Marshall (1980) questioned the differentiation of *Lestoros* from *Caenolestes*.

KEY TO THE LIVING GENERA AND SPECIES OF CAENOLESTIDAE (ADAPTED FROM ALBUJA AND PATTERSON 1996):

1. Incisors 2–4 distinctly and subequally bifid along occlusal edge; upper canine separated from I4 and from first premolar by a gap large enough to accommodate M3; i1 projects beyond alveolus a distance equal to or greater than length of m1–m3; distance from anterior end of nasals to premaxilla–maxillary suture more than 2/3 length of nasals; palatal fenestrae confluent (lack a median bony septum); palatal bridge separating incisive foramina and palatal fenestrae relatively broad, greater than length of M3–M4 . . . . *Rhyncholestes raphanurus*

1′. Incisors 2–4 entire, not distinctly bifid; canine nearly touching I4; i1 less projecting; distance from anterior end of nasals to premaxilla–maxillary suture about 1/2 length of nasals; a usually complete, medial bony septum separates palatal fenestrae; palatal bridge separating incisive foramina and palatal fenestrae narrow, equal to or less than length of M3–M4 2

2. Distance of I4 from canine (and from I3) about equal to alveolar length of I4; canine short, double-rooted, equal to or shorter than I1; P1 minute, less than half the size of P2 . . . . . *Lestoros inca*

2′. I4 tucked closely between I3 and canine; canine large, conical, single-rooted, and exceeds length of I1; P1 nearly equal in size to P2 3

3. Antorbital vacuity (at margin of expanded nasal and maxillary) in the shape of a parenthesis or crescent, or vacuity completely roofed by bone . . . . . *Caenolestes convelatus*

3′. Antorbital vacuity comma-shaped and bounded by nasal, maxillary, and frontal bones 4

4. Size smaller; skull delicate; pelage silky-textured with faint counter-shading; canines short, cranium rests on bullae and incisors (except in some adult males) . . . . . *Caenolestes fuliginosus*

4′. Size usually larger; skull robust; pelage coarse and distinctly counter-shaded; canines longer, cranium rests on bullae and canines (occasionally on labial cusps of M1 or M2) 5

5. Head-and-body length 115 mm; tail 120 mm; condylobasal length 33 mm; 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 1/2 condylobasal length; palatal bridge curved . . . . . *Caenolestes caniventer*

5′. Head-and-body length 135 mm; tail 125 mm; condylobasal length 39 mm; coloration of ventral pelage is drab with an inconspicuous pectoral spot; uppers canines larger and long (3.5 mm); nasal length more than 1/2 of condylobasal length; palatal bridge square . . . . . *Caenolestes condorensis*

Genus *Caenolestes* O. Thomas, 1895

Robert M. Timm and Bruce D. Patterson

Caenolestes contains living caenolestids that have conical, single-rooted incisors in both sexes, I4 mostly filling the space between I3 and canine, P1 and P2 are subequal in size, and the infraorbital foramen opens anteriorly, not laterally (Albuja and Patterson 1996). We recognize four species of *Caenolestes*: *C. caniventer* H. E. Anthony, 1921a, known from the western Andes in southern Ecuador and northern Peru; *C. condorensis* Albuja and Patterson, 1996, from the Cordillera del Cóndor on the Ecuadorian and Peruvian border; *C. convelatus* H. E. Anthony, 1924b, known from the western Andes in Colombia and northern Ecuador; and *C. fuliginosus* (Tomes, 1863a), known mainly from higher elevations in Ecuador, Colombia, and Venezuela. Other authors (e.g., Marshall 1980; Honacki, Kinman, and Koeppl 1982; Nowak and Paradiso 1983) recognized *C. obscurus* O. Thomas, 1895c and *C. tatei* H. E. Anthony, 1923b, as distinct species, but herein we treat these names as synonyms of *C. fuliginosus*. In a revision of the family, Bublitz (1987) treated *Lestoros inca* and *L. gracilis* of southern Peru as members of the genus *Caenolestes*; however, we regard these caenolestids as members of the distinct genus *Lestoros* Oehser, 1934 as do Myers and Patton (this volume).

The four species of *Caenolestes* can be differentiated into two groups that are well defined morphologically and ecologically. Members of the first group (*C. caniventer*, *C. condorensis*, and *C. convelatus*) are large and robust, have coarse pelage that has pronounced counter-shading, and inhabit mid-elevation subtropical forests. The single member of the second group (*C. fuliginosus*) is smaller and has a more slender build; has darker, glossier pelage with reduced counter-shading; and tends to inhabit higher-elevation temperate-zone forests and paramos. The only localities at which two species of *Caenolestes* have been reported (i.e., Mazán, Molleturo, Las Máquinas-Pichincha, and Caicedo; all in Ecuador) lie in subtropical-temperate ecotones and constitute elevational replacements of members of the large-bodied group by the small-bodied *C. fuliginosus* (*caniventer–fuliginosus* at the first two localities and *convelatus–fuliginosus* at the last two). H. E. Anthony (1924b) suggested that the two groups might eventually be distinguished as subgenera.

The anatomy of *Caenolestes* has been considered at length in attempts to interpret its peculiar combination of

polyprotodont (upper dentition) and diprotodont (lower dentition) characters. Accounts include those of O. Thomas (1896a) and subsequent redescriptions of generic characters by Dederer (1909), Broom (1911), Lönnberg (1921), Osgood (1921), Gregory (1922), and Boas (1933). Hayman et al. (1971) and Hayman and Martin (1974) described and analyzed the karyotype of *Caenolestes*, which is considered a primitive $2n = 14$ complement (see also Hayman 1990). Richardson, Bowden, and Myers (1987) and Turner-Erfort (1994) studied the cardiogastric gland and alimentary tract, and Herrick (1921) and Obenchain (1925) described the brain morphology of *C. fuliginosus* in detail. Rodger (1982) described the testes and excurrent ducts of *Caenolestes*; Temple-Smith (1987) reported on sperm morphology and pairing. Szalay (1982) offered a preliminary appraisal of tarsal morphology in the genus.

Little is known of the ecology and behavior of caenolestids. Kirsch and Waller (1979:390) found that, despite marked differences in habitat structure, microhabitats preferred by *C. fuliginosus* and *C. convelatus* were quite similar, being cool, moist, and often moss-covered (see also Osgood 1921; Bublitz 1983). The diets of *Caenolestes* have been reported on by Osgood (1921), Kirsch and Waller (1979), and Barkley and Whitaker (1984), who found them to include a wide array of arthropods as well as some fruit and smaller vertebrates. Known parasites include fleas (Smit 1953; R. E. Lewis 1974), chiggers (Brennan and Reed 1975; Brennan and Goff 1978; Goff and Timm 1985), and chewing lice (Timm and Price 1985). Hershkovitz (1972) described ecological associations and anatomical convergences between *Caenolestes* and species of sigmodontine mice (*Thomasomys* and "*Abrothrix*" [= *Akodon*]).

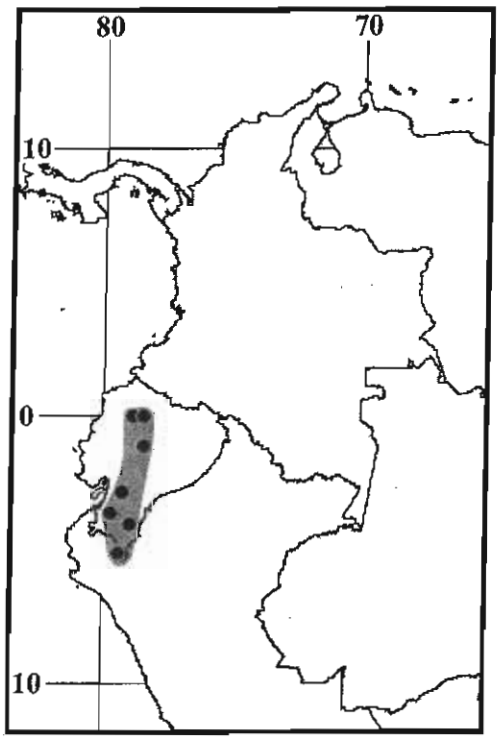
One of the English vernacular names, "shrew-opossums," suggests that caenolestids are shrew equivalents (ecomorphs), and they are found along the same runways as shrews. Competition between caenolestids and *Cryptotis* is undocumented, although both feed on inverterbrates. All species of *Caenolestes* are significantly larger than any species of South American *Cryptotis*; because *Caenolestes* appears to be predaceous, it is possible that they prey upon shrews. Caenolestids are sometimes called "rat opossums," in apparent reference to their rat-like appearance and ability to run quickly.

SYNONYMS:

Hyracodon Tomes, 1863a:50; type species *Hyracodon fuliginosus* Tomes, 1863a, by monotypy; preoccupied by *Hyracodon* Leidy, 1856 (Mammalia: Perissodactyla).

Caenolestes O. Thomas, 1895c:367; replacement name for *Hyracodon* Tomes.

Coenolestes O. Thomas, 1917a:3; incorrect subsequent spelling of *Caenolestes* O. Thomas.



Map 54 Marginal localities for *Caenolestes caniventer* •

Caenolestes caniventer H. E. Anthony, 1921

Gray-bellied Caenolestid

SYNONYMS:

Caenolestes caniventer H. E. Anthony, 1921a:6; type locality "El Chiral, Western Andes; altitude 5350 ft.; Prov. del Oro, Ecuador."

Caenolestes fuliginosus: Barkley and Whitaker, 1984:328; not *Caenolestes fuliginosus* Tomes.

DISTRIBUTION: *Caenolestes caniventer* is recorded from subtropical forests in western Ecuador where it is known from the provinces of Azuay, El Oro, and Pichincha, and in northwestern Peru from the department of Piura.

MARGINAL LOCALITIES (Map 54, localities listed from north to south): ECUADOR: Pichincha, San Antonio (B. E. Brown 2004); Pichincha, Río Saloya, near Mt. Cayambe (Barnett 1991); Tungurahua, San Antonio (B. E. Brown 2004); Azuay, Mazán (Bublitz 1987); El Oro, El Chiral (type locality of *C. caniventer* H. E. Anthony); Zamora-Chinchipe, Zamora (B. E. Brown 2004). PERU: Piura, Cerro Chinguela (Barkley and Whitaker 1984, as *C. fuliginosus*, not mapped); Piura, Km 30, on road from Huancabamba to San Ignacio (Albuja and Patterson 1996).

SUBSPECIES: We treat *C. caniventer* as monotypic.

NATURAL HISTORY: Barkley and Whitaker (1984) reported finding the Gray-bellied Caenolestid using small tunnels and cavities under tree roots along small streams in wet

grasslands, and in patches of humid subtropical and temperate forest at 2,900 m. Barkley and Whitaker (1984) considered "*C. fuliginosus*" (= *C. caniventer*) to be an opportunistic feeder; lepidopteran larvae, centipedes, and arachnids composed over 75% of the food items in stomach contents. Other food items they found included fruit, a bird, and a wide variety of other insects and invertebrates.

Caenolestes condorensis Albuja and Patterson, 1996
Andean Caenolestid

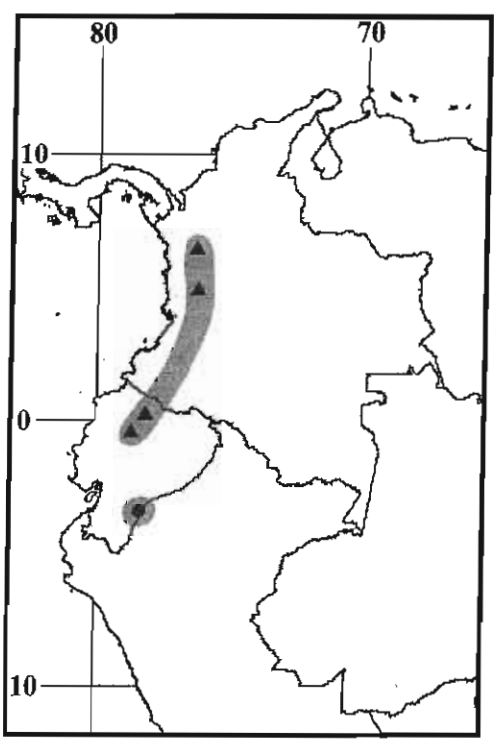
SYNONYM:

Caenolestes condorensis Albuja and Patterson, 1996:42; type locality "'Achupallas'... [a] camp on the upper plateau of the Cordillera del Cóndor, in the Provincia de Morona-Santiago, Ecuador, coordinates 3°27′03″S, 78°29′39″W, elevation 2,080 m."

DISTRIBUTION: *Caenolestes condorensis* is known from only the type locality, which is in the Cordillera del Cóndor on the eastern versant of the Andes along the border between Ecuador and Peru.

MARGINAL LOCALITY (Map 55): ECUADOR: Morona-Santiago, "Achupallas," (type locality of *Caenolestes condorensis* Albuja and Patterson).

SUBSPECIES: *Caenolestes condorensis* is known from only the type series of three specimens.



Map 55 Marginal localities for *Caenolestes condorensis* ● and *Caenolestes convelatus* ▲

NATURAL HISTORY: The Condor Caenolestid is the largest known extant caenolestid. Adult males can attain a mass of 48 g, and a condylobasal length of at least 36 mm. The type series was taken atop a broad plateau composed of Cretaceous ash. The heath-like vegetation of the cold, humid plateau resembles that of the Venezuelan tepuis and is dominated by spiny bromeliads ("achupallas"). *Caenolestes condorensis* was captured on the ground in live traps baited with a mixture of peanut butter and oatmeal. The trapping site was at the juncture between the plateau and the surrounding forested slopes where vegetation included species of *Schefflera* (Araliaceae), *Anthurium* (Araceae), *Ugni* (Myrtaceae), *Spheradenia* (Cyclantaceae), *Clusia* (Clusiaceae), *Leandra* and *Miconia* (Melastomaceae), *Lycopodium* (Lycopodiaceae), *Bennetia* (Theaceae), *Phoradendrom* (Loranthaceae), *Gusmania* and *Tillandsia* (Bromeliaceae), *Chusquea* (Gramineae), *Piper* (Piperaceae), *Monnina* (Polygalaceae), and *Geonoma* (Palmae). Other mammals also acquired at this site include *Artibeus glauca*, *Enchisthenes hartii*, *Sturnira bidens*, *S. erythromos*, *S. oporaphilum*, *Platyrrhinus infuscus*, *P. umbratus*, *Akodon aerosus*, *Oryzomys albigularis*, and *Oryzomys* sp. (Albuja and Patterson 1994).

REMARKS: Although relationships among caenolestids remain uncertain, *C. condorensis* appears to be the only large, coarse-furred caenolestid distributed in lower-elevation forests on the eastern slope of the Andes. Both *C. caniventer* and *C. convelatus* occur on the western slopes and inter-Andean valleys.

Caenolestes convelatus H. E. Anthony, 1924
Northern Caenolestid

SYNONYMS: See under subspecies.

DISTRIBUTION: *Caenolestes convelatus* is known from the western slopes of the Andes in northwestern Ecuador and in northwestern Colombia.

MARGINAL LOCALITIES (Map 55, localities listed from north to south): COLOMBIA: Antioquia, Santa Bárbara (type locality of *Caenolestes convelatus barbarensis* Bublitz); Valle del Cauca, Alto de Galápagos (Albuja and Patterson 1996). ECUADOR: Imbabura, Hacienda La Vega (Albuja and Patterson 1996); Pichincha, 11 km W of Aloag (Kirsch and Waller 1979).

SUBSPECIES: Bublitz (1987) recognized two subspecies based on differences in overall size, especially of the skull, which is larger in *C. c. barbarensis*.

C. c. barbarensis Bublitz, 1987

SYNONYM:

Caenolestes convelatus barbarensis Bublitz, 1987:77; type locality "Santa Barbara (6° 23′0″N, 76° 7′30″W) in [Antioquia] Kolumbien, 3100 m."

This subspecies is in western Colombia.

C. c. convelatus H. E. Anthony, 1924

SYNONYMS:

Caenolestes obscurus: Lönnberg, 1921:4; not *Caenolestes obscurus* O. Thomas, 1895.

Caenolestes convelatus H. E. Anthony, 1924b:1; type locality "Las Maquinas, Western Andes, 7000 feet altitude, on trail from Aloag to Santo Domingo de los Colorados [Pichincha], Ecuador."

Caenolestes convelatus convelatus: Bublitz, 1987:76; name combination.

The nominate subspecies is in northwestern Ecuador.

NATURAL HISTORY: H. E. Anthony (1924b) noted that the holotype was taken in a region of heavy subtropical forest and at an elevation comparable to that inhabited by *C. caniventer*, but lower than elevations where *C. fuliginosus* has been found. R. M. Timm caught an adult male at Hacienda La Vega in thick vegetation along a small stream in pasturelands, using sardine juice as bait. The testes measured 9 × 7 mm, suggesting reproductive activity in September, when the specimen was captured. Two species of ectoparasites were named and described from this specimen: a chewing louse, *Cummingsia perezi* (Timm and Price, 1985) and a chigger, *Peltoculus ecuadorensis* (Goff and Timm, 1985). Kirsch and Waller (1979) captured an adult male (testes = 6 mm) in dense brush along a stream. They reported that a captive *C. convelatus* used its forepaws to direct worms into the side of the mouth where they were sheared into manageable pieces by the cheek teeth.

Caenolestes fuliginosus (Tomes, 1863)

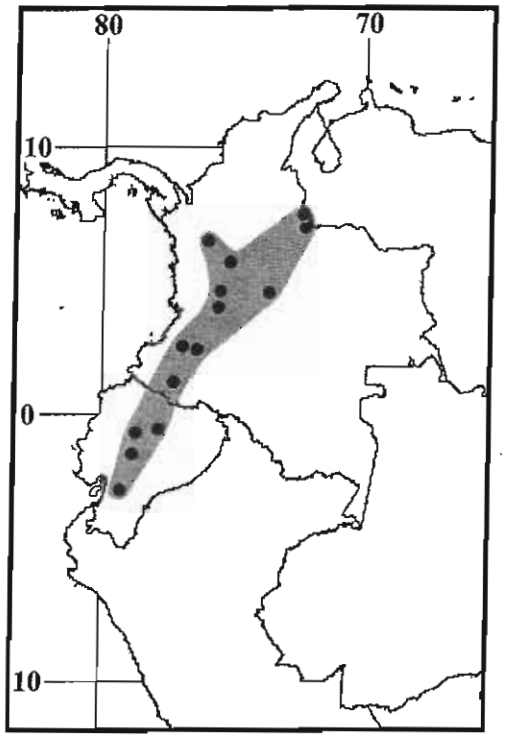
Dusky Caenolestid

SYNONYMS: See under Subspecies.

DISTRIBUTION: *Caenolestes fuliginosus* is in the Andes of Colombia, Ecuador, and northwestern Venezuela.

MARGINAL LOCALITIES (Map 56; from Albuja and Patterson 1996, except as noted): VENEZUELA: Táchira, 41 km SW of San Cristóbal. COLOMBIA: Boyacá, Hacienda La Primavera; Cundinamarca, La Reserva Biológica Carpanta (López-Arevalo, Montenegro-Díaz, and Cadena 1993); Cauca, Páramo de Puracé, 1 km E of Laguna San Raphael (Kirsch and Waller 1979); Nariño, Pasto. ECUADOR: Napo, Cosanga; Azuay; Mazán (Bublitz 1987); Chimborazo, Mt. Chimborazo; Pichincha, Cerro Iliniza. COLOMBIA: Cauca, Munchique (B. E. Brown 2004); Valle del Cauca, Páramo de Barragán; Quindío, Finca Rincón Santo; Antioquia, Páramo de Sonsón, 7 km E of Sonsón; Antioquia, Páramo Frontino.

SUBSPECIES: We follow Bublitz (1987) and treat *C. fuliginosus* as comprising three subspecies.



Map 56 Marginal localities for *Caenolestes fuliginosus* •

C. f. centralis Bublitz, 1987

SYNONYM:

Caenolestes fuliginosus centralis Bublitz, 1987:74; type locality "Rio Termales (4° 56′N, 75° 19′W) in [Caldas] Kolumbien, 2700 m."

This subspecies occurs throughout most of Andean Colombia and in extreme western Venezuela.

C. f. fuliginosus (Tomes, 1863)

SYNONYMS:

Hyracodon fuliginosus Tomes, 1863a:51; type locality "Ecuador" (see Remarks).

Caenolestes fuliginosus: O. Thomas, 1895c:367; name combination.

Caenolestes tatei H. E. Anthony, 1923b:1; type locality "Molleturo, Provincia del Azuay, 7600 feet, Western Andes," Ecuador.

Caenolestes fuliginosus fuliginosus: Bublitz, 1987:72; first use of current name combination.

The nominate subspecies occurs in the high mountains of central Ecuador north to the Colombian border.

C. f. obscurus O. Thomas, 1895

SYNONYMS:

Caenolestes obscurus O. Thomas, 1895c:367; type locality "Bogota," Cundinamarca, Colombia.

Caenolestes fuliginosus obscurus: Bublitz, 1978:73; first use of current name combination.

This subspecies apparently is restricted to the vicinity of Bogotá, Colombia.

NATURAL HISTORY: *Caenolestes fuliginosus* has been found in tall forest with a closed canopy and little undergrowth, in dense undergrowth in scrub forest (Kirsch and Waller 1979), and in vegetated pasture within a few feet of a swiftly flowing stream (Stone 1914). At the northern end of its distribution, the species inhabits cloud forest (Handley 1976), while at its southern limits, *C. fuliginosus* has been taken from the densely forested western slope of the Ecuadorian Andes in a region that receives heavy rainfall (H. E. Anthony 1923b). The species has been documented over an elevational range from 2,150 m in Boyacá, Colombia (FMNH 92299) to 4,300 m on Volcán Pichincha, Ecuador (FMNH 53295).

What little is known concerning the ecology and behavior of *C. fuliginosus* is mainly derived from Kirsch and Waller's (1979) description of vocalizations, locomotion, mastication, and predatory behavior. Kirsch and Waller (1979) reported four lactating females (none with attached young) and one with an enlarged uterus when taken in late August in departamento Cauca, Colombia. They found *C. fuliginosus* at Finca El Soché along with *Cryptotis* and at least five species of rodents. Bublitz (1983) reported *Cryptotis equatoris*, *Reithrodontomys mexicanus*, *Thomasomys laniger*, and *T. paramorum* as associated with *C. fuliginosus* at four localities near Quito, Ecuador. Smit (1953) named and described the flea *Cleopsylla monticola* from Ecuadorian material; Brennan and Goff (1978) described a new chigger, *Crotiscus danae*, from a Venezuelan specimen; and Timm and Price (1985) described a new chewing louse, *Cummingsia albujai*, also from Ecuadorian *C. fuliginosus*.

REMARKS: Tomes's (1860b, 1863a) descriptions of *C. fuliginosus* were inadequate for differentiating this species from other small South American marsupials, and accounts for the early lack of interest that *C. fuliginosus* later excited in mammalogists (see O. Thomas 1896a). The holotype is "A young specimen preserved in spirit" (O. Thomas 1920d:246); its catalog number (BM 7.1.1.191) indicates that it was among the collection of Tomes's types found in rooms of the Zoological Society of London (O. Thomas 1898a; Gardner 1983). Tomes (1863a) gave "Ecuador" as the type locality of *H. fuliginosus*, but earlier he (1860b:211) had written "The greater portion of these [specimens] are thought to have been collected [by Fraser] at Pallatanga, on the western slope of the Cordillera; but the exact locality is not certain, from the specimens having been unfortunately mixed together." Stone (1914:18) suggested that Fraser acquired the type "on Mt. Pichincha" and Osgood (1921:17) thought that it may have come "from the paramos of Mt. Chimborazo or Mt. Pichincha where Fraser also worked." Any of these localities is plausible, and additional information, such as date of collection or Fraser's field number, will be necessary for determining a more specific type locality.

Oldfield Thomas described *Caenolestes obscurus* based on the second known specimen of the genus, obtained near Bogotá, Colombia. The status of *C. obscurus* as a distinct species has long been in doubt. In the original description, O. Thomas (1895c) stated that *C. obscurus* was otherwise similar to, but "double the size" of, *C. fuliginosus*. O. Thomas had seen the holotype of *C. fuliginosus* and relied on Tomes's (1863a) published measurements. Stone (1914) compared external measurements of Ecuadorian and Colombian specimens of *Caenolestes* (specimens from Pichincha and Páramo de Tamá), found them to be "practically identical," and concluded "it looks very much as if *C. obscurus* O. Thomas might become a synonym of *C. fuliginosus* (Tomes)." Bublitz (1987) treated these same populations as conspecific under the names *C. f. fuliginosus* and *C. f. obscurus*. He distinguished these forms mainly through craniometric assessments. The nominate subspecies is the smallest and most gracile, and males have relatively small canines; whereas *C. f. obscurus* is the largest, and males have dagger-like canines; *C. f. centralis* is intermediate. H. E. Anthony (1924b) distinguished *C. tatei* from other *Caenolestes* by its smaller size and darker color, but Bublitz (1987) treated *C. tatei* as a junior synonym of *C. f. fuliginosus*.

Genus *Lestoros* Oehser, 1934

Philip Myers and James L. Patton

Members of the monotypic genus *Lestoros* are small, superficially shrew-like marsupials (head and body length 90–120 mm, tail 105–135 mm, mass 20–35 g), known from only southern Peru and adjacent Bolivia. Pelage color is uniformly slate gray-black or brown above and below; the fur is of medium length, thick, and lax. The pinnae are of moderate length and rounded, without an obvious tragus; the eye is very small but clearly visible. The tail is elongate, unicolored, not incrassate, about equal in length to the head and body, has visible annular scale rows arranged perpendicular to the long axis, and is thinly haired with each hair about the length of two scales. The hind feet are elongated with digits II–V long and with well-developed claws; the hallux is short and non-opposable. The forefeet have five digits, the pollex is non-opposable and about equal in length to digit V, claws are present only on digits II–IV, and nails are present on digits I and V. Vibrissae are present on the chin, sides of the nose, and on the forelimbs at the wrist.

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