A New Species of Thomasomys (Rodentia: Muridae) from Eastern Ecuador, with Remarks on Mammalian Diversity and Biogeography in the Cordillera Oriental

A New Species of *Thomasomys* (Rodentia: Muridae) from Eastern Ecuador, with Remarks on Mammalian Diversity and Biogeography in the Cordillera Oriental

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CONTENTS

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ABSTRACT

A new species of the murid rodent genus *Thomasomys* is described from the Cordillera Oriental of eastern Ecuador, a major range of the northern Andes that remains almost completely unexplored mammalogically. In order to provide a baseline for future faunal inventory work in these mountains, this report summarizes specimen data from the vicinity of Papallacta (0°22′S, 78°08′W), a small village located near tree line on the eastern (Amazonian) slope. In addition to the new *Thomasomys*, the local fauna includes 32 other species of nonvolant mammals, of which several (*Akodon latebricola*, *Thomasomys cinnameus*, and *T. erro*) have not been reported since their original descriptions in the 1920s. Taxonomic research based on this material indicates that at least six taxa currently treated as synonyms or subspecies should be recognized as valid species, including *Thomasomys popayanus* (possibly including *T. nicefori*) and *T. praetor* (both formerly synonymized with *T. aureus*), *T. cinnameus* and *T. hudsoni* (both formerly synonymized with *T. gracilis*), *T. erro* (formerly synonymized with *T. cinereiventer*), and *Coendou quichua* (formerly synonymized with *C. bicolor*). Although the Papallacta fauna includes several clades (''genera'') that extend to south- and north-temperate latitudes, over half of the local species are endemic to the northern Andes (north of the Huancabamba Deflection in northern Peru); among these northern-Andean endemics, three species known only from northeastern Ecuador provide evidence for a distinct center of endemism in the Cordillera Oriental. Quantitative estimates of species-level faunal complementarity indicate substantial horizontal turnover (between ecologically similar highland sites) on the scale of a few hundred kilometers, and almost complete vertical turnover (between adjacent highland and lowland sites) on the scale of about 2000 m. Both phenomena pose significant challenges for timely inventory work across vast Andean landscapes that remain sparsely sampled by mammalogists. In particular, the middle elevations of the eastern slope of the northern Andes, a densely forested region approximately 2 km high and over 1500 km long, remain a mammalogical terra incognita.

INTRODUCTION

Although the Cordillera Oriental (eastern Andes) of Ecuador was first traversed by Europeans in the sixteenth century, scientific knowledge of mammals from this region was not forthcoming until the late 1800s, when a small number of specimens began to arrive in European museums (de Winton, 1896; Cabrera, 1913, 1917). Throughout the first several decades of the 1900s, a period of active biological inventory elsewhere on the continent, only scattered collections amounting to just a few dozen specimens were made in the Cordillera Oriental. To date, no regional species lists or faunal descriptions of any kind have been published. This dearth of information is explained by the fact that only a few primitive trails formerly crossed the rugged eastern Andean escarpment, and those that did were frequently closed by landslides and other accidents. Even today, when all-weather roads provide more-or-less reliable access along several routes, the Cordillera Oriental remains almost unexplored mammalogically. Steep, unstable slopes afford few places to camp, and the dripping-wet

forests are miserable places to run traplines for more than a few days at a time. Most collecting expeditions to eastern Ecuador have hurried downslope to more inviting habitats in the Amazonian lowlands.

One of the few inhabited places in the Cordillera Oriental is Papallacta (0°22′S, 78°08′W), a small village perched several hundred meters below treeline on the eastern slope (fig. 1). Centuries old, and a regular stopping point along the ancient trail from Quito to Baeza, Papallacta was often visited by itinerant naturalists and collectors (e.g., Jameson, 1858; Almagro, 1866; Orton, 1870; Goodfellow, 1901; Sinclair, 1929; Moore, 1934; Webb, 1939). None, however, made substantial collections of mammals there, with the result that only a few species of the local fauna have been recorded in the literature.

In the course of field research on ichthyomyine rodents (Voss, 1988), I collected nonvolant small mammals near Papallacta on several visits from 1978 to 1980, including a new species belonging to the endemic Andean muroid rodent genus *Thomasomys*.
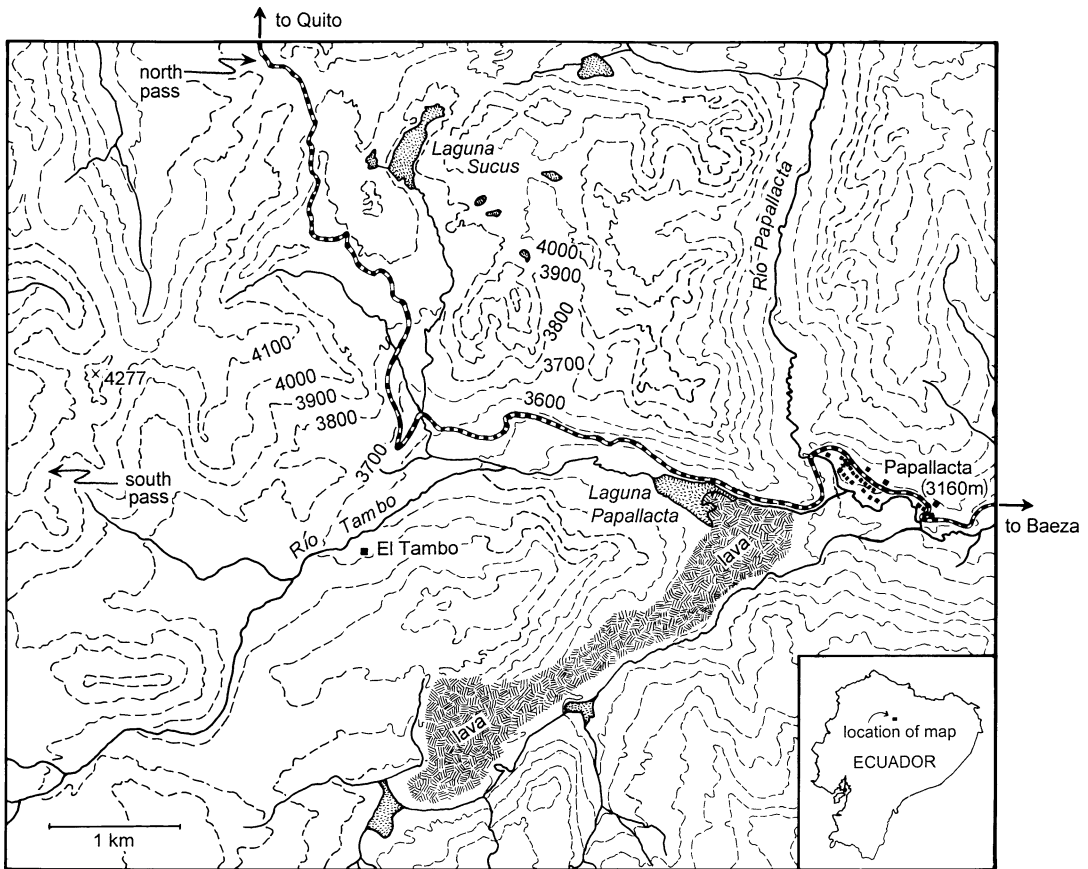
Fig. 1. Map of the Papallacta region (based on IGM, 1978a, 1978b) illustrating local landscape features mentioned in the text. Both the north pass (crossed by the modern road from Quito to Baeza) and the south pass (now roadless) are referred to in the literature as "Guamaní" (see appendix 1). Two nearby localities recorded on specimen tags are outside the limits of this quadrangle: Tablón lies about 3 km to the west, and Cerro Antisana is about 8 km to the south. The continental divide, which runs diagonally across the upper left corner, forms the boundary between Pichincha province (to the west) and Napo province (to the east).

Herein I describe that species and summarize information about other sympatric taxa represented among the material collected. These data, together with records of additional species documented by museum specimens or other reliable information, provide the basis for a preliminary assessment of mammalian diversity and biogeographic relationships on the upper slopes of the Cordillera Oriental. In effect, this study establishes a baseline for future inventory efforts along a still-intact but threatened habitat gradient that extends over 4000 m from snow line to the Amazonian lowlands and harbors one of the least known mammalian faunas in South America.

THE PAPALLACTA REGION

The mean annual temperature at Papallacta—ca. 3200 m above sea level—is almost 17°C (Wernstedt, 1972), but nights are cold throughout the year, mornings are always chilly, and only the rare sunny afternoon is actually warm. Above the town, temperatures are substantially lower. A maximum-minimum thermometer that I installed beneath the forest canopy at 3600 m and checked daily from 9 March to 14 April 1980 recorded a minimum temperature of 4°C and a maximum temperature of 14°C during that interval. Ground frost is common on open hill-

sides from about 3400 m upslope, where stream banks are often rimed with ice in the early morning. Blizzards occasionally blanket the landscape above 4000 m with snow, and local herders sometimes lose cattle to exposure in the months of *invierno* (the local winter, July and August). Permanent snow fields begin at about 4700 m on Cerro Antisana, about 11 km due south of Papallacta (Whymper, 1892; Black, 1982).

Eleven years of weather records from Papallacta indicate that local precipitation is seasonally distributed, with an average monthly minimum of 98 mm in December and an average monthly maximum of 215 mm in July; the total annual average is 1643 mm (Wernstedt, 1972). Although these figures are not impressive by comparison with those from adjacent lowland sites that receive almost 4000 mm of rainfall annually (Ferndon, 1950), Papallacta is persistently humid because it is shrouded in fog and mist for most of the year. Chapman's (1926: 29) inexplicable assignment of Papallacta to the ''Arid Division'' of his so-called Temperate Zone was not based on first-hand experience of this notoriously damp region.[2]

Most of the mineral substrate surrounding Papallacta is igneous, consisting of lava, cinders, and ash from prehistoric eruptions of Antisana (0°30′S, 78°08′W; 5700 m), a now-dormant volcano that is one of the principal peaks of the Cordillera Oriental (see Sauer [1971: 16] for a brief technical account of the local geology). From the continental divide (about 4100 m; see appendix 1) to treeline the local landscape consists of rolling hillsides and rocky peaks dissected by narrow ravines or divided by broad flat-bottomed cirques (fig. 2). The alpine vegetation of this páramo zone consists principally of wiry bunch grass (to 1 m high) on well-drained slopes (fig. 3), but flat valley bottoms are marshy with pools of standing water and low hummocks of moss and other cushion-forming plants. Large terrestrial bromeliads (*Puya*) are scattered on open hillsides, but other kinds of large rosette plants that are common in Colombian and Venezuelan páramos are seldom seen. Almost pure stands of *Polylepis* (Rosaceae) occur as dense thickets whose canopies rarely exceeds 3–4 m. Within these nearly impenetrable tangles, limbs, trunks, and elevated root mats are covered with thick layers of cold, wet moss. Additional floristic, phenological, and anthropogenic aspects of local páramo habitats are described by Grubb (1960), Øllgaard and Balslev (1979), Black (1982), and Laegaard (1992).

Between about 3700 and 3600 m, an ecotone of mixed bunch grass and waist-high shrubs (fig. 4) marks the transition between open páramo vegetation and Subalpine Rain Forest (sensu Grubb, 1977), a distinctive formation of small trees that marks the uppermost limit of continuous forest cover. The canopy of this dwarfed forest seldom exceeds 5 or 6 m. There is no appreciable understory vegetation, but horizontal limbs, sprawling trunks, and fallen logs limit foot travel and visibility. Although epiphytic orchids and bromeliads seem to be absent at this elevation, wet mats of moss, lichens, and climbing ferns completely cover tree trunks and branches (fig. 5). A few thin vines are present, but not woody lianas. Palms, bamboo, and tree ferns are likewise absent. Herbaceous dicots, ferns, and horsetails (*Equisetum*) provide a sparse ground cover. Moss, littered leaves, matted roots, and a deep, peaty humus make the ground soft and springy underfoot.

Below about 3400 m, the forest becomes gradually taller and assumes the characteristics of Upper Montane Rain Forest (sensu Grubb, 1977), but in the immediate vicinity of Papallacta (between about 3200 and 3000 m) most of this natural vegetation has been cleared for agriculture and animal husbandry; only a few stands of dense secondary growth persist along streambanks, at the bases of cliffs, and at the bottoms of steep ravines. Farther downslope, the forest canopy ascends to 25 m or more, vascular epiphytes (e.g., orchids and bromeliads) are conspicuous on tree trunks and branches, and tree ferns and bamboo (*Chusquea*) are abundant

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[2] There is no indication in Chapman's published Ecuadorean itinerary (op. cit.: 15–16) that he ever visited Papallacta. Moore (1934: 99) did, however, and he correctly assigned Papallacta to the ''Humid Temperate Zone'' of Chapman's ecogeographic system. Every traveller's account mentions the cold and the wet near Papallacta, but particularly evocative annecdotes are provided by Øllgaard and Balslev (1979: 17–28).

Fig. 2. Páramo landscape about 12 km (by road) W Papallacta. The road from Quito to Baeza crosses the middle foreground approximately following the 3900 m contour. The open (paler) vegetation is páramo grassland, whereas the darker patches are *Polylepis* thickets. Photographed by Paul Kaarakka, 14 April 1980.

in the understory. Other vegetation formations along this elevational gradient (Lower Montane Rain Forest at 1710 m and Lowland Rain Forest at 380 m) were described in detail by Grubb et al. (1963).

MATERIALS AND METHODS

I worked near Papallacta in May and June of 1978 and in March, April, May, and August of 1980. Traplines were laid out to sample all local habitats as thoroughly as possible, but a special effort was made to collect semiaquatic species by wading in streams and setting traps along the water's edge. Forest traplines always consisted of traps set both in trees and on the ground. Except as noted below I used only snap-traps (Museum Specials and Victor rat traps), which were baited with rolled oats mixed with either canned sardines or peanut butter.

All trapped mammals were prepared as skins and skulls (with skinned carcasses in 10% formalin), or were preserved entire in 10% formalin; formalin-preserved material was subsequently washed and transferred to 70% ethanol for museum storage. Standard external measurements in millimeters (total length from nose to fleshy tail tip, TL; length of tail from dorsal flexure to fleshy tip, LT; length of hindfoot from heel to longest claw, HF; and length of ear from notch to fleshy apex, Ear) and weight in grams were recorded along with habitat notes (see below) and other information in field catalogs that are currently stored as bound volumes in the Division of Mammals at the University of Michigan Museum of Zoology (UMMZ).

Habitat and microhabitat data were recorded in a waterproof notebook at each capture site. In 1980 all trapped animals were placed individually in small paper bags with a chloroform-soaked gauze pad, and the bag was

Fig. 3.   Closeup of páramo vegetation at 3800 m above sea level, approximately 11 km (by road) W Papallacta. Wiry bunch grass (foreground) is the typical vegetation on exposed slopes at this elevation, but *Polylepis* thickets occur on the hill crest and backslope. Photographed by Paul Kaarakka, 19 April 1980.

then twisted shut; each specimen was subsequently combed for ectoparasites, which were preserved in 70% ethanol. All mammalian specimens were given unique field catalog numbers (prefixed by ''RSV''), and the same numbers were used to identify the hosts of collected ectoparasites (e.g., the holotype of *Plocopsylla nungui* Schramm and Lewis, 1987).

Mileages provided in the text were measured from the center of Papallacta by automobile odometer, or were estimated from a 1:25,000 topographic map (IGM, 1978). Altitudes were recorded in the field using a Thommen 2000 pocket altimeter calibrated in feet (ft). Fifteen altimetric readings that I recorded from this instrument in the center of Papallacta from 2 March to 14 April 1980 had a mean of 10,266 ft, a standard deviation of 44 ft, and a range of 10,180–10,325 ft; according to the best available topographic map (IGM, 1978), the elevation in the center

of Papallacta is 3160 m (10,367 ft), suggesting that the altimetric data reported herein are about 30 m less, on average, than corresponding map values. In the following accounts, elevations that I originally recorded in feet are converted to their metric equivalents.

Most of the systematic problems discussed below concern muroid rodents, for which relevant anatomical terminology is referenced or defined by Reig (1977), Carleton (1980), and Voss (1988, 1993). Head-and-Body Length (HBL) was obtained from measurements taken in the field (see above) by subtracting Length of Tail (LT) from Total Length (TL). The following craniodental measurements were taken in the museum with dial calipers (fig. 6): CIL, condylo-incisive length; LD, length of diastema; LM, occlusal length of the maxillary molar row; BM1, breadth of the first maxillary molar; LIF, length of one incisive foramen; BIF,

Fig. 4. The shrubby ecotone at treeline (about 3700 m above sea level) where most specimens of the new *Thomasomys* species were collected, approximately 8 km (by road) W Papallacta. Photographed by the author, 12 May 1978.

breadth across both incisive foramina; BPB, breadth of the palatal bridge; BZP, breadth of the zygomatic plate; LIB, least interorbital breadth; ZB, zygomatic breadth; DI, depth of upper incisor; BIT, breadth across both upper incisor tips.

The specimens reported below are deposited in the following institutional collections, listed in order of their traditional acronyms: The American Museum of Natural History, New York (AMNH); the Natural History Museum, London (BMNH); the Field Mu-

Fig. 5.   Subalpine Rain Forest just below treeline (about 3600 m above sea level), approximately 6 km (by road) W Papallacta. The low, tangled structure of the forest and the thick mats of moss, lichens, and climbing ferns that cover trunks and branches are characteristic features of this habitat. Photographed by Paul Kaarakka, 16 April 1980.

seum of Natural History, Chicago (FMNH); the University of Kansas Museum of Natural History, Lawrence (KU); the Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia'', Buenos Aires (MACN); the Museo de Ciencias Naturales, Instituto Nacional Mejía, Quito (MCN); the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); the Museo Nacional de Ciencias Naturales, Madrid (MNCN); the Museum, Michigan State University (MSU); the Museum of Vertebrate Zoology, Berkeley (MVZ); Museo de Zoología, Pontifica Universidad Católica del Ecuador (QCAZ); the Natural Historie Riksmuseet, Stockholm (NHRS); the University of Michigan Museum of Natural History, Ann Arbor (UMMZ); and the National Museum of Natural History, Washington (USNM). A representative series of the Papallacta material currently cataloged in the UMMZ collection will be transferred to QCAZ in the near future to serve as an in-country resource for specimen identification.

A NEW *THOMASOMYS*

Among the material collected near Papallacta is a previously unknown murid rodent belonging to the sigmodontine genus *Thomasomys* Coues. Formerly construed broadly to include southeastern Brazilian taxa (e.g., by Osgood, 1933; Ellerman, 1940; Cabrera, 1961; Pine, 1980), *Thomasomys* has subsequently been restricted (Voss, 1993; González, 2000) to a smaller but still speciose group that is endemic to tropical Andean cloud forests from Venezuela to Bolivia. Apparently, the center of diversity for the genus includes eastern Ecuador, where the new species described below may occur sympatrically with at least seven other congeners.
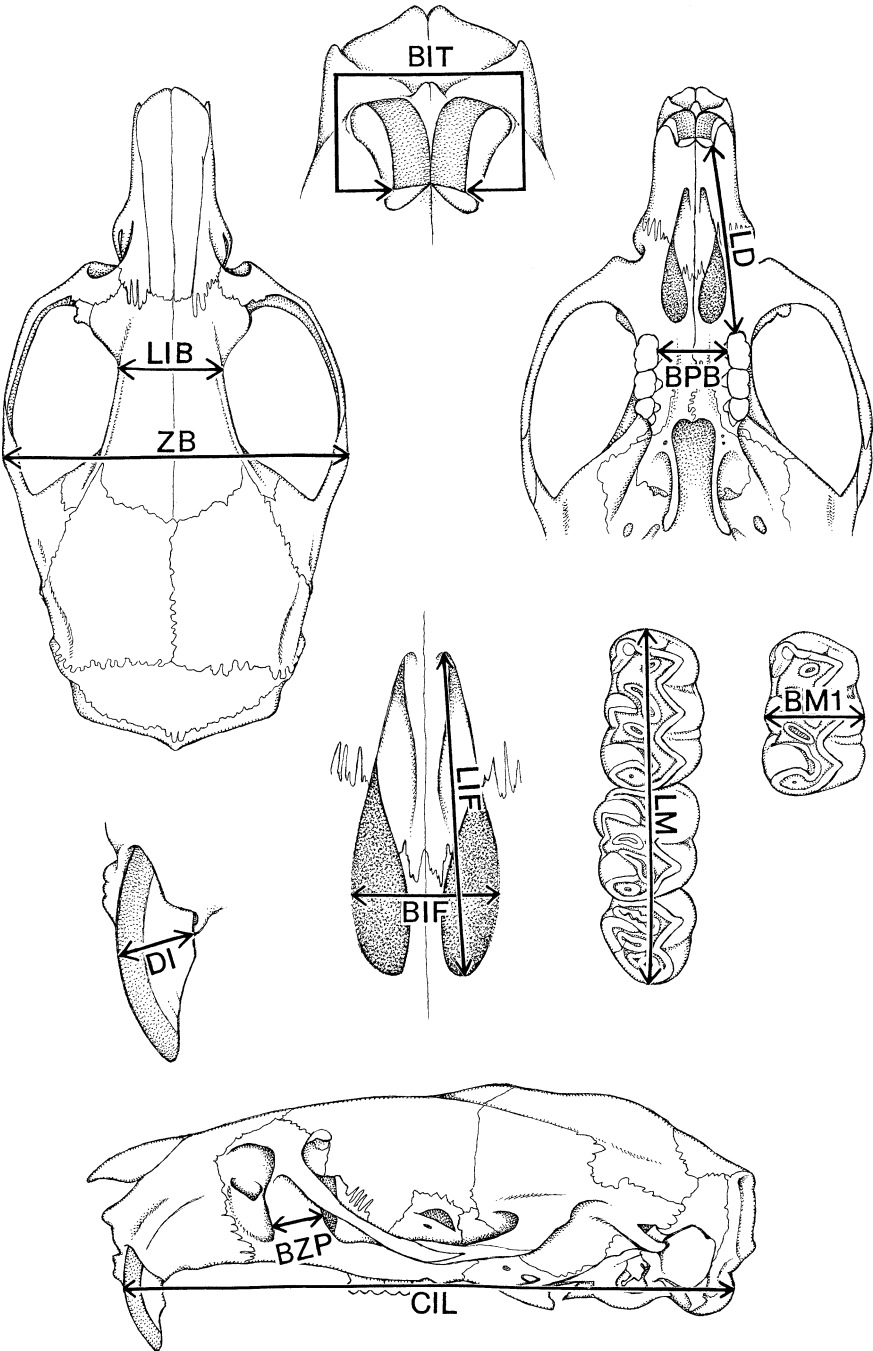
Fig. 6. Anatomical limits of 12 rodent craniodental measurements described in the text (see Materials and Methods).

Thomasomys ucucha, new species
Figures 7–13

TYPE MATERIAL: The holotype, UMMZ 155644 (skin, skull, and fluid-preserved carcass; original number RSV 660), is an adult male that I collected on 26 April 1980 at an elevation of 11,100 ft (3384 m) in the valley of the Río Papallacta (ca. 3–5 km by trail NNW Papallacta), Provincia Napo, Ecuador.

Forty-two other specimens collected in 1978 and 1980, hereby designated as paratypes, are from 8.2 km (by road) W Papallacta, 12,200 ft (UMMZ 127119, 127120, 155717); 7.5 km (by road) W Papallacta, 12,000 ft (UMMZ 155652–155655, 155722–155732); 6.2 km (by road) W Papallacta, 11,700 ft (AMNH 244611–244613; UMMZ 127121, 155742, 155649–155651, 155714–155716, 155718, 155719, 155733–155736); and the Río Papallacta valley [3–5 km by trail NNW Papallacta], 11,100 ft (UMMZ 155643, 155645–155648, 155720, 155721). Three additional paratypes (AMNH 46621, 46622, 46624) were collected in 1903 by L. Söderström at Tablón, in Provincia Pichincha (see appendix 1).

DISTRIBUTION: Known only from the crest of the Cordillera Oriental (between ca. 3400 and 3700 m) just south of the equator in the Ecuadorean provinces of Pichincha and Napo.

ETYMOLOGY: *Ucucha* is the local Quichua word for "mouse" (Orr, 1978), here treated as a noun standing in aposition to the generic name.

DIAGNOSIS: A medium-sized, dark-furred, long-tailed species of *Thomasomys* with short, blunt rostrum; narrow interorbital region with rounded supraorbital margins; widely flaring zygomatic arches; straight fronto-nasal profile; broad, vertically oriented zygomatic plate; short incisive foramina; separate buccinator-masticatory and accessory oval foramina; primitive (pattern 1) carotid circulation; small, uninflated auditory bullae; small, hypsodont molars lacking well-developed cingula and stylar cusps; very small upper third molars; broad and conspicuously procumbent upper incisors; and a distinctive range of morphometric variation (table 1).

DESCRIPTION: Pelage dense, fine, and soft,

TABLE 1
Measurements (mm) and Weights (g) of *Thomasomys ucucha* and *T. hylophilus*[a]

	T. ucucha[b]	*T. hylophilus*[c]
Sex	19 females, 17 males	10 females, 14 males
HBL	110 ± 6 (94–119) 35	115 ± 5 (107–125) 24
LT	140 ± 7 (122–151) 35	142 ± 7 (124–155) 24
HF	28 ± 1 (26–30) 35	26 ± 1 (25–28) 24
Ear	18 ± 1 (17–20) 35	18 ± 1 (17–20) 11
CIL	27.8 ± 0.9 (25.8–29.1) 36	26.9 ± 0.9 (25.2–28.9) 21
LD	8.9 ± 0.4 (7.9–9.6) 36	8.0 ± 0.4 (7.2–8.6) 24
LM	4.4 ± 0.1 (4.2–4.6) 32	4.8 ± 0.2 (4.5–5.2) 24
BM1	1.4 ± 0.0 (1.4–1.5) 36	1.5 ± 0.0 (1.4–1.5) 24
LIF	5.4 ± 0.2 (4.9–5.8) 36	6.1 ± 0.3 (5.4–6.7) 24
BIF	2.3 ± 0.1 (2.0–2.5) 36	2.3 ± 0.2 (1.9–2.6) 22
BPB	3.6 ± 0.2 (3.3–4.0) 36	3.3 ± 0.2 (3.0–3.8) 22
BZP	2.4 ± 0.1 (2.1–2.6) 36	2.4 ± 0.1 (2.2–2.7) 24
LIB	4.8 ± 0.1 (4.5–4.9) 36	4.7 ± 0.1 (4.5–4.9) 23
ZB	15.9 ± 0.6 (14.4–16.8) 36	15.6 ± 0.5 (14.6–16.4) 22
DI	1.5 ± 0.1 (1.3–1.6) 36	1.5 ± 0.1 (1.3–1.7) 24
BIT	2.1 ± 0.2 (1.6–2.3) 36	1.9 ± 0.1 (1.7–2.1) 24
Weight	36 ± 5 (24–46) 35	36 ± 3 (32–40) 11

[a] Tabulated statistics for both species include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size.

[b] AMNH 244611–244613; UMMZ 127119–127121, 155643, 155644, 155646, 155649, 155651–155655, 155714, 155716, 155717, 155719, 155722–155726, 155728–155732, 155734, 155735, 155742, 155745, 155720, 155721, 155727.

[c] AMNH 143667, 143668; FMNH 18563, 18565, 18566, 18576, 18580, 18584, 18587, 18591, 18593, 18595; USNM 259613, 442305, 442308, 442313, 442315–442320, 442322, 442324.

about 13–15 mm long over the back and rump; somberly colored (dark) and not abruptly countershaded. Mass-effect dorsal coloration near Smithe's (1975) Brownish Olive (color 29) along flanks, shading to Dark Grayish Brown (color 20) middorsally. Ventral pelage Dark Neutral Gray (color 83) basally, with superficial wash of Light Neutral Gray (color 85) or Glaucous (color 80); not sharply set off from dorsal coloration. Mystacial vibrissae long, extending just behind pinnae when laid back alongside head. Ears sparsely covered with short, blackish hairs, not contrasting conspicuously with col-

or of head. Hairs over metapodials and digits of manus and pes dark, but tufts of longer hairs at bases of pedal claws silvery. Pes neither very narrow nor conspicuously broad; digit V long (its claw extending almost to base of claw of digit IV), but apparently nonopposable. Tail substantially longer than combined length of head and body, uniformly dark in most specimens but occasionally tipped with white; sparsely haired except for 5–10 mm terminal pencil. Mammae six in inguinal, abdominal, and postaxial pairs.

Skull (in dorsal view) characterized by short, blunt rostrum flanked by shallow zygomatic notches; narrow, hourglass-shaped interorbit with rounded (not beaded or squared) margins; broadly flaring zygomatic arches; and large, oblong braincase unmarked by prominent temporal scars or lambdoidal ridges. Dorsal profile (in lateral view) distinctively flattened from nasal tips to midfrontal region; anterior margin of zygomatic plate straight and nearly vertical, not conspicuously sloping backward from base. Incisive foramina widest just behind premaxillary/maxillary suture and short (averaging 60% of diastemal length), not approaching first molar alveoli. Palatal bridge broad, smooth (without prominent ridges or grooves), and short (not extending posteriorly behind molar rows); posterolateral pits small, simple, inconspicuous perforations (never large, complex, or recessed in shallow fossae). Mesopterygoid fossa broad, straight-sided, extending anteriorly between third molars; bony roof complete or perforated by narrow, slit-like sphenopalatine openings flanking the presphenoid/basisphenoid suture. Parapterygoid fossae narrow, approximately triangular, with shallow (unexcavated) anterior limits. Alisphenoid strut present, separating buccinator-masticatory from accessory oval foramina. Carotid circulation primitive (pattern 1), as indicated by large stapedial foramen, prominent squamosal-alisphenoid groove, and sphenofrontal foramen. Postglenoid foramen and subsquamosal fenestra subequal; tegmen tympani broadly overlaps posterior suspensory process of squamosal. Auditory bullae small, uninflated, flask-shaped; without sharply defined transition between capsular part and bony eustacian tube. Tympanic membrane pars flaccida

present, large. Malleus with large orbicular apophysis.

Mandible with distinct capsular process for lower incisor alveolus on lateral surface posteroventral to base of coronoid process. Basihyal more-or-less straight (not strongly arched), without entoglossal process.

Upper incisors large, broad, and conspicuously procumbent, with heavily pigmented enamel bands (near Smithe's [1975] Spectrum Orange [color 17] in fresh material). Upper molars in parallel left and right series, small, pentalophodont, hypsodont when unworn (by comparison with more brachydont congeners), and lacking well-developed cingula and stylar cusps. M1 anterocone divided by anteromedian flexus into subequal anterolabial and anterolingual conules. Paralophs and metalophs (on M1 and M2) connect corresponding labial cusps to mesolophs and posterolophs, respectively, or to median mures, not to opposing lingual cusps. M3 conspicuously smaller than M2 (<50% as estimated by occlusal areas) and usually lacking a distinct lingual fold (hypoflexus). Lower molars similar to upper teeth in general design, but m1 anteroconid often undivided (even in unworn dentitions), and m3 not conspicuously reduced. Molar root formulas unknown (no specimens are available with loose teeth), but M1 and m1 apparently without accessory rootlets.

Stomach unilocular-hemiglandular. Adult males with one pair each of dorsal prostate, anterior prostate, ampullary, vesicular, and bulbo-urethral glands; and with two pairs of ventral prostate glands. Macroscopic preputial glands absent. Glans penis small, short, and subcylindrical (weakly divided into right and left halves by a shallow middorsal trough and an inconspicuous midventral raphe but otherwise unmarked by external folds); externally covered with coarse spines except for broad rim of soft, crenulated tissue surrounding terminal crater; crater contents include three bacular mounds, bifurcate urethral flap, and one dorsal papilla; two small spinous patches of rugose epithelium present dorsolateral to bacular mounds, but remaining crater contents unarmed.

COMPARISONS: As restricted by Voss (1993) and González (2000), the genus *Thomasomys* consists of 6-mammate pentalopho-
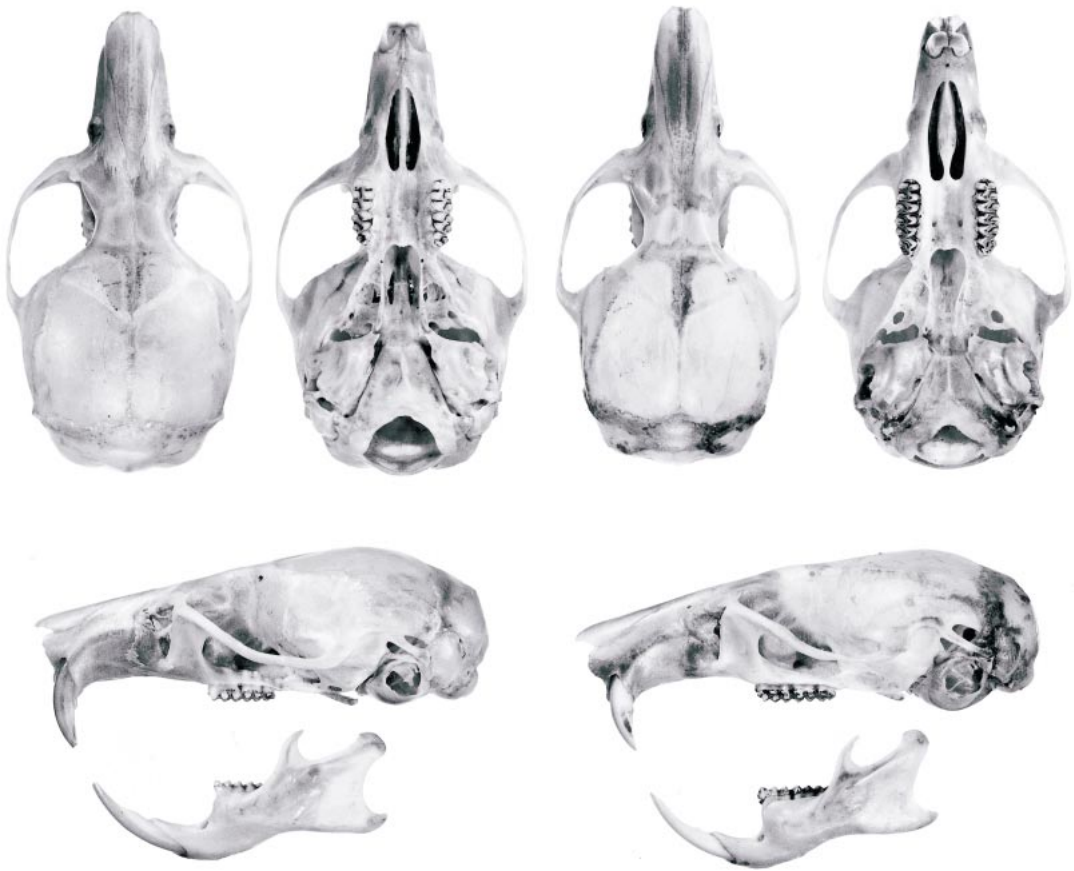
Fig. 7.   Dorsal, ventral, and lateral cranial views of *Thomasomys ucucha* (**left,** UMMZ 155644, holotype) and *T. hylophilus* (**right,** FMNH 18593, paratype). Approximately twice life size.

dont Andean sigmodontines with very shallow zygomatic notches; hourglass-shaped interorbital regions that lack well-developed beads or projecting supraorbital shelves; short palates lacking prominent posterolateral pits; and auditory bullae firmly attached to the skull by overlap of the tegmen tympani with a posterior suspensory process of the squamosal. Because all of these traits are currently thought to be plesiomorphies within the Neotropical muroid radiation (Voss, 1993), the genus lacks compelling evidence of monophyly. Pending a comprehensive phylogenetic analysis of the ''thomasomyine'' group, however, there is no more restricted taxonomic category within which to assess the relationships of *T. ucucha*. Phenetically, the new species most closely resembles *T. hylophilus* Osgood (1912), an al-

lopatric taxon that occurs in northeastern Colombia and western Venezuela.[3]

Thomasomys ucucha and *T. hylophilus* overlap in all external and craniodental measurements (table 1), and they share many qualitative traits in common: both lack genal vibrissae but have moderately long mystacial hairs; relatively long tails; similarly proportioned hind feet; flattened fronto-nasal profiles; narrow interorbital regions with round-

[3] Specimens of *Thomasomys hylophilus* examined for this report include the holotype (FMNH 18583) together with 43 other specimens collected in or near the Páramo de Tamá on the border between Venezuela (Estado Táchira) and Colombia (Departamento Norte de Santander): AMNH 143667, 143668; FMNH 18563, 18565, 18566, 18576, 18580, 18584, 18587, 18591, 18593, 18595; USNM 259613, 442305, 442307–442311, 442313–442320, 442322–442331, 442336–442341.
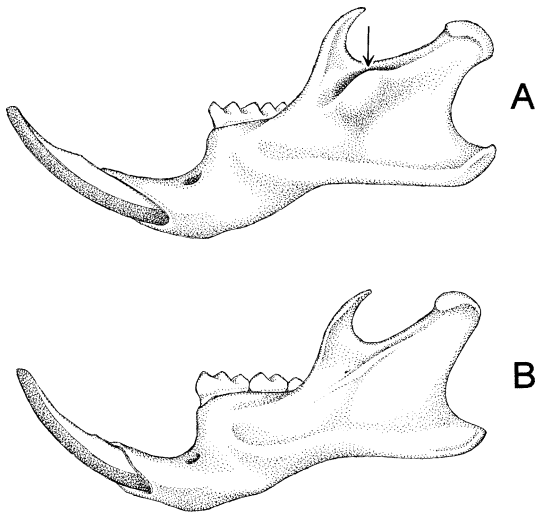
Fig. 8. Lateral mandibular views of *Thomasomys ucucha* (**A,** UMMZ 155644, holotype) and *T. hylophilus* (**B,** FMNH 18593, paratype). Among other species differences, a distinct capsular process for the lower incisor alveolus is present posteroventral to the coronoid process in *T. ucucha* (arrow), whereas this structure is absent in *T. hylophilus*.

ed supraorbital margins; straight, vertically oriented zygomatic plates; broad palates; alisphenoid struts that separate buccinator-masticatory and accessory oval foramina; complete (pattern 1) carotid arterial circulations; oblong braincases; small, uninflated auditory bullae; relatively hypsodont molars that lack well developed cingula and stylar cusps; and unilocular-hemiglandular stomachs. Despite this suite of resemblances, *ucucha* and *hylophilus* differ in other points of comparison.

In dorsal cranial view (fig. 7), *Thomasomys ucucha* is distinguishable at a glance by its relatively short, broad rostrum and by its widely flaring, rounded zygomatic arches. By contrast, the rostrum of *T. hylophilus* is proportionately longer and narrower, and the zygomatic arches converge anteriorly from a widest point across their squamosal roots. In ventral view, the incisive foramina of *ucucha* are absolutely shorter than those of *hylophilus*, and they are also proportionately shorter in relation to the diastema: the ratio LIF/LD averages about 61% in the former species versus about 76% in the latter. The posterior opening of the alisphenoid canal, a tiny per-

foration behind each parapterygoid fossa in *ucucha*, is a conspicuously larger orifice in *hylophilus*.

Thomasomys ucucha and *T. hylophilus* are also dentally distinctive. The upper incisors of *ucucha* are broader, more deeply pigmented, and more procumbent than those of *hylophilus*. In side-by-side comparisons, the contrast in upper incisor procumbency between the two species is visually obvious (fig. 7), but measurements provide a more objective basis for discrimination. Measured with an ocular goniometer, the chord that subtends the exposed greater curvature of these teeth defines an average anterior angle of 87° with the occlusal plane of the upper molars in *ucucha* (observed range, 85–89°; N = 14), whereas the homologous angle has an average value of 77° in *hylophilus* (observed range, 76–79°; N = 11).[4] A correlated species difference in the lower incisors is likewise apparent: whereas the lower incisor root of *ucucha* is contained in a prominent capsular process on the lateral mandibular surface just below the base of the coronoid process (fig. 8A), the lower incisor root of *hylophilus* terminates in an inconspicuous bony ridge without a distinct process (fig. 8B).

The molar dentition provides several additional traits of diagnostic value. The upper toothrow is shorter on average in *Thomasomys ucucha* than in *T. hylophilus* (table 1), a difference that is primarily attributable to the size of M3. That tooth ranges from 0.8 to 1.0 mm long and accounts for just 21% of average toothrow length in *ucucha*, versus 1.2–1.3 mm long and 25% of toothrow length in *hylophilus*. Correlated species differences in occlusal complexity are also apparent (fig. 9). In the upper molars, the anterolophs and mesolophs of M1 and M2 are much more weakly developed in *ucucha* than in *hylophilus*, and M3 usually lacks a distinct lin-

[4] This angle is equivalent to the incisive index of Thomas (1919), who defined the standard descriptive terminology for rodent incisor procumbency. According to Thomas's definitions, proodont incisors are those with index values >90°, orthodont incisors are those with index values close to 90°, and opisthodont incisors are those with index values <90°. Therefore, the incisors of *Thomasomys ucucha* are orthodont, whereas those of *T. hylophilus* are opisthodont.
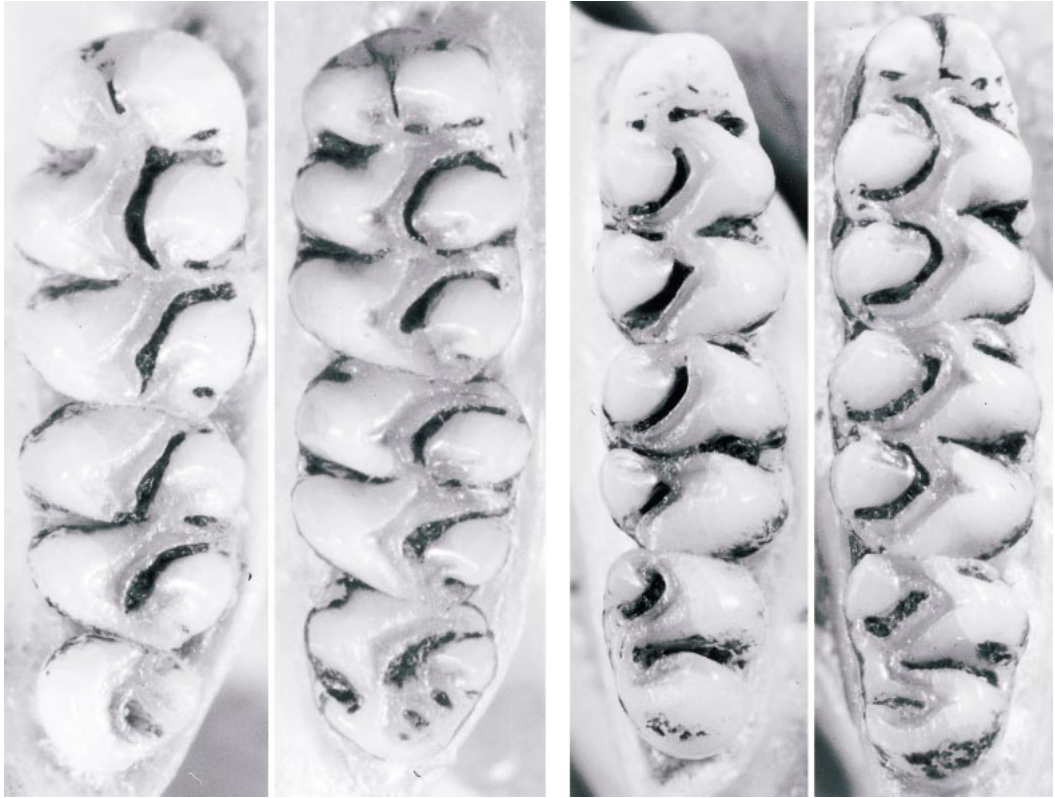
Fig. 9.   Left upper and right lower molars of *Thomasomys ucucha* (left-hand photo of each pair, UMMZ 155722) and *T. hylophilus* (right-hand photo of each pair, USNM 442322). Note the relatively smaller M3 of *T. ucucha*, the presence of a distinct lingual fold on the M3 of *T. hylophilus*, and the relatively larger (more robust) anterolophs and mesolophs of the latter species.

gual fold (hypoflexus) in *ucucha* that is consistently present in *hylophilus*. In the lower dention, the anteromedian flexid of m1 is shallower, less persistent with wear, or altogether absent in *ucucha*, whereas this fold is always present and usually persistent in *hylophilus*.

Incisor procumbency alone is sufficient to set *Thomasomys ucucha* apart from other congeners, only two of which approach the orthodont condition (defined in footnote 4, above). However, both of those species—*T. australis* with an index value of 85°, and *T. daphne* with an index value of 90°—have chisel-like incisors that are much shorter and narrower than the more scooplike, longer, and broader teeth of *ucucha* (fig. 10), and neither species closely resembles *ucucha* in other respects. *Thomasomys ucucha* is readily distinguished from other congeneric species known

to occur in the Cordillera Oriental of northern Ecuador (*T. aureus*, *T. baeops*, *T. cinnameus*, *T. erro*, *T. paramorum*, *T. rhoadsi*, *T. silvestris*; see below) by numerous qualitative and quantitative character differences that are summarized in table 2.

REMARKS: In a previous list of Papallacta mammals (Voss, 1988: table 43), I referred to this taxon as "*Thomasomys* sp."

FIELD OBSERVATIONS: The 42 specimens of *Thomasomys ucucha* that I collected near Papallacta in 1978 and 1980 were trapped at elevations ranging from 3380 to 3720 m. Of these, 3 were taken in grassy páramo, 22 were taken in the shrubby páramo/forest ecotone or in grassy glades surrounded by forest, and 17 were taken deep inside Subalpine Rain Forest. Most recorded captures were on the ground, of which 18 were in rabbit trails or runways through dense grass or low herbs;
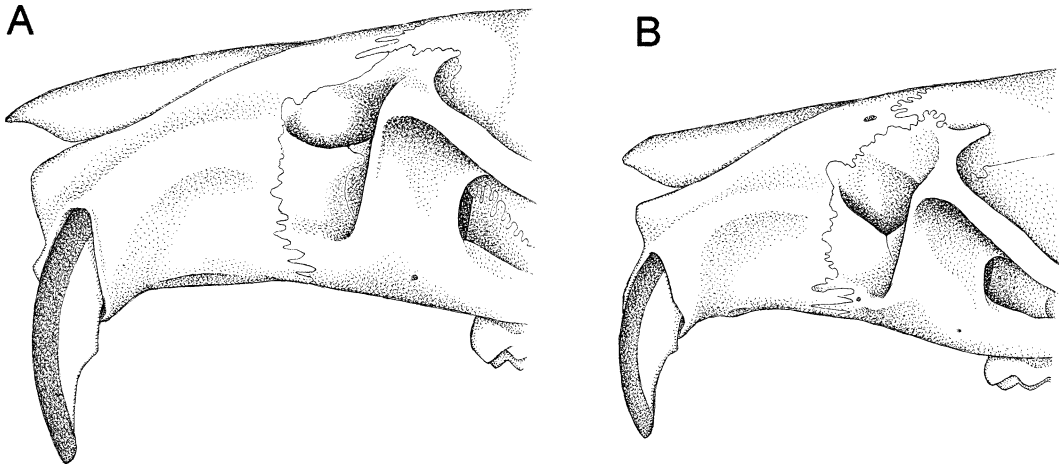
Fig. 10. Lateral view of rostrum of *Thomasomys ucucha* (**A,** UMMZ 155652) and *T. daphne* (**B,** UMMZ 160579). Although both species have procumbent (orthodont) incisors, those of *ucucha* are longer, broader, and more scoop-like than the shorter, narrower, chisel-like teeth of *daphne*.

16 were in runways through moss or damp litter, under mossy debris, or at the bases of mossy trees; and 7 were along the wet margins of small streams. Only one specimen was trapped off the ground, on the mossy limb of a low tree. Other muroid species that were trapped syntopically (in the same habitats) with *T. ucucha* include *Akodon latebricola*, *Akodon mollis*, *Anotomys leander*, *Chilomys instans*, *Microryzomys altissimus*, *M. minutus*, *Neusticomys monticolus*, *T. aureus*, *T. baeops*, *T. cinnameus*, *T. erro*, and *T. paramorum*.

OTHER SYMPATRIC TAXA

In addition to *Thomasomys ucucha*, 32 other species of nonvolant mammals are definitely known to occur along the crest of the Cordillera Oriental near Papallacta, including some that I collected in 1978 and 1980, others that were previously reported in the literature, and a few that are here documented for the first time based on earlier collections. The geographic scope of the following review includes localities above 3000 m on both the western slope (Provincia Pichincha) and the eastern slope (Provincia Napo) from about 0°20′S to 0°30′S. The two most distant collection sites within these limits are only about 15 airline km apart.

The species accounts below summarize information about available specimens from this region, together with notes on taxonomy, habitats, and relevant literature references. Identifications of *Thomasomys* species were a significant challenge in working up this material due to the virtually complete absence of any modern revisionary literature on this large and difficult genus (the unique exception is Gómez-Laverde et al., 1997). In the absence of other taxonomic resources, I compared specimens with holotypes and/or original descriptions of all of the 40 nominal taxa listed by Musser and Carleton (1993), together with the recently described species *T. apeco* Leo and Gardner (1993), *T. macrotis* Gardner and Romo (1993), and *T. onkiro* Luna and Pacheco (2002). In some cases the results of such exercises indicated that the current nomenclature is incorrect, and these accounts therefore recommend several necessary taxonomic changes.

Caenolestes fuliginosus (Tomes)

SPECIMENS COLLECTED: 10.6 km (by road) W Papallacta, 12,600 ft (UMMZ 155581); 6.2 km (by road) W Papallacta, 11,700 ft (AMNH 248261–248271; UMMZ 127107–127109, 127152–127157, 155571–155580, 155688–155689, 155692–155695); Río Papallacta Valley, 11,100 ft (UMMZ 155570, 155690, 155691).

OTHER MATERIAL: Three additional speci-

TABLE 2
Morphological Comparisons Among Eight Species of *Thomasomys* from the Cordillera Oriental

T. aureus	*T. baeops*	*T. cinnameus*	*T. erro*
Size: large (HF = 38-40 mm; LM = 7.2-7.7 mm; weight 75-100+ g).	*Size*: medium (HF = 24-27 mm; LM = 4.2-4.5 mm; weight 27-45 g).	*Size*: small (HF = 21-23 mm; LM = 3.8-4.0 mm; weight 14-19 g).	*Size:* medium (HF = 28-32 mm; LM = 4.5-4.8 mm; weight 28-46 g).
Tail relatively long (LT about 130% of HBL).	*Tail* relatively long (LT about 126% of HBL).	*Tail* relatively long (LT about 140% of HBL).	*Tail* relatively long (LT about 132% of HBL).
Dorsal pelage uniformly rich yellowish- to reddish- brown.	*Dorsal pelage* dull olive-brown, darker middorsally than along flanks.	*Dorsal pelage* uniformly warm reddish-brown.	*Dorsal pelage* uniformly dark grayish-brown.
Genal vibrissae present.	*Genal vibrissae* absent.	*Genal vibrissae* absent.	*Genal vibrissae* absent.
Mystacial vibrissae very long, extending posteriorly well behind pinnae.	*Mystacial vibrissae* very long, extending posteriorly well behind pinnae.	*Mystacial vibrissae* long, extending posteriorly just behind pinnae.	*Mystacial vibrissae* short, usually not extending posteriorly behind pinnae.
Rostral tube absent.[a]	*Rostral tube* absent.[a]	*Rostral tube* absent.[a]	*Rostral tube* present.[a]
Interorbital region very narrow,[b] with squared supraorbital margins.	*Interorbital region* narrow,[b] with squared supraorbital margins.	*Interorbital region* narrow,[b] with rounded supraorbital margins.	*Interorbital region* very broad,[b] with rounded supraorbital margins.
Zygomatic plate broad.[c]	*Zygomatic plate* broad.[c]	*Zygomatic plate* broad.[c]	*Zygomatic plate* narrow.[c]
Incisive foramina very long, usually extending posteriorly between molar alveoli.	*Incisive foramina* long, usually extending posteriorly to but not between molar alveoli.	*Incisive foramina* long, usually extending posteriorly to but not between molar alveoli.	*Incisive foramina* short, usually not extending posteriorly to molar alveoli.
Palate narrow.[d]	*Palate* broad.[d]	*Palate* broad.[d]	*Palate* broad.[d]
Alisphenoid strut present.	*Alisphenoid strut* present.	*Alisphenoid strut* present.	*Alisphenoid strut* usually absent.
Carotid circulation pattern 3.	*Carotid circulation* pattern 3.	*Carotid circulation* pattern 1.	*Carotid circulation* pattern 1.
Auditory bullae small and uninflated	*Auditory bullae* small and uninflated	*Auditory bullae* small and uninflated	*Auditory bullae* small and uninflated
Capsular process of lower incisor alveolus indistinct or absent.	*Capsular process of lower incisor alveolus* large well developed.	*Capsular process of lower incisor alveolus* indistinct or absent.	*Capsular process of lower incisor alveolus* absent.
Upper incisors opisthodont, not procumbent.	*Upper incisors* opisthodont, not procumbent.	*Upper incisors* opisthodont, not procumbent.	*Upper incisors* opisthodont, not procumbent.
Molars hypsodont when unworn; without well-developed cingulae or stylar cusps.	*Molars* brachydont, even when unworn; with well-developed cingulae and stylar cusps.	*Molars* hypsodont when unworn; without well-developed cingulae or stylar cusps.	*Molars* hypsodont when unworn, without well-developed cingulae or stylar cusps.

[a] Character defined by Voss (1993: 15).

[b] Expressed as a percentage of zygomatic breadth, relative interorbital breadth ranges from 25 to 39% among these species. Qualitative descriptors ("narrow", "broad", etc.) are arbitrary partitions of this continuum.

TABLE 2
(Continued)

T. paramorum	T. rhoadsi	T. silvestris	T. ucucha
Size: small (HF = 23-25 mm; LM = 3.8-4.3 mm; weight = 17-26 g).	*Size:* medium (HF = 28-31 mm; LM = 5.1-5.6 mm; no weight data).	*Size:* medium (HF = 28-30 mm; LM = 4.8-5.1 mm; no weight data).	*Size:* medium (HF = 26-30 mm; LM = 4.2-4.6 mm; weight = 24-46 g).
Tail relatively long (LT about 132% of HBL).	*Tail* relatively short (LT about 95% of HBL).	*Tail* relatively long (LT about 140% of HBL).	*Tail* relatively long (LT about 128% of HBL).
Dorsal pelage uniformly dull olive-brown.	*Dorsal pelage* uniformly dark grayish-brown.	*Dorsal pelage* uniformly dark grayish brown.	*Dorsal pelage* uniformly dark grayish-brown.
Genal vibrissae absent.	*Genal vibrissae* absent.	*Genal vibrissae* absent.	*Genal vibrissae* absent.
Mystacial vibrissae long, extending posteriorly just behind pinnae.	*Mystacial vibrissae* short, usually not extending posteriorly behind pinnae.	*Mystacial vibrissae* long, extending posteriorly just behind pinnae.	*Mystacial vibrissae* long, extending posteriorly just behind pinnae.
Rostral tube absent.[a]	*Rostral tube* absent.[a]	*Rostral tube* absent.[a]	*Rostral tube* absent.[a]
Interorbital region narrow,[b] with rounded supraorbital margins.	*Interorbital region* broad,[b] with rounded supraorbital margins.	*Interorbital region* narrow,[b] with rounded supraorbital margins.	*Interorbital region* narrow,[b] with rounded supraorbital margins.
Zygomatic plate broad.[c]	*Zygomatic plate* broad.[c]	*Zygomatic plate* broad.[c]	*Zygomatic plate* broad.[c]
Incisive foramina very long, usually extending posteriorly between molar alveoli.	*Incisive foramina* short, usually not extending posteriorly to molar alveoli.	*Incisive foramina* short, usually not extending posteriorly between molar alveoli.	*Incisive foramina* very short, not approaching level of molar alveoli.
Palate broad.[d]	*Palate* broad.[d]	*Palate* broad.[d]	*Palate* broad.[d]
Alisphenoid strut present.	*Alisphenoid strut* present.	*Alisphenoid strut* present.	*Alisphenoid strut* present.
Carotid circulation pattern 1.	*Carotid circulation* pattern 1.	*Carotid circulation* pattern 1.	*Carotid circulation* pattern 1.
Auditory bullae large and conspicuously inflated.	*Auditory bullae* small and uninflated.	*Auditory bullae* small and uninflated.	*Auditory bullae* small and uninflated.
Capsular process of lower incisor alveolus indistinct or absent.	*Capsular process of lower incisor alveolus* indistinct or absent.	*Capsular process of lower incisor alveolus* indistinct or absent.	*Capsular process of lower incisor alveolus* usually distinct.
Upper incisors opisthodont, not procumbent.	*Upper incisors* opisthodont, not procumbent.	*Upper incisors* opisthodont, not procumbent.	*Upper incisors* orthodont, conspicuously procumbent.
Molars hypsodont when unworn; without well-developed cingulae or stylar cusps.	*Molars* hypsodont when unworn; without well-developed cingulae or stylar cusps.	*Molars* hypsodont when unworn; without well-developed cingulae or stylar cusps.	*Molars* hypsodont when unworn; without well-developed cingulae or stylar cusps.

[c] Expressed as a proportion of condylo-incisive length, the relative breadth of the zygomatic plate ranges from 5 to 9% among these species. Qualitative descriptors ("narrow", "broad", etc.) are arbitrary partitions of this continuum.

[d] Character defined by Hershkovitz (1962: 54).

mens (FMNH 43164–43166) were collected on Cerro Antisana by R. Olalla in 1930.

TAXONOMY: The genus *Caenolestes* was revised by Bublitz (1987), who examined eight of the specimens listed above and identified the local population as belonging to the nominotypical subspecies *C. f. fuliginosus*.

FIELD OBSERVATIONS: The 40 specimens of *Caenolestes fuliginosus* that I collected near Papallacta in 1978 and 1980 were trapped at elevations ranging from 3380 to 3840 m. Of these, 39 were taken in Subalpine Rain Forest, and one was trapped in a *Polylepis* thicket in the páramo zone. Most recorded captures were on the ground: 24 along mossy or muddy stream margins, 5 in narrow runways or tunnels through wet moss, 5 in wet leaf litter beneath tangled shrubs or branches, and 3 in shallow cavities beneath earth banks or root mats. Only three individuals were taken above ground level, on the inclined trunks or horizontal limbs of low, moss-covered trees.

Didelphis pernigra J.A. Allen

SPECIMENS COLLECTED: 1.4 km (by road) E Papallacta, 9980 ft (UMMZ 155582).

OTHER MATERIAL: Apparently none.

TAXONOMY: The white-eared Neotropical *Didelphis* were recently revised by Lemos and Cerqueira (2002), who distinguished the Andean form (*D. pernigra*) as a distinct species from the predominantly lowland taxon *D. albiventris* Lund, with which it was formerly synonymized (e.g., by Gardner, 1993).

FIELD OBSERVATIONS: The single specimen of *Didelphis pernigra* that I collected near Papallacta in 1980 was taken at 3040 m in a wire live trap set on the ground in wet secondary growth surrounded by pastures and agricultural fields.

Cryptotis cf. *montivagus* (Anthony)

SPECIMENS COLLECTED: 7.5 km (by road) W Papallacta, 12,000 ft (UMMZ 155585); 6.2 km (by road) W Papallacta, 11,700 ft (UMMZ 155583, 155584, 155704, 155705).

OTHER MATERIAL: A single specimen (AMNH 63844) labeled ''Guamaní'' on one side of the original label and ''Cerro Guamaní'' on the other side was collected by the Olallas in 1922. Additional shrews from the Cordillera Oriental include one (MCN 150)

collected at Papallacta by C. Olalla in 1931 and another (QCAZ 307) collected on Antisana by R. Sierra in 1985 (D. Tirira, personal commun.).

TAXONOMY: The Ecuadorean species of *Cryptotis* were recently reviewed by Vivar et al. (1997), who identified the Guamaní specimen (AMNH 63844) as *C. montivagus*. The five Papallacta shrews, collected only a few kilometers from Guamaní, appear to be indistinguishable from AMNH 63844 and presumably represent the same taxon. However, measurements of these six specimens (from Papallacta and Guamaní) indicate that they have slightly narrower zygomatic plates and broader interorbits than typical *montivagus*, and side-by-side comparisons reveal that they have much less robust anterior unicuspids than any specimen of the type series (AMNH 47197–47201; from Bestión, in the Ecuadorean province of Azuay). The possible taxonomic significance of these and other differences (V. Pacheco and N. Woodman, personal commun.) remain to be determined by a more comprehensive evaluation of character variation in Ecuadorean shrews.

REMARKS: In a previous list of Papallacta mammals (Voss, 1988: table 43), I misidentified this material as *Cryptotis thomasi* (Merriam, 1897).

FIELD OBSERVATIONS: The five shrews that I collected near Papallacta in 1980 were taken at elevations ranging from 3570 to 3660 m. Of these, three were trapped on the ground in runways or small tunnels through moss in Subalpine Rain Forest, one was found dead on a trail in Subalpine Rain Forest, and one was trapped in a runway though tall grass at the páramo/forest ecotone.

Pseudalopex culpaeus (Molina)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: I examined a single specimen (AMNH 66739) collected at 4145 m elevation on Cerro Antisana by G.H.H. Tate in 1923. Another specimen (MNCN 3652), which I have not seen, was collected on Antisana by M. Jiménez de la Espada in 1865 (J. Barreiro, personal commun.).

TAXONOMY: There has been no comprehensive revision of the wolf-like canid taxa currently referred to this species. According

to Lönnberg (1922) and Cabrera (1958) the local form is *reissii* Hilzheimer (1906), which was originally described from material collected on Volcán Cotopaxi (0°40′S, 78°26′W).

REMARKS: According to Emerson and Johnson (1960) and Black (1982), *Pseudalopex culpaeus* is common in the páramo landscapes surrounding Cerro Antisana.

Lynchailurus pajeros (Desmarest)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: A single specimen (FMNH 43291) was collected by R. Olalla at 4000 m elevation on Cerro Antisana in 1934.

TAXONOMY: The pampas cat genus *Lynchailurus* was revised by García-Perea (1994), who examined FMNH 43291 and identified the local population as *L. pajeros thomasi* Lönnberg (1913). Wozencraft (1993) included this taxon in the synonymy of *Oncifelis colocolo* (Molina).

Puma concolor (Linnaeus)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: Apparently none.

REMARKS: Pumas are hunted along the crest of the Cordillera Oriental, where they are said to follow the movements of deer in remote parts of the páramo near Cerro Antisana (Emerson and Johnson, 1960), but I did not observe any in the course of my work near Papallacta.

Conepatus cf. *semistriatus* (Boddaert)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: I examined a single specimen (AMNH 66719) that was collected by H.E. Anthony at 4145 m on Cerro Antisana in 1923. Other material that I have not seen (Diego Tirira, personal commun.) includes one specimen from 4200 m on Cerro Antisana (QCAZ 0638), and another from 2800 m near Cuyuja (E of Papallacta on the road to Baeza; QCAZ 0726).

TAXONOMY: Ecuadorean hog-nosed skunks are currently referred to *Conepatus semistriatus* (e.g., by Cabrera, 1958; Kipp, 1965; Wozencraft, 1993), but no substantive analysis of character data is apparently available

to justify this convention.[5] Van Gelder's (1968) detailed analysis of variation in cranial and pelage traits within a very large Uruguayan sample of *Conepatus* could serve as the basis for a much-needed revision of this genus in South America.

REMARKS: Although none were seen in the course of our fieldwork, skunks are said to be common in local páramo habitats (Black, 1982).

Mustela frenata Lichtenstein

SPECIMENS COLLECTED: None.

OTHER MATERIAL: I examined two specimens from the Stockholm museum collected by L. Söderström in 1918. One (NHRS A58/6157) is an adult male labeled ''side of Guamani near Papallacta 11,000 ft'' [3353 m], and the other (NHRS A58/6145) is an adult female labeled ''below Papallacta 9000 ft'' [2743 m]; both are skins and skulls in good condition.

TAXONOMY: Lönnberg (1921) and Hall (1951) examined the material described above and provided qualitative descriptions and measurements in their systematic accounts. However, whereas Lönnberg identified the local population as *Mustela macrura* Taczanowski (1874), Hall treated *macrura* and other South American long-tailed weasels as subspecies of *M. frenata* (the type locality of which is in Mexico). Hall's concept of *frenata* (the basis for Wozencraft's [1993] synonymy) implies genetic continuity among populations of long-tailed weasels from Canada to Bolivia, a hypothesis that has yet to be tested by any geographically extensive analysis of morphometric or molecular data.

REMARKS: Although uncommon and rarely seen, weasels are locally regarded as pests that enter houses to kill domesticated guinea pigs (*Cavia porcellus*). Hall (1951: 402) incorrectly copied the locality of NHRS A58/6157 as ''Nára [sic] Papallacta'' from the Swedish museum label rather than from Söderström's original (English) specimen tag.

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[5] Kipp's (1965) paper, cited as a generic revision by Wozencraft (1993), only analyzed character data from Patagonian material.

Tremarctos ornatus (F. Cuvier)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: Apparently none.

REMARKS: The local population of spectacled bears was studied by Suárez (1988), who described their seasonal distribution and diet on the eastern slopes of Cerro Antisana. No locally collected specimens, however, are apparently preserved in museums. Although I did not see any bears in the course of my fieldwork, signs of their foraging (consisting of shredded terrestrial bromeliads whose pith is an important item of diet) were sometimes observed above treeline.

Hippocamelus antisiensis (D'Orbigny)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: An adult female specimen and a juvenile male, formerly preserved in the Museo Nacional de Ciencias Naturales (Madrid), were collected on Cerro Antisana in 1865 by M. Jiménez de la Espada. This material was originally reported by Cabrera (1917), whose taxonomic identification can be accepted as authoritative. Unfortunately, both specimens were lost during the Spanish Civil War or its aftermath, when the collections of the MNCN remained uncurated for several decades (J. Barreiro, personal commun).

REMARKS: The huemal is thought to be extinct in Ecuador (Albuja, 1991), and only four specimens appear to have ever been collected there. Mysteriously, all are now lost. In addition to the Madrid specimens, a single skull (MACN 31.69) alleged to have come from eastern Ecuador was formerly preserved in Buenos Aires (Tirira, 1999), and another specimen (from "Ecuador" without other locality data) was formerly in the FMNH (Elliot, 1907).

Odocoileus peruvianus (Gray)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: The holotype of *Odocoileus peruvianus consul* Lönnberg is an adult female specimen (NHRS A63/0094), collected by L. Söderström in 1920 at "Guamani on the road to Papallacta, altitude 12,000 feet" (Lönnberg, 1922: 13; O. Grönwall, personal commun.). Additional specimens of white-tailed deer (AMNH 66743, 66744) were collected by H.E. Anthony between 4100 and 4300 m on Cerro Antisana in 1923.

TAXONOMY: Cabrera (1961) and most subsequent authors (including Grubb, 1993) treated *Odocoileus peruvianus* as a synonym or subspecies of *O. virginianus*, but all South American white-tailed deer appear to be diagnostically distinct from the latter species (Molina and Molinari, 1999). Pending a comprehensive revision of the Neotropical forms of *Odocoileus*, I recognize *peruvianus* (with type locality in the Peruvian highlands) as a distinct species following Molina and Molinari's (1999) provisional taxonomy.

REMARKS: White-tailed deer are said to be common throughout the páramo landscapes surrounding Cerro Antisana (Black, 1982), but I did not observe any in the course of my fieldwork.

Pudu mephistopheles (de Winton)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: The holotype of the northern pudu (BMNH 96.1.28.5), which I have not examined, was collected in the "Paramo of Papallacta" by native collectors in the employ of Ludovic Söderström, the Swedish consul in Quito (de Winton, 1896). Another Söderström specimen (which I did examine) is NHRS A58/4636, a dried skin with the skull inside labeled "Papallacta 12000 ft", collected in 1908 and originally reported by Lönnberg (1913).

TAXONOMY: The genus *Pudu* was revised by Hershkovitz (1982), who reviewed the scant literature on these rare deer and summarized information about the diagnostic characters, geographic distribution, and natural history of *P. mephistopheles*.

REMARKS: Pudus are avidly hunted everywhere they occur and appear to be uncommon or hard to observe throughout their dwindling geographic range. I did not see any in the course of my fieldwork near Papallacata, but Black (1982) reported recent sightings of spoor in the páramos surrounding Cerro Antisana.

Tapirus (*Pinchacus*) *pinchaque* (Roulin)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: Two specimens of the

woolly tapir are known from Papallacta. The first (AMNH 70521), consisting of a skull collected by the Olallas (a family of professional collectors) in 1925, is unaccompanied by other geographic data. The second (AMNH 149370) is the skin and skull of an individual that was captured alive by C. Cordier, who sold it to the New York Zoological Society in 1952; an index card in the AMNH collection archives indicates that this specimen was captured at 11,500 ft (3505 m), but Hershkovitz (1954: 476) reported the capture elevation as 3150 m.

TAXONOMY: The taxonomy of living Neotropical tapirs was revised by Hershkovitz (1954), who diagnosed the subgenus *Pinchacus* and established that Roulin's is the oldest valid name for the woolly montane species.

REMARKS: Woolly tapirs have long been hunted in the vicinity of Papallacta and Antisana, from which hides and meat are still exported for sale in the street markets of Quito (Downer, 1997). Although tracks and droppings are commonly encountered (Black, 1982), the animal itself is seldom seen.

Akodon latebricola (Anthony)

SPECIMENS COLLECTED: 10.6 km (by road) W Papallacta, 12,600 ft (UMMZ 155616); 7.5 km (by road) W Papallacta, 12,000 ft (UMMZ 155607–155615, 155768–155772, 155774); 6.2 km (by road) W Papallacta, 11,700 ft (UMMZ 155773, 155775, 155776); Río Papallacta valley [3–5 km by trail NNW Papallacta], 11,100 ft (UMMZ 155617, 155618).

OTHER MATERIAL: None.

TAXONOMY: Originally described as *Microxus latebricola*, this species has long been known only from the holotype (AMNH 67506) collected by G.H.H. Tate in 1924 at Hacienda San Francisco, a locality in the Cordillera Oriental east of Ambato (Anthony, 1924b: 3). A peculiar feature of AMNH 67506 is its intensely black fur, which is quite unlike the normal coloration of any other muroid rodent species known to me. Anthony (1924b) considered and rejected the hypothesis that the holotype was a melanistic mutant, but the rediscovery of this taxon at

Papallacta lends support to the opposite conclusion.

Except in pelage color, the Papallacta specimens are qualitatively indistinguishable from the type of *latebricola*, and measurements of the type fall within the range of morphometric variation in the Papallacta series. By contrast with the unnatural appearance of AMNH 67506, the Papallacta skins are dark grizzled-brown dorsally, and the ventral fur is gray-based with a superficial brownish wash; the ears, feet, and the dorsal surface of the tail are likewise dark brown, but the ventral surface of the tail is covered with long silvery hairs. Because brownish pigmentation is almost universal among the small akodontine rodents that inhabit humid Andean habitats, it is more parsimonious to assume that this is the normal coloration of *Akodon latebricola*, and that the coloration of the type is not, in point of fact, typical.

This species closely resembles *Akodon bogotensis* Thomas (1895a), another eastern-Andean species that was formerly referred to the genus *Microxus*. Among other shared similarities, both species differ from typical *Akodon* by their very small size; possession of a slender, tapering rostrum flanked by very shallow zygomatic notches (versus a shorter, stouter rostrum flanked by deeper zygomatic notches); origin of the superficial masseter from an indistinct tubercle or scar on the anterior margin of the zygomatic plate (versus from a scar posteroventral to the anterior edge of the zygomatic plate); confluence of the buccinator- masticatory foramen and foramen ovale (versus buccinator masticatory foramen and foramen ovale accessorius separated by a vertical strut of the alisphenoid); proportionately shorter incisive foramina, wider parapterygoid fossae, and more inflated bullae; and highly distinctive molars with opposite (versus alternating) cusps. Although phylogenetic analyses of mitochondrial DNA sequences do not support the separate generic status of *Microxus* (as represented by the type species *mimus* Thomas; see Smith and Patton [1993] and references cited therein), sequence data from *latebricola* and *bogotensis* have not been analyzed. Despite their current generic classification, these two northern-Andean endemics clearly form a distinct clade that merits nomenclatural recognition.

Subtle but consistent craniodental differences (M. Gómez-Laverde, personal commun.) distinguish *latebricola* from *bogotensis* and support their current status as valid species.

REMARKS: In a previous list of Papallacta mammals (Voss, 1988: table 43), I misidentified this material as *Microxus bogotensis*.

FIELD OBSERVATIONS: The 21 specimens of *Akodon latebricola* that I collected near Papallacta in 1980 were trapped at elevations ranging from 3380 to 3840 m. Of these, 16 were taken in the shrubby páramo/forest ecotone, 2 in Subalpine Rain Forest, 2 in grassy glades surrounded by Subalpine Rain Forest, and 1 in grassy páramo. All recorded captures were on the ground: 9 in runways under dense bunch grass, 8 among mixed grasses and mossy shrubs, and 4 under moss mats or low herbs. Unlike other murid rodents that I collected near Papallacta (which appear to be strictly nocturnal), several individuals of *A. latebricola* were captured in broad daylight, between the time when traps were checked just after dawn and when they were rebaited in the late afternoon.

Akodon mollis Thomas

SPECIMENS COLLECTED: 12.5 km W (by road) Papallacta, 13,520 ft (UMMZ 155597); 10.6 km W (by road) Papallacta, 12,600 ft (UMMZ 155596, 155777); 7.5 km W (by road) Papallacta, 12,000 ft (UMMZ 155591–155595); 6.2 km W (by road) Papallacta, 11,700 ft (UMMZ 155586–155590, 155778–155780).

OTHER MATERIAL: Three additional specimens were collected at ''Tablon, road to Papallacta'' with recorded elevations of 10,500–11,500 ft [3200–3505 m] by L. Söderström in 1903 and 1913. Another nine specimens (AMNH 47156–47164) taken by the same collector in 1914 are labeled ''Mt. Antisana 12000 feet'' [3658 m]. Forty-two more specimens (AMNH 66450–66491) were collected by H.E. Anthony and G.H.H. Tate between 4115 and 4570 m on Antisana in 1923. Lastly, three specimens (AMNH 67330, 67332, 67334) collected in 1924 by R. Olalla are labeled ''Mt. Guamaní, road to Papallacta'' with recorded elevations of 12,000–13,000 ft [3658–3962 m].

TAXONOMY: The Papallacta material closely resembles the type of *Akodon mollis altorum* as originally described by Thomas (1913) based on a specimen collected at 2600 m in the Ecuadorean province of Cañar. No substantive analysis of character data, however, is available to support the current hypothesis (Cabrera, 1961; Musser and Carleton, 1993) that *altorum*, a highland taxon, is really conspecific with the geographically adjacent lowland forms *mollis* Thomas (1894) and *fulvescens* Hershkovitz (1940). As noted by Myers and Patton (1989), *Akodon mollis* as currently recognized has a very large geographic range and exhibits substantial geographic variation. Given their conclusion that *fumeus* Thomas (1902)—another taxon formerly ranked as a subspecies or synonym of *mollis*—is a valid species, a comprehensive revision of this complex is long overdue.

FIELD OBSERVATIONS: The 16 specimens of *Akodon mollis* that I collected near Papallacta in 1980 were trapped at elevations ranging from 3600 to 4160 m. Of these, 13 were taken in the shrubby páramo/forest ecotone, and 3 in grassy páramo. All recorded captures were on the ground: 5 in tunnels among the bases of tall bunch grass, 5 among wet litter under mossy shrubs, 4 in runways through mixed bunch grass and bushes, 1 in a rabbit trail beneath low herbaceous cover, and 1 beneath an earth bank.

Anotomys leander Thomas

SPECIMENS COLLECTED: 8.9 km (by road) W Papallacta, 12,480 ft (AMNH 244607; UMMZ 126294); 8.2 km (by road) W Papallacta, 12,000 ft (UMMZ 155603); 6.2 km (by road) W Papallacta, 11,700 ft (AMNH 244605, 244606; UMMZ 126295, 126296, 155598–155602).

OTHER MATERIAL: None.

TAXONOMY: The murid rodent tribe Ichthyomyini was revised by Voss (1988), who summarized available information about the diagnostic morphological characters of *Anotomys leander* based in part on this material.

FIELD OBSERVATIONS: The 12 specimens of *Anotomys leander* that I collected near Papallacta in 1978 and 1980 were trapped at elevations ranging from 3600 to 3750 m. All were taken along swift, cold, turbulent streams bordered by Subalpine Rain Forest

or grassy páramo. Eight recorded captures were in traps set on rocky ledges or gravel beneath undercut banks at the water's edge, but four specimens were trapped on rocks or logjams surrounded by swift current. More detailed habitat information about this series was summarized by Voss (1988: 412–413).

Chilomys instans (Thomas)

SPECIMENS COLLECTED: 7.5 km (by road) W Papallacta, 12,000 ft (UMMZ 155795); 6.2 km (by road) W Papallacta, 11,700 ft (UMMZ 155619, 155620).

OTHER MATERIAL: None.

TAXONOMY: The morphologically distinctive genus *Chilomys* Thomas (1897a) is currently thought to contain only a single valid species, *C. instans* (Thomas, 1895b); another nominal taxon, *fumeus* Osgood (1912) is either a subspecies or synonym according to Cabrera (1961) and Musser and Carleton (1993). The Papallacta specimens closely resemble the holotype of *instans* (BMNH 95.10.14.1, from Bogotá) in qualitative characters, but they have slightly broader interorbits and shorter molar rows. A revision of this long-neglected northern-Andean endemic genus is necessary in order to evaluate the taxonomic significance of character variation among these and other specimens from Ecuador, Colombia, and western Venezuela.

FIELD OBSERVATIONS: The three specimens of *Chilomys instans* that I collected near Papallacta in 1980 were trapped at elevations ranging from 3600 to 3690 m. One specimen was trapped on a mossy log over a stream in Subalpine Rain Forest, another on the ground in a narrow runway beneath mossy shrubs in the same habitat, and the third in a mossy tunnel beneath bunch grass in the páramo/forest ecotone.

Microryzomys altissimus (Osgood)

SPECIMENS COLLECTED: 10.6 km (by road) W Papallacta, 12,600 ft (UMMZ 155799); 8.9 km (by road) W Papallacta, 12,480 ft (AMNH 248497); 8.2 km (by road) W Papallacta, 12,200 ft (UMMZ 155677); 7.5 km (by road) W Papallacta, 12,000 ft (UMMZ 155672–155676, 155802); 6.9 km (by road) W Papallacta, 12,020 ft (AMNH 248279, 248280); 6.2 km (by road) W Papallacta, 11,700 ft (UMMZ 155798); near Papallacta, 10,480 ft (UMMZ 127125); 1.6 km (by road) E Papallacta, 10,250 ft (AMNH 248277).

OTHER MATERIAL: Three specimens collected by L. Söderström in 1913 and 1914 are labeled ''Papallacta 11,000 ft'' (AMNH 47068, 47071) or ''Tambo above Papallacta 12,000 ft'' (AMNH 47069). Four others (AMNH 66577–66580) were collected by G.H.H. Tate in 1923 on Cerro Antisana at 13,500–13,600 ft [4116–4146 m].

TAXONOMY: The genus *Microryzomys* was revised by Carleton and Musser (1989), who provided morphological diagnoses of both currently recognized species based in part on the material listed above and below.

FIELD OBSERVATIONS: The 14 specimens of *Microryzomys altissimus* that I collected near Papallacta in 1978 and 1980 were trapped at elevations ranging from 3124 to 3840 m. Of these, five were taken in the shrubby páramo/forest ecotone, four in grassy páramo, and three in Subalpine Rain Forest; two captures in anthropogenic habitats (secondary vegetation surrounded by cow pastures) were the only ones below 3600 m. All recorded captures were in traps set on the ground, five of which were placed along the margins of small streams; of the remaining nine captures (away from streams), six were in runways under tall bunch grass and/or low shrubs mixed with grass, two were in relatively open sites without grass inside the forest, and one was under a mossy bank.

Microryzomys minutus (Tomes)

SPECIMENS COLLECTED: 6.2 km (by road) W Papallacta (UMMZ 155678); Río Papallacta valley [3–5 km by trail NNW Papallacta], 11,100 ft (UMMZ 155679, 155801); 1.4 km (by road) E Papallacta (UMMZ 155797); 1.6 km (by road) E Papallacta, 10,250 ft (AMNH 248278; UMMZ 127126).

OTHER MATERIAL: A single specimen (AMNH 46804) collected by L. Söderström in 1914 is labeled ''Papallacta 11,000 ft''.

TAXONOMY: Carleton and Musser (1989) reviewed the morphological characters and taxonomy of this species, based in part on the material listed above.

FIELD OBSERVATIONS: The six specimens of *Microryzomys minutus* that I collected near

Papallacta in 1978 and 1980 were trapped at elevations ranging from 3040 to 3570 m. Of these, three were taken in dense secondary growth surrounded by pastures (below 3200 m), and three were in Subalpine Rain Forest (above 3300 m). Five specimens were trapped on the ground (two on the banks of small streams, two under tangles of mossy debris, one inside a hollow trunk), but one was trapped on the mossy limb of a small tree.

Neusticomys monticolus Anthony

SPECIMENS COLLECTED: 8.2 km W Papallacta, 12,200 ft (UMMZ 155605, 155606); 6.2 km W Papallacta, 11,700 ft (UMMZ 155604); 1.6 km E Papallacta, 10,250 ft (UMMZ 126297; AMNH 244608, 244609).

OTHER MATERIAL: None.

TAXONOMY: The murid rodent tribe Ichthyomyini was revised by Voss (1988), who provided a morphological diagnosis of the genus *Neusticomys* and its constituent species based in part on this material.

FIELD OBSERVATIONS: The six specimens of *Neusticomys monticolus* that I collected near Papallacta in 1978 and 1980 were trapped on the ground at elevations ranging from 3042 to 3719 m. Of these, three were taken along small rivulets descending narrow ravines choked with secondary vegetation, and three others were taken along the wet margins of larger streams bordered by Subalpine Rain Forest or grassy páramo vegetation.

Phyllotis haggardi Thomas

SPECIMENS COLLECTED: None.

OTHER MATERIAL: Nine specimens in the American Museum of Natural History (AMNH 66624–66632) were collected by H.E. Anthony and G.H.H. Tate between 4115 and 4570 m on Cerro Antisana in 1923. Other specimens from the vicinity of Papallacta are labeled "Papallacta 11,500 ft about" (AMNH 46824, collected by L. Söderström in 1903) and "Antisana 12,000 ft" (AMNH 36293–36296, collected by W.B. Richardson in 1913).

TAXONOMY: The genus *Phyllotis* was revised by Pearson (1958) and by Hershkovitz (1962), both of whom examined the material listed above. However, whereas Pearson re-

ferred the local population to the subspecies *P. haggardi fuscus* Anthony (1924a), Hershkovitz attributed phenotypic variation among samples of *P. haggardi* to clinal environmental factors and did not recognize specific taxa.

Reithrodontomys (*Aporodon*) *mexicanus* (Saussure)

SPECIMENS COLLECTED: 8.9 km (by road) W Papallacta, 12,480 ft (UMMZ 127159).

OTHER MATERIAL: None.

TAXONOMY: The single available specimen of a harvest mouse from the Papallacta region, a fluid-preserved old adult with extracted skull, is referable to *Reithrodontomys mexicanus* as that taxon was recognized in Hooper's (1952) generic revision. According to Hooper, three valid subspecies of *R. mexicanus* are present in northern Ecuador, including *soderstromi* Thomas (1898), *milleri* Allen (1912), and *eremicus* Hershkovitz (1941). Unfortunately, none can be effectively diagnosed by cranial characters, and meaningful pelage color comparisons are impossible with the alcohol-bleached material at hand.

FIELD OBSERVATIONS: The specimen I collected in 1978 was trapped at an elevation of 3754 m next to a rocky stream bordered by grassy páramo vegetation.

Thomasomys aureus (Tomes)
Figures 11–13

SPECIMENS COLLECTED: 6.2 km (by road) W Papallacta, 11,700 ft (AMNH 248281, 248498; UMMZ 127114, 155621–155624, 155626, 155707); Río Papallacta valley [3–5 km by trail NNW Papallacta], 11,100 ft (UMMZ 155625).

OTHER MATERIAL: None.

TAXONOMY: The holotype of *Thomasomys aureus* (BMNH 7.1.1.104) consists of the skin only of a specimen collected by Louis Fraser, allegedly at Pallatanga (1°59′S, 78°57′W; 1500 m above sea level) in the Ecuadorean province of Chimborazo (Allen, 1914; Ellerman, 1941; Cabrera, 1961), or at Gualaquiza (3°24′S, 78°33′W; 971 m above sea level) in the Ecuadorean province of Morona-Santiago (Thomas, 1920). Neither locality, however, is within the usual altitudinal

Fig. 11. Dorsal cranial views of eight *Thomasomys* species that occur in the Cordillera Oriental of northern Ecuador. Top row (left to right): *T. aureus* (UMMZ 127114), *T. baeops* (UMMZ 155708), *T. cinnameus* (UMMZ 155671), *T. erro* (UMMZ 155713). Bottom row (left to right): *T. paramorum* (UMMZ 155737), *T. rhoadsi* (AMNH 66256), *T. silvestris* (USNM 513592), *T. ucucha* (UMMZ 155644).

range of this species (ca. 3000–4000 m), and the exact provenance of Fraser's Ecuadorean material is uncertain due to inadequate labelling and the lack of detailed field records (Gardner, 1983). Despite the absence of cranial material and a definite geographic da-

tum, however, the type serves to establish that *aureus* is a distinctively large, shaggy rat with grizzled yellowish-brown dorsal fur; yellow-washed, gray-based ventral fur; long, blackish mystacial vibrissae; dark, broad hind feet with semiopposable fifth digits; and
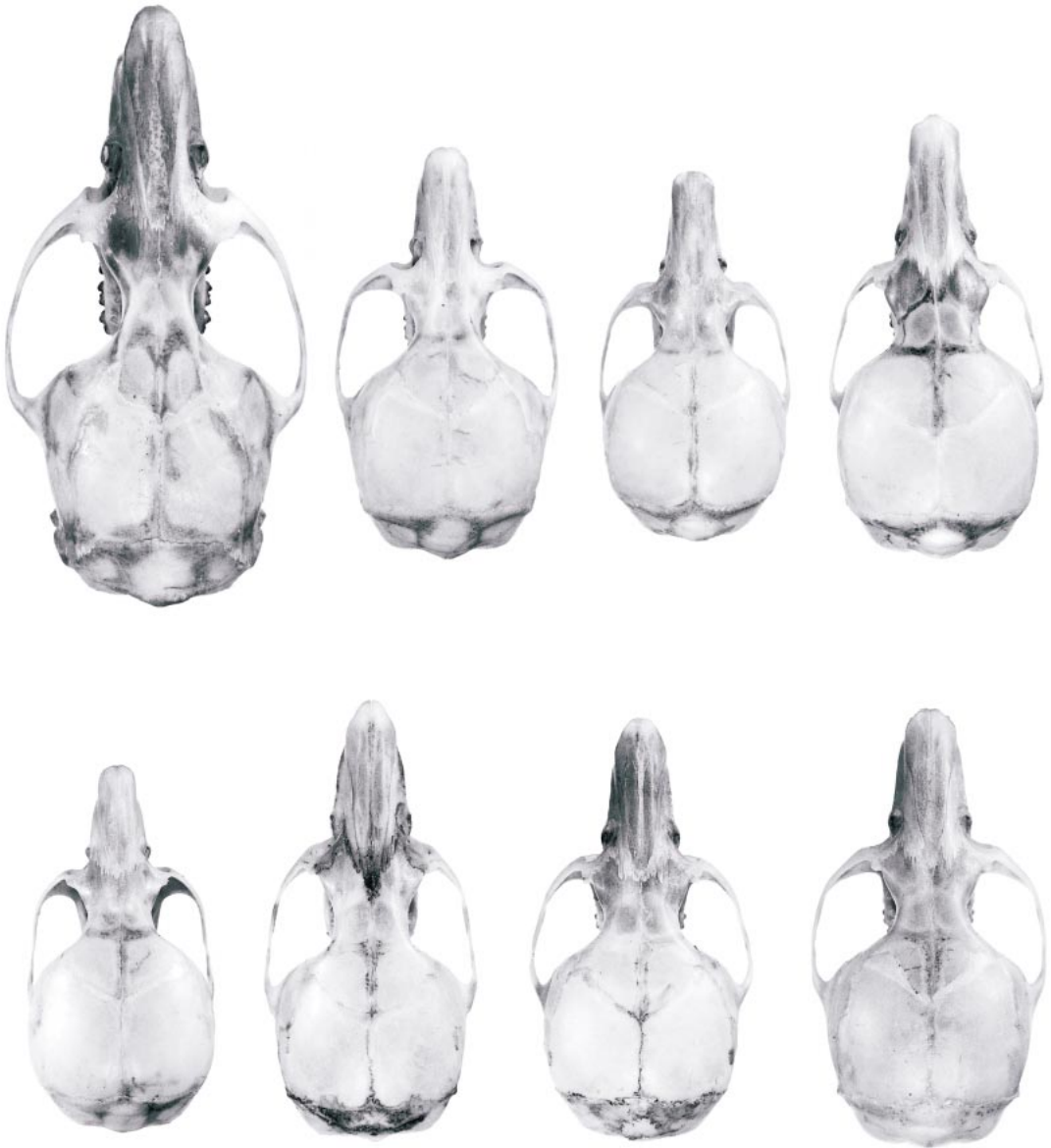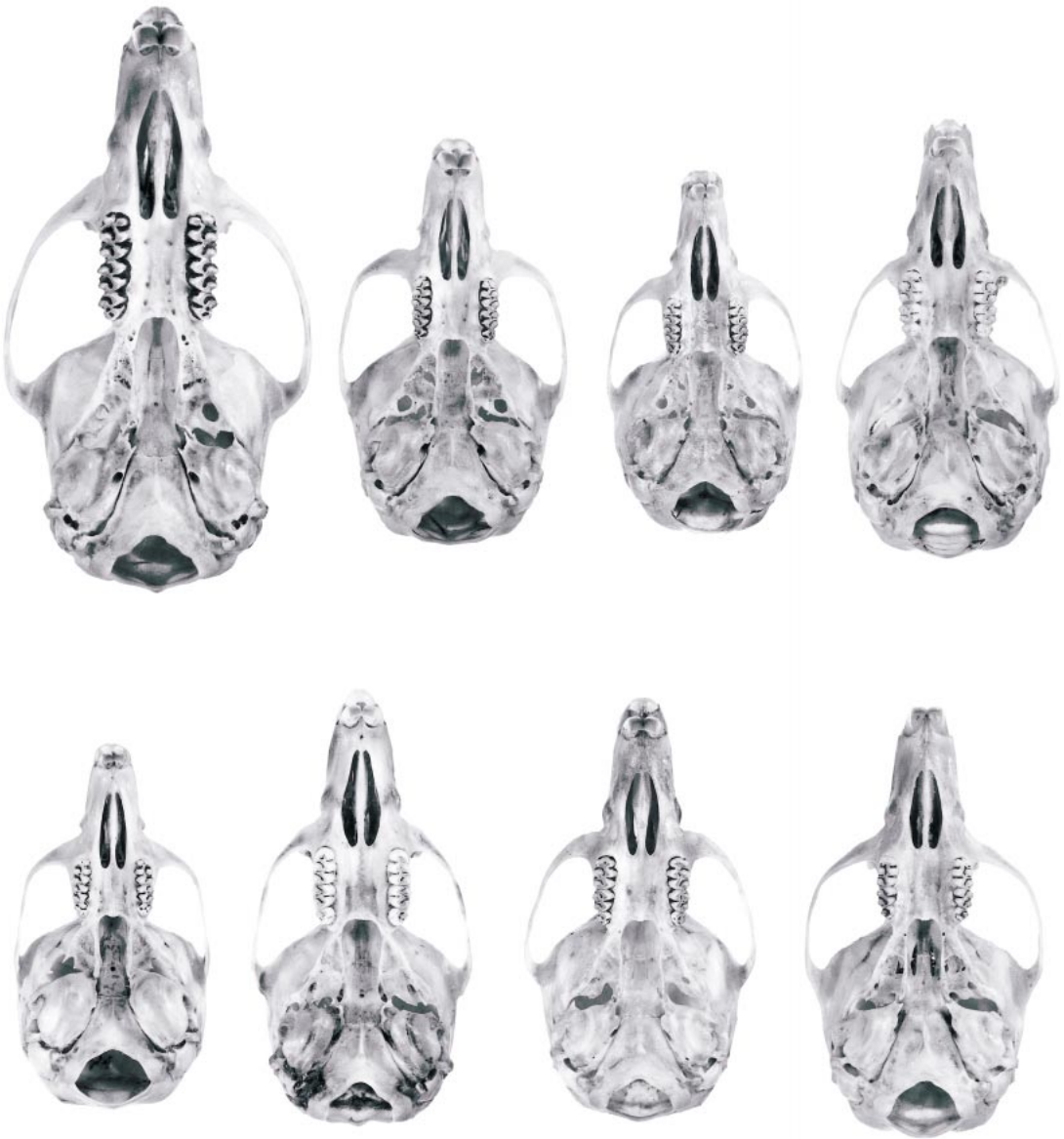
Fig. 12. Ventral cranial views of eight *Thomasomys* species from the Cordillera Oriental of northern Ecuador. Top row (left to right): *T. aureus* (UMMZ 127114), *T. baeops* (UMMZ 155708), *T. cinnameus* (UMMZ 155671), *T. erro* (UMMZ 155713). Bottom row (left to right): *T. paramorum* (UMMZ 155737), *T. rhoadsi* (AMNH 66256), *T. silvestris* (USNM 513592), *T. ucucha* (UMMZ 155644).

a tail that is much longer than the combined length of head-and-body. Other Ecuadorean specimens with these external characters exhibit the qualitative craniodental characters listed in table 2 and approximate the range of morphometric variation summarized in table 3.

Among the several nominal taxa currently synonymized with *Thomasomys aureus* by Musser and Carleton (1993), the same qualitative and morphometric traits are shared by *princeps* Thomas (1895a) from the eastern Andes of Colombia and by *altorum* Allen (1914) from the western Andes of Ecuador.

Fig. 13. Lateral cranial and mandibular views of eight *Thomasomys* species from the Cordillera Oriental of northern Ecuador. Left side (top to bottom): *T. aureus* (UMMZ 127114), *T. baeops* (UMMZ 155708), *T. cinnameus* (UMMZ 155671), *T. erro* (UMMZ 155713). Right column (top to bottom): *T. paramorum* (UMMZ 155737), *T. rhoadsi* (AMNH 66256), *T. silvestris* (USNM 513592), *T. ucucha* (UMMZ 155644).

TABLE 3
Measurements (mm) and Weights (g) of
Thomasomys aureus

	Papallacta series[a]
Sex	3 females, 4 males
HBL	168 (143–178) 6
LT	218 (186–234) 6
HF	38 (38–40) 6
Ear	23 (20–25) 6
CIL	35.9 (32.4–38.3) 6
LD	10.4 (9.0–11.2) 6
LM	7.4 (7.2–7.7) 6
BM1	2.2 (2.1–2.3) 6
LIF	8.4 (7.3–9.1) 6
BIF	3.1 (2.8–3.4) 6
BPB	3.3 (3.0–3.8) 6
BZP	3.4 (2.9–3.6) 6
LIB	5.1 (4.9–5.5) 6
ZB	20.8 (18.6–22.2) 6
DI	2.0 (1.6–2.2) 6
BIT	2.8 (2.3–3.1) 6
Weight[b]	>100 (75–100+) 6

[a] Tabulated statistics include the mean, the observed range (in parentheses), and the sample size for each measurement of the following series: UMMZ 127114, 155621–155626.

[b] Specimens were weighed with scales having a maximum capacity of 100 g.

Other putatively synonymous taxa, however, differ conspicuously from *aureus* in side-by-side morphological comparisons: *popayanus* Allen (1912) from the western Andes of Colombia and *nicefori* Thomas (1921) from the Colombian central Andes have substantially shorter (33–34 mm) hind feet and smaller (6.0–6.6 mm) molar toothrows, whereas *praetor* Thomas (1900) from northern Peru has grayish dorsal fur, pale-silvery ventral fur, pale hind feet, shorter tail, narrower interorbit, and a broad, distinctively flattened braincase. These three taxa were first treated as conspecific with *T. aureus* by Cabrera (1961), who (as usual) offered no explanation for his nomenclatural changes. In view of such trenchant character differences, at least four species appear to be represented in this complex: *T. aureus* (including *altorum* and *princeps*), *T. praetor*, and *T. popayanus* (possibly including *nicefori*).

FIELD OBSERVATIONS: The 10 specimens of *Thomasomys aureus* that I collected near Papallacta in 1978 and 1980 were all taken in Subalpine Rain Forest at elevations ranging from 3380 to 3570 m. Six were trapped in well-worn paths through mats of moss and liverworts on horizontal tree limbs, and four were trapped on the ground. Of the latter, two were trapped at the edge of a stream, one was trapped among tall grass in a clearing, and one was trapped in a runway through dense mats of moss.

Thomasomys baeops (Thomas)
Figures 11–13

SPECIMENS COLLECTED: 6.2 km (by road) W Papallacta, 11,700 ft (AMNH 248499; UMMZ 127117, 155630–155632, 155708, 155739); Río Papallacta valley (3–5 km by trail NNW Papallacta), 11,100 ft (UMMZ 155629); 1.4 km (by road) E Papallacta, 9,980 ft (UMMZ 127118, 155627, 155628, 155767).

OTHER MATERIAL: Another specimen (KU 109495) was collected by W.E. Duellman in 1967 near Laguna Papallacta at 3350 m elevation.

TAXONOMY: The type material of *Thomasomys baeops* consists of a single specimen (BMNH 98.8.1.7) collected near the Río Pita in the Ecuadorean province of Pichincha, from which a small series of topotypes is also available for comparisons. The Papallacta series is essentially indistinguishable from this material in qualitative characters of the skin and skull, as well as in measurements (table 4). No synonyms of *T. baeops* are currently recognized.

FIELD OBSERVATIONS: The 12 specimens of *Thomasomys baeops* that I collected near Papallacta in 1978 and 1980 were trapped at elevations ranging from 3040 to 3565 m. Of these, one was taken in the shrubby páramo/forest ecotone, seven were in Subalpine Rain Forest, and four were in dense thickets of secondary growth at the bottom of a narrow ravine surrounded by pastures. Eight specimens were trapped on the ground: three along the wet margins of small streams, three in narrow trails through mossy debris and damp leaf litter, one under a mossy log, and one in a hole in a bank under the roots of a tree. Four specimens were trapped on the mossy branches of small trees.

TABLE 4
Measurements (mm) and Weights (g) of *Thomasomys baeops*

	Papallacta series[a]	Topotypes[b]
Sex	3 females, 8 males	5 females, 4 males
HBL	107 ± 6 (98–117) 11	105 (95–120) 9
LT	135 ± 8 (119–147) 11	125 (106–140) 9
HF	25 ± 1 (24–27) 11	25 (24–26) 9
Ear	18 ± 1 (16–19) 11	—
CIL	25.7 ± 0.8 (24.1–27.0) 11	25.8 (24.4–27.7) 9
LD	7.4 ± 0.3 (6.9–7.9) 11	7.2 (6.5–8.0) 9
LM	4.4 ± 0.1 (4.2–4.5) 11	4.6 (4.4–4.8) 9
BM1	1.3 ± 0.0 (1.3–1.4) 11	1.3 (1.2–1.4) 9
LIF	5.7 ± 0.2 (5.2–6.1) 11	5.3 (4.8–5.6) 9
BIF	2.1 ± 0.1 (1.9–2.3) 11	1.8 (1.6–2.0) 9
BPB	3.2 ± 0.2 (2.9–3.5) 11	3.1 (2.8–3.4) 9
BZP	2.3 ± 0.1 (2.1–2.5) 11	2.4 (2.2–2.7) 9
LIB	4.5 ± 0.1 (4.2–4.7) 11	4.3 (4.2–4.5) 9
ZB	15.3 ± 0.5 (14.5–15.9) 10	15.1 (14.1–15.8) 9
DI	1.6 ± 0.1 (1.4–1.7) 11	1.6 (1.5–1.7) 9
BIT	1.8 ± 0.1 (1.6–1.9) 11	1.7 (1.6–1.9) 9
Weight	36 ± 5 (27–45) 10	—

[a] Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 248499; UMMZ 127117, 127118, 155627–155629, 155631, 155632, 155708, 155739, 155767.

[b] From the Río Pita, Provincia Pichincha, Ecuador (including sublocalities "Cañon of Río Pita", "Upper Río Pita", and "Santa Rosa above Río Pita"). The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 65006, 65007, 65009–65011, 64994, 64996–64998).

Thomasomys cinnameus Anthony
Figures 11–13

SPECIMENS COLLECTED: 1.6 km (by road) W Papallacta, 10,500 ft (UMMZ 155668–155670); Río Papallacta valley [3–5 km by trail NNW Papallacta], 11,100 ft (AMNH 155671, 155800).

OTHER MATERIAL: None.

TAXONOMY: This material of *Thomasomys cinnameus* was the first to be reported (by Voss, 1988: table 43) since the original description based on a single specimen collected at 8000 ft (2438 m) near Hacienda San Francisco, Provincia Tunguragua, Ecuador (Anthony, 1924b). Side-by-side comparisons indicate that the Papallacta series closely resembles the holotype (AMNH 67401) in all qualitative and most quantitative characters.

Although the holotype slightly exceeds the Papallacta specimens in several external and craniodental measurements (table 5), the differences are so small and the number of Papallacta specimens (five) is so few that these discrepancies do not seem taxonomically significant.

One of the smallest known species of the genus, *Thomasomys cinnameus* is currently regarded as a subspecies or junior synonym of *T. gracilis* Thomas (1917), originally described from a specimen collected at Machu Picchu in southern Peru (Cabrera, 1961; Musser and Carleton, 1993). However, the hypothesis that *cinnameus* and *gracilis* (with type localities separated by 1500 km of highly dissected mountainous terrain) are conspecific is unsupported by any published analysis or discussion of character data. Rather, my examination of both holotypes and other representative material[6] indicates that these are unambiguously diagnosable taxa that should be recognized as distinct species.

Although similar to *Thomasomys gracilis* in size, external proportions, and pelage coloration, *T. cinnameus* consistently lacks genal vibrissae, long black tactile hairs of the upper cheek that are consistently present in *gracilis*. Among other trenchant craniodental comparisons, *cinnameus* is distinguished by (1) incisive foramina that are widest posteriorly, behind the maxillary/premaxillary suture; (2) absence of sphenopalatine vacuities; (3) smaller and less inflated auditory bullae; and (4) larger and more hypsodont molars with weakly developed cingula and stylar cusps. By contrast, *gracilis* exhibits (1) incisive foramina that are widest anteriorly, at or near the maxillary/premaxillary suture; (2) large sphenopalatine vacuities that perforate the bony roof of the mesopterygoid fossa on each side of the basisphenoid/presphenoid suture; (3) larger and more inflated auditory bullae; and (4) smaller, brachydont molars with better developed cingula and stylar cusps.

[6] The comparative material of *Thomasomys gracilis* that I examined included the holotype (USNM 194816), two topotypes (USNM 194799, 194801), and 12 other specimens (AMNH 95206, 95207; USNM 194785–194787, 194790, 194807, 194808, 194811–194813), all of which were collected between 2774 and 4267 m above sea level in the Peruvian department of Cusco.

TABLE 5
Measurements (mm) and Weights (g) of
Thomasomys cinnameus

	Papallacta series[a]	Holotype[b]
Sex	3 females, two males	female
HBL	84 (82–87) 5	90
LT	118 (110–128) 5	120
HF	22 (21–23) 5	24
Ear	15 (14–16) 5	–
CIL	22.4 (22.0–23.0) 4	23.4
LD	6.8 (6.5–7.1) 5	7.0
LM	3.9 (3.8–4.0) 5	4.1
BM1	1.2 (1.2–1.3) 5	1.3
LIF	5.0 (4.8–5.3) 5	5.5
BIF	1.9 (1.8–2.0) 4	1.9
BPB	3.1 (2.9–3.3) 4	3.3
BZP	1.7 (1.6–2.0) 5	1.6
LIB	4.2 (4.1–4.4) 4	4.1
ZB	13.4 (12.9–13.6) 4	13.5
DI	1.2 (1.1–1.2) 5	1.2
BIT	1.6 (1.5–1.7) 5	1.6
Weight	17 (14–19) 5	–

[a] Tabulated statistics include the mean, the observed range (in parentheses), and the sample size for each measurement of the following series: UMMZ 155668–155671, 155800.

[b] AMNH 67401, from Hacienda San Francisco, Provincia Tugurahua, Ecuador.

Thomasomys hudsoni Anthony (1923) is another small Ecuadorean taxon that has been treated without explanation as a synonym or subspecies of *T. gracilis* (see Cabrera, 1961; Musser and Carleton, 1993). However, I agree with Anthony (1924b) that *hudsoni* is a distinct species, differing from both *gracilis* and *cinnameus* in details of coloration and craniodental morphology. Unlike any specimens of the other small species, the type of *hudsoni* (AMNH 47690, from Bestión in Provincia Azuay) has a rostrum that is peculiarly produced beyond the incisors as a flaring bony tube with a concave (rather than convex) dorsal profile. As in *cinnameus* (and unlike *gracilis*) genal vibrissae and sphenopalatine vacuities are absent in *hudsoni*, but as in *gracilis* (and unlike *cinnameus*) the incisive foramina are widest anteriorly (near the maxillary/premaxillary suture). The auditory bullae of *hudsoni* are larger and more inflated than those of *cinnameus* but smaller and less inflated than those of *gracilis*. Unfortunately, the molars

of the type (and only known specimen) of *hudsoni* are too worn to support confident dental comparisons.

FIELD OBSERVATIONS: The five specimens of *Thomasomys cinnameus* that I collected near Papallacta in 1980 were trapped at elevations ranging from 3200 to 3380 m. Of these, three were taken among mossy boulders in an old lava flow that impounds the Río Tambo to form Laguna Papallacta (fig. 1), and two were trapped on the ground in Subalpine Rain Forest in the valley of the Río Papallacta 3–5 km (by trail) NNW of the town.

Thomasomys erro Anthony
Figures 11–13

SPECIMENS COLLECTED: 6.2 km (by road) W Papallacta, 11,700 ft (UMMZ 155711); Río Papallacta valley [3–5 km by trail NNW Papallacta], 11,100 ft (UMMZ 155640–155642, 155712, 155713); 1.4 km (by road) E Papallacta (AMNH 248283; UMMZ 155633–155639, 155709, 155710); 9 km (by road) E Papallacta, 9280 ft (UMMZ 127133).

OTHER MATERIAL: None.

TAXONOMY: *Thomasomys erro* was originally described on the basis of a single specimen (AMNH 68195) collected by the Olallas on the "upper slopes of Mt. Sumaco, exact altitude unknown, but probably 8000–9000 feet [2440–2740 m], at head of the Río Suno, a tributary of the Río Napo, eastern Ecuador; June 10, 1924" (Anthony, 1926: 5). Although only about 50 km SE of Papallacta, Volcán Sumaco (0°34′S, 77°38′W) is an isolated peak that is separated from the main range of the Cordillera Oriental by the lowland valley of the Río Quijos (fig. 14). Populations of montane organisms on the upper slopes of Sumaco are therefore likely to be ecologically disjunct from those in the vicinity of Papallacta.

The Papallacta specimens are the only additional material of *Thomasomys erro* to have been collected since 1924 and merit close comparison with the holotype (AMNH 68195). No noteworthy differences in pelage color or other external characters are apparent, however. The skull of AMNH 68195 is partially crushed, so only an incomplete set of measurements can be taken, but most of

Fig. 14. The type locality of *Thomasomys erro*, Volcán Sumaco (0°34′S, 77°38′W) is an isolated peak that rises to 3840 m above sea level in Provincia Napo, eastern Ecuador. Photographed by the author, looking northeast from the crest of the Cordillera de los Guacamayos on the road between Baeza and Tena, 3 August 1980.

these fall within the range of variation observed among the Papallacta specimens; the exceptions are two molar dimensions in which the type is slightly larger (table 6). In all qualitative craniodental comparisons, the holotype appears to be indistinguishable from the Papallacta series and appears to represent the same taxon.

Cabrera (1961) listed *Thomasomys erro* as a subspecies of *T. cinereiventer* Allen (1912) without explanation, and no discussion of character information has been published to justify the current treatment of *erro* as a junior synonym of that species (e.g., by Musser and Carleton, 1993). However, side-by-side comparisons of the holotypes and other representative material of *erro* and *cinereiventer* do not support the hypothesis that these taxa are conspecific. Among other differences, typical *cinereiventer* from the Cordillera Oc-

cidental of southern Colombia[7] is a much bigger animal with longer hind feet (33–36 mm); deeper zygomatic notches; less inflated interorbital region; more strongly convergent zygomatic arches; more elongate (less globular) braincase; broader and more vertically oriented zygomatic plates; consistently separate buccinator-masticatory and accessory oval foramina; larger (5.7–6.2 mm), incipiently lophodont molars with interpenetrating lingual and labial flexi (see illustrations and discussion of this trait in Voss, 1993); and relatively much broader incisors. Other Col-

[7] In addition to the holotype of *Thomasomys cinereiventer* (AMNH 32436), I examined 17 paratypes (AMNH 32417, 32419, 32421–32425, 32427, 32428, 32430, 32433–32435, 32437–32440), all of which were collected at 3152 m on the Pacific slope of the Cordillera Occidental west of Popayán in Departamento Cauca, Colombia.

TABLE 6
Measurements (mm) and Weights (g) of
Thomasomys erro

	Papallacta series[a]	Holotype[b]
Sex	6 females, 5 males	male
HBL	114 ± 8 (104–130) 11	–
LT	150 ± 13 (131–175) 11	–
HF	31 ± 1 (28–32) 11	31
Ear	20 ± 1 (19–21) 11	–
CIL	26.5 ± 1.3 (25.0–28.6) 11	–
LD	7.7 ± 0.5 (6.9–8.5) 11	8.3
LM	4.6 ± 0.1 (4.5–4.8) 11	5.0
BM1	1.6 ± 0.0 (1.5–1.6) 11	1.7
LIF	5.5 ± 0.3 (5.1–6.0) 11	5.5
BIF	2.4 ± 0.2 (2.2–2.9) 11	2.4
BPB	3.2 ± 0.3 (2.7–3.7) 11	3.2
BZP	1.4 ± 0.1 (1.3–1.7) 11	1.6
LIB	5.7 ± 0.2 (5.4–5.9) 11	5.8
ZB	14.8 ± 0.6 (13.9–15.6) 11	–
DI	1.4 ± 0.1 (1.2–1.6) 11	1.4
BIT	1.4 ± 0.1 (1.3–1.6) 11	1.4
Weight	38 ± 7 (28–46) 11	–

[a] Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the same size for each measurement of the following series: AMNH 248283; UMMZ 127133, 155634, 155636, 155637, 155639–155642, 155712, 155713.

[b] AMNH 68195, from Volcán Sumaco, Provincia Napo, Ecuador.

ombian taxa that are currently considered to be subspecies or synonyms of *T. cinereiventer*—including *contradictus* Anthony (1925) from the Cordillera Central and *dispar* Anthony (1925) from the Cordillera Oriental—are smaller than the nominotypical form but do not exhibit any other noteworthy similarities with *T. erro*.

FIELD OBSERVATIONS: I collected 17 specimens of *Thomasomys erro* in the vicinity of Papallacta, at elevations ranging from 2830 to 3570 m. Of these, 11 were taken in dense secondary vegetation, 5 in Subalpine Rain Forest, and 1 in Upper Montane Rain Forest. All recorded captures were on the ground. Eleven specimens were trapped in runways through wet leaf litter and mossy debris; three were trapped beneath mossy logs, branches, or roots; and one was trapped inside the trunk of a hollow tree.

Thomasomys paramorum Thomas
Figures 11–13

SPECIMENS COLLECTED: 10.6 km (by road) W Papallacta, 12,600 ft (UMMZ 155662–155667); 7.5 km (by road) W Papallacta, 12,000 ft (UMMZ 155661, 155745–155747); 6.2 km (by road) W Papallacta, 11,700 ft (AMNH 248282; UMMZ 127123, 127124, 155656–155660, 155737, 155738, 155740–155744, 155748–155751).

OTHER MATERIAL: Five specimens (AMNH 46627, 46628, 46631, 46633, 46636) were collected at "El Tambo, Papallacta 12,000 ft" by L. Söderström between 1912 and 1914, and another specimen (AMNH 46643) taken by the same collector at the same time is labeled "Tablon, road to Papallacta 11,000 ft about". Five additional Söderström specimens (AMNH 46629, 46630, 46634, 46641, 46642) are labeled "Cuyuco [probably Cuyuja] below Papallacta, 7000 ft".

TAXONOMY: The type material of *Thomasomys paramorum* consists of a single specimen collected at an Ecuadorean locality that Thomas (1898: 454) described vaguely as "Paramo, south of Chimborazo", but a small series from Urbina (1°30′S, 78°44′W) just a few kilometers SE of Chimborazo can be considered topotypic. Although these topotypes average larger than the Papallacta sample in most measurements and have proportionately narrower zygomatic plates (table 7), the two series are similar in qualitative external and craniodental traits and appear to represent the same taxon. No synonyms of *T. paramorum* are currently recognized.

FIELD OBSERVATIONS: I recorded 29 captures of *Thomasomys paramorum* near Papallacta in 1978 and 1980 (one specimen was lost in the field), at elevations ranging from 3570 to 3840 m. Of these, 15 were taken in Subalpine Rain Forest, 7 in *Polylepis* thickets in the páramo, and 7 in the shrubby páramo/forest ecotone. Twenty-two captures were on the ground, of which nine were trapped in runways through moss, six along the banks of small streams, six in wet leaf litter under shrubs and branches, and one under a clump of grass. Seven specimens were trapped in low, mossy trees.

TABLE 7
Measurements (mm) and Weights (g) of *Thomasomys paramorum*

	Papallacta series[a]	Topotypes[b]
Sex	14 females, 10 males	6 females, 3 males
HBL	92 ± 5 (80–103) 24	99 (91–106) 9
LT	121 ± 5 (113–133) 24	122 (114–129) 9
HF	24 ± 1 (23–25) 24	25 (24–26) 9
Ear	18 ± 1 (16–19) 24	–
CIL	23.3 ± 0.6 (21.8–24.3) 24	24.3 (23.0–25.4) 9
LD	6.6 ± 0.3 (6.0–7.1) 24	6.9 (6.2–7.5) 9
LM	4.0 ± 0.1 (3.8–4.3) 24	4.4 (4.2–4.5) 9
BM1	1.2 ± 0.0 (1.1–1.3) 24	1.4 (1.3–1.4) 9
LIF	5.3 ± 0.2 (4.9–5.7) 24	5.7 (5.4–6.1) 9
BIF	1.9 ± 0.1 (1.8–2.1) 24	2.0 (1.9–2.1) 9
BPB	3.0 ± 0.2 (2.7–3.4) 24	3.1 (2.7–3.4) 9
BZP	2.1 ± 0.1 (1.8–2.3) 24	2.0 (1.8–2.2) 9
LIB	4.3 ± 0.1 (4.1–4.5) 24	4.4 (4.2–4.5) 9
ZB	13.5 ± 0.3 (13.0–14.2) 24	14.3 (13.7–14.8) 8
DI	1.2 ± 0.1 (1.1–1.3) 24	1.3 (1.2–1.4) 9
BIT	1.5 ± 0.1 (1.3–1.6) 24	1.6 (1.4–1.8) 8
Weight	21 ± 2 (17–26) 24	–

[a] Tabulated statistics include the mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 248501; UMMZ 127123, 127124, 155656–155667, 155737, 155738, 155740–155744, 155746, 155749, 155750.

[b] From Urbina, Provincia Chimborazo, Ecuador (see text). Tabulated statistics include the mean, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 64871, 64872, 64874, 64877–64880, 64882, 64883.

TABLE 8
Measurements (mm) of *Thomasomys rhoadsi*[a]

	Antisana series[b]	Topotypes[c]
Sex	2 females, 1 male	6 females, 4 males
HBL	131 (130–132) 3	123 (112–128) 10
LT	116 (114–118) 3	117 (110–123)
HF	29 (29–30) 3	29 (28–31) 10
Ear	18 (18–19) 3	–
CIL	30.0 (30.0–30.0) 1	29.0 (28.3–29.8) 7
LD	9.4 (9.3–9.4) 2	9.0 (8.5–9.4) 10
LM	5.4 (5.4–5.5) 3	5.4 (5.1–5.6) 10
BM1	1.6 (1.5–1.6) 3	1.6 (1.5–1.6) 10
LIF	7.0 (7.0–7.1) 2	6.6 (6.2–7.0) 10
BIF	2.9 (2.9–2.9) 2	2.7 (2.6–2.9) 10
BPB	4.0 (3.9–4.1) 3	3.6 (3.4–3.9) 10
BZP	2.2 (2.1–2.4) 2	2.3 (2.1–2.4) 10
LIB	5.5 (5.4–5.7) 3	5.6 (5.2–5.8) 10
ZB	16.4 (16.2–16.7) 2	15.8 (15.4–16.3) 8
DI	1.6 (1.4–1.6) 3	1.5 (1.3–1.5) 10
BIT	1.9 (1.8–2.0) 2	1.8 (1.5–2.0) 10

[a] Tabulated statistics for each measurement of both series include the mean, the observed range (in parentheses), and the sample size. Measurements of the ear and weights were not recorded by the collectors of these series.

[b] FMNH 43247, 43249, 43250.

[c] From Volcán ("Mount") Pichincha, Provincia Pichincha, Ecuador: AMNH 66252–66257, 66259–66262.

Thomasomys rhoadsi Stone
Figures 11–13

SPECIMENS COLLECTED: None.

OTHER MATERIAL: Five specimens (FMNH 43246–43250) collected by R. Olalla in 1934 are labeled "Cerro Antisana, Andes Orientales", and two others (BMNH 54.553, 55.554) collected by C.S. Webb in 1937 are labeled "Mt. Antisana, E. Andes 12,500–13,000 ft".

TAXONOMY: *Thomasomys rhoadsi* was originally described from material collected in 1911 by S.N. Rhoads on Volcán ("Mt.") Pichincha in the western Andes above Quito (Stone, 1914: 12). The Antisana specimens listed above were compared with a series of topotypes, which they resemble qualitatively despite averaging slightly larger in several external and craniodental dimensions (table 8). In the absence of other character differences between these samples, I assume that they represent the same taxon. An apparently related form originally described as *T. rhoadsi fumeus* is substantially smaller than typical *rhoadsi* and also differs from it in qualitative external and cranial characters as remarked by Anthony (1924b).

REMARKS: Although Olalla's and Webb's labels do not state whether their specimens were collected on the eastern or western slopes of Antisana, it seems probable they were collected near Hacienda Antisana on the western side, the only inhabited site described in published accounts of visitors to this famous mountain (e.g., Orton, 1870; Whymper, 1892; Emerson and Johnson, 1960).

Thomasomys silvestris Anthony
Figures 11–13

SPECIMENS COLLECTED: None.

OTHER MATERIAL COLLECTED: A single

TABLE 9
Measurements (mm) of *Thomasomys silvestris*[a]

	Antisana specimen[b]	Type series[c]
Sex	female	8 females, 4 males
HBL	117	106 ± 9 (95–127) 10
LT	148	148 ± 6 (139–157) 10
HF	27	29 ± 1 (28–30) 10
Ear	18	–
CIL	–	26.6 ± 0.7 (25.4–27.3) 12
LD	8.7	8.0 ± 0.3 (7.6–8.5) 12
LM	–	4.9 ± 0.1 (4.8–5.1) 11
BM1	–	1.6 ± 0.0 (1.6–1.7) 12
LIF	5.7	5.6 ± 0.3 (5.1–6.1) 12
BIF	2.7	2.3 ± 0.2 (1.9–2.6) 12
BPB	–	3.3 ± 0.3 (2.8–3.9) 12
BZP	2.1	2.0 ± 0.1 (1.8–2.2) 12
LIB	5.4	5.1 ± 0.1 (4.9–5.3) 12
ZB	16.6	15.6 ± 0.5 (14.8–16.4) 10
DI	1.4	1.4 ± 0.1 (1.3–1.6) 12
BIT	1.8	1.8 ± 0.2 (1.5–2.0) 12

[a] Weights were not recorded for specimens in either series.

[b] FMNH 43251, an old adult (TWC 5) with molars worn below the widest part of the crown, and therefore unmeasurable (see text).

[c] On the road to Santo Domingo ("Santo Domingo Trail") northwest of Volcán Corazón (0°32′S, 78°39′W), Provincia Pichincha, Ecuador (including sublocalities "Las Maquinas" and "Forest N.W. of Corazon"). Tabulated statistics include the sample mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 66280, 66283–66289, 66293, 66296, 63364, 63365.

specimen (FMNH 43251) was collected on Cerro Antisana by R. Olalla in 1934.

TAXONOMY: *Thomasomys silvestris* was originally described from a large series of specimens collected on the densely forested western slope of the western Andes south of Quito in the Ecuadorean provinces of Pichincha and Bolívar (Anthony, 1924a). I compared the Antisana specimen with the type series, which it exactly resembles in qualitative characters. The Antisana specimen is an old adult, however, with molars that are worn below the widest part of the crowns, so most of its measurements are larger than those of adults with measurable teeth in the type series (table 9). No synonyms of *T. silvestris* are currently recognized.

REMARKS: It seems probable that the Antisana specimen of *Thomasomys silvestris* was collected on the western side of Antisana

as previously remarked for similarly labeled specimens of *T. rhoadsi* collected at the same time by the same collector.

Coendou quichua Thomas

SPECIMENS COLLECTED: None.

OTHER MATERIAL: I examined three NHRS specimens (A58/2822, A58/2962, A59/2962) collected by Ludovic Söderström in 1911 at "Tablon above Tumbaco" with recorded elevations of 9000–11,000 ft [2744–3354 m].

TAXONOMY: *Coendou quichua* is a morphologically distinctive porcupine whose diagnostic characters were accurately described by Thomas (1899). Cabrera (1961), however, treated *quichua* as a subspecies of *C. bicolor* Tschudi without providing any justification for doing so. Although Emmons (1990), Albuja (1991), Tirira (1999), and Alberico et al. (1999) have subsequently recognized that *quichua* is a valid species, some checklists (e.g., Woods, 1993) continue to treat this name as a synonym of *bicolor*.

To date, no rationale has been provided for the zoogeographically incoherent and morphologically divergent collection of taxa that Cabrera (1961) lumped together as *Coendou bicolor*. Although this name has been applied by authors to a wide range of morphologies, specimens collected in the vicinity of the Peruvian type locality (e.g., AMNH 147500, FMNH 65799) are distinctively large porcupines (ca. 900 mm total length) with tails that are almost as long as the combined length of head-and-body; the visible dorsal pelage consists entirely of bicolored (black-tipped) quills, of which those over the forequarters are conspicuously longer than those over the lower back and rump. By contrast, *C. quichua* is much smaller (ca. 600 mm or less) with a proportionately much shorter tail (approximately half the length of head-and-body) and tricolored (pale-tipped) dorsal quills that are not conspicuously longer over the forequarters than on the lower back and rump. Cranially, *quichua* has a proportionately narrower rostrum than *bicolor*, smaller orbits, less expanded jugals, and less inflated frontal sinuses. Other relevant morphological comparisons will be provided in an upcoming generic revision (Voss, in prep.), but the characters given here together with other

traits mentioned by Emmons (1990) and Alberico et al. (1999) are sufficient for unambiguous identifications of these dissimilar taxa.

REMARKS: The original specimen tag of NHRS A58/2822 notes that the animal was "found in the underbrush". Lönnberg (1913) originally reported this material as having been collected above Tumbaco, without mentioning the actual collecting site (Tablón).

Cuniculus (*Stictomys*) *taczanowskii* (Stolzmann)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: A single specimen that I have not examined (QCAZ 954) was collected in the páramo near Paso de Guamaní by G. Onore in 1993 (D. Tirira, personal commun.).

TAXONOMY: The mountain paca is morphologically distinctive (Thomas, 1924) and was formerly distinguished generically (as *Stictomys*) from the lowland paca (*Cuniculus paca*). Although only a single species of mountain paca is currently recognized, no critical analysis of morphological or molecular data is currently available to test the hypothesis that *C. taczanowskii* (from Ecuador and Peru) is actually conspecific with populations from Venezuela and Colombia that were formerly known as *C. sierrae* (e.g., by Thomas, 1905; Krumbiegel, 1940). The International Commission on Zoological Nomenclature (ICZN, 1998) recently ruled that *Cuniculus* Brisson, 1762, is the oldest available name for pacas, previously referred by most American authors to *Agouti* Lacépède, 1799.

Sylvilagus brasiliensis (Linnaeus)

SPECIMENS COLLECTED: None.

OTHER MATERIAL: The type of *Sylvilagus nivicola* is a specimen collected at 4800 m "en el límite de nieves perpetuas" on Cerro Antisana, about 10 km south of Papallacta (Cabrera, 1913: 6). Ten additional specimens of rabbits from Antisana (AMNH 66659–66668) were subsequently collected between 4115 and 4265 m by H.E. Anthony in 1923. Other material from Antisana (in the BMNH) was reported by Laurie (1955), and a few more specimens are scattered among other museums (e.g., MCN, MNCN).

TAXONOMY: All of the material at hand is referable to *Sylvilagus brasiliensis* in the sense of Hershkovitz (1950), the last comprehensive taxonomic review of South American lagomorph taxonomy. Hershkovitz (1950) treated *nivicola* Cabrera (1913) as a valid subspecies of *S. brasiliensis*, but Laurie (1955) synonymized *nivicola* with *S. b. andinus* (Thomas, 1897b). The current treatment (Hoffmann, 1993) of 41 nominal taxa ranging from southern Mexico to northern Argentina as synonyms or subspecies of *S. brasiliensis* obviously merits critical scrutiny, but is far beyond the scope of this faunal report.

REMARKS: Although I did not collect any rabbits near Papallacta, they were abundant in grassy habitats throughout the páramo zone.

DISCUSSION

The discovery less than 50 km east of the Ecuadorean capital of a new species of numerically abundant rodent, and the rediscovery in the same place of several other species previously known only from type material, indicates how much yet remains to be learned about mammalian diversity and endemism in the northern Andes. Indeed, the mammalogical exploration of the Cordillera Oriental has hardly begun. The following paragraphs summarize what can be inferred about mammalian faunal composition above 3000 m in these mountains and briefly sketches the dimensions of our ignorance about almost everything between this elevation and the Amazonian lowlands to the east.

SAMPLING COMPLETENESS

On 50 sampling days between 8 May 1978 and 7 May 1980, inclusive, I trapped 241 individual small mammals belonging to 16 species near Papallacta. As is typically the case when cumulative species richness is plotted against cumulative captures (fig. 15), new species were encountered at a relatively rapid rate early in the sampling process and at a relatively slow rate in the later stages. In fact, no new species were encountered among the last 102 trapped individuals. Be-
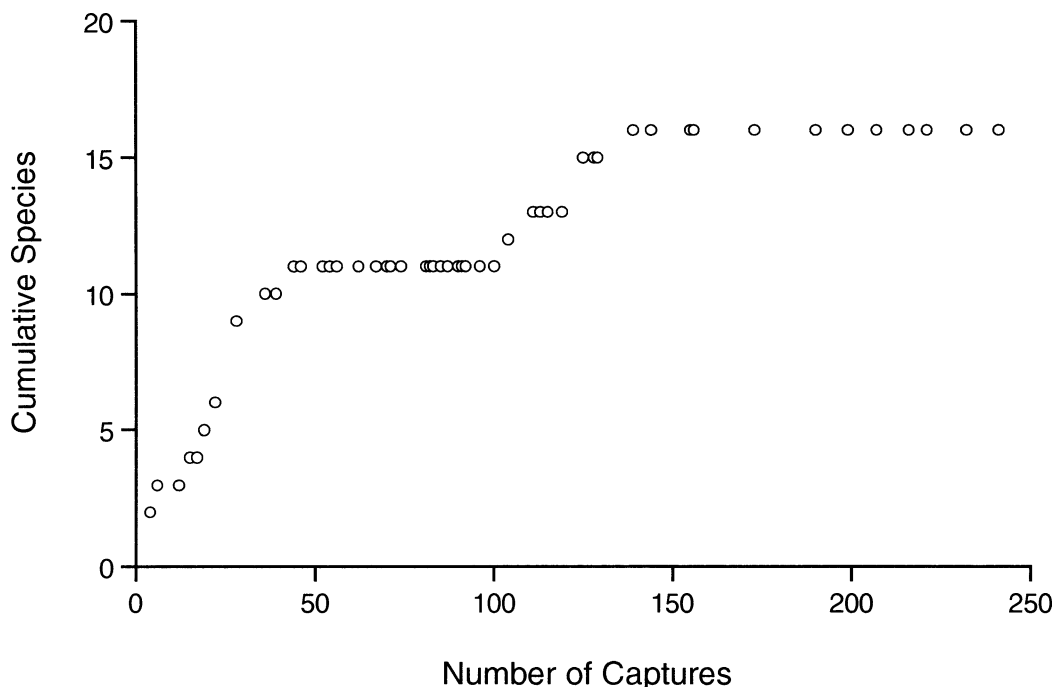
Fig. 15. Species accumulation for small mammal trapping near Papallacta, where 16 species of caenolestid marsupials, shrews, and murid rodents were taken over 50 sampling days in 1978 and 1980 (see text). The stepped appearance of the graph merits comment. Traps were first deployed along streams to capture ichthyomyines, where a total of 11 species were taken after 11 nights; 19 subsequent nights of streamside trapping more than doubled the number of recorded captures but yielded no additional species. The second increase in species richness resulted from moving traplines away from streams onto neighboring hillsides, where five more species were encountered.

cause the traps I used are known to be effective for a wide range of species, and because I made a sustained effort to sample all recognizable macro- and microhabitats above 3000 m, these results suggest that few small (ca. <300 g) nonvolant species remain to be discovered here. Nevertheless, the fact that I did not trap some small species known to occur locally (e.g., *Phyllotis haggardi*) and the possibility that new species might occur in habitats that I was unable to sample effectively (e.g., páramo bogs, marshy lake shores, Upper Montane Rainforest) are compelling arguments for continued inventory efforts in the region.

Sampling completeness for the larger fauna, which I did not systematically attempt to survey, is more difficult to assess because there are no records of the methods and effort used by earlier collectors. However, only five additional species seem likely to occur

locally based on the distributional data compiled by Tirira (1999): *Mazama rufina*, *Leopardus tigrinus*, *Lontra longicaudis*, *Nasuella olivacea*, and *Sciurus granatensis*.[8] At least some of these species probably inhabit Upper Montane Rain Forest, a vegetation type that no longer remains intact on accessible slopes above 3000 m near Papallacta.

BIOGEOGRAPHIC COMPOSITION

As summarized in this report, the known nonvolant mammalian fauna of the crest of the Cordillera Oriental in northeastern Ecuador is a distinctive assemblage of several biogeographic groups, including (1) clades with distributions that extend to south-temperate latitudes (*Pseudalopex*, *Lynchailurus*,

[8] This list does not include domesticated (or semidomesticated) species, such as *Cavia porcellus* and camelids, the indigenous status of which seems debatable.

Hippocamelus, *Pudu*, *Akodon*, *Phyllotis*); (2) clades with distributions that extend to north-temperate latitudes (*Cryptotis*, *Odocoileus*, *Reithrodontomys*); (3) clades with distributions that extend to both south- and north-temperate latitudes (*Didelphis*, *Puma*, *Conepatus*, *Mustela*, *Sylvilagus*); (4) widespread tropical clades (*Tapirus*, *Neusticomys*, *Coendou*, *Cuniculus*); and (5) clades that are endemic to the tropical Andes (*Caenolestes*, *Tremarctos*, *Anotomys*, *Chilomys*, *Microryzomys*, *Thomasomys*). At the species level, a substantial fraction of the fauna (17 of 33 species) is endemic to the northern Andes—north of the Huancabamba Deflection in northern Peru—including representatives from all of the groups enumerated above: *Caenolestes fuliginosus*, *Cryptotis montivagus*, *Pudu mephistopheles*, *Tapirus pinchaque*, *Akodon latebricola*, *Anotomys leander*, *Chilomys instans*, *Neusticomys monticolus*, *Phyllotis haggardi*, *Thomasomys baeops*, *T. cinnameus*, *T. erro*, *T. paramorum*, *T. rhoadsi*, *T. silvestris*, *T. ucucha*, and *Coendou quichua*. Among these northern-Andean endemics, three species are only known from northeastern Ecuador (*Akodon latebricola*, *Thomasomys erro*, *T. ucucha*) and provide some support for the existence of a distinct center of endemism in the Cordillera Oriental.

Unfortunately, *Akodon latebricola*, *Thomasomys erro*, and *Thomasomys ucucha* are each known from so few localities that the geographic limits of any center of endemism they might represent is necessarily speculative. However, the lowland gap formed by the headwaters of the Río Pastaza to the south (in central Ecuador) and a nother corresponding to the headwaters of the Río Caquetá to the north (in southern Colombia) seem likely candidates. Volcán Sumaco (fig. 14) is presumably a vicariant part of this endemic center because its biota is clearly derived from the adjacent slopes of the Cordillera Oriental (Chapman, 1926; Løjtnant and Molau, 1982). Also within these hypothetical limits, inter alia, are the Cordillera de los Llanganates (rising from the left bank of the upper Pastaza), the Cordillera El Diviso (including Volcán Cayambe), the Cordillera de Pimampiro (northeast of Ibarra), and the Páramos de las Juntas (east of Ipiales). Only

future collecting in these poorly known regions will help resolve the currently obscure picture of mammalian montane endemism in northeastern Ecuador and southern Colombia.

HORIZONTAL COMPLEMENTARITY: COMPARISONS WITH OTHER HIGHLAND FAUNAS

In terms of higher-taxonomic composition, the nonvolant mammalian fauna near Papallacta broadly resembles faunas from other northern-Andean localities, of which the best-sampled is the Cajas Plateau of southern Ecuador (Barnett, 1999). Meaningful comparisons are possible between Papallacta and Cajas because small nonvolant mammals were intensively trapped at both sites with similar equipment over elevational gradients that each included montane forest, a shrubby ecotone, grassy páramo, and *Polylepis* thickets. Both faunas (table 10) contain caenolestid marsupials and shrews, together with akodontine, ichthyomyine, oryzomyine, phyllotine, and ''thomasomyine'' murid rodents; *Thomasomys* is the most speciose genus at each site.

Despite such methodological, environmental, and higher-taxonomic similarities, these inventories document a surprising degree of species-level complementarity (sensu Colwell and Coddington, 1994). Counting just those small nonvolant mammals recorded above 3000 m, a total of 26 species is represented in the two lists, of which 16 are uniques (occurring at just one site). Colwell and Coddington's C is therefore $16/26 \times 100 = 62\%$ between ecologically comparable sites separated by less than 300 airline km. Although it is possible that additional collecting at both sites will discover more shared species, an equally plausible result is the discovery of more uniques. Pending new fieldwork, there is no basis for thinking that 62% is a biased estimate of complementarity from the data at hand.

Defensible quantitative comparisons with other highland faunal inventories are complicated by methodological differences, ecological disparities, and other problems, but a limited number of studies available for ad hoc inference (Aagaard, 1982; López-Arév-

TABLE 10
Nonvolant Small Mammals from Two Well-Sampled Highland Faunas in Ecuador

	Papallacta[a]	Cajas[b]
Caenolestidae		
Caenolestes caniventer[c]		X
Caenolestes fuliginosus	X	
Caenolestes tatei[c]		X
Soricidae		
Cryptotis montivagus	X	X
Muridae: Akodontini		
Akodon latebricola	X	
Akodon mollis	X	X
Akodon orophilus		X
Muridae: Ichthyomyini		
Anotomys leander	X	
Chibchanomys orcesi		X
Neusticomys monticolus	X	
Muridae: Oryzomyini		
Microryzomys altissimus	X	X
Microryzomys minutus	X	X
Oligoryzomys destructor		X
Oryzomys albigularis[c]		X
Muridae: Peromyscini		
Reithrodontomys mexicanus	X	
Muridae: Phyllotini		
Phyllotis andium		X
Phyllotis haggardi	X	X
Muridae: Sigmodontini		
Sigmodon inopinatus		X
Muridae: "Thomasomyines"		
Chilomys instans	X	
Thomasomys aureus	X	X
Thomasomys baeops	X	X
Thomasomys cinnameus	X	X
Thomasomys erro	X	
Thomasomys "gracilis"		X
Thomasomys paramorum	X	X
Thomasomys pyrrhonotus		X
Thomasomys rhoadsi	X	
Thomasomys sylvestris	X	
Thomasomys ucucha	X	

[a] Species records based on material examined for this report.

[b] Species records from Barnett (1999); the Cajas region lies about 25 km W of Cuenca (2°52′S, 78°54′W) in Provincia Azuay.

[c] Species not recorded above 3000 m elevation.

between Andean sites separated by as little as 500–700 km, even in the absence of major habitat discontinuities. Obviously, species turnover on this scale poses a significant challenge for timely inventory work across many thousands of kilometers of high-Andean landscapes that remain sparsely sampled by mammalogists.

VERTICAL COMPLEMENTARITY: COMPARISONS WITH ADJACENT LOWLAND FAUNAS

The mammalian fauna of the Amazonian lowlands of northeastern Ecuador (≤1000 m in the provinces of Napo and Sucumbíos) includes 80 nonvolant species vouchered by museum specimens or documented by other reliable sources (appendix 2). Although no inventory to date has recorded all of these species from any local community, it is probable that most of them are sympatric near the base of the Cordillera Oriental, where an additional 12 species could also be predicted to occur based on distributional information compiled by Tirira (1999).[9] Among the most striking differences between this lowland fauna and that of the adjacent highlands (>3000 m) near Papallacta is the sparse representation or disappearance at the higher elevation of several speciose lowland clades, including didelphid marsupials, edentates, primates, and caviomorph rodents (table 11). By contrast, carnivores, perissodactyls, artiodactyls, and murid rodents maintain almost equivalent diversity at both elevations. Caenolestid marsupials and insectivores are the only higher taxa present in the highlands but not in the lowlands. Overall, these data suggest that nonvolant mammalian species richness declines by about 60% from the piedmont to the crest of the Cordillera Oriental.

The highland fauna near Papallacta, however, is not simply an attenuated version of the adjacent lowland fauna. Only three species are known to occur at both elevations (*Didelphis pernigra*, *Puma concolor*, *Sylvilagus brasiliensis*), so the total number of species represented in these faunas (high-

alo et al., 1993; Cadena and Malagón, 1994; Soriano et al., 1999) suggest that horizontal complementarity at the species level could approach 90% for small nonvolant mammals

[9] *Cabassous unicinctus, Priodontes maximus, Myrmecophaga tridactyla, Atelocynus microtis, Speothos venaticus, Herpailurus jaguarondi, Leopardus tigrinus, L. wiedii, Panthera onca, Galictis vittata, Pteronura brasiliensis, Mazama gouazoubira.*

TABLE 11
Taxonomic Distribution of Nonvolant Mammalian Species Richness at Papallacta and in the Adjacent Amazonian Lowlands of Eastern Ecuador

	Papallacta[a]	Lowlands[b]
Marsupialia		
Caenolestidae	1	0
Didelphidae	1	15
Insectivora	1	0
Xenarthra	0	6 (9)
Primates	0	15
Carnivora	6 (9)	9 (17)
Perissodactyla	1	1
Artiodactyla	3 (4)	3 (4)
Rodentia		
Sciuridae	0 (1)	3
Muridea	17	14
Caviomorpha[c]	2	13
Lagomorpha	1	1
TOTAL SPECIES:	33 (38)	80 (92)

[a] Species counts from records documented in the text of this report; parenthetical counts include expected species for which local records are currently unknown (see text).

[b] Species counts from appendix 1; parenthetical counts include expected species for which local records are currently unknown (see text footnote 8).

[c] Caviomorphs include erethizontids, hydrochoerids, cuniculids, dasyproctids, and echimyids.

TABLE 12
Nonvolant Mammalian Collecting Effort at Three Elevational Intervals in Northeastern Ecuador[a]

Interval	Specimens collected	% Effort
Lowlands (≤1000 m)	837	67
Middle Elevations (1001–3000 m)	34	3
Highlands (>3000 m)	371	30

[a] Collecting effort in northeastern Ecuador (Napo and Sucumbíos) was estimated as the number of nonvolant mammalian specimens from each elevational interval (N_i) in the computerized databases of AMNH, FMNH, KU, MVZ, UMMZ, and USNM. The total number of specimen records summed over all three intervals (N_T) from those sources is 1242. Percent effort was estimated as $(N_i \div N_T) \times 100$.

lands and lowlands combined) is $33 + 80 - 3 = 110$, of which 107 are "uniques". Colwell and Coddington's C is therefore $107/110 \times 100 = 98\%$. Such high complementarity obviously results from wholesale species turnover across the intervening middle elevations—between 1000 and 3000 m—of the Cordillera Oriental. Unfortunately, almost nothing is known about patterns of species replacement in that interval.

THE UNKNOWN MIDDLE ELEVATIONS

As remarked in the Introduction, most faunal sampling in northeastern Ecuador has been done along the crest of the Cordillera Oriental or in the adjacent Amazonian lowlands, not on the intermediate slopes. Attempting to quantify this historical collecting bias, I compiled Ecuadorean specimen records from six computerized museum databases (AMNH, FMNH, KU, MVZ, UMMZ, USNM). A total of 1242 specimens of non-

volant mammals represented in those databases are from the adjoining northeastern provinces of Napo and Sucumbíos, each of which extends from the crest of the Cordillera Oriental to the Amazonian lowlands. Sorting specimen records by elevational intervals (≤1000 m, 1001–3000 m, >3000 m) resulted in the counts and proportions summarized in table 12.

These data clearly indicate that the middle elevations of the Cordillera Oriental remain a virtual terra incognita from the mammalogical perspective. Although substantial collections of Ecuadorean material are in museums with uncomputerized catalogs (e.g., BMNH, NHRS), I am not aware that any contain significant numbers of additional specimens from Napo or Sucumbíos collected in the interval between 1000 and 3000 m; at most, perhaps a few dozen middle-elevation specimens remain uncounted. In effect, two thousand vertical meters of densely forested habitat have never been sampled effectively by mammalogists in northeastern Ecuador. Just how significant is this collecting hiatus likely to be?

The eastern slopes of the Andes harbor diverse faunas of amphibians, squamates, and birds, many species of which are known to be endemic to intermediate elevations (Duellman, 1979; Stotz et al., 1996), and there is compelling evidence from elevational transects in southern Peru that nonvolant mammals likewise show substantial endemism between 1000 and 3000 m (Cadle and

Patton, 1988; Patterson et al., 1998). Unfortunately, virtually nothing is known about mid-elevational mammalian endemism in the northern Andes because the same pattern of collecting bias documented in table 12 seems to hold throughout eastern Ecuador and Colombia, approximately from 5°S to 8°N. No more than incidental collecting (nothing like sustained attempts at faunal inventory) has been attempted along any elevational transect in this extensive region of eastern-slope forests, even along such long-established routes as the road from Baños to Puyo in Ecuador or the road from Bogotá to Villavicencio in Colombia. The result is an elevational band at least 2000 m high and more than 1500 km from south to north that is currently unrepresented by any significant collections of mammals.

DIRECTIONS FOR FUTURE RESEARCH

There can be few higher priorities for siting new faunal inventory work anywhere in South America than in the middle elevations of the eastern Andes of Ecuador and Colombia. Although habitat destruction has been extensive along the few roads that currently descend these slopes, the forest remains undisturbed by man from timberline to piedmont in many roadless areas. Cutting trail and siting camps in virgin territory where intact mid-elevational faunas can still be sampled by transect collecting will not be easy, but ongoing road construction along the base of the Andes will shortly make most eastern-slope valleys accessible to land-hungry colonists. Such opportunities as now exist may soon be lost to subsequent generations of mammalogists.

The present report establishes a baseline for future inventory efforts in the Cordillera Oriental of northern Ecuador. Due to extensive clearing along the road from Papallacta to Baeza, it seems unlikely that mid-elevational forests can be effectively sampled for mammals along this particular route, but better opportunities may exist in the valley of the Río Oyacachi to the north, and in the valley of the Río Antisana/Verdeyacu to the south. A logical starting point for productive collecting would be to establish a base camp at or near the 2000 m contour where small

field teams could return for several years to explore the effectiveness of different faunal-sampling methods in this logistically challenging region of almost-continuous rainfall. New species and novel insights about equatorial-montane faunal gradients are certain to reward such initiatives.

ACKNOWLEDGMENTS

derson, Marcela Gómez-Laverde, Mike Carleton, and Diego Tirira read the manuscript and offered helpful suggestions for its revision.

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APPENDIX 1

Geographic Notes

Place names associated with specimens known to have been collected along the old trail from Quito to Baeza are a source of lingering confusion in the zoological literature. In order to better document the provenance of specimens examined for this report, I tried to locate every published first-hand description of this journey and the surrounding landscape. Apparently, two alternative routes were formerly used to cross the summit of the Cordillera Oriental and arrive at Papallacta. The following summary may prove helpful for other researchers working with old material from this region.

The only published survey of a route from Quito to Baeza appears to be the stadia and plane-table traverse in Sinclair (1929). From the northeastern outskirts of Quito (0°13′S, 78°30′W) the road to Baeza passed through the towns of Guapulo (0°12′S, 78°29′W), Cumbayá (0°12′S,

78°26′W), Tumbaco (0°13′S, 78°24′W), and Pifo (0°14′S, 78°20′W). A short distance beyond Pifo was an hacienda known as Paluguillo (0°15′S, 78°18′W), which was said to be the last permanently inhabited place before Papallacta was reached by this route (Sinclair, 1929; Moore, 1934). Leaving Paluguillo (at 9452 ft [2881 m] according to Sinclair), the trail climbed ESE to the northernmost of the two passes referred to in the literature as Guamaní (ca. 0°20′S, 78°12′W). From this pass, a broad saddle at 4070 m, the road descended to a lake variously referred to as ''Sugchoscocha'' (Sinclair, 1929: 205) or ''Laguna de Sugchos'' (op. cit.: pl. 3); on modern maps (e.g., IGM, 1978b) it is labeled as ''Laguna Sucus''. The next prominent landscape feature along this route was Laguna Papallacta, from which the trail descended to the town itself (fig. 1).

Nineteenth-century travelers and some 20th century collectors, however, followed another route that crossed the continental divide farther to the south. According to Jiménez de la Espada (1928), whose posthumously published journal described a journey made in 1865, this trail diverged from the itinerary described above at Tumbaco (0°13′S, 78°24′W), passed through an hacienda called Itulcache or Itulcachi (0°17′S, 78°20′W), and continued southward and eastward to the small village of Tablón (0°22′S, 78°15′W). From Tablón the trail ascended to another pass called Guamaní, about 5–6 km SW of the homonymous northern pass described above. This southern pass was described by Orton (1870) and Jiménez de la Espada (1928) as a sharp ridge, as it is currently depicted on modern maps (near 0°22′S, 78°14′W) at an elevation of 4150 m (IGM, 1978b). From this high point, the trail descended to a tambo (traditional resting place or shelter), probably the spot mapped as Hacienda El Tambo (ca. 0°23′S, 78°12′W) at 3780 m on the south bank of the Río Tambo (fig. 1). This southern route then converged on the northern road at or near Laguna Papallacta.

The modern all-weather road from Quito to Baeza follows the northern route described above, but does not pass by Laguna Sucus as the old road once did (fig. 1). The southern route is not marked on modern maps but perhaps remains as a footpath used by herders, fishermen, or hunters. Not knowing of its existence or historical significance, we did not attempt to find it when we worked near Papallacta from 1978 to 1980.

The literature contains several erroneous references to various places near Papallacta, especially with regard to the two passes confusingly known as Guamaní. Paynter's (1993) coordinates refer to the northern pass, but his elevation (3600 m) is much too low and at least some of the collectors he lists as working at Guamaní (e.g., the Olallas) probably visited the southern pass instead. The distinction is potentially important because the eastern and western approaches and the summit of the northern pass are mostly open páramo, whereas Jameson (1858), Orton (1870), and Jiménez de la Espada (1928) described the trail to the southern pass as passing through a forest on the western slope. "Cerro Guamaní", a place name that occurs on several specimen tags, may refer to a peak that rises to 4277 m between the north and south passes; on modern maps (e.g., IGM, 1978b) it is labeled as "Singunay". Alternatively, Guamaní may have been used in a regional sense—for the entire crest of the eastern cordillera south of Cayambe (0°02′N, 77°59′W) and north of Antisana—as defined by Reiss (1872).

The location of Tablón, another source of local specimens, is also problematic. According to Paynter (1993), this place is in Provincia Napo on the eastern slope of the Cordillera Oriental (Paynter, 1993), but first-hand accounts by travellers on the southern route describe the spectacular view westward from this point (e.g., Orton, 1870: 179) as well as the subsequent eastward climb to the pass; the coordinates of Tablón in modern gazetteers (e.g., USBGN, 1987) likewise place it at least 3 km west of the continental divide in Provincia Pichincha.

APPENDIX 2

Nonvolant Lowland Mammals from Napo and Sucumbíos

The following list comprises published and unpublished records of mammals collected or observed below 1000 m elevation in the provinces of Napo and Sucumbíos, both of which extend from the crest of the eastern Andes to the Amazonian lowlands of northeastern Ecuador.[10] Taxa are listed in the systematic sequence of Wilson and Reeder (1993), but names have been updated to conform with current usage (ICZN, 1998; Musser et al., 1998; Patton et al., 2000; Voss et al.,

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[10] Unbeknownst to us when we compiled these records, Napo was recently (1998) divided into two provinces: "Napo" was retained as the name for the western part, but the eastern part is now called "Francisco de Orellana" (D. Tirira, personal commun.). Almost all of our Napo records are from the western half of the old province.

2001). Institutional collections in which voucher material is deposited are listed parenthetically after each Latin binomial. Most voucher material was not examined to confirm identifications, which were obtained secondhand from electronic databases (FMNH, KU, MVZ, UMMZ, USNM), publications on museum holdings (e.g., Cabrera, 1917; Lönnberg, 1913, 1921, 1922; Baker, 1974), and the revisionary literature (Lawrence, 1941; Hall, 1951; Patton, 1987; Voss, 1988; Musser et al., 1998; Voss and da Silva, 2001). Five unvouchered sightings (marked with asterisks below) are included from a 1996 visit to La Selva Jungle Lodge (0°30′S, 76°22′W; in Sucumbíos province) by R.S. Voss and L.H. Emmons; supporting fieldnotes are preserved in the archives of the AMNH Department of Mammalogy.

MARSUPIALIA
  Didelphidae
    Caluromys lanatus (AMNH, FMNH, KU, MSU, USNM)
    Chironectes minimus (MSU)
    Didelphis pernigra (FMNH)
    Didelphis marsupialis (AMNH, KU, USNM)
    Glironia venusta (AMNH)
    Marmosa lepida (KU)
    Marmosa murina (AMNH, KU)
    Marmosa rubra (AMNH, FMNH)
    Marmosops impavidus (AMNH)
    Marmosops noctivagus (AMNH, KU, MSU, UMMZ, USNM)
    Metachirus nudicaudatus (AMNH, KU, UMMZ)
    Micoureus demerarae (FMNH)
    Micoureus regina (AMNH, MSU, UMMZ)
    Monodelphis adusta (AMNH)
    Philander andersoni (AMNH, FMNH, MSU, UMMZ, USNM)
XENARTHRA
  Bradypodidae
    Bradypus variegatus (FMNH)
  Megalonychidae
    Choloepus didactylus (MNCN)
  Dasypodidae
    *Dasypus kappleri**
    *Dasypus novemcinctus**
  Myrmecophagidae
    Cyclopes didactylus (UMMZ)
    Tamandua tetradactyla (MSU)
PRIMATES
  Callitrichidae
    Callithrix pygmaea (MNCN, MSU, UMMZ, USNM)
    Saguinus fuscicollis (AMNH, MNCN)
    Saguinus nigricollis (AMNH, FMNH, KU, MNCN, UMMZ, USNM)
    Saguinus tripartitus (UMMZ)
  Cebidae
    Alouatta seniculus (FMNH, MNCN, MVZ)
    Aotus vociferans (AMNH, FMNH, KU, USNM)
    Ateles belzebuth (USNM)
    Callicebus cupreus (FMNH, MNCN, MSU, UMMZ)
    Callicebus torquatus (see Torre et al., 1995)
    Cebus albifrons (FMNH, MVZ, UMMZ)
    Cebus apella (MNCN, USNM)
    Lagothrix lagotricha (AMNH, FMNH, MNCN, UMMZ, USNM)
    Pithecia aequatorialis (AMNH)
    Pithecia monachus (AMNH, UMMZ)
    Saimiri sciureus (FMNH, UMMZ)
CARNIVORA
  Felidae
    Leopardus pardalis (AMNH, FMNH, MSU, MVZ, UMMZ)
    Puma concolor (AMNH, MSU, MVZ)
  Mustelidae
    Eira barbara (AMNH)
    Mustela africana (MCZ)
    Lontra longicaudis (FMNH, MNCN, MVZ)
  Procyonidae
    *Bassaricyon gabbii**

    Nasua nasua (AMNH, FMNH, MSU)
    Potos flavus (AMNH)
    *Procyon cancrivorus**
PERISSODACTYLA
  Tapiridae
    Tapirus terrestris (FMNH)
ARTIODACTYLA
  Cervidae
    Mazama americana (KU, MVZ, UMMZ)
  Tayassuidae
    Pecari tajacu (AMNH, MNCN)
    Tayassu pecari (MVZ)
RODENTIA
  Sciuridae
    Microsciurus flaviventer (AMNH, FMNH, KU, MSU, UMMZ, USNM)
    Sciurus igniventris (AMNH, FMNH, MNCN, UMMZ, USNM)
    Sciurus spadiceus (FMNH, MNCN, UMMZ, USNM)
  Muridae
    Ichthyomys stolzmanni (AMNH, BMNH, NHRS)
    Melanomys robustulus (AMNH, UMMZ)
    Neacomys spinosus (AMNH, FMNH, UMMZ, USNM)
    Neacomys cf. *tenuipes* (MCZ)
    Nectomys apicalis (AMNH, FMNH, MSU, MVZ, UMMZ, USNM)
    Oecomys bicolor (AMNH, FMNH, KU, MSU, UMMZ)
    Oecomys superans (AMNH, FMNH, KU, MVZ)
    Oligoryzomys cf. *fulvescens* (KU, UMMZ)
    Oryzomys macconnelli (AMNH, MCZ)
    Oryzomys perenensis (AMNH, FMNH, KU, MVZ, UMMZ, USNM)
    Oryzomys yunganus (AMNH, UMMZ)
    Rhipidomys leucodactylus (AMNH, FMNH, MVZ, USNM)
    Scolomys melanops (USNM)
  Erethizontidae
    Coendou cf. *prehensilis* (USNM)
    *Coendou ichillus**
  Hydrochoeridae
    Hydrochoeris hydrochaeris (FMNH)
  Cuniculidae
    Cuniculus paca (FMNH, MVZ)
  Dasyproctidae
    Dasyprocta fuliginosa (AMNH, FMNH, MNCN, MVZ)
    Myoprocta pratti (AMNH, FMNH, MVZ, UMMZ)
  Echimyidae
    Dactylomys dactylinus (KU, MSU, USNM)
    Echimys saturnus (KU, MSU)
    Isothrix bistriata (see Tirira, 1999: 141)
    Makalata sp. (KU)
    Mesomys sp. (AMNH, USNM)
    Proechimys cf. *brevicauda* (AMNH, MVZ, FMNH, UMMZ)
    Proechimys cf. *simonsi* (AMNH, KU, MVZ, UMMZ, USNM)
    Proechimys cf. *steerei* (MVZ, UMMZ)
LAGOMORPHA
  Leporidae
    Sylvilagus brasiliensis (FMNH, MSU)

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