coati, the raccoon is not considered a type of coati. Few Matses have seen a crab-eating raccoon, and not all are familiar with its name. Some of our informants had heard of them, but none had seen one. The raccoon is of no economic importance to the Matses.

Since raccoons are so rarely encountered, the Matses have no specific beliefs regarding them and no special medicinal plants for contagions by a raccoon spirit. However, Matses medicine men say that they could make a child ill if touched or looked upon, and certain medicinal plants (“coati otter medicine”) would be expected to be effective.

MATSES NATURAL HISTORY: The raccoon is similar to the coati, but bigger and darker colored.

Perissodactyla (Tapiridae)

Only one valid species of perissodactyl, the Brazilian tapir (*Tapirus terrestris*), occurs in

TABLE 16

Measurements (mm) of Specimens of *Tapirus terrestris* Collected in the Yavari-Ucayali Interfluvium

	AMNH 74119	AMNH 73766	FMNH 88794
Age ^a	young adult	full adult	young adult
Sex	female	male	male
Head-and-body length	—	—	1935
Length of tail	—	—	85
Length of hind foot	—	—	353
Ear	—	—	130
Condylbasal length	—	377.0	371.6
Condylolincisive length	—	381.9	374.3
Length of nasals	89.4	106.8	97.2
Breadth of nasals	66.5	64.2	61.0
Least interorbital breadth	84.4	84.7	85.3
Least postorbital breadth	68.1	60.0	63.0
Zygomatic breadth	178.2	180.5	165.8
Cheektooth row (P1–M3)	142.0	136.5	—

^a After Hulbert (2010): “young adults” have fully erupted P4 and M2, but M3 is incompletely erupted and/or unworn; “full adults” have completely erupted toothrows and M3 shows moderate wear.

Amazonia, where it is ubiquitously distributed from the Andean foothills to the Atlantic coast. Although a second nominal species of Amazonian tapir, *T. “kabomani,”* was recently described by Cozzuol et al. (2013), analyses of mtDNA sequence data suggest that it is not genetically distinct from the widespread Brazilian species (Voss et al., 2014; Ruiz-García et al., 2016).

Tapirus terrestris (Linnaeus, 1758)

VOUCHER MATERIAL (TOTAL = 5): Boca Río Yaquerana (FMNH 88794), Nuevo San Juan (MUSM 11181), Orosa (AMNH 73766, 74118, 74119).

OTHER INTERFLUVIAL RECORDS: Divisor (Jorge and Velazco, 2006), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: Tapir specimens collected in the Yavari-Ucayali interfluvial region conform to the typical morphology of *Tapirus terrestris*

described by Hershkovitz (1954) and Husson (1978), and they do not include any examples of the unusual cranial phenotype described by Haggmann (1908) and Cozzuol et al. (2013). Measurements of our material (table 16) are all within a few millimeters of homologous values obtained from Surinamese specimens (Husson, 1978: table 55), suggesting little geographic variation in cranial dimensions across vast Amazonian landscapes despite modest mtDNA heterogeneity in this species (Thoisly et al., 2010; Ruiz-García et al., 2016).

ETHNOBIOLOGY: The principal name for the tapir is *nēishamē*, which can be analyzed as meaning “large game animal.” There are three archaic synonyms: *awad* (a monomorphemic pan-Panoan term), *wisu* (an archaic term that also means “black”), and *danchish* (synchronically unanalyzable, but seems to include the prefix *dan-*, meaning “knee”). The tapir is the only animal with pet vocative¹³ terms: *dampiyada* and *choada* (both synchronically unanalyzable, but

¹³ Pet vocatives are special words used for calling tame animals kept as pets (Dienst and Fleck, 2009).

the first also seems to include the prefix *dan-*). In the language used in the Matses' *komok* ceremony, the tapir is called *dëpachi*, a term that means "soft snout."

The Matses recognize three types of tapirs: *nëishamëdapa* ("large tapir"), *nëishamë chëshë* ("black tapir"), and *nëishamë mëbëdi* ("striped-foreleg tapir"). According to Matses hunters, the type with striped forelegs is the smallest of the three varieties, prefers upland forest (as opposed to floodplain forest), and when chased by dogs runs without tiring out. The large variety is found along large rivers and is the type that most readily takes refuge in the water when chased by dogs.

The tapir is a principal game animal for the Matses, although tapirs are killed infrequently compared to other game species. In addition to providing a bonanza of meat, a butchered tapir is much appreciated for its fat, which is carefully rendered for frying manioc and plantains, and to make an oily broth thickened with grated manioc. Tapirs are desirable pets that quickly become tame when captured as juveniles. Even as adults, pet tapirs roam the village peacefully.

Tapirs are killed by the Matses in various ways. A hunter may happen upon a tapir as it sleeps on the forest floor and shoot it with a shotgun (formerly it would have been shot with a bow and arrows). Or, a hunter may find tapir spoor and track the animal to where it is sleeping or feeding, and then shoot it. Hunters also encounter tapirs at mineral licks. When a tapir has been scared off or runs off when shot and injured, the hunter whistles, imitating the tapir's call. Interestingly, the tapir often replies with a whistle or comes to where the hunter has whistled, even if it has been shot. Often a shot tapir escapes, and killed tapirs are sometimes found to have healed shotgun wounds.

Tapirs are also hunted with dogs. The best hunting dogs will chase a tapir, nipping at its legs. If the dogs do this, or if the tapir tires out, it may take refuge by submerging itself in a deep bend of a stream. (If the dogs do not follow the tapir closely or far enough, the tapir will just keep run-

ning and the hunter will not be able to catch up.) Once the hunter reaches the place where the tapir is submerged, he kills it. In the past the tapir would be killed in such a situation with a spear as it lay underwater. If the stream is too deep, the hunter will try to get the tapir to move away from the deep river bend and shoot it (with a shotgun or, formerly, with arrows) when it emerges into a shallower part of the stream.

Now that the Matses have acquired flashlights, they sometimes wait for tapirs at mineral licks at night. A hunter may visit a mineral lick during the day and find fresh tapir tracks. Since tapirs often return to the same mineral licks, the hunter builds a platform about 2 m off the ground and returns at dusk to wait, sitting on the platform.

An additional method for killing tapirs, which is not employed frequently anymore, is to build a trap along a tapir path, usually at the edge of a mineral lick or where tracks reveal that a tapir comes every night to feed on fallen fruits. A pole some three meters long is cut from a sapling and lashed with epiphyte stems to a tree that is right next to the tapir path; the pole is lashed parallel to the tree, with the lashed end at the top and the bottom end about 40 cm above the ground (about tapir-chest height). Next, a daggerlike bamboo blade about 50 cm long is lashed to the pole (pointing toward the tree). Thus armed, the pole is bent away from the tree and held in place by an ingenious trigger mechanism actuated by a trip wire (figs. 17, 18). When the tapir walks by, it hits the trip wire with its foreleg, releasing the spring-loaded pole with the bamboo blade. If the bamboo blade stabs it in the chest, the tapir will die close to where the trap was set. Often, however, the tapir is not mortally wounded. The trap is checked every three days or so, and if the trap has been sprung, the hunter follows the blood trail to find the dead or injured tapir. The tapir may need to be finished off with a club or by shooting.

Because an adult tapir is too large to be carried by a single person, a successful tapir hunter will return to his village to recruit other Matses,

especially women, to come to the kill site and help butcher the carcass. The tapir is skinned and butchered by the women, after which everyone carries back a portion of the carcass to his or her own household. The hunter who killed the tapir takes home the ribs and other choice portions and then invites others to eat at his house. In this way, everyone in the village partakes of the tapir.

The Matses believe that, while packing tapir meat back to the village, one must not look back over one's shoulder toward the butchering site, lest someone in the family die. Women and young men cannot eat the tail or the part of the rump near the tail, lest they begin to walk bent over like an old man. While waiting at home for a tapir trap to be sprung, the hunter who set the trap follows several dietary restrictions (e.g., he does not eat tortoise or spider monkey meat) and must abstain from sexual intercourse, lest the trap not be sprung or the tapir not be mortally injured. Additionally, men who regularly set tapir traps do not eat the liver and intestines of tapirs. Pregnant women do not eat young tapirs (or young game animals in general), lest they grow weak while giving birth. Young men likewise do not eat young tapirs (or young animals in general), lest they become cowards. Thus, only old people may safely eat immature tapirs.

When a hunter kills, eats, or sees a tapir, the spirit of the tapir may cause one of his young children to fall ill. Occasionally a tapir's spirit makes a child ill even if there has been no contact with a tapir. The symptoms for contagion by tapir spirits are a high fever and the rolling of eyes into the back of the head. When a child exhibits these symptoms after the father has eaten or had contact with a tapir, a medicine man will collect medicinal plants known as "tapir medicine" and bathe the child with an infusion of the leaves.

MATSES NATURAL HISTORY: The tapir is dark colored. It has large ears with white tips. Its snout is soft and flexible and can be curled upward. Its feet are flat. It has much fat and a thick hide. The male has a large penis.

The tapir uses all types of habitats, including floodplain and upland forest, palm swamps, primary forest, secondary forest from blowdowns, and secondary forest from abandoned swiddens. Tapirs are especially common in the floodplains of rivers and streams. They come to Matses swiddens to eat manioc leaves, but only in swiddens that people do not visit regularly, such as those made at hunting camps.

The tapir is mostly nocturnal. It is more wary when the moon is bright. It sleeps during the day on the ground, often on dry hilltops or at the edge of a treefall. It does not sleep in the same spot every night. It does not walk around in the late morning if the sun is shining, but does when it is cloudy or raining. It travels far, crossing streams and rivers. It has many paths in the forest. It leaves its path, foraging in a large circle, and return to the same place where it had left the path.

It visits mineral licks between 7 PM and midnight, and between 2 AM and dawn (as noted by hunters that wait for tapirs at mineral licks). The tapir eats mud and drinks muddy water at mineral licks (small areas in the forest with poor drainage where minerals collect and the activity of animals make the area muddy). It always returns to the same mineral licks to drink the muddy water; that is, it visits several different mineral licks, but returns to the same ones. There is often a well-worn tapir path leading to a mineral lick. Sometimes several tapirs congregate at mineral licks and a tapir may use a mineral lick together with deer.

The tapir walks around constantly eating the leaves or succulent stems of understory plants. It bends down saplings to eat the leaves. In secondary forest it frequently bends over small *Cecropia* trees to eat the leaves (but not the stems). It pulls down certain types of soft vines and chews and sucks on them. It drinks water in deep bends of large streams. It defecates in the deep parts of little streams.

The tapir is usually solitary. It gives birth to a single large young. The tapir gives birth in the open, at the edge of a blowdown. It goes to eat without



FIG. 17. Tapir trap, ready for action near Estirón, 2017 (photo by D.W.F.). A flexible pole (a) is tightly lashed to a tree with an epiphyte-stem binding (b); a sharp bamboo blade (c, partially sheathed with palm leaflets) is firmly attached to the other end, which is bent away from the tree and held in place by a camouflaged trigger mechanism (d). The trigger mechanism (close-up in figure 18) is released by a trip-wire (e).

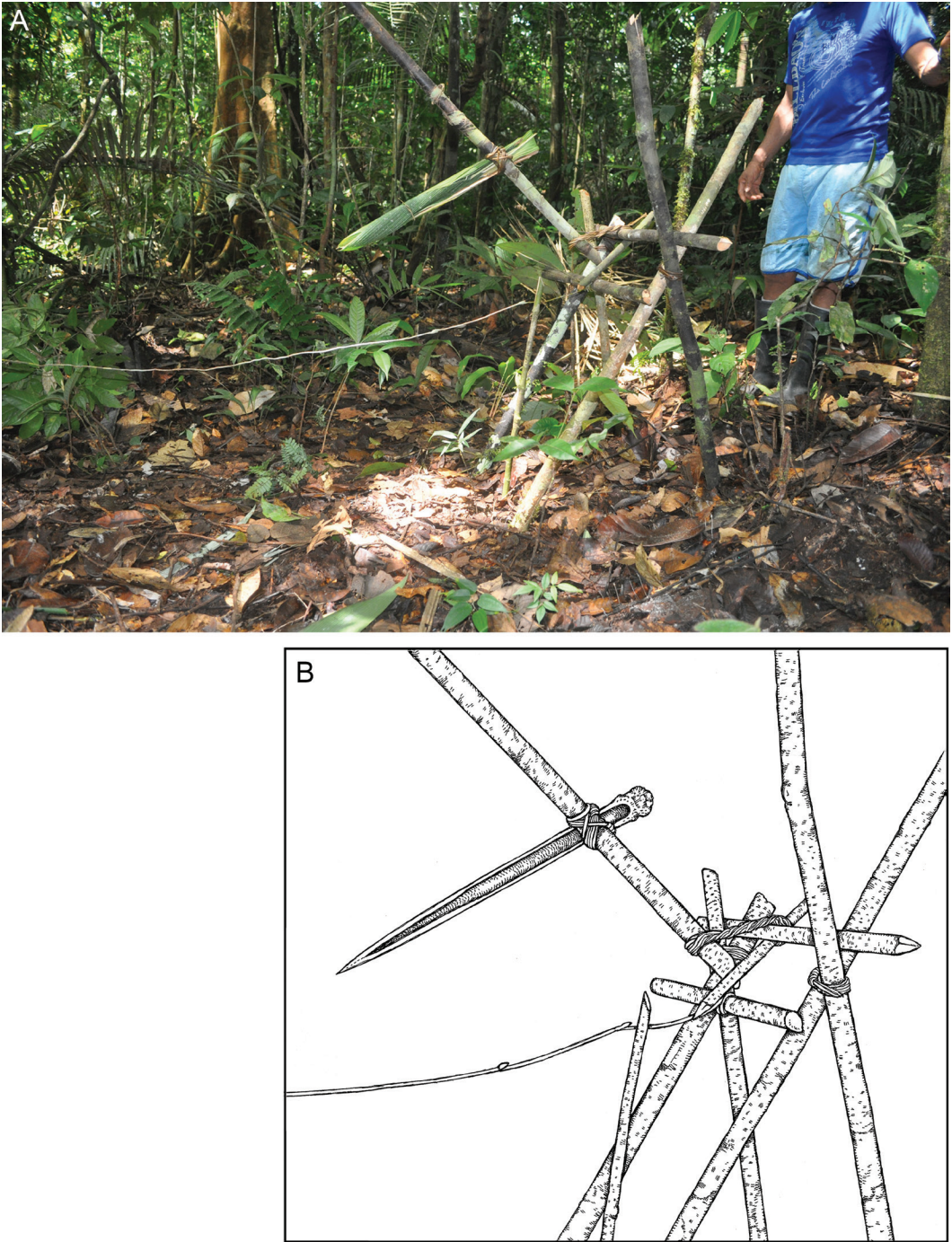


FIGURE 18. Close-up of tapir-trap trigger stripped of camouflage (A), but with bamboo blade still sheathed with palm leaflets; and diagram of the trigger mechanism (B), with bamboo blade exposed.

going far and comes back to suckle its young repeatedly. It suckles its young while lying on its side. When the young tapir grows strong, the mother takes it to forage for fruits at night, and the young tapir eats the fruits too. Then the mother takes the young tapir to a good place to sleep during the day. The young tapir leaves the mother when it becomes black (i.e., loses its stripes).

Tapirs are eaten by jaguars, but not by pumas. Large anacondas occasionally capture and eat tapirs. Large tabanid flies are always biting tapirs.

The tapir whistles loudly, saying “pin.” When a Black Caracara (a vulturelike falcon, *Daptrius ater*) calls out, the tapir answers with this same whistling call, and goes to where the caracara is calling. The young tapir whines saying “chee-oo chee-oo chee-oo” when its mother leaves it. It snorts and stamps its feet. It travels through the forest making a lot of noise as it crushes through the vegetation.

The tapir eats the young leaves of dicot plants and small trees, including those of shuishèn chete (?*Alchornea* sp. [Euphorbiaceae]) and cecropias (*Cecropia* spp. [Moraceae]). It also sucks on and eats the stems of soft vines and the leaves of harder vines that it pulls down to the ground. It eats the leaves of epiphytes that grow close to the ground. It also eats the stems (and leaves) of succulent plants.

It eats many types of fallen dicot tree fruits, including those of the rubber tree (*Castilla* [Moraceae]), dadain (*Clarisa racemosa* [Moraceae]), figs (*Ficus* spp. [Moraceae]), diden këku (*Parahancornia peruviana* [Apocynaceae]), nuëkkid neste tree (*Bellucia* sp. [Melastomataceae]), nëishamë naësh (unidentified), echo (*Jacaratia* sp. [Caricaceae]), and pënkad (an unidentified large tree with large fruits that the Matses also eat). It eats the mesocarp of the fruits of swamp palms (*Mauritia flexuosa* [Arecaceae]) and isan palms (*Oenocarpus bataua*). It also eats fallen fruits of some types of epiphytes in the family Araceae.

REMARKS: Matses interviews about tapirs include many familiar aspects of the biology of this culturally important species, including its

marked preference for floodplain habitats, use of paths, nocturnal visitation of mineral licks, solitary behavior, mixed diet of browse and fruit, and curious habit of defecating in water (Salas, 1996; Salas and Fuller, 1996; Henry et al., 2000; Tober et al., 2009; Link et al., 2012). Additionally, several food-plant taxa mentioned by our informants have previously been reported in tapir dietary studies (e.g., Bodmer, 1990; Salas and Fuller, 1996; Henry et al., 2000). However, the Matses state unequivocally that tapirs are killed and eaten by jaguars and large anacondas, whereas Salas (1996) claimed that adult tapirs are immune from predation. Because jaguars in the Pantanal and Cerrado are definitely known to kill tapirs as well as cattle (which are substantially larger than adult tapirs; Cavalcanti and Gese, 2010; Sollmann et al., 2013), and because green anacondas (*Eunectes murinus*) are also known to prey on tapirs (Martins and Oliveira, 1999), we do not doubt that the Matses are correct, although their accounts do not explicitly report the age of tapirs taken by these formidable predators.

Artiodactyla (“Cetartiodactyla”)

Six species of artiodactyls in four families (including cetaceans) are definitely known to occur in the Yavari-Ucayali interfluvium. Whereas the families of terrestrial artiodactyls (Tayassuidae and Cervidae) are each represented by two species in our region, the aquatic families (Iniidae and Delphinidae) are represented by a single species each.

Tayassuidae

Two tayassuid species, the collared peccary (*Pecari tajacu*) and the white-lipped peccary (*Tayassu pecari*), are definitely known to occur in the Yavari-Ucayali interfluvium. As currently recognized, both species occur throughout Amazonia, and no other tayassuids are expected in our region. Although a third Amazonian tayassuid, *Pecari maximus*, was recently described from the Madeira-Tapajós interfluvium (Roosmalen et al., 2007) and was subsequently alleged to also occur

TABLE 17
**Measurements (mm) and Weights (kg) of Adult Specimens of *Pecari tajacu*
 from the Yavari-Ucayali Interfluve**

	FMNH 88799	FMNH 88800	FMNH 88802	FMNH 88803	FMNH 89176	FMNH 89177	MUSM 11182	MUSM 11183
Sex	female	female	female	male	male	male	male	male
Head-and-body length	905	905	990	1007	955	945	887	905
Length of tail	23	25	25	25	20	32	40	40
Hind foot	210	210	215	210	214	210	206	201
Ear	83	84	88	85	88	85	89	88
Weight	—	—	—	—	—	—	27.5	29.0
Condylobasal length	201.8	206.1	215.1	223.5	208.7	210.2	205.8	221.0
Condylolincisive length	204.1	208.5	217.0	—	212.0	211.1	205.6	220.9
Length of diastema	17.0	16.2	20.5	21.3	19.9	15.4	17.5	21.4
Rostral breadth at diastema	33.1	32.7	34.0	34.9	34.4	36.8	35.7	30.0
Least interorbital breadth	51.6	51.3	57.0	61.7	57.7	54.5	56.8	57.0
Zygomatic breadth	98.6	104.7	105.1	116.0	115.6	104.7	110.4	113.9
Cheektooth row (P2–M3)	67.5	70.4	62.7	70.6	68.8	69.8	67.9	66.2
Breadth of M2	12.7	14.0	13.0	13.9	14.5	14.1	14.3	13.5

in Bolivia (near the Peruvian border; Moravec and Böhme, 2009), molecular sequence data suggest that *P. maximus* is not genetically distinct from the collared species (Gongora et al., 2011).

The generic taxonomy of peccaries has been historically unstable. Husson (1978), for example, referred the white-lipped species to *Dicotyles* Cuvier, 1816, and the collared species to *Tayassu* Fischer, 1814, whereas previous authors (e.g., Cabrera, 1961) often referred both species to *Tayassu*. The current use of *Pecari* Reichenbach, 1835, for the collared species (Grubb, 2005) follows Miller (1912), whereas current usage of *Tayassu* for the white-lipped species follows Hershkovitz (1963). Although it is now widely agreed that the white-lipped and collared species should be placed in separate genera, and despite the fact that the binomina used below are now well established in the literature, it is only too likely that some future reinterpretation of the technical rules governing type species of genus-group names (ICZN, 1999: Chapter 15) will suggest different combinations.

Pecari tajacu (Linnaeus, 1758)

VOUCHER MATERIAL (TOTAL = 9): Boca Río Yaquerana (FMNH 88799–88802, 89176, 89177), Nuevo San Juan (MUSM 11182, 11183), Quebrada Esperanza (FMNH 88803).

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Choncó (Amanzo, 2006), Divisor (Jorge and Velazco, 2006), Itia Tëbu (Amanzo, 2006), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Specimens of *Pecari tajacu* collected in the Yavari-Ucayali interfluve externally resemble the widespread Amazonian phenotype (Husson, 1978; Emmons 1997), and craniodental measurements of our material (table 17) broadly overlap those of Surinamese specimens (Husson, 1978: table 58) for most dimensions. Although skulls of *P. tajacu* from the Yavari-Ucayali interfluve seem to average a bit larger than conspecific Surinamese specimens,

they are much smaller than the skulls of *P. maximus* measured by Roosmalen et al. (2007: table 1). For example, whereas the mean and standard deviation for condyloincisive length in our material ($N = 7$, males and females combined) is 211.3 ± 6.0 mm, the homologous dimensions of two specimens of *P. "maximus"* (sex unknown) are reported as 260 and 262 mm (Roosmalen et al., 2007). Although sample size and sample composition are obviously problematic in this comparison, the estimated mean difference between our material and Roosmalen et al.'s (about 50 mm, equivalent to eight standard deviations) is too large to be easily dismissed as intraspecific variation. If *P. tajacu* populations sometimes include "extremely large" individuals—equivalent in size to Roosmalen et al.'s material, as Gongora et al. (2011) suggest—we have not seen any evidence of it.

Analyses of mtDNA control region sequences (Gongora et al., 2006, 2011) suggest the existence of two moderately well-supported phylogroups of *Pecari tajacu*, consisting of predominantly North American and Central American sequences on the one hand and of South American sequences on the other. Unfortunately, the relevance of this analytic result for assessing the plethora of currently recognized subspecies (Grubb, 2005) is unclear, because no sequence data are available from the type localities of several key nominal taxa, including the nominotypical form (restricted by convention to Pernambuco, Brazil; Cabrera, 1961; Hershkovitz, 1963). At the moment, no trinomial classification of *P. tajacu* seems justified by the analytic results in hand, although Amazonian material is often referred to *P. t. patira* Kerr, 1792.

ETHNOBIOLOGY: The principal term for the collared peccary is *shëkten*, a monomorphemic term that is not found in any other Panoan language. The collared peccary has two archaic synonyms: *unkin* and *matosh*, both of which are monomorphemic terms found in other Mayoruna languages, but not in other Panoan languages.¹⁴ In

the language used in the Matses' *komok* ceremony, the collared peccary is called *pani tuku*, a term that is not synchronically analyzable.

Two varieties of collared peccaries are recognized: *shëkten chëshë* ("black" or "dark-colored" collared peccary) and *shëkten uşhu* ("white" or "light-colored" collared peccary). The dark variety is said to be larger. The light colored variety does not enter holes quickly when chased by dogs and its hide dries more quickly than that of the darker variety.

The collared peccary is a primary game animal for the Matses, who encounter them in various ways. Hunters hear collared peccaries crunching up palm nuts and then approach quietly and shoot them with a shotgun (formerly with arrows). Hunters also visit mineral licks during the day to see if peccaries or other game animals are there. When one collared peccary is killed, the rest of the herd will run off, but if the hunter remains hidden and quiet, the rest of the herd often returns (even if a shotgun was used), and the hunter can kill a second peccary. The herd may even return a third and fourth time.

Hunters also track collared peccaries after finding their spoor. Collared peccaries often sweep away leaf litter, root, defecate, rub their scent gland on saplings, and leave tracks right on Matses paths. Hunters follow spoor until they can hear the animals, or until their hunting dogs pick up the scent.

One hunting method that, as far as we know, is employed only by the Matses, is to chase down a collared peccary with dogs until it enters a hole in a headwater gully or a hollow log, and then to strangle it with a noose on a stick. When Matses hunting dogs find a herd of collared peccaries, they chase them as the hunter follows, encouraging the dogs. If the dogs follow a peccary closely enough, the peccary (usually one, but occasionally two or three) may seek refuge in a hole in a stream headwater gully. These holes are cavities in the bank that have been formed over time by erosion; often the roof of such a hole will be close to the surface of the ground overhead. Alternatively, the peccary may enter a hollow log. When

¹⁴ See Fleck (2013: table 1) for a classification of Mayoruna and other branches of the Panoan language family.

the hunter catches up to the dogs and the cornered peccary, he blocks the entrance to the hole or log with any dry or rotten woody debris that he can find nearby. Then he prepares a noose from the hard vinelike stems of an epiphyte called *ayash* (*Heteropsis* spp. [Araceae]) and attaches it to the end of a stick about 1 m long. Next, the hunter pokes a small hole in the roof of the hole or hollow trunk, introduces the noose, works it around the peccary's neck using the stick, and garrotes the animal.

Slain peccaries—both collared and white-lipped—are prepared for packing home in a particular way (figs. 19, 20). First, the lower jaw is tied to the ankles of the forelegs with an epiphyte stem (the same stem used to make the noose, if the peccary was killed in this manner). Then the ankles of the hind legs are tied to those of the front legs. Next, a tumpline is fashioned from the inner bark of certain trees, one end of which is tied to the upper jaw and the other end to the rump. The lower tusks keep the lashing from slipping, and the upper tusks keep the tumpline from slipping. If the animal was killed far from the village, the carcass is gutted to lighten the load. Before carrying the peccary, the hunter rubs his dogs' noses on the peccary's caudal scent gland so that they will follow peccaries readily in the future.

The carcass is skinned at home by a woman. Other women will come to where the skinner is working and ask for a leg or part of the viscera, and she will give it to them. Different cuts are given or fed to different people, for example, an old woman typically eats the intestines, visiting men the ribs, a young woman is given the leg, etc. If the peccary was killed by dogs, the dogs will be fed some of the meat.

The Matses raise collared peccaries as pets. The young are often left behind when the adult peccaries flee, and these can be chased down and caught. Tame young peccaries are allowed to roam the village, but peccaries become aggressive when they are older and must be kept in a pen. Peccaries are not raised in sufficient numbers or in conditions that would allow them to reproduce in captivity, and the Matses do not eat their pets.

Collared peccary hides can be legally sold, but currently the hides are not worth much, so the Matses only occasionally prepare the skins of peccaries they have killed. Some Matses smoke peccary meat for sale to non-Indians at Colonia Angamos and Requena. However, it is mainly those who live close to these markets who do so regularly, because the money earned by selling smoked meat barely covers the cost of the gasoline needed for canoe travel from more distant Matses villages.

Men do not eat the intestines of peccaries, lest they scrape themselves with a rough-barked vine while they are chasing animals during a hunt. Hunters do not eat peccary spleens, lest their spleens hurt while chasing game animals.

MATSES NATURAL HISTORY: The collared peccary has a white stripe around its neck. It has large ears and a flat-tipped nose. It has two hooves on each foot. It has a tiny tail. Even newborns have a caudal scent gland, which emits a very strong smell that is different from the scent of white-lipped peccaries. Its feces are seed-shaped pellets.

The collared peccary is found in all habitats, including floodplain and upland forest, and primary and secondary forest. They are especially commonly found along small and medium-sized streams. They seem to be more abundant in areas that are near abandoned Matses villages, where there are large stretches of secondary forest growing in abandoned swiddens. They also come to active Matses swiddens to eat manioc tubers and cush-cush yams.

Collared peccaries are diurnal. They travel far looking for fruits to eat. They chew loudly on palm nuts. They follow streams, rooting for earthworms in the rich soil of the stream floodplain and digging in the streambed for aquatic snails. They leave the water turbid where they have foraged in the streambed, and in areas where they have rooted the leaf litter is swept away. They also root on hilltops, leaving the ground swept clear.

Collared peccaries drink muddy water, eat mud, and bathe at mineral licks. They also root for earthworms at the edge of mineral licks and



FIG. 19. White-lipped peccary carcass with tumpline attached for carrying. The epiphyte-stem binding that formerly attached the forelegs to the lower jaw and the hind legs to the forelegs has been cut (photo by D.W.F.; Estirón, 2013). The tumpline, tied to the upper jaw and the rump, is made from the inner bark of a *tote* tree (*Eschweilera* or *Lecythis* spp. [Lecythidaceae]), the preferred material for this purpose (compare with fig. 22).

palm swamps. They come to swiddens where they root in the ground with their noses to expose manioc tubers.

Collared peccaries take mud baths in small muddy depressions in the ground. A depression used for this purpose is often created when a tree is blown over and its roots are uplifted. Peccaries return again and again to bathe in the same mud holes, and are often caked in mud. As they travel through the forest they leave their scent on saplings by rubbing their scent glands on them.

Collared peccaries sleep on the ground wherever they are when it becomes night. They sleep on hilltops, stream valleys, and even on hillsides if the slope is not too steep. They sweep a small patch of ground (but do not dig a

depression, as they do to give birth) and sleep on it. They sleep near each other, but not touching, with a space of about 1 m separating one from another.

Collared peccaries live in herds of 5 to about 15 individuals. Occasionally one finds a solitary peccary, or a pair. Collared peccaries are fattest at the end of the rainy season (May). The female gives birth to a single young during the rainy season after digging a depression in level ground. It suckles its young right in the same place where it gave birth. During the first day, the female leaves her young to eat fruits and then comes back to suckle it again. By the second day the newborn peccary begins to travel, very slowly, with the herd. During the first day the rest of the herd stays around the area where the female gave



FIG. 20. Use of the tumpline for carrying white-lipped peccary carcass (photo by D.W.F.; Estirón, 2013).

birth, and after that they walk slowly so the newborn can keep up (the female does not separate herself from the herd to give birth).

Collared peccaries are eaten by jaguars, pumas, and (less frequently) by anacondas.

Adults make groanlike grunts. They clack their teeth when they become aggressive. The young also grunt, saying “wek wek wek.”

Peccaries crunch the hard nuts of pinchuk palms (*Astrocaryum murumuru*, *A. chambira*, and *A. jauari* [Arecaceae]) to eat the endosperm. They also eat the endosperm of shuinte mapi (*Attalea tessmanii* [Arecaceae]) nuts and the mesocarp and endosperm of swamp palm (*Mauritia flexuosa* [Arecaceae]) fruits and isan (*Oenocarpus bataua* [Arecaceae]) fruits. Among the dicot tree fruits they eat are kuëte ise (unidentified), poshton tonte (?*Macoubea guianensis* [Apocynaceae]), tonnad (a general term for trees

in the family Myristicaceae), kuëte mëdiad (an unidentified tree with starchy fruits), and tote (*Eschweilera* spp. and *Lecythis* spp. [Lecythidaceae]). Collared peccaries also eat the new unrolled leaves of wild banana plants. They gnaw on the pith of fallen budëd palms (*Attalea butyracea* [Arecaceae]).

They also eat invertebrates, including aquatic snails, clams, crabs, freshwater shrimp, and earthworms. They occasionally find and eat rotten meat.

REMARKS: Matses observations about collared peccaries are richly detailed and suggest long and intimate familiarity with this primary game species. All the salient facts about collared peccary natural history documented in the literature are reported by the Matses, including diurnality, small herd size, use of wallows and mineral licks, scent-marking, feline predators, and a mostly frugivorous/gra-

TABLE 18
 Measurements (mm) and Weights (kg) of Adult Specimens of *Tayassu pecari*
 from the Yavari-Ucayali Interfluve

	FMNH 88795	FMNH 88796	FMNH 88797	FMNH 88798	MUSM 11184
Sex	female	female	male	male	male
Head-and-body length	1170	1125	1085	1098	1090
Length of tail	35	30	30	32	25
Hind foot	243	235	233	241	226
Ear	79	79	76	79	79
Weight	—	—	—	—	41.0
Condylobasal length	258.0	252.2	249.1	252.6	243.0
Condylolincisive length	—	252.7	250.5	251.3	243.7
Length of diastema	31.1	27.1	27.5	27.4	32.0
Rostral breadth at diastema	53.6	53.6	52.8	51.9	58.9
Least interorbital breadth	61.8	59.8	62.3	61.2	62.5
Zygomatic breadth	118.5	117.8	117.8	121.4	124.0
Cheektooth row (P2–M3)	80.6	83.8	78.4	81.5	81.1
Breadth of M2	15.2	16.6	16.1	15.9	15.8

nivorous diet supplemented by invertebrates and browse (Kiltie, 1981, 1982; Kiltie and Terborgh, 1983; Byers, 1985; Bodmer, 1989; Tobler et al., 2009; Blake et al., 2012). Matses observations confirm the fondness of this species for the very hard, golf-ball-size nuts of *Astrocaryum* spp., the coconutlike endosperm of which is an important trophic resource otherwise accessible only to capuchin monkeys (Terborgh, 1983; Voss and Fleck, 2011), white-lipped peccaries (Kiltie, 1982; see below), and rodents (Emmons, 1997; Voss and Fleck, in prep.). Interestingly, the Matses claim that collared peccaries consume the dense, ivory-hard endosperm of *Mauritia flexuosa* seeds, which Kiltie (1982) believed to be eaten only by white-lipped peccaries. Other noteworthy dietary items are aquatic mollusks and crustaceans, both seemingly improbable food resources, but snail opercula were reported from peccary stomachs by Kiltie (1981). Many other behavioral details (e.g., of nocturnal bivouacking) are not described in the literature we consulted.

Tayassu pecari (Link, 1795)

VOUCHER MATERIAL (TOTAL = 5): Boca Río Yaquerana (FMNH 88795–88798), Nuevo San Juan (MUSM 11184).

OTHER INTERFLUVIAL RECORDS: Choncó (Amanzo, 2006), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirím (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: Specimens of *Tayassu pecari* collected in the Yavari-Ucayali interfluve agree in all qualitative respects with near-topotypical material described by Husson (1978), and measurements of our material (table 18) overlap broadly with Husson's (1978: tables 56, 57). As usual, the current subspecific classification (Grubb, 2005) is difficult to reconcile with the results of analyzing mtDNA sequence data (Ruiz-García et al., 2015).

ETHNOBIOLOGY: The Matses term for the white-lipped peccary is *shëktenamë*, analyzable as meaning "large collared peccary." As with the term *shëkten*, the term *shëktenamë* is not found

in other languages. The archaic term for the white-lipped peccary, chede, is monomorphemic and found in some other Mayoruna languages. In the language used in the Matses' komok ceremony, the white-lipped peccary is called pashankid, a term whose meaning seems to contain the nominalizing suffix -kid, but the meaning of pashan is not clear.

As with the collared peccary, two varieties are recognized, shëktenamë çhëshë ("black" or "dark-colored" white-lipped peccary) and shëktenamë uşhu ("white" or "light-colored" white-lipped peccary). The dark variety is said to be larger and has a very white jaw, while the lighter variety is said to have a grayish, less contrastingly colored jaw. An additional name is panchu, which uniquely designates the leader of a white-lipped peccary herd.¹⁵

White-lipped peccaries are a primary game species for the Matses. The Matses find them while hunting in the forest by smell, or when dogs pick up their scent, or when they are heard grunting or crunching palm nuts. Hunters also find their tracks, or see muddied water flowing downstream from where a herd has foraged in the streambed. White-lipped peccaries are sometimes encountered by canoe travellers, who find herds crossing rivers, see their tracks on the bank where they have crossed, or smell or hear them eating in the forest near the banks. Unless he encounters white-lipped peccaries far from the village, a hunter is expected to refrain from killing them and to return to the village to recruit other men to come and hunt them collectively. If the herd is found at the end of the day, the hunt will begin at dawn the following day.

Matses hunters usually kill white-lipped peccaries with shotguns or arrows. Since there are seldom enough shotguns to arm all the men in a village, bows and arrows are still used in these collective hunts. Also, because there is often a shortage of ammunition, spears are

often made on the spot from the trunks of sinnad palms (*Bactris* spp. [Arecaceae]), oninansiante (*Iriartella stenocarpa* [Arecaceae]), or from the petioles of the stemless budëd uşhu (*Attalea microcarpa* [Arecaceae]). If it is a very large herd, the peccaries may not run off when hunters start to kill them, defending themselves by trying to bite the hunters. In such cases the Matses can easily kill many individuals, although hunters may have to climb trees if they are attacked. If the peccaries run off, as is most frequently the case, the hunters will chase after them. Because white-lipped peccaries do not run quickly and can be headed off, they are easily killed, and one can even get right next to them while running and kill them with a spear or club. When the leader of the herd is killed, the peccaries run aimlessly, often circling back toward the hunters. When clubbed on the head, right where its ears are, the peccary dies immediately.

Dogs are also used to hunt white-lipped peccaries. Dogs can help tire out the peccaries, giving the hunters a chance to catch up, if the herd had a good head start. Additionally, a white-lipped peccary that is chased by a dog may stop, turn to face the dog, and try to bite it. If the hunter can catch up in time, he kills the peccary. However, dogs are often bitten during such hunts.

White-lipped peccaries are considered potentially dangerous, and any children present during a hunt are told to climb trees in case the peccaries become fierce. Baby white-lipped peccaries are often captured during hunts and kept as pets, although captive animals become fierce as adults and must be kept in a pen. White-lipped peccary hides could formerly be sold legally, so the Matses used to prepare them for sale, but only collared peccary hides are purchased now. Some hunters smoke white-lipped peccary meat for sale at nearby non-Indian towns.

Men do not eat the heart, lest they lose their endurance while running after game.

MATSES NATURAL HISTORY: White-lipped peccaries are larger than collared peccaries. Their

¹⁵ Panchu is not used for the leader of the herd, troop, pack, or flock of any other animal.

lower cheeks and jaws are white. Their feet have two hooves. They emit a strong, foul smell, different from that of collared peccaries.

White-lipped peccaries walk and sleep in all types of habitats, including upland and floodplain forest, and palm swamps.

White-lipped peccaries are diurnal. They sleep at night on the ground and set out at dawn. They travel very far, swimming across rivers, and come back after a long time. When the Matses kill some of them, the rest of the herd travels very far away and comes back only after a very long time. They travel slowly when there are many recently born young. They go around looking for fallen tree fruits and fallen palm nuts that they crunch loudly. They follow streams rooting in the floodplain earth for earthworms and digging into the streambed looking for mollusks and crustaceans. They make the water turbid where they dig into streambeds. They leave a wide path where they travel and leave large cleared areas where they have rooted. They raise the hair on their back and clack their teeth facing upward when they become aggressive.

White-lipped peccaries frequent mineral licks, where they drink the muddy water, eat mud, and bathe. They root beside mineral licks for earthworms.

White-lipped peccaries live in large herds (of up to 200 individuals) or in smaller herds (of 20 or 30 individuals). A large old male leads them.

White-lipped peccaries are fattest at the end of the rainy season (May). The female gives birth to a single young during the rainy season where the herd stops to sleep for the night. The first day the young does not walk, and the mother suckles it while the rest of the herd forages in the vicinity, without leaving the new mother. The next day, while its umbilical cord is still hanging, she takes it traveling around with the rest of the herd, moving slowly. The rest of the herd also travels slowly to let the newborn(s) keep up. The female eats and lies down frequently to suckle her young.

Jaguars and pumas eat white-lipped peccaries.¹⁶

White-lipped peccaries grunt, snort, scream, and clack their teeth. The young grunt saying "wek wek." They travel through the forest making a lot of noise.

White-lipped peccaries eat aquatic snails, clams, crabs, freshwater shrimp, earthworms, snakes (including pitvipers), and rotten meat. They eat many types of dicot tree fruits. They are especially fond of pinchuk (*Astrocaryum* spp. [Arecaceae]) nuts. They eat the mesocarp and endosperm of swamp palm (*Mauritia flexuosa* [Arecaceae]) fruits. They eat the new leaves of wild banana plants.

REMARKS: Matses interviews about white-lipped peccaries are much less informative than those about collared peccaries, presumably because this species is encountered at infrequent intervals. Although broadly consistent with the scattered literature (e.g., Kiltie and Terborgh, 1983; Fragoso, 1998, 1999; Tobler et al., 2009) in most respects, Matses observations do not suggest that this species routinely eats any item not also eaten by collared peccaries (contra Kiltie, 1982; see above), with the possible exception of venomous snakes.

Cervidae

There are two species of deer in Matses territory, the red brocket (*Mazama americana*) and the gray brocket (*M. nemorivaga*). The general term that designates both of these species is senad (monomorphemic and absent from other Panoan languages), and its archaic synonym is chashu (monomorphemic, but a common name for deer in other Panoan languages). While the two species of local deer have specific names, and two overdifferentiated varieties of one species are recognized and named, the Matses almost always use the term senad, unmodified, to talk about deer.

¹⁶ But pumas are said to eat only the young of this species (see the account for *Puma concolor*, above).

TABLE 19

Measurements (mm) and Weights (kg) of Adult Specimens of *Mazama americana* and *M. nemorivaga* from the Yavari-Ucayali Interfluve

	<i>M. americana</i>			<i>M. nemorivaga</i>	
	AMNH 74117	MUSM 11185	FMNH 88806	MUSM 11186	FMNH 86898
Sex	female	female	male	female	male
Head-and-body length	—	1200	1115	1011	975
Length of tail	—	150	125	131	100
Hind foot	—	312	300	298	302
Ear	—	100	92	87	85
Weight	—	36.0	—	24.0	—
Condylobasal length	216.3	197.0	196.9	170.4	177.1
Length of nasals	63.1	63.7	63.7	56.8	56.3
Least interorbital breadth	42.9	40.7	44.2	34.7	39.0
Least postorbital breadth	48.9	54.8	—	46.6	—
Zygomatic breadth	95.1	90.6	92.6	80.0	78.4
Breadth of braincase	67.2	62.8	62.4	52.7	56.5
Cheektooth row	61.9	64.6	63.0	55.0	55.6
Breadth of M2	13.7	14.3	15.2	13.0	13.0

Mazama americana (Erxleben, 1777)

VOUCHER MATERIAL (TOTAL = 6): Boca Río Yaquerana (FMNH 88806–88808), Nuevo San Juan (MUSM 11185), Orosa (AMNH 74117), Santa Cecelia (FMNH 86900).

OTHER INTERFLUVIAL RECORDS: Chonco (Amanzo, 2006), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006).

IDENTIFICATION: Several of our voucher specimens of red brockets (FMNH 86900, 88807, 88808) are immature individuals that retain their milk premolars (dP2–dP4), but only one of these (FMNH 88807) has the immature markings of a fawn. Of our three adult specimens, two are antlerless females (AMNH 74117, MUSM 11185) and the third (FMNH 88806) is a very young male with tiny antlers that measure less than 20 mm (not including the bony pedicel). In pelage characters (the FMNH specimens are accompanied by well-preserved skins) and adult cranial

measurements (table 19), this material agrees closely with Husson's (1978) descriptions and measurements of almost-topotypical (Surinamese) material of *Mazama americana*.

Although the identification of our material does not seem problematic based on morphological criteria, karyological and molecular studies of *Mazama americana* suggest that specimens sharing the red brocket phenotype are genetically heterogeneous. In fact, phylogenetic analyses of cytochrome-*b* sequence data do not support the monophyly of *Mazama americana*, which was recovered as two weakly supported haplogroups in an unresolved polytomy with *Odocoileus hemionus*, *O. virginianus*, and two other species of *Mazama* by Duarte et al. (2008). Subsequently, Abril et al. (2010) recovered two haplogroups of *M. americana* with stronger support by sequencing the mitochondrial control region and by omitting sequences from some of the other odocoileine taxa included in Duarte et al.'s (2008) analysis. Abril et al. (2010) referred to these haplogroups as morphologically cryptic "species,"



FIG. 21. Matsigenka boy with pet red brocket fawn (photo by D.W.F.; Estirón, 2016).

but this conclusion is not supported by their karyological data.¹⁷ In effect, the taxonomic interpretation of the cytogenetic and molecular data at hand is not straightforward, nor is it known which (if either) of the two haplogroups recovered in published analyses of mtDNA sequence data occurs in French Guiana (the type locality of *M. americana*).

Grubb (2005) recognized numerous allegedly valid subspecies of *Mazama americana* for which (as usual) he cited no supporting revisionary study. According to Cabrera (1961), the western Amazonian form is *M. a. zamora* Allen, 1915, the type locality of which is in the southeastern Andean foothills of Ecuador. In light of molecular studies cited above, a comprehensive taxonomic revision of the many nominal taxa currently treated as synonyms or subspecies of *M. americana* is clearly needed.

¹⁷ One cytotype (“Santarém”) is shared between the two haplogroups, which do not form convex sets on Abril et al.’s (2010: fig. 4) hypothesized network of chromosomal evolution.

ETHNOBIOLOGY: The red brocket is called senad piu (“reddish deer”). The Matsigenka recognize and name two varieties of this species, senad maçhësh (“black-headed deer”) and senad bēdimpi (“little spotted deer”). The latter would seem to designate young individuals, yet the Matsigenka insist that this variety does not grow any larger, does not lose its spots, and runs as fast as an adult. Additionally, a third variety is simply called senad piu.¹⁸ The spotted variety is rarely encountered and is only found in upland forest, the senad piu variety is the most commonly encountered, and the black-headed variety is the largest.

The red brocket is a primary game animal for the Matsigenka. Deer fat sticks to the mouth when one eats it, so the Matsigenka are not fond of deer fat.

¹⁸ One could interpret this either as an unnamed variety or as an example of multilevel polysemy (a single name designating both a superordinate and a subordinate entity; e.g., the English term *cat* referring either to the house cat or to felids in general).



FIG. 22. Red brocket trussed for carrying (photo by Steven Romanoff; upper Quebrada Chobayacu, ca. 1975). Here the tumpline is made from stems of the *ayash* epiphyte (*Heteropsis* spp. [Araceae]), a less desirable material for this purpose than the inner bark of the *tote* tree (see. fig. 19).

However, lean meat is appreciated, and a red brocket carcass has a lot of meat on it. The Matses sometimes keep fawns as pets (fig. 21), but tame deer wander away when they become adults.

Deer are difficult to kill because they almost always run off before one can shoot them. The Matses often kill deer when they happen upon one that is sleeping in the daytime and can be approached before it wakes up. The Matses often

visit mineral licks during the day to look for deer and other game species that visit mineral licks.

Now that the Matses have flashlights, they hunt at night by walking down forest paths. The intention of night hunting is primarily to kill pacas, which are common in secondary forest near villages, especially when peach-palm (*Bactris gasipaes* [Araceae]) fruits are ripe (from January to March). Hunters also occasionally encounter red

brockets that come to secondary forest near villages at night, and they occasionally kill deer while waiting at night for game at a mineral lick.

Slain deer are prepared for packing home in a certain way (fig. 22). The front legs are lashed to the neck with epiphyte stems, and the hind legs are lashed to the front legs. Then a strip of the inner bark of certain types of trees is tied to the neck and rump to make a tumpline. If the deer is large and is killed far from the village, it is gutted before being tied up for carrying. A hunter might also skin and butcher the deer and carry it back in a palm leaf basket that is woven on the spot.

Young men and women do not eat the head, lest they stab themselves in the thigh with a sharp (antlerlike) stick when chasing after an animal while hunting (women often help men chase down animals, especially while guiding hunting dogs). Old people, however, may eat the head.

When a hunter kills, eats, or sees a deer, the deer's spirit may make one of his children ill. Occasionally the deer's spirit makes a child ill even if there has been no contact with a deer. The symptoms for contagion by deer spirits are the same as those by tapir spirits: high fever and rolling of eyes into the back of the head. When a child exhibits these symptoms after the father has had contact with a deer, a medicine man will collect certain medicinal plants ("deer medicine") and bathe the child with an infusion of the leaves. Interestingly, "tapir medicine" is also used to treat ailments caused by deer spirits, suggesting that the Matses perceive an affinity between these two ungulates.

MATSSES NATURAL HISTORY: Red brockets are reddish, the color of some dogs. Males have antlers, but females do not. The antlers are very hard. Red brockets have a white tail, large ears, and large nostrils. Their hindquarters have a lot of meat. They have thin lower legs and ankles, and two parallel hooves, similar to those of a collared peccary, but smaller. The young are spotted.

Red brockets walk around in all habitats, including upland and floodplain forest, primary

and secondary forest, and along streams and rivers. They come to the edges of Matses swiddens and sometimes enter Matses swiddens to eat manioc leaves.

Red brockets do not make nests. They clear a small patch of ground and lie down to sleep, curled up on their sides like dogs. In the daytime they often sleep in forest with an open canopy. They do not sleep in the same place twice.

Red brockets are mostly nocturnal. They sleep during the day. Sometimes they walk around during the day, but not when it is dry. They walk around in the rain by day or night. They travel far, looking for leaves and fruits to eat. The places where they eat fruits are swept clear of leaf litter. After eating their fill, they lie down to rest, often in a sunny spot in a treefall, in streamside forest on high ground where a stream bends, at the foot of a hill, or on a hilltop.

Red brockets visit several different mineral licks by day or at night, and they always return to the same mineral licks. They make the water in the mineral lick turbid with their feet and then slurp up the muddied water. Unlike tapirs and other animals that use mineral licks, red brocket deer do not eat the mud if the mineral lick is not waterlogged. Red brockets do not usually make paths, but one can find deer paths that lead to a mineral lick.

Red brockets are generally solitary. Very rarely two adults may be encountered together. The male does not live with the female. They mate when they encounter each other. The deer gives birth to a single young under the shelter of a stemless palm with large simple leaves, or at the edge of a blowdown. It suckles its newborn at the same place where it gave birth to it, lying on its side, like a dog does. It goes to drink muddied water at a mineral lick and then returns to suckle its young. Then it goes to eat ripe fruits and comes back to suckle its young again. The young deer stands up after two days and starts to walk around and forage with the mother. Once it is large and strong, it leaves its mother.

Red brockets are a favorite prey of jaguars and pumas. Large anacondas and black caimans occasionally capture deer.

Red brockets call out saying “mia” (a sort of high-pitched whine). Females call out saying “ooo” (a sort of howl) when they are in heat. They stamp their feet when they see a person at a distance (if they are not wary).

Red brockets eat the fruits of many types of dicot trees—particularly sweet fruits—including those of *shannëd* (?*Brosimum* [Moraceae]), figs (*Ficus* spp. [Moraceae]), *shëshun* (*Spondias mombin* [Anacardiaceae]), *taëpa* (unidentified), and *piuṣh bëchi* (*Helicostylis tomentosa* [Moraceae]). They don’t just eat the pulp of the fruits, but also swallow the seeds. Their favorite dicot tree fruit is that of *echo* (*Jacaratia* sp. [Caricaceae]), which is like a wild papaya. They also eat papayas that have fallen to the ground in Matses swiddens. They also eat the seeds of some palms, including those of bottle palms (*Iriarteia deltoidea* [Arecaceae]) and stilt palms (*Socratea exorrhiza* [Arecaceae]). Red brockets also eat the leaves of many dicot trees and understory plants, including cecropia trees (*Cecropia* sp. [Moraceae]), which grow in secondary forest. They eat manioc leaves and papaya leaves when they come to Matses swiddens. Pet deer are fed papaya, *echo* fruits, and the otherwise discarded pulp of strained plantain beverages.

REMARKS: Matses interviews about red brockets include most of the well-established natural history facts about this widespread species, including its use of floodplain habitats and secondary vegetation (avoided by gray brockets); solitary habits; feline predators; mixed diet of fruit, seeds, and browse; and propensity for visiting mineral licks (e.g., Bodmer, 1989, 1991; Gayot et al., 2004; Tobler et al., 2009; Blake et al., 2013). Many other behavioral details, however, are not reported in the literature we consulted, including information about daily movements, geophagy, reptilian predators, and sexual vocalizations. Although the Matses say red brockets are mostly nocturnal, this is perhaps a result of local hunting pressure; at un hunted western Amazonian sites red brockets are often active by day (Gómez et al., 2005; Blake et al., 2013).

Mazama nemorivaga (Cuvier, 1817)

VOUCHER MATERIAL (TOTAL = 3): Nuevo San Juan (MUSM 11186, 13148), Santa Cecilia (FMNH 86898).

OTHER INTERFLUVIAL RECORDS: Anguila (Escobedo-Torres, 2015), Quebrada Pobreza (Escobedo-Torres, 2015), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Tapiche (Jorge and Velazco, 2006), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: The voucher material we examined corresponds closely to the qualitative description of *Mazama nemorivaga* provided by Rossi et al. (2010), who recognized the Amazonian brown brocket as a distinct species from *M. gouazoubira*, with which it was formerly synonymized (e.g., by Grubb, 2005). Among other diagnostic craniodental traits of *M. nemorivaga*, the premaxillary does not contact the nasal, from which it is widely separated on each side by a dorsolateral process of the maxillary. Unusually, one of our vouchers (FMNH 86898) retains well-developed canine teeth.

Measurement data that we obtained from adult specimens collected in the Yavarí-Ucayali interfluvium (table 19) broadly overlap those previously reported from Amazonian brown brockets by Husson (1978: table 61) and Bisbal (1991: table II), although an adult male from Santa Cecilia (FMNH 86898) is somewhat larger than the topotypical specimens measured by Voss et al. (2001: table 16).

The recognition of *Mazama nemorivaga* as a species distinct from *M. gouazoubira* by recent authors is consistent with molecular evidence that these are not sister taxa (Duarte et al., 2008), but the same analyses also suggest that *Mazama* is not monophyletic. Since the type species of *Mazama* is *M. americana*, it is plausible that *M. nemorivaga* will eventually be referred to another genus if Duarte et al.’s results are confirmed by additional research. However, few of the relevant nodes in Duarte et al.’s phylogeny are strongly supported, so it is not clear what nomenclatural

solution is appropriate. Additionally, few morphological characters apart from size and pelage color appear to distinguish *M. nemorivaga* from *M. americana*, so describing new genera based only on molecular results is likely to cause problems for generic assignments of fossil odocoileines.

ETHNOBIOLOGY: The gray brocket is called senad tanun (“gray deer”). A few Matses recognize a small and large variety of this species, but most do not.

The gray brocket is a game animal of secondary importance (due to its small size). It is hunted in the same manner as the red brocket.

All the Matses beliefs associated with deer are the same for red and gray brockets.

MATSES NATURAL HISTORY: The gray brocket is gray, has light-colored undersides, and is smaller than the red brocket. The male’s antlers are shorter than those of the red brocket. The young are spotted and thin.

The gray brocket prefers upland forest, away from rivers and large streams. It does not come near Matses villages, nor does it enter secondary forest growing in abandoned swiddens. It is often found on hilltops where the understory is dominated by thatch palms (*Lepidocaryum tenue* [Arecaceae]). The gray brocket is encountered much less frequently than the red brocket.

(The rest of the natural history information for this species is the same as for the red brocket, except for the foods eaten in abandoned and active swiddens.)

REMARKS: The only ecological distinction that the Matses report between the gray and red brockets, that *Mazama nemorivaga* is an upland species that avoids river floodplains, is corroborated by field research (Bodmer, 1991; Tobler et al., 2009). However, the Matses’ failure to distinguish these sympatric cervids in other ecobehavioral respects is hard to reconcile with published evidence that gray brockets are primarily diurnal and do not visit mineral licks, whereas red brockets are often active at night and commonly visit mineral licks (Tobler et al., 2009; Blake et al., 2012, 2013).

Cetaceans (Delphinidae and Iniidae)

The Matses recognize both of the species of dolphins present in the Yavari-Ucayali interfluvium, the gray dolphin (*Sotalia fluviatilis* [Delphinidae]) and the pink Amazon river dolphin (*Inia geoffrensis* [Iniidae]). Their general term for dolphin is chishkan, an unanalyzable term that does not occur in other Panoan languages. There are no archaic synonyms or ceremonial terms for dolphins.

Inia geoffrensis (Blainville, 1817)

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Actiamë (Amanzo, 2006), Jenaro Herrera (Pavlinov, 1994), Nuevo San Juan (this report), Río Yavari (Salovaara et al., 2003), Río Yavari-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: Identifications of pink Amazon river dolphins are not problematic.

ETHNOBIOLOGY: The pink Amazon river dolphin is named chishkan piu (“reddish dolphin”) by the Matses.

Dolphins are of no economic importance to the Matses, but they are sometimes a nuisance. The Matses now purchase nylon gill nets, which they set up in rivers, streams, and lakes near their homes. Dolphins, especially Amazon pink river dolphins often steal fish caught in the gill nets, tearing holes in the nets when they do so.

The Matses traditionally believed that pink Amazon river dolphins are spirits. Pink Amazon river dolphins (but not gray dolphins) tend to follow the Matses when they travel in canoes, which make the Matses nervous.

MATSES NATURAL HISTORY: The pink Amazon river dolphin is reddish. It has a very long snout with pointy teeth and a ball-shaped lump on its forehead. Its tail is similar to that of a fish, but oriented laterally. The dorsal fin is like the keel of a canoe. They have nipples.

Pink Amazon river dolphins are found in rivers and large streams, and in ox-bow lakes and flooded forest during the high-water season.

They are especially fond of deep river bends. They congregate at the mouths of streams.

Pink Amazon river dolphins swim following the river looking for fish. They may stay a long time in deep river bends and at the mouths of streams, catching fish. They chase fish down and eat them underwater. They especially chase fish close to the bank and near river beaches. When Matses travel by canoe, they follow the canoe and exhale loudly through their blowholes to scare Matses.

Pink Amazon river dolphins are most frequently seen alone, but it is also common to see a pair or a group of three. Larger numbers can be seen where large streams feed into the Río Yaquerana. They copulate on river beaches.

They eat all types of fish, especially large catfishes.

REMARKS: Matses observations about *Inia geoffrensis* are limited in scope but agree in several details with the scientific literature on this species, notably about their numerical abundance at stream confluences, seasonal use of flooded forests, predominantly piscivorous diet, and uncanny habit of following canoes and frightening people (Martin and da Silva, 2004; Martin et al., 2004; Gomez-Salazar et al., 2012; Paschoal et al., 2013). We have not seen any explicit description of the copulatory behavior of this species in the wild, but the common Amazonian superstition that pink dolphins have sexual relationships with people may have something to do with mating on or near river beaches, as alleged by the Matses.

Sotalia fluviatilis (Gervais and Deville, 1853)

VOUCHER MATERIAL: None.

OTHER INTERFLUVIAL RECORDS: Nuevo San Juan (this report), Río Yavarí (Salovaara et al., 2003), Río Yavarí-Mirim (Salovaara et al., 2003), San Pedro (Valqui, 1999), Wiswincho (Escobedo-Torres, 2015).

IDENTIFICATION: Identifications of gray dolphins are not problematic.

ETHNOBIOLOGY: The gray dolphin is called chishkan ushu (“white” or “light-colored dol-

phin”). Some Matses recognize a darker variety that they call chishkan umu (“blue dolphin”), although most speakers consider the color variation to be continuous.

Dolphins are of no economic importance to the Matses.

The Matses are not afraid of gray dolphins (as they are of pink Amazon river dolphins).

MATSES NATURAL HISTORY: Gray dolphins are light gray to dark gray.

Gray dolphins are found in rivers and large streams, but not in smaller streams or flooded forest. They are also found in ox-bow lakes when they are flooded.

Gray dolphins travel through the rivers and streams chasing down fish and eating them. Unlike pink Amazon river dolphins, they do not follow canoes, and they can jump high out of the water.

Gray dolphins are solitary and often travel in pairs. They feed in groups of up to 5.

Gray dolphins exhale audibly when they surface, but not as loudly as pink Amazon river dolphins do.

Gray dolphins eat fish.

REMARKS: The Matses do not have much to say about gray dolphins, but they accurately note several behavioral differences from pink Amazon river dolphins, notably their fondness for acrobatic aerial displays (*Inia* seldom jumps clear of the water) and their avoidance of flooded forest (an important seasonal habitat of *Inia*; da Silva and Best, 1996; Emmons, 1997; Martin and da Silva, 2004). The benign attitude of the Matses toward gray dolphins is similar to those of other native Amazonians, who do not fear this species as they do pink Amazon river dolphins (McGuire, 2010; Paschoal et al., 2013).

Sirenia (Trichechidae)

The Amazonian manatee (*Tichechus inunguis*) occurs—or formerly occurred—along the margins of the Yavarí-Ucayali interfluvium and in some of its interior waterways, but it does not occur in Matses tribal territory, and its habits are not

known to the Matses, who traditionally avoided major rivers.

Trichechus inunguis (Natterer, 1883)

VOUCHER MATERIAL: Río Tapiche (AMNH 98691).

OTHER INTERFLUVIAL RECORDS: Jenaro Herrera (Tovar, 2011), Reserva Comunal Tamshiyacu-Tahuayo (Bodmer, 1994), Río Orosa (Mármol, 1995), Río Tapiche (Reeves et al., 1996), Río Yavarí (Mármol, 1995).

IDENTIFICATION: Only a single species of manatee is known to occur in the upper Amazon Basin. Our voucher consists of the skull of a mature adult of unknown sex. Selected cranial measurements of AMNH 98691 are all within the range of variation for *Trichechus inunguis* tabulated by Domning and Hayek (1986): condylobasal length, 383.1 mm; breadth across postorbital processes of frontals, 130.1 mm; least postorbital breadth, 54.1 mm; zygomatic breadth, 214.1 mm.

REMARKS: The holotype skull of an allegedly new species of “dwarf” manatee recently described by Roosmalen (2015: figs. 20, 21) from the Rio Aripuanã basin of Amazonas, Brazil, is an obviously immature individual with open basicranial and occipital sutures.

DISCUSSION

The terrestrial groups treated in this report (Xenarthra, Carnivora, Perissodactyla, Tayasuidae, and Cervidae) together with Primates (treated by Voss and Fleck, 2011) comprise most of the mammalian biomass but only a small fraction of the taxonomic diversity in Amazonian habitats, where bats, rodents, and marsupials probably make up 80% or more of the species in well-sampled local faunas (Voss and Emmons, 1996). Therefore, any general inferences about mammalian diversity, endemism, community ecology, and ethnobiology in the Yavarí-Ucayali interfluvium are premature, and the following discussion is restricted to the

taxa of immediate interest. Because our results contribute little to the existing literature on Amazonian aquatic mammals, we do not discuss them further here.

Diversity and Endemism

Available information about the diversity of xenarthrans, carnivores, and ungulates in the Yavarí-Ucayali interfluvium is based on specimens collected at seven localities in the region, interviews with Matses hunters, published sight-censuses from 10 inventory sites (appendix 4), and two short-term camera-trap surveys (Jorge and Velazco, 2006; Escobedo-Torres, 2015). These sources, and the results of our taxonomic research as summarized in the preceding accounts, document the local occurrence of 30 species (table 20). The total faunal-sampling effort represented by these data is hard to quantify, but our interview results alone effectively summarize the life experiences of several hunters with daily exposure to the local fauna, so it seems likely that our list of species is nearly complete. Indeed, geographic range data suggest that only a single additional xenarthran, the two-toed sloth *Choloepus didactylus*, could be expected to occur in our region. No additional species of carnivore or ungulate are expected to occur here based on known geographic ranges.

All of the species of terrestrial mammals treated in this report are widespread, but they can be sorted into three biogeographic categories. (1) The first and most numerous category includes 24 species currently thought to occur throughout Amazonia wherever suitable habitat is present, except where locally extirpated by human activities. (2) By contrast, three local species (*Dasypus pastasae*, *Bradypus variegatus*, *Choloepus hoffmanni*) belong to subgenera or genera with geographically replacing species, different members of which occur in other parts of Amazonia. *Dasypus* (*Hyperoambon*) *pastasae*, for example, is replaced by *D. (H.) beniensis* in southeastern Amazonia (east of the Rio Madeira

TABLE 20
**Species of Xenarthrans, Carnivores, and Ungulates Recorded from the
 Yavari-Ucayali Interfluve**

	Specimens ^a	Interviews ^b	Sightings ^c	Photos ^d
<i>Cabassous unicinctus</i>	X	X		
<i>Priodontes maximus</i>	X	X	X	X
<i>Dasypus novemcinctus</i>	X	X	X	
<i>Dasypus pastasae</i>	X	X		
<i>Bradypus variegatus</i>	X	X	X	
<i>Choloepus</i> sp. ^e	X	X	X	
<i>Cyclopes didactylus</i>	X	X		
<i>Myrmecophaga tridactyla</i>	X	X	X	
<i>Tamandua tetradactyla</i>	X	X	X	
<i>Atelocynus microtis</i>		X	X	X
<i>Speothos venaticus</i>		X	X	
<i>Leopardus pardalis</i>	X	X	X	X
<i>Leopardus wiedii</i>	X	X		
<i>Panthera onca</i>		X	X	
<i>Puma concolor</i>		X		
<i>Puma yagouaroundi</i>		X	X	
<i>Eira barbara</i>	X	X	X	X
<i>Galictis vittata</i>	X	X	X	
<i>Mustela africana</i>		X		
<i>Lontra longicaudis</i>	X	X	X	
<i>Pteronura brasiliensis</i>	X	X	X	
<i>Bassaricyon alleni</i>	X	X	X	
<i>Nasua nasua</i>	X	X	X	X
<i>Potos flavus</i>	X	X	X	
<i>Procyon cancrivorus</i>	X	X		
<i>Tapirus terrestris</i>	X	X	X	
<i>Pecari tajacu</i>	X	X	X	
<i>Tayassu pecari</i>	X	X	X	
<i>Mazama americana</i>	X	X	X	X
<i>Mazama nemorivaga</i>	X	X	X	X

^a Specimens examined for this report.

^b With Matses informants (this report).

^c From visual transect censuses conducted at sites listed in appendix 4.

^d From camera-trapping described by Jorge and Velazco (2006) and Escobedo-Torres (2015).

^e Positively identified as *Choloepus hoffmanni* from examined specimens, but unvouchered observations could be based on *C. didactylus*.

and south of the lower Amazon) and by *D. (H.) kappleri* in NE Amazonia (east of the Rio Negro and north of the lower Amazon; Feijó and Cordeiro-Estrela, 2016). (3) Three other local species (*Atelocynus microtis*, *Mustela africana*, and *Basaricyon alleni*) might occur throughout western Amazonia, but they have restricted distributions east of the Rio Negro and/or the Rio Madeira (Pitman and Williams, 2004; Helgen et al., 2013; Ramírez-Chavez et al., 2014).

In effect, the Yavari-Ucayali interfluvial harbors a typically western Amazonian fauna of xenarthrans, carnivores, and ungulates, all of which could be expected to occur together in adjacent interfluvial regions, although some inventory sites might have smaller species lists for a number of reasons. Several species treated in this report (e.g., *Cabassous unicinctus*, *Cyclopes didactylus*, *Atelocynus microtis*, *Speothos venaticus*, *Mustela africana*) are notoriously elusive, so they are often absent from site inventories based on short-term faunal sampling. Upland sites might lack otters and raccoons, which inhabit rivers and riparian habitats, respectively, whereas inventories sited in extensive floodplains might lack species that favor upland habitats (e.g., *Dasyurus pastasae*, *Mazama nemorivaga*). Vulnerable game species (e.g., tapirs, white-lipped peccaries) and a few other taxa valued for their hides, teeth, or claws (e.g., jaguars, giant anteaters) are often extirpated by commercial hunting near large population centers. Therefore, if our list of xenarthrans, carnivores, and ungulates is longer than those previously reported from most other western Amazonian inventories (e.g., Hutterer et al., 1995; Voss and Emmons, 1996; Hice and Velazco, 2012), the discrepancies are probably artifacts of sampling or site selection rather than biogeography.

Matses Knowledge of Local Species

Matses knowledge of local mammals is based on direct observation of diurnal taxa, shrewd interpretation of spoor, information obtained from butchering carcasses, and familiarity with the behavior of orphaned offspring kept as pets.

Direct observation comes primarily from hunting, a key subsistence activity, and the traditional source of almost all Matses dietary protein (Romanoff, 1984). Indeed, it is difficult to exaggerate the importance of hunting for the Matses, who practice stalking and archery skills from early childhood, and for whom the habits of game species are a routine topic of conversation. Hunting is also key to male reproductive success, because men who cannot hunt well are considered worthless and cannot attract wives or sex partners (Fleck and Voss, 2006). Traditional Matses hunting methods—described in detail by Romanoff (1984), Voss and Fleck (2011), and this report—rely for their success on detailed knowledge of animal behavior. Among other senses honed by constant use, the hunter's sense of smell is engaged to a greater extent than many urban dwellers may easily credit.

Interpretation of spoor (tracks, feces, food remains, and other sign) is another crucial Matses hunting skill. Spoor provides the primary source of information about the behavior, habitat, and diet of species that are seldom directly observed, a category that includes both nocturnal mammals and elusive diurnal taxa. Butchering carcasses, a chore routinely performed by women, provides information about litter size and stomach contents.

Pet-keeping is a widespread practice of indigenous Amazonians (Erikson, 2000), among whom the Matses are fairly typical in adopting the offspring of animals orphaned by hunters. Animals adopted as pets are almost always game species, and they are not mistreated, killed, or eaten even after they have grown to adulthood and become a nuisance. Tame monkeys, two-toed sloths, peccaries, deer, and tapirs are often found wandering unmolested around Matses villages. These companion animals (typically nurtured by children and adolescents) provide first-hand experience with species-specific vocalizations and other behaviors.

Matses knowledge of nongame species results from chance encounters over a lifetime of hunting and other subsistence activities (principally

slash-and-burn horticulture and fishing) carried out daily in or adjacent to the most extensive primary tropical forest that still exists on our planet. Some common diurnal nongame species (e.g., small monkeys, squirrels, acouchies, dolphins) are seen routinely, whereas others (e.g., tamanduas, tayras, jaguarundis, ocelots, jaguars) are probably encountered by every hunter several times a year. A few (tayras, ocelots) are pests that enter villages or lurk on the outskirts of clearings to eat chickens, and the spoor of potentially dangerous large cats always merits close attention. Nocturnal arboreal species (e.g., kinkajous, porcupines) are sometimes observed when trees are felled to clear new garden plots, an activity in which men are engaged for weeks at a time early in the dry season.

Despite such extensive lifetime experience, the Matses are not infallible observers, and they have many superstitious beliefs about the local fauna, notably concerning the magical ability of animal spirits to sicken children. In general, such superstitions are easily distinguished from the factual content of our interviews, but even the latter are not necessarily free of errors, which might arise from anthropomorphic interpretations of animal behavior, incorrect inferences from spoor, or imperfect observations. Nevertheless, detailed comparisons of Matses natural history knowledge with the scientific literature (Voss and Fleck, 2011; Fleck and Voss, 2016) suggest that, in general, the Matses are highly accurate observers whose knowledge of the local fauna and flora merits high credibility.

Matses interviews about xenarthran, carnivore, and ungulate natural history are, in general, less detailed than the accounts of primate natural history summarized by Voss and Fleck (2011). This is, undoubtedly, because most primates are diurnal, noisy, social, and conduct their lives openly in well-lit canopy and subcanopy vegetation, whereas most nonprimate mammals are nocturnal, quiet, solitary, or inhabit deeply shaded, densely vegetated understory habitats where their behavior is harder to observe. Also, many nonprimate species (e.g., felids) are elusive

by nature, and others (e.g., *Myrmecophaga*, *Speothos*) occur at low densities, so encounters are correspondingly infrequent.

Nevertheless, Matses natural history accounts for some culturally important species—especially *Dasybus pastasae*, *Cholepus hoffmanni*, *Panthera onca*, and *Pecari tajacu*—are richly detailed, and other accounts, although less detailed, provide much new information of interest. Many examples of new natural history information contained in these accounts are discussed above, but accounts that are noteworthy for new information include those for *Dasybus pastasae*, *Cholepus hoffmanni*, *Myrmecophaga tridactyla*, *Speothos venaticus*, *Puma yagouaroundi*, and *Nasua nasua*. None of these species have ever been the focus of scientific study in Amazonian rainforest, so Matses information about them provides a useful baseline for future research and hypothesis testing.

Matses natural history information about local xenarthrans and carnivores suggest that members of these assemblages are well separated ecologically based on diurnal activity, locomotion, diet, and social behavior (tables 1, 8, 11). Most of these traits are not new to the scientific literature, but such comparisons have seldom been compiled for sympatric members of a single fauna, and they serve to focus attention on pairs of ecologically similar species that seem likely to compete with one another. *Atelocynus microtus* and *Speothos venaticus*, for example, are both diurnal-terrestrial canids (routinely described as “hypercarnivores” in the literature), but Matses-derived information suggest that one is a solitary generalist predator, whereas the other is uniquely adapted to extracting armadillos, pacas, and other medium-size prey from refugia where they might be otherwise immune from predation. The Matses are not, however, always well informed about ecological distinctions among closely related sympatric taxa. Their accounts offer no insights about niche separation (if any) between olingos and kinkajous, nor do they seem well informed about ecological differences between *Mazama americana* and *M. nemo-*

TABLE 21
**Fruits and Seeds Eaten by Xenarthrans, Carnivores, and Ungulates
 Based on Matses Interviews**

	Consumers of fruits/seeds
Monocots	
Arecaceae (Palmae)	
<i>Astrocaryum</i> spp.	<i>Pecari, Tayassu</i>
<i>Attalea tessmanii</i>	<i>Pecari</i>
<i>Iriartea deltoidea</i>	<i>Potos, Mazama</i>
<i>Mauritia flexuosa</i>	<i>Dasyopus pastasae, D. novemcinctus, Priodontes, Atelocynus, Nasua, Tapirus, Pecari, Tayassu</i>
<i>Oenocarpus bataua</i>	<i>Dasyopus pastasae, D. novemcinctus, Priodontes, Panthera, Puma concolor, Nasua, Tapirus, Pecari</i>
<u>kuëbun isan</u> ^a	<i>Dasyopus novemcinctus</i>
<u>pëdi</u> ^b	<i>Mazama</i>
Dicots	
Anacardiaceae	
<i>Spondias mombin</i>	<i>Mazama</i>
Apocynaceae	
? <i>Macoubea guianensis</i>	<i>Pecari</i>
<i>Couma macrocarpa</i>	<i>Eira, Potos</i>
<i>Parahancornia peruviana</i>	<i>Eira, Tapirus</i>
Caricaceae	
<i>Jacaratia</i>	<i>Puma yagouarondi, Tapirus, Mazama</i>
Guttiferae (Clusiaceae)	
<i>Rhedia longifolia</i>	<i>Choloepus</i>
Lecythidaceae	
<u>tote</u> ^c	<i>Pecari</i>
Melastomataceae	
<i>Bellucia</i> sp.	<i>Tapirus</i>
Mimosoideae	
<u>mannan tsipuis</u> ^d	<i>Choloepus</i>
Moraceae	
? <i>Brosimum</i>	<i>Mazama</i>
<i>Castilla</i>	<i>Tapirus</i>
<i>Cecropia</i> spp.	<i>Eira</i>
<i>Clarisa racemosa</i>	<i>Panthera, Tapirus</i>
<u>bata</u> ^e	<i>Atelocynus, Panthera, Puma concolor, P. yagouarondi, Eira, Nasua, Potos</i>
<u>chiuish</u> ^f	<i>Bradypus, Tapirus, Mazama</i>
<u>piuësh bëchi</u> ^g	<i>Choloepus, Mazama</i>
Myristicaceae	
<u>tonnad</u> ^h	<i>Dasyopus novemcinctus, Choloepus, Pecari</i>

Consumers of fruits/seeds	
Sterculiaceae	
<i>Theobroma</i>	<i>Choloepus</i>
<i>Theobroma subincanum</i>	<i>Choloepus</i>
Undetermined	
<u>taëpa</u>	<i>Mazama</i>
<u>kuëte mëdiad</u>	<i>Pecari</i>
<u>pënkad</u>	<i>Tapirus</i>
<u>kuëte ise</u>	<i>Pecari</i>
<u>nëishamë naësh</u>	<i>Tapirus</i>

^a *Oenocarpus mapora* and *O. balickii*.

^b *Socratea exorrhiza*, *S. salazarii*, and *Wettinia angusta*.

^c *Eschweilera* spp., *Lecythis* spp., and *Cariniana*.

^d *Inga* spp. and *Pithecellobium auriculatum*.

^e *Pseudolmedia* spp. and *Maquira* spp.

^f *Ficus* spp. and *Coussapoa* spp.

^g *Helicostylis tomentosa* and *H. elegans*.

^h Undetermined (a generic term for trees of this family).

rivaga, perhaps because neither procyonids nor gray brockets are of much cultural importance.

Fruit pulp sustains a large fraction of mammalian biomass in Amazonia (Janson and Emmons, 1990; Peres, 1999). Matses interviews confirm that frugivory is widespread among the mammalian taxa treated in this report, and they enlarge the roster of Amazonian species known to eat fruit, at least occasionally, by including several felids previously thought to be exclusively carnivorous (*Panthera onca*, *Puma concolor*, *Pu. yagouaroundi*). Our list of plant species with fruits or seeds¹⁹ that the Matses claim to be eaten by xenarthrans, carnivores, and ungulates (table 21) include many of the same botanical and folk taxa eaten by monkeys (Voss and Fleck, 2011: table 21), notably including two palms (*Oenocarpus bataua*, *Mauritia flexuosa*) and the folk taxon known as bata (including species of *Pseudolmedia* and possibly also *Maquira* [Moraceae]). However, some fruit taxa said to be eaten by large terrestrial mammals do not appear in Matses-reported primate diets (e.g., *Jacaratia* [Caricaceae]), and some popular monkey fruits (e.g., machiste

[Apocynaceae] and *Chrysophyllum prieurii* [Sapotaceae]) are not mentioned in these accounts. Whether such omissions reflect observer bias, errors, or different syndromes of frugivory by monkeys on the one hand and large nonprimate mammals on the other remains to be determined.

Ethnobiological Nomenclature, Cultural Importance, and Food Taboos

Matses folk taxonomy of mammals has been discussed extensively in previous reports (e.g., Fleck and Voss, 2006; Voss and Fleck, 2011) and we have no new insights or interpretation to offer here. Matses names for xenarthrans, carnivores, and ungulates (table 22) illustrate the familiar correlation between cultural importance and linguistic elaboration: culturally unimportant (inedible, nondangerous) species are typically known by a single name, whereas culturally important (edible or dangerous) species are typically known by multiple synonyms and hyponyms.²⁰ The contrast in terminology

¹⁹ Frugivory and granivory are difficult to distinguish consistently in our interview data.

²⁰ Synonyms, in this context, are terms with the same zoological referent as the principal term, whereas hyponyms are names for phenotypic varieties of the same zoological species.

TABLE 22

**Species of Xenarthrans, Carnivores, and Ungulates Annotated for Cultural Importance,^a
with Corresponding Matses Names**

	Interpretation ^b
<i>Cabassous unicinctus</i> (not eaten, unimportant)	
<u>menkudu</u>	principal term
<i>Priodontes maximus</i> (not eaten, unimportant)	
<u>tsawesamë</u>	principal term
<u>panu</u>	archaic synonym
<i>Dasybus novemcinctus</i> (secondary game species)	
<u>sedudi</u>	principal term
<u>sedudimpi</u>	overdifferentiated variety
<u>sedudidapa</u>	overdifferentiated variety
<u>akte tsawes</u>	overdifferentiated variety
<i>Dasybus pastasae</i> (primary game species)	
<u>tsawes</u>	principal term
<u>yosh</u>	archaic synonym
<u>tsawes çhëshe</u>	overdifferentiated variety
<u>tsawes uşhu</u>	overdifferentiated variety
<u>tsawes uşhu</u>	overdifferentiated variety
<i>Bradypus variegatus</i> (not eaten, unimportant)	
<u>mëinkançhuşh</u>	principal term
<i>Choloepus hoffmanni</i> (primary game)	
<u>şhuinte</u>	principal term
<u>nai</u>	archaic synonym
<u>posën</u>	archaic synonym
<u>tabidiate</u>	archaic synonym
<u>uşhtud kudu</u>	ceremonial term
<u>şhuinte uşhu</u>	overdifferentiated variety
<u>şhuinte piu</u>	overdifferentiated variety
<u>şhuinte poçhëşh</u>	overdifferentiated variety
<u>chompish</u>	overdifferentiated variety ^c
<i>Cyclopes didactylus</i> (not eaten, unimportant)	
<u>tsipud</u> or <u>tsekeded</u>	principal terms
<i>Myrmecophaga tridactyla</i> (not eaten, unimportant)	
<u>shaë</u>	principal term
<i>Tamandua tetradactyla</i> (not eaten, unimportant)	
<u>bëwi</u>	principal term
<i>Atelocynus microtis</i> (not eaten, unimportant)	
<u>mayanën opa</u> or <u>nimëduk opa</u>	principal terms
<i>Speothos venaticus</i> (not eaten, unimportant)	

	Interpretation ^b
<u>achu kamun</u>	principal term
<i>Leopardus pardalis</i> (not eaten, unimportant)	
<u>bëdimpi</u>	principal term
<i>Leopardus wiedii</i> (not eaten, unimportant)	
<u>tëstuk mawekid</u>	principal term
<i>Panthera onca</i> (not eaten, but dangerous)	
<u>bëdi</u>	principal term
<u>kamun</u>	archaic synonym
<u>winsad</u>	archaic synonym
<u>chuisad</u>	archaic synonym
<u>bëdidapa</u>	overdifferentiated variety
<u>wispan kamun</u>	overdifferentiated variety
<i>Puma concolor</i> (not eaten, but potentially dangerous)	
<u>bëdi piu</u>	principal term
<u>bëdi piu</u>	overdifferentiated variety
<u>sipidin</u>	overdifferentiated variety
<i>Puma yagouaroundi</i> (not eaten, unimportant)	
<u>bëdi chëshë</u> or <u>shododon</u>	principal terms
<i>Eira barbara</i> (not eaten, unimportant)	
<u>batachued</u>	principal term
<i>Galictis vittata</i> (not eaten, unimportant)	
<u>bosen uşhu</u>	principal term
<i>Mustela africana</i> (not eaten, unimportant)	
<u>mayanën opampi</u>	principal term
<i>Lontra longicauda</i> (not eaten, unimportant)	
<u>bosen</u>	principal term
<i>Pteronura brasiliensis</i> (not eaten, unimportant)	
<u>onina</u>	principal term
<i>Bassaricyon alleni</i> (not eaten, unimportant)	
<u>shëmën</u>	principal term
<i>Nasua nasua</i> (secondary game species)	
<u>tsise</u>	principal term
<u>tsisedapa</u>	overdifferentiated variety
<u>tsisempi</u>	overdifferentiated variety
<i>Potos flavus</i> (not eaten, unimportant)	
<u>kuichikkekid</u>	principal term
<i>Procyon cancrivorus</i> (not eaten, unimportant)	
<u>tsisebiekkid</u>	principal term
<i>Tapirus terrestris</i> (primary game species)	
<u>nëishamë</u>	principal term

	Interpretation ^b
<u>awad</u>	archaic synonym
<u>wisu</u>	archaic synonym
<u>danchish</u>	archaic synonym
<u>dëpachi</u>	ceremonial term
<u>nëishamëdapa</u>	overdifferentiated variety
<u>nëishamë çhëshë</u>	overdifferentiated variety
<u>nëishamë mëbëdi</u>	overdifferentiated variety
<i>Pecari tajacu</i> (primary game species)	
<u>shëkten</u>	principal term
<u>unkin</u>	archaic synonym
<u>matoşh</u>	archaic synonym
<u>pani tucu</u>	ceremonial term
<u>shëkten çhëshë</u>	overdifferentiated variety
<u>shëkten uşhu</u>	overdifferentiated variety
<i>Tayassu pecari</i> (primary game species)	
<u>shëktenamë</u>	principal term
<u>chede</u>	archaic synonym
<u>pashankid</u>	ceremonial term
<u>shëktenamë çhëshë</u>	overdifferentiated variety
<u>shëktenamë uşhu</u>	overdifferentiated variety
<i>Mazama americana</i> (primary game species)	
<u>senad piu</u>	principal term
<u>senad maçhësh</u>	overdifferentiated variety
<u>senad bëdimpi</u>	overdifferentiated variety
<i>Mazama nemorivaga</i> (secondary game species)	
<u>senad tanun</u>	principal term

^a Primary game species are large animals that the Matses prefer to eat and are the object of hunts. Secondary game species are generally smaller and are killed when encountered, but no special effort is made to find them. Other categories under this heading are self-explanatory.

^b See text and Fleck and Voss (2006) for definitions of “principal term,” “archaic synonym,” “ceremonial term,” and “overdifferentiated varieties.”

^c Possibly a distinct species (*Choloepus didactylus*; see text).

for inedible three-toed sloths (*Bradypus variegatus*, with one folk-taxon name) and edible two-toed sloths (*Choloepus hoffmanni*, with eight or nine names) exemplifies a pattern that occurs throughout the Matses zoological lexi-

con and seems to be perpetuated by cultural mechanisms that involve public displays of hunting jargon (Fleck and Voss, 2006).

Amazonian food taboos have received much anthropological attention, but there is little consensus about why animal species that are esteemed as food by one tribe are rejected as inedible by neighboring cultures. By compari-

“Dog” and “pooch” are synonyms, for example, but “German Shepherd” and “Great Dane” are hyponyms.

son with other indigenous Amazonians, the Matses eat a wider range of large nonprimate mammals than some tribes (the Achuarä, for example, are said not to eat sloths, tapirs, or deer; Ross, 1978) but have a more restricted diet than others (e.g., the Amahuaca, who eat everything the Matses eat, as well as anteaters; Carneiro, 1970). For some anthropologists, food taboos are ethnic markers that serve to set one tribe apart from another (Milton, 1991), whereas statistical analyses by wildlife biologists suggest that dietary taboos simply reflect cultural pickiness wherever game is abundant (Jerzolimski and Peres, 2003). These viewpoints are not mutually exclusive, and we have no insights to offer on this topic based on Matses examples from this report. However, we note that one effect of partial food taboos (e.g., that young people may not eat *Dasybus novemcinctus*, immature tapirs, or deer heads) is to ensure a food supply for the elderly. Similarly, the somewhat elaborate rules regarding the distribution of butchered *Dasybus pastasae* and *Choloepus hoffmanni* would seem to guarantee that everyone in the hunter's household gets something from these prized but not overly large kills. As noted in the accounts for several species, traditional dietary taboos are increasingly ignored by younger generations exposed to the omnivorous diets of detribalized Peruvians, so many of the customs described here, along with other aspects of Matses ethnobiology, may disappear completely in the next few decades.

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APPENDIX 1

Exemplar Interview Text

The composite natural history summaries in our systematic accounts do not resemble typical Matses monologs, which often contain narrative material, expressed opinions, and comparisons of animal behavior with Matses culture, all of which were edited out by us. To provide the reader with a more authentic notion of a typical Matses monolog, we provide a free English translation of a recorded description of the greater long-nosed armadillo (*Dasyops pastasae*) by César Nacua Uaqui Canshë, a skilled hunter who is renowned among the Matses for his detailed knowledge of natural history. In this monolog (recorded at the Matses village of Estirón on 23 October 2011), César first narrates a typical night in the life of a greater long-nosed armadillo as it travels around foraging for food and then prepares its burrow for sleeping. He also relates an incident when he and his wife found an armadillo and its newborn young. Lastly, he tells about how jaguars and bush dogs hunt and eat greater long-nosed armadillos.

For ease of reading we paraphrased some material, combined sentences into paragraphs, and eliminated repetition. Explanatory notes are provided in footnotes, and information that is implied by context but not stated explicitly is enclosed in parentheses. The interested reader can access the original audio file, accompanied by the transcription (in Matses), original (more

literal) English and Spanish translations, and technical annotations (linguistic, ethnographic, and biological) at the Endangered Languages Archive (<https://elar.soas.ac.uk/Record/MPI165966>).

“I’m going to tell about that one, so listen up, because this is how the greater long-nosed armadillo is. The greater long-nosed armadillo²¹ is one that does not walk around during the day. It sets out at night, when it is dark. Just before dusk it is still sitting in its burrow rustling the leaves in its bed. It keeps on rustling the leaves in its bed for a long time while waiting for dusk. I once said mistakenly to the Matses who had stopped to sleep with me along the route, “The armadillo is exiting its burrow.”²² Rather, right at dusk it quickly runs out. At the edge of a stream, where we had stopped to pass the night along the way to see the non-Indians,²³ there was a burrow with many white flies at the entrance. An armadillo had been rustling the leaves there for a while before finally exiting the burrow, such that it would have been easy to kill if I had been waiting ready with a shotgun.

“So, after sitting in its nest rustling the leaves in its bed for a while, right at dusk it exits and begins searching for its food. It stops where there is a rotten log and remains there for a while. It searches there and quickly finds its food, including armored millipedes and round millipedes, of which there are many in rotten logs. It digs into the rotten log looking for those, including red armored millipedes and little light-colored armored millipedes.

“After doing that it roots in the ground for earthworms. After finding and eating those, it continues on its way. After foraging along its path in that manner, it leaves its path. While foraging far from its path, it finds its other favored food, isan palm fruits.²⁴ While gnawing on the isan palm fruits, it also smells and digs around at

²¹ Hereafter just “armadillo.”

²² Saying that an armadillo is about to leave its burrow is bad luck.

²³ On the trail to a mestizo village.

²⁴ The fruits of isan (*Oenocarpus bataua* [Arecaceae]) have an oily and very nutritious mesocarp.

the base of the isan palm tree searching for earthworms. It leaves a cleared area where it has rooted at the base of the isan palm at night.

"After eating that, it sets out again, traveling far all night long, crossing a stream. Then it begins to root in the soft earth of the stream floodplain. Then it crosses the stream coming back to where it was before and follows the stream upstream, eating earthworms along the way. It roots out the earthworms, digging into the earth with its snout and grabbing the earthworms with its thin tongue. Then it continues rooting and finds armored millipedes, earthworms, and all types of invertebrates.

"After eating those for a while, it goes to a swamp-palm swamp.²⁵ It does not root in palm swamps when they are flooded. It roots at the edge of the palm swamp and eats many earthworms and gnaws on swamp-palm fruits.

"After gnawing on swamp-palm fruits for a long while, it sets out again. It arrives at its mud hole, its little 'clay pot,' where collared peccaries also bathe (during the day), and bathes in the mud there.²⁶

"After bathing, it sets out again and descends into the valley of another stream. It goes following the sandy stream downstream, eating earthworms along the way. It finds and eats another kind of armored millipede that has hairs on its underside and many legs. It eats that sort of thing without passing up any. It chews them up well. Then it gnaws again on ripe isan palm fruits that have fallen to the ground. Where there are many fallen ripe isan fruits there are many chukë ants (which it also eats). It also eats earthworms there, rooting intensely.

"After having eaten there, it begins to follow a larger stream. Then it finds its path again and begins to follow it, going very far. If comes upon one of its old burrows, it enters and inspects it. It decides not to sleep there and comes back out. It

continues to follow its path. It leaves its path, forages going in a large circle, eating earthworms, and then returns to its path. Then it crosses another stream and continues on, leaving its path. It roots and returns again to its path.

"Meanwhile, the day begins to dawn. Perhaps the armadillo knows dawn is coming soon because it gets cold.²⁷ Then it goes along its path without leaving its path again. It crosses a small stream and follows another tributary stream, still going along its path. When it reaches its burrow it begins to collect dead leaves for its bed, repeatedly collecting leaves and dragging them into the burrow, leaving an area clear of leaf litter.

"Just as the day dawns, it goes into its burrow where it has refreshed its leaf bed. Then it fixes up its leaf bed by rolling on it. It rolls around in its nest making a rustling noise for a while. Then it goes to sleep, sleeping comfortably. Then, it stays in its burrow all day.

"The male armadillo does not say to the female 'Let's live together.' Rather, they live separately. They copulate when they find each other (while foraging). The Matses, by contrast, live with their wives. The armadillo gets pregnant without living with its husband. Then, it gives birth to its young right there, in the absence of the male. It gives birth to two offspring.

"One time I heard much rustling and whining. 'What could it be?' I asked my wife. 'What could it be? Could it be a pitviper? The sound is coming from a burrow into which an armadillo has evidently entered,' I said to her. 'It must be an armadillo that is making that noise, so let's stop up the hole (with rotten logs) so I can have a look,' I told her. After stopping up the hole, I dug a hole where the sleeping chamber was. There were a lot of white flies there at the burrow entrance. It was a burrow that was easy to flood out. The armadillo was growling and rustling the dry leaves of the nest chamber. Then, when it saw that I had perforated its burrow, it went into the retreat tunnel. Upon looking in the hole I saw that there was a lot of

²⁵ Swamp palms (*Mauritia flexuosa* [Arecaceae]) grow in permanently waterlogged soil, where they are often the dominant tree.

²⁶ The narrator is comparing the wallow with a clay pot, since the Matses formerly sometimes bathed with water collected in a clay pot.

²⁷ There is a predawn chill in the forest between 03:00 and 05:00.

blood. 'Oh, it was giving birth to its young, so come look' I told my wife. Then I told her, 'Make a (palm) frond basket, because there is a stream nearby. I'm going flood the burrow and see.' My wife made the frond basket, and I told her, 'Line the frond basket with wild banana leaves and then fetch water! I'm going to make a fence across the burrow entrance, in order to kill it. I want to see how small the young she has just given birth to are.' The newborns had gone into the retreat tunnel with their mother. When I flooded the burrow, one little baby armadillo came out first, splashing the water. It was all pink. Its snout, its undersides, and its feet were all pink. It did not have a placenta attached to its umbilical cord. Its mother had eaten it. Then the other newborn came out of the burrow. My wife said 'Grab it! Grab it!' I gave them to her and told her 'Place them right here, so that a jaguar can kill them. Or are you going to breast feed them?'²⁸ After taking them, she set them down them outside the burrow. They were trembling intensely. Meanwhile, their big mother came to the burrow entrance. My wife and I killed the mother together.

"That is how the armadillo gives birth. Not together with its husband. The male's 'house' is far away, in a burrow at another small stream, where it lives. It has many 'houses.' Do you think that it lives with the male? It does not live with the male. And the young likewise do not live with their mother for long. They leave her, such that the female ends up alone. They go to another burrow. The armadillo's young leave, crossing to another stream. They do not live with their mother. By contrast, woolly monkeys live together. The armadillo does not do that. By contrast, the collared peccary lives with its offspring. The armadillo does not do that.

"Armadillos also live in burrows along the middle course of streams (as opposed to only at the headwaters). It leaves many of its white flies at the hole that is along the middle course of a stream, while the other half of its flies follow it.

²⁸ Since the narrator planned to kill the mother and the young were too small to take home to eat, the narrator suggests leaving them outside the burrow so a jaguar could eat them, rather letting them starve.

Where it stays to sleep again, the flies perch at the entrance in the same number. Many buzz around the entrance. Many hang out at the edge of the hole. The greater long-nosed armadillo is one that lives like that.

"Greater long-nosed armadillos are often eaten by jaguars as they walk around at night. I once saw evidence that a jaguar had pounced on an armadillo from above, after waiting for it sitting on a tree branch. The jaguar had eaten the armadillo right there. It had removed its carapace cleanly. In the same manner that one removes the carapace after cooking it, it had gnawed the meat away from the part of the carapace that is above the ribs. Then, it had skinned it after placing it on a log. After doing that, it had peeled the rear portion of its carapace. In the same manner as it had done with the other part of the carapace, it had peeled the rear portion of the carapace well, such that there wasn't even a little piece of meat on it. The jaguar does not eat it all, but leaves a piece to eat later. It had covered its head and one of its legs with leaves. It had eaten it cutting it in half at the middle of its back. That is how the jaguar eats an armadillo, at night, since the armadillo does not walk around during the day. The jaguar eats collared peccaries and other animals walking around during the day. The armadillo does not walk around during the day. When a big rain falls at dusk, only then does it walk around when it is still light. The armadillo walks around after exiting its burrow when it sees that its 'house' is leaking during a rainstorm.

"Also, bush dogs smell an armadillo as it lies in its burrow during the day. After making it go into its retreat tunnel, a bush dog goes all the way to the end of its burrow and grabs it and brings it out. Then right there the whole pack eats it. Those little ones live in packs of about five. They eat greedily, taking bits of meat away from each other. They eat the whole armadillo without leaving any of it. By contrast, the big jaguar eats leaving a portion. It eats like that because it walks around alone.

"That is how the greater long-nosed armadillo lives."

APPENDIX 2

Gazetteer

Below we list the principal localities from which xenarthrans, carnivorans, perissodactyls, and terrestrial artiodactyls have been collected or observed in the Ucayali-Yavarí interfluvial region. Boldface identifies locality names as they appear in the text (alternative names or spellings are cited parenthetically). Except as noted otherwise, all localities are mapped in figure 2.

- Actiamë** (6°19'S, 73°09'W; Vriesendorp et al., 2006a): inventory site in the floodplain of the Río Yaquerana surveyed for large mammals from 2–7 November 2004 (Amanzo, 2006).
- Angamos** (also known as “Colonia Angamos” [not mapped]; 5°11'S, 72°53'W; DMA, 1989): military outpost on the left bank of the Río Yavarí (q.v.) just downstream from the confluence of the Río Gálvez (q.v.) and the Río Yaquerana.
- Anguila** (6°16'S, 73°55'W; Pitman et al., 2015): inventory site in the headwaters of the Quebrada Yanayacu, a minor right-bank affluent of the Río Tapiche (q.v.), surveyed for mammals by M. Escabedo-Torres from 14 to 20 October 2014 (Pitman et al., 2015).
- Boca Río Yaquerana** (ca. 5°12'S, 72°53'W): collecting locality of C. Kalinowski at the confluence of the Yaquerana with the Río Gálvez (q.v.) from 3–30 August 1957. The combined waters of the Yaquerana and the Gálvez form the Río Yavarí (Faura-Gaig, 1964), but the Yaquerana is sometimes also known as the Alto Yavarí (Faura-Gaig, 1964), not the “Alto Yaquerana” (contra Stephens and Traylor, 1983).
- Choncó** (5°33'S, 73°36'W; Vriesendorp et al., 2006a): inventory site in hilly terrain between the Río Tapiche (q.v.) and the Río Gálvez (q.v.) surveyed for large mammals by J. Amanzo from 25–28 October 2004 (Amanzo, 2006).
- Divisor** (7°12'S, 73°53'W; Vriesendorp et al., 2006b): inventory site near Tapiche (q.v.) east of the upper Río Tapiche (q.v.) in the Sierra del Divisor (250–600 m), surveyed for mammals by M.L.S.P. Jorge and P.M. Velazco from 19 to 23 August 2005 (Jorge and Velazco, 2006).
- Estación Biológica Quebrada Blanco** (EBQB; 4°21'S, 73°09'W; Heymann et al., 2011): research station near San Pedro (q.v.) on the Quebrada Blanco (q.v.) and adjacent to the Reserva Comunal Tamshiyacu-Tahuayo (q.v.).
- Itia Tëbu** (5°51'S, 73°46' W; Vriesendorp et al., 2006a): inventory site in white sand forest on the right bank of the Río Blanco (q.v.), surveyed for large mammals by J. Amanzo from 29 October to 2 November 2004 (Amanzo, 2006).
- Jenaro Herrera** (sometimes misspelled “Genaro Herrera” or “Henaro Errera”; 4°55'S, 73°40'W): botanical field station ca. 2.5 km inland from the right bank of the Río Ucayali surveyed for mammals by various research teams from 1978 to 2003 (Voss and Fleck, 2011: 10).
- Nuevo San Juan** (5°15'S, 73°10'W; IGN, 1995): Matses village on the right bank of the Río Gálvez, intensively sampled for mammals from 1995 to 1999 by D.W. Fleck and from 19 May to 12 July 1998 by R.S. Voss.
- Orosa** (ca. 3°32'S, 72°11'W; Wiley, 2010): collecting locality on the right (south) bank of the Amazon, where Alfonso and Ramón Olalla worked from 30 August to 11 December 1926 (probably near the modern village of San José de Orosa with above coordinates; Wiley, 2010). Hershkovitz (1977: 928) placed this locality on the Río Marañón, but Orosa lies well below the confluence of the Marañón and the Ucayali, so it is unambiguously on the Amazon (Río Amazonas; for Peruvian fluvial nomenclature, see Faura-Gaig, 1964).
- Quebrada Blanco** (also known as “Río Blanco”; mouth at ca. 4°19'S, 73°14'W; Valqui, 2001: fig. 2-2): right-bank tributary of the Río Tahuayo and site of faunal inventory fieldwork, some of which extended into the nearby Reserva Comunal Tamshiyacu-Tahuayo (q.v.). Valqui's (1999, 2001) inventory site at San Pedro (q.v.) was on the lower Quebrada Blanco. Not to be confused with the Río Blanco (q.v.), a tributary of the Río Tapiche.

- Quebrada Esperanza** (ca. 4°20'S, 71°55'S; Stephens and Traylor, 1983): collecting locality of C. Kalinowski on the left bank of the Río Yavarí-Mirím (q.v.) from 6–27 September 1957. Faura-Gaig (1964) gave the coordinates of Quebrada Esperanza at its confluence with the Yavarí-Mirím as 4°18'S, 71°56'W.
- Quebrada Pobreza** (5°59'S, 73°46'W; Pitman et al., 2015): inventory site on the eponymous stream, a left-bank affluent of the Río Blanco (q.v.), surveyed for mammals by M. Escobedo-Torres from 20–26 October 2014 (Pitman et al., 2015).
- Reserva Comunal Tamshiyacu-Tahuayo** (recently renamed the “Área de Conservación Regional-Comunal Tamshiyacu-Tahuayo”): a protected area of predominantly well-drained upland forest extending from the headwaters of the Río Tamshiyacu and the Río Tahuayo (both are right-bank tributaries of the Amazon) to the upper Río Yavarí-Mirím (a left-bank tributary of the Yavarí), comprising about 322,500 ha (Puentes and Bodmer, 1993: fig. 1).
- Río Blanco** (mouth at 5°34'S, 73°52'W; DMA, 1989): a right-bank tributary of the Río Tapiche (q.v.). This river is not labelled on our map (fig. 2), but it is the stream that separates Itia Tëbu from Quebrada Pobreza.
- Río Gálvez** (mouth at 5°12'S, 72°53'W; DMA, 1989): one of two principal headwater tributaries of the Río Yavarí (see Boca Río Yaquerana, above). Our inventory site at Nuevo San Juan (q.v.) is on the right bank of the middle Gálvez.
- Río Manítí** (mouth at 3°27'S, 72°51'W; DMA, 1989): minor right-bank tributary of the Amazon downstream from Iquitos.
- Río Orosa** (mouth at 3°29'S, 72°03'W; Wiley, 2010): minor right-bank tributary of the Amazon, probably with mouth near Orosa (q.v.) in the early 1900s but now shifted downstream (Wiley, 2010: 40).
- Río Tapiche** (see fig. 1; mouth at 5°03'S, 73°51'W; DMA, 1989): major right-bank tributary of the Ucayali upstream from Jenaro Herrera (q.v.).
- Río Yavarí** (mouth at 4°21'S, 70°02'W; DMA, 1989): major right-bank tributary of the Amazon, formerly an important source of wild rubber but now almost uninhabited (Bodmer and Puertas, 2003). Three sites along the left bank of the Yavarí between Angamos (q.v.) and the mouth of the Río Yavarí-Mirím (q.v.) were surveyed for large mammals by Salovaara et al. (2003): Quebrada Curacinha (5°03'S, 72°44'W), Quebrada Buenavista (4°50'S, 72°23'W), and Quebrada Limera (4°31'S, 71°54'W).
- Río Yavarí-Mirím** (also known as the “Yavarí-Mirí”, “Yavari-Mirín”, or “Yavarí Chico”; mouth at 4°31'S, 71°44'W): principal left-bank tributary of the Río Yavarí. The results of extensive transect census studies conducted at various sites along the upper and middle Yavarí-Mirím were reported by Puertas and Bodmer (1993) and Salovaara et al. (2003).
- San Pedro** (4°20'S, 73°12'W; Valqui, 2001): ribereño village on the lower Quebrada Blanco (q.v.) adjacent to Reserva Comunal Tamshiyacu-Tahuayo (q.v.). San Pedro was the site of a faunal inventory study by Valqui (1999, 2001), whose results were based on fieldwork conducted from 1993 to 1999. Local habitats include flooded and unflooded primary forest and secondary growth.
- Santa Cecilia** (3°33'S, 72°53'W; Robbins et al., 1991): collecting locality of C. Kalinowski on the right bank of the Río Manítí (q.v.) from 27 December 1956 to 21 January 1957. According to Robbins et al. (1991), who collected birds around Santa Cecilia in 1983, the predominant natural habitat is well-drained forest on level terrain.
- Tapiche** (7°12'S, 73°56'W; Vriesendorp et al., 2006b): inventory site on the right bank of the upper Río Tapiche, surveyed for mammals by M.L.S.P. Jorge and P.M. Velazco from 12–17 August 2005 (Jorge and Velazco, 2006).
- Wiswincho** (5°49'S, 73°52'W; Pitman et al., 2015): inventory site about 2 km from the left bank of the lower Río Blanco (q.v.), surveyed for mammals by M. Escobedo-Torres from 9–14 October 2014 (Pitman et al., 2015).

APPENDIX 3

LIST OF MAPPED AMAZONIAN COLLECTION
LOCALITIES FOR THREE-TOED SLOTHS
(*BRADYPUS VARIEGATUS*)

Below we list the Amazonian localities from which we examined specimens of three-toed sloths for this report. Numbers correspond to specimen records plotted on the map that accompanies our account for *Bradypus variegatus* (fig. 10), and italic font indicates major political divisions (state/department/province) within each country. Geographic coordinates are provided with a cited reference (in square brackets). Trinomial nomenclature follows usages explained in the text (“ssp.” = not assigned to subspecies)

BRAZIL

1. *Amazonas*, Rio Amazonas, “Villa Bella Imperatriz” (= Parintins, on right bank; 2°36’S, 56°44’W [Paynter and Traylor, 1991]): *Bradypus variegatus* ssp. (AMNH).
2. *Amazonas*, Rio Madeira, Rosarinho (on left bank; 3°42’S, 59°06’W [Vanzolini, 1992]): *Bradypus variegatus* ssp. (AMNH).
3. *Amazonas*, Rio Madeira, Santo Antonio [do] Guajará (4°20’S, 59°46’W [Vanzolini, 1992]): *Bradypus variegatus* ssp. (AMNH).
4. *Amazonas*, Rio Negro, “Cacao Pereira” (= Cacao-Pirera, on right bank; 3°09’S, 60°05’W [Vanzolini, 1992]): *Bradypus variegatus* ssp. (AMNH).
5. *Amazonas*, Rio Negro, “Javanari” (= Iauari, on right bank; 0°31’S, 64°50’W [Paynter and Traylor, 1991]): *Bradypus variegatus* ssp. (AMNH).
6. *Amazonas*, Rio Negro, Manaus (on left bank; 3°08’S, 60°01’W [Paynter and Traylor, 1991]): *Bradypus variegatus* ssp. (AMNH).
7. *Amazonas*, Santo Antonio de Amatary (ca. 3°00’S, 58°00’W [Gardner, 2008]): *Bradypus* ssp. (AMNH).
- 8a. *Amazonas*, Codajás (3°50’S, 62°05’W; Paynter and Traylor, 1991): *Bradypus variegatus* ssp. (BMNH).
- 8b. *Amazonas*, “Solimoens” (= Manacapuru, on left bank of upper Amazon; 3°18’S, 60°37’W [Paynter and Traylor, 1991]): *Bradypus variegatus* ssp. (AMNH).
9. *Pará*, Ilha de Marajó, Currálinho (1°48’S, 49°47’W [USBGN, 1963]): *Bradypus variegatus variegatus* (AMNH).
10. *Pará*, Patagonia (1°17’S, 47°58’W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (AMNH).
11. *Pará*, “Rio Majary” (= Rio Majari, right-bank tributary of lower Xingu [Vanzolini, 1992]), Recreio (ca. 1°42’S, 52°12’W [Paynter and Traylor, 1991]): *Bradypus variegatus variegatus* (AMNH).
12. *Pará*, Rio Tapajós, “Aramanay” (= Aramaná, on right bank; 2°45’S, 55°11’W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (AMNH).
13. *Pará*, Rio Tapajós, Caxiricatuba (on right bank; 2°36’S, 54°56’W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (AMNH).
14. *Pará*, Rio Tapajós, Inajatuba (apparently on left bank near Surucua, ca. 2°53’S, 55°11’W; Silva and Braga, 2016): *Bradypus variegatus variegatus* (AMNH).
15. *Pará*, Rio Tapajós, Igarapé Brabo (= Igarapé Bravo, on left bank, ca. 2°40’S, 55°10’W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (AMNH).
16. *Pará*, Rio Tapajós, “Igarapé Amarin” (= Amarin, on left bank; 2°32’S, 55°47’W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (AMNH).
17. *Pará*, Rio Tapajós, near Santarém (on right bank; 2°26’S, 54°42’W [Paynter and Traylor, 1991]): *Bradypus variegatus variegatus* (AMNH, FMNH).
18. *Pará*, Rio Tapajós, São Raimundo (on left bank; 3°44’S, 55°28’W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (FMNH).
19. *Pará*, Rio Tapajós, Fordlândia (on right bank; 3°40’S, 55°30’W [Paynter and Traylor, 1991]): *Bradypus variegatus variegatus* (FMNH).

20. *Pará*, Rio Tocantins, Baião (on right bank; 2°41'S, 49°41'W [Paynter and Traylor, 1991]): *Bradypus variegatus variegatus* (AMNH).
21. *Pará*, Rio Tocantins, "Ilha do Taiuna" (= Ilha do Iraúna, in midstream; 2°15'S, 49°28'W [Vanzolini, 1992]): *Bradypus variegatus variegatus* (AMNH).
22. *Pará*, Rio Tocantins, Mocajuba (on right bank; 2°35'S, 49°30'W [Paynter and Traylor, 1991]): *Bradypus variegatus variegatus* (AMNH).
- COLOMBIA
23. *Putumayo*, San Antonio (ca. 0°31'N, 76°45'W [Paynter, 1997]): *Bradypus variegatus infuscatus* (FMNH).
- ECUADOR
24. *Napo*, Río Suno below Loreto (ca. 0°38'S, 77°19'W [Paynter, 1993]): *Bradypus variegatus infuscatus* (FMNH).
25. *Pastaza*, east of Puyo (ca. 1°28'S, 77°59'W [Paynter, 1993]): *Bradypus variegatus infuscatus* (MSU).
26. *Pastaza*, Sarayacu (1°44'S, 77°29'W; Paynter, 1993): *Bradypus variegatus infuscatus* (BMNH).
- PERU
27. *Amazonas*, Huampami (4°28'S, 78°10'W [Patton et al., 1982]): *Bradypus variegatus infuscatus* (MVZ).
28. *Amazonas*, La Poza (4°03'S, 77°46'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (MVZ).
29. *Loreto*, Apayacu (3°29'S, 72°11'W [Wiley, 2010]): *Bradypus variegatus infuscatus* (AMNH).
30. *Loreto*, Boca Río Amasa on Río Morona (not located; arbitrarily plotted halfway between mouth of Río Morona and Ecuadorian border): *Bradypus variegatus infuscatus* (FMNH).
31. *Loreto*, Boca Río Curaray (2°22'S, 74°5'W; [Wiley, 2010]): *Bradypus variegatus infuscatus* (AMNH).
32. *Loreto*, Cocamilla on Río Ianacu (4°49'S, 74°10'W): *Bradypus variegatus infuscatus* (MUSM).
33. *Loreto*, Cocha Tacari on Río Ianacu (5°01'S, 74°13'W): *Bradypus variegatus infuscatus* (MUSM).
34. *Loreto*, Iquitos (3°46'S, 73°15'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (AMNH).
35. *Loreto*, Mishana on Río Nanay (ca. 3°53'S, 73°27'W; Stephens and Traylor, 1983): *Bradypus variegatus infuscatus* (MUSM).
36. *Loreto*, Nuevo San Juan on Río Gálvez (5°15'S, 73°10'W): *Bradypus variegatus infuscatus* (MUSM).
37. *Loreto*, Puerto Arturo (5°50'S, 76°03'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (FMNH).
38. *Loreto*, Puerto Indiana (3°30'S, 73°03'W [Wiley, 2010]): *Bradypus variegatus infuscatus* (AMNH).
39. *Loreto*, Río Samiria (mouth at 4°42'S, 74°13'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (AMNH).
40. *Loreto*, Santa Elena on Río Samiria (ca. 4°50'S, 74°13'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (FMNH).
41. *Loreto*, Sarayacu on Río Ucayali (ca. 6°47'S, 75°07'W [Wiley, 2010]): *Bradypus variegatus infuscatus* (AMNH).
42. *Ucayali*, Balta on Río Curanja (10°08'S, 71°13'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (LSUMZ, MVZ).
43. *Ucayali*, Pucallpa (8°23'S, 74°32'W [Stephens and Traylor, 1983]): *Bradypus variegatus infuscatus* (AMNH).
- VENEZUELA
44. *Amazonas*, Brazo Río Casiquiare (2°01'N, 67°07'W [Paynter, 1982]): *Bradypus variegatus infuscatus* (AMNH).
45. *Amazonas*, Esmeralda (3°10'N, 65°33'W [Paynter, 1982]): *Bradypus variegatus infuscatus* (AMNH).

APPENDIX 4

INVENTORY SITES IN THE YAVARÍ-UCAYALI INTERFLUVE SAMPLED BY VISUAL CENSUS FOR LARGE NONPRIMATE MAMMALS

	Census type	km ^a	Reference
Actiamë	diurnal and nocturnal	?	Amanzo (2006)
Anguila	mostly diurnal	31	Escobedo-Torres (2015)
Choncó	diurnal and nocturnal	?	Amanzo (2006)
Divisor	diurnal and nocturnal	65	Jorge & Velazco (2006)
Itia Tëbu	diurnal and nocturnal	?	Amanzo (2006)
Quebrada Pobreza	mostly diurnal	37	Escobedo-Torres (2015)
Río Yavarí ^b	diurnal	507	Salovaara et al. (2003)
Río Yavarí-Mirím ^c	diurnal	1827	Salovaara et al. (2003)
Tapiche	diurnal and nocturnal	111	Jorge and Velazco (2006)
Wiswincho	mostly diurnal	16	Escobedo-Torres (2015)

^a Total distance (kilometers) of walked transects, including repeats, as reported by authors.

^b Three sites on left bank below Angamos.

^c Two study areas.

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ON THE COVER: JUVENILE TWO-TOED SLOTH (*CHOLOEPUS HOFFMANNI*) KEPT AS A PET BY MATSES CHILDREN AT ESTIRÓN, ON THE LOWER QUEBRADA CHOBAYACU, LORETO, PERU.