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A NEW SPECIES OF NORTHERN SHREW-OPOSSUM (PAUCITUBERCULATA: CAENOLESTIDAE) FROM THE CORDILLERA DEL CÓNDOR, ECUADOR

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A preliminary biological survey of the remote Cordillera del Cóndor revealed a new species of northern shrew-opossum (*Caenolestes*), the fourth species known from the northern Andes. The new form is distinguished from congeners by numerous metrical characters, especially of the skull and teeth; it is the largest living caenolestid. Its habitat is at the interface of densely forested montane slopes and the more open, low-lying vegetation that covers the main plateau. This vegetation is reminiscent of that in the tepuis of Venezuela and the Guianas. Diagnosis of the new species accompanies qualitative and morphometric comparisons to other caenolestid genera and species. Because the related species *C. convelatus* and *C. caniventer* occur mainly on the Pacific slope of the Andes, the presence of the new species on the Cordillera del Cóndor, an eastern foothill range, is remarkable.

Key words: new species, marsupials, *Caenolestes*, Neotropics, biogeography

Although living marsupials are most diverse in Australasia, the Neotropics are home to an impressive and diversified array. Ranging from Canada to Patagonia and from the Atlantic to Pacific oceans, the didelphimorphs are the best known and most widely distributed of American marsupials; this group includes ca. 15 genera and 65 species arrayed in one to four families (Gardner, 1993; Hershkovitz, 1992b). However, two additional marsupial orders are now restricted to the Andean cordilleras of South America, both remnants of more diversified and widespread Cenozoic radiations (Marshall, 1980, 1982). Microbiotheria now contains only the Valdivian Forest "monito del monte" (*Dromiciops* Thomas), an enigmatic form often regarded as the sole American member of the Australasian radiation (Springer et al., 1994) or, alternatively, as sister to all other marsupial lineages, living and extinct (Hershkovitz, 1992a, pers. comm.). Similarly, the order Paucituberculata includes only three extant genera in a single unspecialized family,

Caenolestidae (Melville, 1983). Genera of "shrew-opossums" are disjunct, with *Caenolestes* Trouessart in westernmost Venezuela, Colombia, Ecuador, and northernmost Peru, *Lestoros* Oehser in southern Peru, and *Rhyncholestes* Osgood in southern Chile and Argentina.

Although caenolestid marsupials have been known for >130 years (Thomas, 1895a, 1895b, Tomes, 1860), their biology and interrelationships remain poorly known. This ignorance is partly a consequence of their remote high-elevation and high-latitude habitats, which have limited access and scientific sampling. However, when suitable habitats have been sampled, caenolestids are not difficult to collect and are often as abundant and readily caught as other sympatric small mammals (Patterson et al., 1989; Tate, 1931). Fieldwork during the past decade has yielded many new records, e.g., more than two-thirds of the localities known for *Rhyncholestes* by Patterson and Gallardo (1987) were based on captures made since 1980. Similarly, the range

of *Lestoros* has been greatly enlarged by recent collecting in southern Peru (J. L. Patton, pers. comm.).

Because *Lestoros* and *Rhyncholestes* are regarded as monotypic (Gardner, 1993; but see Bublitz, 1987), new records have served mainly to refine their distributions. However, the northern shrew-opossums *Caenolestes* include at least three species: *C. fuliginosus* (Tomes, 1863) occurring at higher elevations from central Ecuador into all three Andean cordilleras of Colombia and westernmost Venezuela; *C. convelatus* Anthony (1924) at lower elevations of western Colombia and northern Ecuador; and *C. caniventer* Anthony (1921) at lower elevations in southwestern Ecuador and northwestern Peru. All three species occur in central Ecuador, and the characters known to distinguish them are subtle and often overlapping. Complicating matters, the most recent catalog of caenolestids (Gardner, 1993) was unaccompanied by diagnoses or keys and differs from the last comprehensive and definitive revision (Bublitz, 1987).

In 1993, the senior author and his associates collected three specimens of a large *Caenolestes* with unknown affinities. Here, we characterize the new shrew-opossum and detail its relationships to other *Caenolestes*, which includes caenolestids with conical single-rooted incisors in both sexes, I4 mostly filling the space between I3 and C, similar-sized P1 and P2, and infraorbital foramen open to anterior (not lateral) view.

MATERIALS AND METHODS

This study was an outgrowth of a Rapid Assessment Program (RAP) expedition focused on the Cordillera del Cóndor, which lies on the Ecuadorian and Peruvian border to the east of the main axis of the Andes. Separated from the Cordillera Real de los Andes by the course of the Río Zamora, the Cordillera del Cóndor runs roughly parallel to the main axis of the Andes between 3°S and 3°20'S. Three camps were established during this biological reconnaissance; Destacamento Militar Coangos (1,666 m elevation), Destacamento Militar Miazí (900 m), and

Achupallas (at 2,100 m, atop the main block of the Cóndor). All three specimens of the new *Caenolestes* were taken during standard mammalian sampling at the last-named site.

Provenance and collection abbreviations are listed in Appendix I. External measurements (in millimeters unless otherwise indicated) were taken from specimen tags; length of head and body (obtained as total length minus length of tail), length of tail, length of hind foot, and weight (grams). Dental and tooth-gap measurements were taken at 25× magnification using an eyepiece micrometer (120 units) in a Wild M5A dissecting microscope. Because ontogenetic criteria were unavailable for assessing the dental homologies of paucituberculate marsupials to other mammals (Luckett, 1993), and because cheektooth formulae of marsupials remain controversial, our dental notations imply only position within the toothrow. Measurements of crowns were generally chordal distances from the labial alveolus to the tip of the cusp; however, for P3, measurements also were made along the leading edge of the tooth from the anterior alveolus to the anterior style (P3—anterior style) and also to the tooth crown (P3—chordal height). Measurements for gaps began and ended at alveoli of successive maxillary teeth.

Measurements were taken using digital calipers and INCAL software running on a Toshiba laptop computer. These include condylobasal length, nasal length, premaxillary length, zygomatic breadth, mastoid breadth, postorbital constriction, cranial depth, mandibular length, height of mandibular ramus (from the ventral border of the ramus to the labial alveolus of m1), palatilar length (to the elevated border of the palatine bridge), length of anterior palatal foramen, length of posterior palatal foramen, and length of maxillary cheekteeth (from the anterior alveolus of P3 to the posterior alveolus of M4). Statistical analyses were conducted and graphs generated on a personal computer using STATISTICA for Windows (StatSoft, 1984–1994).

RESULTS

Caenolestes condorensis, new species

Holotype.—Fully adult male; skin and skull with mandibles in excellent condition; FMNH 152134; obtained 23 July 1993 by Luis Albuja V. and Alfredo Luna; formerly EPN 933886.

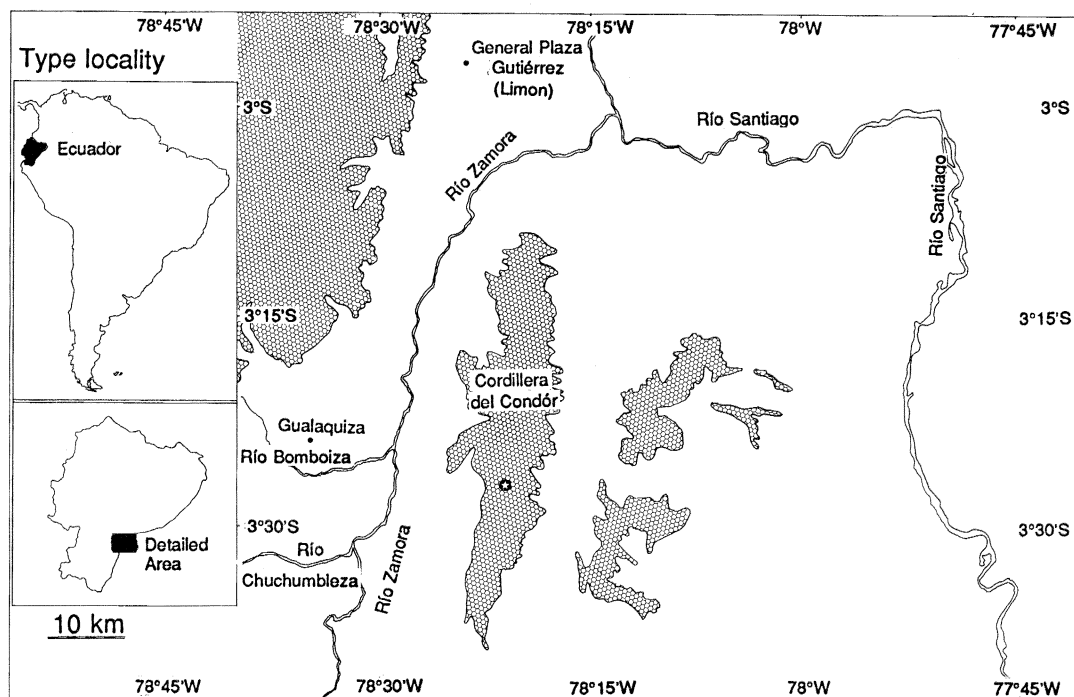


FIG. 1.—Type locality and only known record of the new species of *Caenolestes* from Ecuador is indicated by the star. Stippled area corresponds to elevations >1,000 m.

Paratypes.—EPN 933874 (Escuela Politécnica Nacional, Ciencias Biológicas, Quito), subadult female (preserved in alcohol), and EPN 933875, adult male (skin and skull with mandibles), both collected by L. Albuja and A. Luna, 22 July 1993.

Type locality.—“Achupallas” is a place name coined by members of the Rapid Assessment Program expedition for their camp on the upper plateau of the Cordillera del Cóndor, in the Provincia de Morona-Santiago, Ecuador, coordinates 3°27'03"S, 78°21'39"W, elevation 2,080 m. Paratypes were taken at the same locality as the holotype.

Etymology.—The specific epithet refers to the Cordillera del Cóndor, where the type and only known specimens were collected.

Distribution.—Insofar as known, *Caenolestes condorensis* is found only in the Cordillera del Cóndor of southeastern Ecuador, probably extending in the same cordillera into Peru (Fig. 1).

Diagnosis.—A large species of caenolestid marsupial with the following distinguishing traits: canines large and massive; nasals long and exceeding half of greatest length of skull; p2 large with its anterior cusp elevated; crown of p3 enlarged; posterior margin of palate squared; anterior palatal foramen opens far anteriorly, between P1 and P2; posterior palatal foramen opens level with anterior margins of P3; antorbital vacuity is bordered by premaxilla, nasal, and frontal bones; gaps between anterior maxillary teeth, particularly I3–I4 and C–P13 larger, in some cases exceeding the lengths of anterior teeth; I4 in contact with the anterior margin of C; color of dorsal pelage fuscous, browner below, and coarse-textured; sides of rhinarium and mystacial vibrissae whitish.

Description.—The largest species yet known in the family Caenolestidae (measurements of holotype in millimeters; see Tables 1–3 for measurements of hypo-

digm): total length, 260; length of tail, 130; length of hind foot, 30; length of ear, 18, weight, 48 g. Dorsal pelage fuscous, distinctly contrasting with the drab ventral pelage, which bears a faintly darker pectoral spot. Length of pelage on back and rump is ca. 10 mm, with two plainly visible bands on the hairs: the basal 7 mm is dark gray and the apical 3 mm is fuscous. On the venter, hairs are 7–8 mm long, again with two distinct bands; the basal 5–6 mm pale gray and the apical 2 mm drab. Pelage is darker around the eyes and rostrum than elsewhere dorsally; the tip of the nose, the lips, and digits of both manus and pes are rose-colored in life. The mystacial vibrissae are whitish, the tail and ears are fuscous (Fig. 2).

The skull is large (37.60) and massive, the nasals are long (19.47), premaxillary bones extend posteriorly past the level of the anterior margin of P2, and the braincase is deep (11.08). The antorbital vacuity is shaped liked a comma and is bordered by the nasal, maxillary, and frontal bones. The palate is long, with its posterior margin quadrate. The anterior palatal foramen extends posteriorly to a level midway between P1 and P2; the posterior foramen opens at the level of the anterior margin of P3 and is long (8.64). The caudal region of the mandible (i.e., that part containing the condylar, angular, and coronoid processes) is enlarged.

The dentition (Fig. 3) is typical of the genus, with incisors shorter than the canines, which are long (3.71) and curved; P1 and P2 almost the same height and size; height of P3 slightly larger than the anterior cusp of M1. Gaps between I3 and I4 are about equal to the breadth of I4; gaps between C and P1 are about equal to the breadth of P1; median lower incisors are well developed and strongly procumbent; p2 larger than p3 and with the posterior cusp distinct and elevated; p3 with the crown nearly triangular in lateral view, the posterior cusp almost consolidated with the anterior one.

Comparisons.—In numerous metrical characters, *Caenolestes condorensis* is the largest Recent caenolestid known. Its nasals are longer than in any living species (including *Rhyncholestes*) and comprise more than one-half the length of the skull, not less than one-half as in other *Caenolestes*. Cranial depth and length of posterior palatal foramen are two other characters in which *C. condorensis* appears larger than and non-overlapping with any other Recent caenolestid (Fig. 4). Palatilar length of *C. condorensis* is longer than in other *Caenolestes*, but equalled by some *Rhyncholestes*.

From *C. caniventer*, the new species can be distinguished by its larger cranial and external dimensions (Table 1). The two available specimens of *C. condorensis* do not overlap with examined samples of *C. caniventer* in condylobasal length, premaxillary length, palatilar length, zygomatic breadth, mastoid breadth, or mandibular length. In addition to being substantially longer, the palate of *C. condorensis* has a posterior margin that is squared, not curved. The new species also has darker dorsal pelage, ventral coloring that is drab (not grayish), and a pectoral spot that is faint, almost inconspicuous (not defined by nearly the same color as the dorsal pelage). Its median upper incisors are one-half again as long as those in *C. caniventer*, and the gaps between tooth-pairs I3–I4 and C–P1 are noticeably larger (Tables 2 and 3).

From *C. convelatus*, the new species differs in being slightly larger (non-overlapping in condylobasal length, nasal length, palatilar length, cranial depth, or length of posterior palatal foramen). Externally, it is predominantly grayish (not dark brown) in dorsal pelage, with fuscous (not tan) tips to individual hairs; below, it is appreciably darker, with hairs tipped by drab- (not cream-) colored bands. The antorbital vacuity of *C. condorensis* is more open anteriorly, forming the shape of a comma (not a narrow crescent or parenthesis), and is bordered by nasal, maxillary, and frontal bones (not solely the former two). On the



FIG. 2.—*Caenolestes condorensis* showing contrasting coloration of nose, ear pinnae, and digits(a), and vegetation at type locality, showing the ecotone of open and forested habitats where *C. condorensis* was captured(b). Photographs by L. Albuja V.

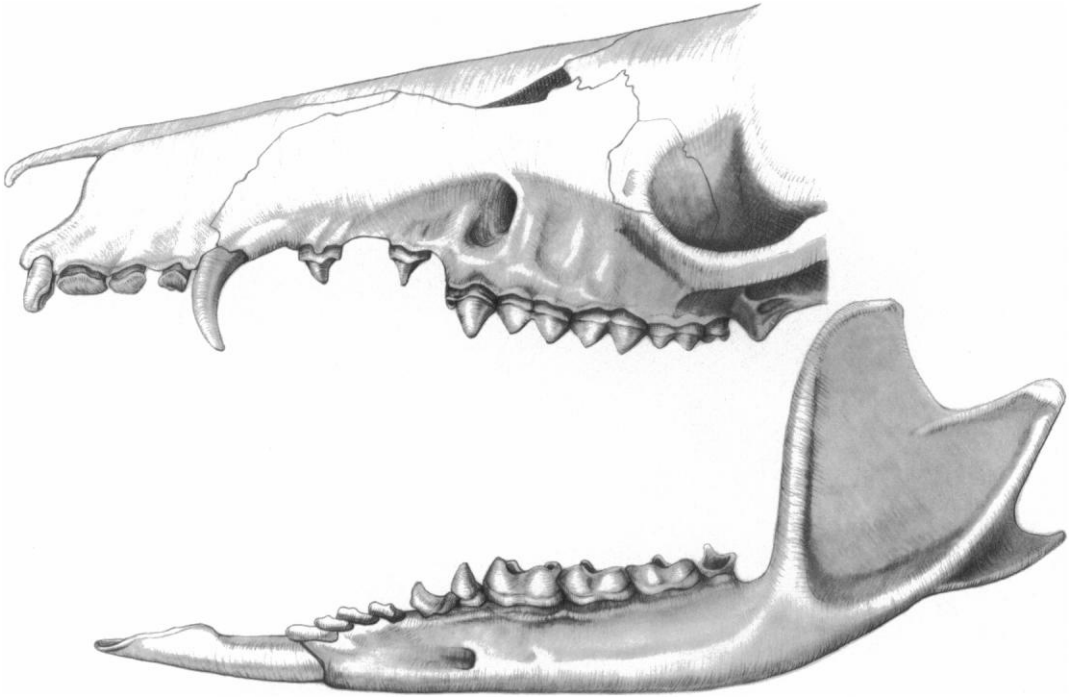


FIG. 3.—Maxilla and mandible of male holotype (FMNH 152134) of *Caenolestes condorensis*, showing location and shape of antorbital vacuity, size and shape of dentition, and dental gaps considered diagnostic of the new species.

mandible, the principal cusp of p3 is broader (not narrower) in lateral aspect and the posterior cusp on p2 is more distinct from the primary cusp.

From *C. fuliginosus*, the new species differs in larger size (non-overlapping in condylobasal length, premaxillary length, palatal length, zygomatic breadth, mastoid breadth, or mandibular length). It has darker and coarser pelage (not sooty brown above and slightly paler below, with silky texture and little counter-shading), with dorsal hairs tipped by fuscous (not reddish). *C. condorensis* is easily distinguished by its longer and more massive upper canines. The labial cusp of P3 is nearly equal in height to those on the molars.

As in other species of the genus, *C. condorensis* exhibits sexual dimorphism in size, with larger adult males than females. A single fluid-preserved female of unknown age had the following external mea-

surements: total length, 228; length of tail, 124; length of hind foot, 25; weight, 43 g (cf. measurements of males in Table 1). Differences among species of *Caenolestes* may be summarized by the accompanying key, but individuals of comparable age and sex are needed for metrical comparisons.

Key to Living Species of *Caenolestes*

1. Antorbital vacuity in the shape of a parenthesis or crescent, or else completely roofed by bone; located at margin of nasal and maxillary bones *C. convelatus*
- 1'. Antorbital vacuity comma-shaped and bounded by nasal, maxillary, and frontal bones 2
2. Size smaller, skull delicate; pelage silky-textured with faint counter-shading; skull rests on bullae and incisors (except in some adult males) *C. fuliginosus*
- 2'. Size generally larger, skull robust; pelage coarse and distinctly counter-shaded; skull rests on bullae and canines (occa-

sionally on labial cusps of M1 or M2)

- 3
3. Length of head and body, 115; length of tail, 120; condylobasal length, 33; coloration of ventral pelage is grayish with a dark and conspicuous pectoral spot; upper canines moderately long (1.9 mm); length of nasals less than one-half condylobasal length; palatal bridge curved *C. caniventer*
- 3'. Length of head and body, 135; length of tail, 125; condylobasal length, 39; coloration of ventral pelage is drab with an inconspicuous pectoral spot; uppers canines large (3.5 mm); nasal length larger than one-half of condylobasal length; palatal bridge square *C. condorensis*

Ecological notes.—The type locality of *C. condorensis* is distinguished geologically by an ash deposit filled with sandy quartz of Cretaceous age. According to Alwyn Gentry (pers. comm.), the vegetation of the area in which *C. condorensis* was collected shows strong resemblances to that of the Venezuelan tepuis. The locality is cold and extremely humid, presenting two well-defined habitats: a plain covered by low heath-like vegetation <1.5 m in height, dominated by spiny bromeliads (achupallas) and an adjacent slope with a dense forest and shrubs 5–6 m in height. Vegetation at the collection site included *Schefflera* (Araliaceae), *Anthurium* (Araceae), *Ugni* (Myrtaceae), *Spheradenia* (Cyclantaceae), *Clusia* (Clusiaceae), *Leandra* and *Miconia* (Melastomaceae), *Lycopodium* (Lycopodiaceae), *Bennetia* (Theaceae), *Phoradendrom* (Loranthaceae), *Tillandsia* and *Gusmania* (Bromeliaceae), *Chusquea* (Gramineae), *Piper* (Piperaceae), *Monnina* (Polygalaceae), and *Geonoma* (Palmae).

Caenolestes condorensis was taken at the ecotone between the shorter vegetation of the plateau and the forest-covered slopes. Traps capturing the specimens had been placed on the ground in existing runways between dense vegetation or outside burrows. Two specimens were captured alive in National live traps (13 by 13 by 40 cm), and the third in a Victor rat trap. In each

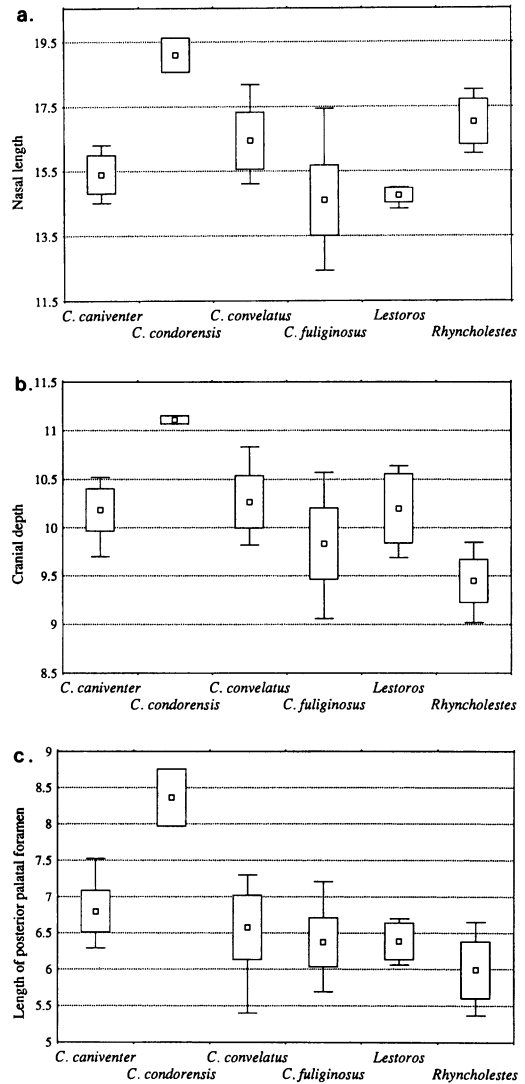


FIG. 4.—Morphological comparisons of caenolestid species in (a) nasal length, (b) cranial depth, and (c) length of posterior palatal foramen. Plotted values (in mm) include means, standard deviations, and ranges for adult males and females (pooled) of all four species of *Caenolestes*, plus *Lestoros* and *Rhyncholestes*. See text for discussion and Appendix 1 for specimens examined.

instance, the bait used was ground roasted peanuts mixed with oats. Other mammals captured at this site included *Platyrrhinus infuscus*, *P. umbratus*, *Sturnira bidens*, *S.*

TABLE 1.—Measurements of skulls and mandibles of adult *Caenolestes*. All measurements in millimeters; see text for discussion. Sample sizes are given in parentheses.

Variable	<i>C. caniventer</i>			<i>C. condorensis</i>	<i>C. convelatus</i>			<i>C. fuliginosus</i>		
	♀ ♀ (10)	♂ ♂ (6)	Pooled (16)	♂ ♂ (2)	♀ ♀ (15)	♂ ♂ (7)	Pooled (22)	♀ ♀ (25)	♂ ♂ (45)	Pooled (70)
Condylobasal length										
Mean	31.91	32.93	32.32	36.88	32.46	34.73	33.25	29.87	31.30	30.77
Min	30.53	31.69	30.53	36.15	31.00	33.97	31.00	27.53	27.56	27.53
Max	33.45	35.79	35.79	37.60	33.31	35.77	35.77	32.51	34.27	34.27
Nasal length										
Mean	15.32	15.75	15.49	19.10	15.86	17.01	16.28	13.98	14.72	14.46
Min	14.50	15.35	14.50	18.73	15.10	16.01	15.10	12.43	12.48	12.43
Max	16.30	16.29	16.30	19.47	16.88	18.20	18.20	16.34	16.90	16.90
Premaxillary length										
Mean	9.80	10.49	10.07	12.10	9.97	10.50	10.16	8.87	9.61	9.34
Min	8.77	10.07	8.77	12.02	8.62	9.14	8.62	7.74	7.73	7.73
Max	10.59	11.39	11.39	12.18	11.06	12.58	12.58	10.02	10.80	10.80
Zygomatic breadth										
Mean	14.68	14.88	14.76	17.29	15.15	16.65	15.67	14.02	14.52	14.34
Min	13.91	13.95	13.91	17.13	14.28	15.72	14.28	12.80	13.24	12.80
Max	15.40	16.45	16.45	17.44	16.11	17.48	17.48	15.31	16.15	16.15
Mastoid breadth										
Mean	11.56	11.33	11.47	13.11	11.83	12.52	12.05	11.04	11.29	11.20
Min	11.04	10.86	10.86	13.07	10.99	11.86	10.99	10.46	10.33	10.33
Max	12.13	11.87	12.13	13.14	12.72	13.49	13.49	12.01	11.98	12.01
Postorbital constriction										
Mean	7.70	7.66	7.69	7.39	7.49	7.37	7.45	7.44	7.50	7.48
Min	7.36	7.39	7.36	7.28	6.96	6.65	6.65	7.00	6.87	6.87
Max	7.94	7.96	7.96	7.51	7.86	7.94	7.94	8.04	8.16	8.16
Cranial depth										
Mean	10.21	10.12	10.18	11.11	10.16	10.50	10.27	9.74	9.88	9.83
Min	9.72	9.70	9.70	11.08	9.82	10.36	9.82	9.06	9.10	9.06
Max	10.52	10.37	10.52	11.14	10.71	10.83	10.83	10.57	10.54	10.57
Mandibular length										
Mean	20.00	20.54	20.20	23.62	20.22	22.06	20.80	18.25	19.46	19.05
Min	18.93	19.63	18.93	23.27	19.58	21.38	19.58	16.45	16.40	16.40
Max	20.72	22.19	22.19	23.96	21.04	22.70	22.70	20.72	22.29	22.29
Mandibular ramus height										
Mean	2.60	2.53	2.58	3.03	2.88	2.99	2.91	2.50	2.62	2.57
Min	2.42	2.21	2.21	2.99	2.30	2.59	2.30	2.23	2.09	2.09
Max	3.04	3.05	3.05	3.08	3.18	3.55	3.55	2.75	3.03	3.03
Palatilar length										
Mean	16.97	17.36	17.13	19.94	17.08	18.57	17.60	15.55	16.56	16.20
Min	16.36	16.25	16.25	19.70	16.33	17.94	16.33	14.08	14.58	14.08
Max	17.86	18.99	18.99	20.17	18.33	19.07	19.07	17.51	18.39	18.39
Anterior palatal foramen										
Mean	6.05	6.34	6.17	6.99	6.21	6.77	6.41	5.70	6.06	5.93
Min	5.56	5.85	5.56	6.98	5.74	6.35	5.74	4.90	5.08	4.90
Max	6.90	7.13	7.13	7.00	6.77	7.46	7.46	6.43	7.24	7.24
Posterior palatal foramen										
Mean	6.78	6.81	6.79	8.36	6.30	7.01	6.54	6.20	6.39	6.32
Min	6.36	6.29	6.29	8.08	5.40	6.78	5.40	5.69	5.74	5.69
Max	7.10	7.52	7.52	8.64	6.66	7.23	7.23	6.57	7.10	7.10
Length of maxillary cheekteeth										
Mean	7.50	7.46	7.48	8.09	7.68	7.71	7.69	6.94	7.13	7.06
Min	7.06	7.21	7.06	8.08	7.30	6.92	6.92	6.50	6.41	6.41
Max	7.83	7.67	7.83	8.10	8.12	8.12	8.12	7.21	7.60	7.60

TABLE 2.—Measurements of dental crowns for *Caenolestes*. All measurements in millimeters. Sample sizes are given in parentheses.

Dental crown	<i>C. caniventer</i>			<i>C. condorensis</i>	<i>C. convelatus</i>			<i>C. fuliginosus</i>		
	♀ ♀ (6)	♂ ♂ (5)	Pooled (11)	♂ ♂ (2)	♀ ♀ (12)	♂ ♂ (8)	Pooled (20)	♀ ♀ (6)	♂ ♂ (14)	Pooled (20)
C height										
Mean	1.650	1.844	1.736	3.418	2.290	3.022	2.656	1.706	2.106	1.980
Min	1.520	1.719	1.523	3.125	1.953	2.422	1.953	1.211	1.641	1.211
Max	1.800	1.914	1.914	3.711	2.734	3.555	3.555	2.031	2.734	2.734
I1 height										
Mean	1.393	1.359	1.378	1.875	1.736	1.802	1.765	1.344	1.426	1.404
Min	1.172	1.016	1.016	1.875	1.367	1.484	1.367	1.055	1.172	1.055
Max	1.680	1.562	1.680	1.875	2.148	2.070	2.148	1.641	1.680	1.680
P1 height										
Mean	0.833	0.937	0.881	1.035	1.090	1.128	1.105	0.827	0.896	0.875
Min	0.781	0.859	0.781	1.016	0.898	0.898	0.898	0.508	0.781	0.508
Max	0.859	1.016	1.016	1.055	1.250	1.328	1.328	0.977	1.055	1.055
P2 height										
Mean	0.905	0.908	0.906	0.996	1.051	1.099	1.070	0.898	0.940	0.927
Min	0.859	0.898	0.859	0.977	0.937	1.016	0.937	0.781	0.820	0.781
Max	0.977	0.937	0.977	1.016	1.211	1.250	1.250	1.016	1.055	1.055
P3 chordal height										
Mean	2.259	2.164	2.216	2.344	2.350	2.510	2.414	1.940	2.148	2.083
Min	2.070	2.031	2.031	2.227	2.187	2.266	2.187	1.680	1.875	1.680
Max	2.344	2.227	2.344	2.461	2.617	2.734	2.734	2.188	2.422	2.422
P3 anterior style										
Mean	1.022	0.945	0.987	1.309	1.087	1.239	1.143	0.924	1.010	0.984
Min	0.781	0.859	0.781	1.016	0.898	1.094	0.898	0.703	0.781	0.703
Max	1.250	1.055	1.250	1.602	1.406	1.445	1.445	1.055	1.406	1.406
P3 height										
Mean	1.810	1.943	1.863	1.855	1.982	1.987	1.984	1.647	1.829	1.769
Min	1.641	1.836	1.641	1.797	1.797	1.758	1.758	1.406	1.680	1.406
Max	1.992	2.031	2.031	1.914	2.383	2.187	2.383	1.797	2.187	2.187
M1 height										
Mean	1.439	1.586	1.506	1.523	1.575	1.602	1.586	1.315	1.487	1.435
Min	1.172	1.445	1.172	1.445	1.133	1.250	1.133	0.820	1.250	0.820
Max	1.602	1.719	1.719	1.602	1.914	1.797	1.914	1.602	1.680	1.680

erythromos, *S. ludovici*, *Dermanura glauca*, *Enchisthenes hartii*, *Oryzomys albigularis*, *Oryzomys* sp., and *Akodon aerosus*.

Biogeographic remarks.—Two ecological groups of shrew-opossums are recognized within the genus *Caenolestes* (Timm and Patterson, in press). The first, represented by *C. fuliginosus*, inhabits cloud forests and páramos, habitats typical of high elevations. Although geographically variable, *C. fuliginosus* tends to have dark, silky pelage, reduced countershading, and a delicate, gracile skull. The second group, represented by both *C. convelatus* and *C.*

caniventer, inhabits sub-tropical and montane forests at lower elevations. These tend to be larger, heavier, and more robust, with coarser pelage and more strongly defined countershading. Morphological comparisons and habitat associate *C. condorensis* with the latter group.

Until now, lower-elevation *Caenolestes* were known only from intermontane valleys and the Pacific slope; the Sierra de Santa Barbara in Colombia, the Cordillera Occidental in southern Colombia and Ecuador (*C. convelatus*), and the Cordillera Occidental in Ecuador and Peru (*C. cani-*

TABLE 3.—Measurements of gaps between tooth-pairs in *Caenolestes*. All measurements in millimeters. Sample sizes are given in parentheses.

Variable	<i>C. caniventer</i>			<i>C. condorensis</i>	<i>C. convelatus</i>			<i>C. fuliginosus</i>		
	♀ ♀ (6)	♂ ♂ (5)	Pooled (11)	♂ ♂ (2)	♀ ♀ (12)	♂ ♂ (8)	Pooled (20)	♀ ♀ (6)	♂ ♂ (14)	Pooled (20)
I1–I2 gap										
Mean	0	0	0	0.176	0.117	0	0.064	0	0	0
Min	0	0	0	0.156	0	0	0	0	0	0
Max	0	0	0	0.195	0.312	0	0.312	0	0	0
I2–I3 gap										
Mean	0	0	0	0.195	0.039	0	0.021	0.019	0.014	0.016
Min	0	0	0	0.195	0	0	0	0	0	0
Max	0	0	0	0.195	0.117	0	0.117	0.117	0.117	0.117
I3–I4 gap										
Mean	0.247	0.125	0.192	0.449	0.046	0	0.025	0.013	0.008	0.010
Min	0.117	0	0	0.391	0	0	0	0	0	0
Max	0.352	0.195	0.352	0.508	0.156	0	0.156	0.078	0.117	0.117
I4–C gap										
Mean	0.104	0.062	0.085	0.234	0	0.023	0.011	0	0.017	0.012
Min	0	0	0	0.234	0	0	0	0	0	0
Max	0.195	0.156	0.195	0.234	0	0.117	0.117	0	0.234	0.234
C–P1 gap										
Mean	0.892	0.773	0.838	1.406	1.048	1.141	1.090	0.488	0.597	0.564
Min	0.625	0.469	0.469	1.367	0.781	0.703	0.703	0.273	0.117	0.117
Max	1.25	1.094	1.25	1.445	1.328	1.289	1.328	0.586	1.094	1.094
P1–P2 gap										
Mean	0.944	0.891	0.920	1.113	0.915	0.992	0.947	0.534	0.594	0.576
Min	0.781	0.742	0.742	1.094	0.664	0.820	0.664	0.312	0.391	0.312
Max	1.172	1.172	1.172	1.133	1.211	1.172	1.211	0.703	0.781	0.781
P2–P3 gap										
Mean	0.124	0.156	0.132	0.098	0.039	0	0.026	0	0	0
Min	0	0.117	0	0.078	0	0	0	0	0	0
Max	0.312	0.195	0.312	0.117	0.078	0	0.078	0	0	0

venter). The range of the last-named species includes forests of the Huancabamba Deflection in northern Peru (Timm and Patterson, in press; Barkley and Whitaker, 1984 reported these specimens as *C. fuliginosus*). There, the axis of the Andes changes abruptly, creating some of the lowest Andean passes between the Caribbean and Tierra del Fuego. These low-elevation passes (and the adjacent arid valley of the Río Marañón) constitute significant barriers to north-south distributions of high-elevation species (Parker et al., 1985). Vuilleumier (1984) found that almost one-third (31%) of high-elevation species of birds reached their northern or southern limits at the deflection and that most remaining species

(62%) were differentiated on either side. However, many lower-elevation species of birds and mammals range widely through the passes, uniting the Pacific and Marañón slopes of the cordilleras into the Western Slope region of endemism (Chapman, 1926; Patterson et al., 1992; Pearson, 1982; Vuilleumier, 1984). However, this region of endemism is not known to extend onto the eastern versant of the Cordillera Oriental (Chapman, 1926; Patterson et al., 1992).

Caenolestes condorensis might have reached the eastern versant of the Andes through a low-elevation Huancabamba corridor, but we find few characters allying the new species with neighboring *C. caniventer*. In a number of mensural characters (in-

cluding premaxillary length, mastoid breadth, zygomatic breadth, and gaps between anterior incisors), *C. condorensis* overlaps *C. convelatus*, but not *C. caniventer*. In postorbital constriction, the only cranial character in which *C. caniventer* averages larger than *C. convelatus*, *C. condorensis* is shorter than both. The explanation for this biogeographic puzzle, in which geographically adjacent forms appear more distantly related, undoubtedly lies in further fieldwork and systematic revision.

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APPENDIX I

The following specimens were examined during the course of this analysis. Owing to incomplete growth, damage, missing preparations, or specific analytical requirements, only a subset of these specimens were included in any given comparison. Abbreviations are: AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum, London; EPN, Ciencias Biológicas, Escuela Politécnica Nacional (Quito); FMNH, Field Museum of Natural History (Chicago); UV, Departamento de Zoología, Universidad del Valle (Cali).

Caenolestes caniventer.—Ecuador: El Oro; El Chiral, 5,350 feet (AMNH 5♂♂). Pichincha; Molleturo, 7,600 feet (AMNH 3♂♂). Peru: Piura; "Batan," on Zapalache-Carmen trail, 2,250

m (LSU 11♀); Cerro Chinguela, ca. 5 km N Sapalache, 2,900 m (LSU 5♂♂, 5♀♀); Huanabamba, km 30 on road to San Ignacio, 3,000 m (FMNH 2♂♂, 7♀♀).

Caenolestes condorensis.—Ecuador: Morona-Santiago; Achupallas, 2,100 m (EPN 2 ♂♂, 1 ♀).

Caenolestes convelatus.—Colombia: Antioquia; Páramo Frontino, 3,600 m (FMNH 1♀); Santa Barbara, 2,700 m (FMNH 3♂♂, 2♀♀), 2,800 m (FMNH 8♀♀), 3,000 m (FMNH 1♂), 3,100 m (FMNH 1♂ 1♀). Ecuador: Imbabura; Hacienda La Vega, 5 km ESE San Pedro del Lago (FMNH 1♂). Pichincha; El Castillo (FMNH 1♀); El Hato, Antisana, 4,100 m (FMNH 1♀); Galaya [=Saloya] West, 1,100 m (FMNH 1♀); Guala, Illambo Valley, 1,800 m (FMNH 1♂); Las Máquinas, Santo Domingo Trail, 7,000 feet (AMNH 5♂♂, 5♀♀); Santa Rosa, Mindo (EPN 1 unknown). No locality data (EPN 1♂).

Caenolestes fuliginosus.—Colombia: Antioquia; Páramo Frontino, 3,100 m (FMNH 1♀); 3,300 m (FMNH 4♂♂, 1♀); Páramo [Sonsón], 7 km E, 3,000 m (FMNH 1♂), 3,100 m (FMNH 1♂, 2♀♀); Páramo Sonsón, 7 km E, 3,050 m (FMNH 1♂). Boyacá; East Andes, E Side, Hacienda La Primavera, 7,000 feet (FMNH 1♂). Caldas; Río Termales (FMNH 1♂), 2,600 m (FMNH 3♂♂), 3,100 m (FMNH 1♂ 1♀), 3,200 m (FMNH 2♂♂, 2♀♀), 3,300 m (FMNH 1♂); Termales del Ruiz, 3,100 m (FMNH 1♀), 3,200 m (FMNH 1♀). Cauca; Lago San Rafael, 3,375 m (FMNH 1♀); Laguna San Rafael, Páramo Puracé (UV 2♂♂); Páramo de Guanacas, km 51 entre Totoró e Inzá (UV 1♀). Cundinamarca; Bogotá (type; BMNH 1♂); Río Balcones (FMNH 5♂♂, 1♀), 2,700 m (FMNH 6♂♂, 3♀♀), 2,750 m (FMNH 1♀); San Cristobal, 2,800 m (FMNH 1♀), 2,900 m (FMNH 5♂♂, 8♀♀); Soacha, Finca El Soche, 2,800 m (UV 7♂♂, 3♀♀); Soacha, San Miguel-Sibaté, 2,600 m (UV 3♂♂, 3♀♀). Huila; Río Magdalena, 2,300 m (FMNH 6♂♂, 2♀♀); Río Ovejeras, 2,350 m (FMNH 1♂, 1♀); San Antonio, 2,200 m (FMNH 2♂♂, 2♀♀), 2,300 m (FMNH 1♂, 1♀); Santa Marta, 2,700 m (FMNH 1♂). Nariño; Pasto, km 33 E (UV 1♂). Norte de Santander; Páramo de Tamá [3,330 m] (FMNH 3♂♂, 3♀♀). Quindío; Finca "Bengala," carretera Salento-Cocora (UV 1♀); Finca Rincón Santo, 6 km carretera Salento, 2,750 m (UV 1♂); Finca Rincón Santo, carretera Salento-Cocora, 3,250

m (UV 1♂); Finca Rincón Santo, Municipio Salento (UV 1♂). Valle del Cauca; Páramo de Baragán, 6 km S, 40 km W Tuluá (UV 1♀). Ecuador: Bolívar ["Pinchincha"]; Sinche, 11,100 feet (AMNH 1♀). Chimborazo; Chimborazo Mt., 4,000 m (FMNH 1♀). Napo; Cerro Antisana, oriente (FMNH 1♂, 2♀♀); Cosanga, Río Aliso (EPN 1♀); Río Bermejo (EPN 1 unknown, 1♂); Río Bermejo, Oriente (EPN 1♀). Pichincha; Chinchin Cocha (FMNH 5♂♂, 1♀); Faldas Iliniza (EPN 1♂); Faldas Occidentales del Pichincha (EPN 1♂); Inga Pirca (EPN 1♀); Laderas Iliniza (EPN 1♂); Mt. Pichincha, San Ignacio (AMNH 6♂♂, 6♀♀); Páramos of Chimborazo or Pichincha (type; BMNH juvenile); Pichán (Pichincha) (EPN 1♂); Pichincha (EPN 1♂); Quebrada de Pichán (EPN 1♂, 2♀♀); Saloya Occidente (EPN 1♂); Tablahuasi occidente (EPN 1♀); Verdecocha (AMNH 1♂, 2♀♀); Volcán Pichincha (EPN 3♂♂, 2♀♀, 1 unknown), 3,300 m (FMNH 1♂), 3,600 m (FMNH 1♂), 3,800 m (FMNH 1♂, 1♀), 4,000 m (FMNH 1♂), 4,200 m (FMNH 1♂), 4,300 m (FMNH 1♂, 2♀♀); Volcán Pichincha, oriente, 3,700 m (FMNH 1♂), Volcán Pichincha? (EPN

1 unknown). Venezuela: Táchira; Páramo de Tamá, [3,330 m] (FMNH 1♀); San Cristobal, 41 km SW, near Páramo de Tamá (USNM 2♂♂).

Lestoros inca.—Peru: Cuzco; Limacpunco, 2,400 m (FMNH 6♂♂, 4♀♀); Machu Picchu, 12,000 feet (FMNH 1♂).

Rhyncholestes raphanurus.—Chile: Los Lagos; Chiloé Island, Río Inio (type; FMNH 1♀, 1♂); Contao, 19.7 km N Río Negro and 26.7 km S Contao, 200 m (FMNH 1♀); Maicolpue, 2 km S Bahía Mansa, 110 m (FMNH 1♀); Osorno, 32 km SSE and Puerto Octay, 15 km NNW, 140 m (FMNH 1♀); Parque Nacional Puyehue, 94 km NW Antillanca and 74 km SE Aguas Calientes, 700 m (FMNH 1♀); Parque Nacional Puyehue, Centro de Ski Antillanca, 9.4 km W Los Malines (FMNH 1♀); Río Negro, 11.1 km WNW Río Negro, 200 m (FMNH 1♀); Río Negro, 12.4 km WNW, 150 m (FMNH 1♂, 1♀); Valle de La Picada, 425 m (FMNH 2♂♂, 2♀♀), 505 m (FMNH 3♂♂, 1♀), 715 m (FMNH 1♂); Valle de La Picada, 84 km SE Osorno and 32 km ESE Puerto Octay, 450 m (FMNH 1♂); Valle de La Picada, La Picada Alto, 595 m (FMNH 1♂), 600 m (FMNH 2♀♀); Valle de La Picada, Refugio, 820 m (FMNH 1♂).