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# Tonatia evotis and Tonatia silvicola.

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## *Tonatia* Gray, 1827

*Vampyrus* Spix, 1823:65. Type species *Vampyrus bidens* Spix.
*Tonatia* Gray, 1827:71. Type species *Vampyrus bidens* Spix.
*Lophostoma* D'Orbigny, 1836:11. Type species *Lophostoma silvicolum* D'Orbigny.
*Phyllostoma* Gray, 1838:488. Type species *Phyllostoma childreni* (=*Vampyrus bidens* Spix).
*Tylostoma* Gervais, 1855:49. Type species *Tylostoma bidens* Gervais.
*Chrotopterus* Allen, 1910:147. Type species *Chrotopterus carrikeri.*

**CONTEXT AND CONTENT.** Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Phyllostominae. The genus *Tonatia* contains six living species (Davis and Carter, 1978; Koopman, 1978). A key to the species, modified from Genoways and Williams, 1984, follows (measurements in mm):

1 Forearm less than 40; greatest length of skull less than 22 ..... *T. brasiliensis*
Forearm more than 40; greatest length of skull more than 22 ..... 2
2 (1) Forearm less than 45; greatest length of skull less than 24. Wart-like granulations on limbs, ears and noseleaf ..... *T. schulzi*
Forearm more than 45; greatest length of skull more than 24. Limbs, ears and noseleaf without wart-like granulations ..... 3
3 (2) Size large, forearm more than 55. Ears less than 32. Postorbital constriction more than 5. Faint pale stripe on top of head ..... *T. bidens*
Size variable, if forearm more than 50, then ears more than 32. Postorbital constriction less than 5. No pale stripe on top of head ..... 4
4 (3) Underparts pure white except chin and sides of venter. Present only in South America ..... *T. carrikeri*
Underparts dusky to pale. If there is any white, it is only a small gular patch. From southern Mexico to northern Argentina ..... 5
5 (4) Maxillary toothrow 9.5 or more; pale patches at bases of ears. Underparts paler, frequently with a white gular patch ..... *T. silvicola*
Maxillary toothrow 9.2 or less. No pale patches at bases of ears. Underparts dusky, contrasting only slightly with dorsum ..... *T. evotis*

## *Tonatia evotis* Davis and Carter, 1978

### Davis' Round-eared Bat

*Tonatia evotis* Davis and Carter 1978:8. Type locality "25 km. SSW Puerto Barrios, 75 m., department of Izabal, Guatemala."

**CONTEXT AND CONTENT.** Context noted in generic summary above. Davis and Carter (1978) erected the species *T. evotis* for the smallest representatives of the *T. silvicola* complex in the northern part of the range. *T. evotis* is a monotypic species (Davis and Carter, 1978).

**DIAGNOSIS.** *Tonatia evotis* (Fig. 1) is a middle-sized phyllostomid, varying in color from pale lead gray or brownish to dusky brown or dark gray. They resemble large *Micronycteris megalotis* (forearm of *T. evotis* >47.2 mm; *M. megalotis* <39 mm) and have four (rather than two) lower incisors. The only other genera within the subfamily Phyllostominae that possess only two lower incisors are *Mimon* and *Chrotopterus.* Species of the genus *Tonatia* can be distinguished from the former by the rounded ears and the presence of a third lower premolar, and from the latter by the much smaller size, and by having the second lower premolar crowded to the labial side, rather than the lingual. *T. evotis* is middle-sized for the genus, but is easily distinguishable from the two other *Tonatia* that occur in its range. *T. brasiliensis* is much smaller, having a forearm at least 5 mm shorter. *T. bidens* is larger, forearm 54.5 to 60.5 mm, and has a whitish stripe on top of the head. From the adjacent populations of *T. silvicola*, *T. evotis* differs in the less massive teeth, shorter toothrow, lack of auricular patches, and overall darker color. Also, *T. silvicola* generally has a larger sagittal crest than *T. evotis* (Davis and Carter, 1978).

**GENERAL CHARACTERS.** The ears of *T. evotis* are round and long. The noseleaf is narrow and short, and as in some other phyllostomids (for example, *Artibeus hartii*) the lower element is fused and indistinguishable from the upper lip. The lower lip has two V-shaped pads, covered with weakly developed granular warts. Color is generally dark gray uniform dorsally and ventrally. Hair of the back is long (about 8 mm), but shorter on the venter. The hair extends to the proximal half of the forearm and femur. The interfemoral membrane is wide and reaches the base of the feet, and the short tail is completely encased in it, reaching its center. The thumb is included in the propatagium, except for its free last phalanx. Calcars are long and robust. The wings are broad and relatively short. Range of external and cranial measurements (in mm) are: total length, 79 to 91; length of tail, 14 to 18; length of ear, 33 to 35; length of forearm, 47.2 to 52.7; greatest length of skull, 24.3 to 26.9; zygomatic breadth, 11.6 to 12.7; breadth of braincase, 9.5 to 10.4; length of maxillary toothrow, 8.4 to 9.0; breadth across M3–M3, 7.5 to 8.2 (Davis and Carter, 1978; Medellín, 1986; Sánchez-H. et al., 1986).

The skull of *T. evotis* (Fig. 2) is elongated and robust, with large cheek teeth and long canines. Two pairs of incisors fill completely the space between the canines, and the internal pair is much larger than the external. Molar lophs show a clear W shape from an occlusal view. The rostrum is narrow and relatively long. The braincase is swollen and extends backwards conspicuously. The low

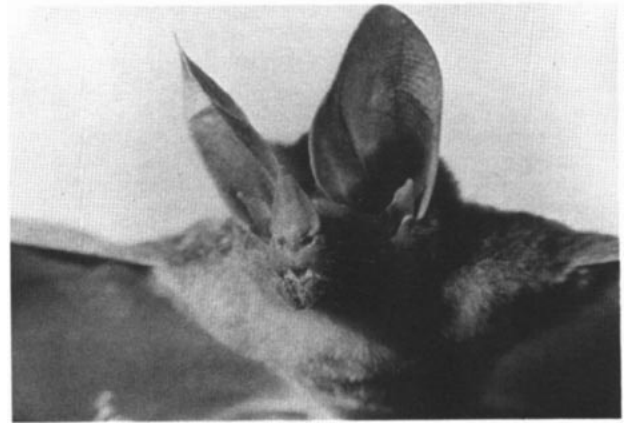

FIG. 1. *Tonatia evotis* from Chajul, Lacantún River, Chiapas, México. Photograph by R. A. Medellín.


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tonatia evotis* (United States National Museum of Natural History 506465) from Columbia Forest, Toledo, Belize. Greatest length of skull is 23.6 mm. Photographs courtesy of D. E. Wilson.

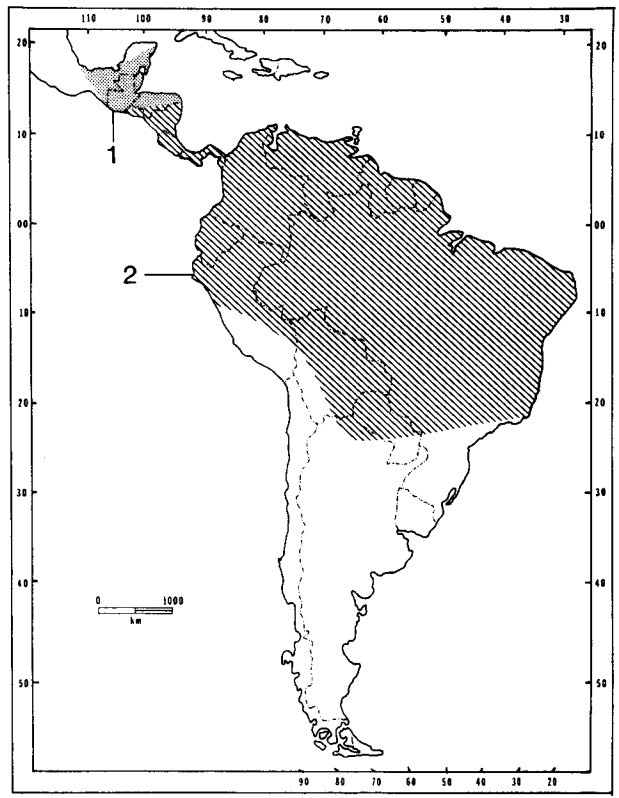


FIG. 3. Distribution of 1) *Tonatia evotis* and 2) *T. silvicola*.

forehead is continued onto the top of the head by a weakly developed sagittal crest. A strong postorbital constriction is present. Body mass of *T. evotis* is near 20 g. Dental formula for all species of *Tonatia* is i 2/1, c 1/1, p 2/3, m 3/3.

**DISTRIBUTION.** *Tonatia evotis* occupies the lowland tropical rain forests of the extreme northern Neotropics (Fig. 3), from central Honduras northward to the moist tropical regions of Chiapas, Tabasco, southern Veracruz, Campeche, and southern Quintana Roo (Davis and Carter, 1978; Medellín, 1986; Sánchez-H. et al., 1986). This species occurs below 100 m in elevation. There are no fossil records.

**ONTOGENY AND REPRODUCTION.** Litter size is one. *T. evotis* probably behaves as a monoestrous species. One female from Chiapas had a small embryo in January (Medellín, 1986), one female from Belize captured in March and two more from Quintana Roo captured in April contained one large fetus each (McCarthy, 1987; Medellín, 1986; Sánchez-H. et al., 1986). This suggests that parturition coincides with the beginning of the rainy season.

**ECOLOGY.** There are no records of predators or endoparasites of this species. *T. evotis* from Quintana Roo were carrying unidentified streblids (Sánchez-H. et al., 1986).

*Tonatia evotis* was captured in Quintana Roo in nets stretched across a path in secondary forest, with trees such as *Lysiloma latisiliqua*, *Bursera simaruba*, *Manilkara zapota*, *Cordia* sp., and *Cecropia obtusifolia* (Sánchez-H. et al., 1986). Other species caught in the same area were *Pteronotus parnellii*, *Carollia perspicillata*, *Artibeus phaeotis*, and *Desmodus rotundus*. In Chiapas, México, *T. evotis* was found inside mature primary tropical rainforest, with 45 additional species of bats (Medellín, 1986). Stomachs of four *T. evotis* collected in Quintana Roo (Sánchez-H. et al., 1986) contained katydids (Orthoptera) and beetles (Coleoptera—J. J. Belwood, pers. comm.).

**BEHAVIOR.** In Quintana Roo, *T. evotis* was inactive during times when moonlight was bright (Sánchez-H. et al., 1986). Bats caught in Quintana Roo and Chiapas (Medellín, 1986; Sánchez-H. et al., 1986) were flying in the understory of secondary and mature forest.

## *Tonatia silvicola* (D'Orbigny, 1836)

### Round-eared Bat

*Lophostoma silvicolum* D'Orbigny, 1836:11. Type locality "... des grandes forêts qui bordent le pied oriental de la Cordillére bolivienne, au pays des sauvages Yuracarés [... large forests bordering the east of the Bolivian mountain range, in the country of the Yuracaré Indians]." Hall (1981) mentions as restricted type localty Yungas de Bolivia between Rio Secure and Rio Isibara.

*Phyllostoma childreni* Gray, 1838:488. Type locality "South America."

*Phyllostoma amblyotis* Wagner, 1843:365. Type locality "Matto Grosso, Brazil."

*Tonatia laephotis* Thomas, 1910:184. Type locality "River Supinaam, tributary of the lower Essequibo [Guyana]."

*Chrotopterus colombianus* Anthony, 1920:84. Type locality "Rio Quatequia, near Bogota, Colombia."

**CONTEXT AND CONTENT.** Context as for *T. evotis*. *T. silvicola* contains four subspecies (Davis and Carter, 1978), as follows:

*T. s. centralis* Davis and Carter, 1978:7, type from "El Castillo, 40 m., department of Río San Juan, Nicaragua."

*T. s. laephotis* Thomas, 1910:184, see above.

*T. s. occidentalis* Davis and Carter, 1978:6. Type from "4 mi. W Suyo, 1000 ft., department of Piura, Perú."

*T. s. silvicola* (D'Orbigny, 1836:11), see above.

**DIAGNOSIS.** *Tonatia silvicola* are middle-sized leaf-nosed bats. The color varies from deep gray to dusky reddish brown or blackish. They can be separated from other genera of sympatric phyllostomids by the characters discussed in the account of *T. evotis*. *T. silvicola* is a large representative of the genus. Diagnostic characters separating *T. silvicola* from *T. evotis* were given above. In many areas of South America, particularly in Suriname, *T. silvicola* is the largest species of the genus, being slightly larger than *T. bidens*, that has a faint whitish stripe on top of the head, shorter ears, with a small and simple tragus, and the ears not connected by a band. *T. silvicola* has longer ears, a long tragus with three tooth-like projections near the base of outer border, and a small connecting band between the ears that meets in the middle of forehead (Genoways and Williams, 1984). *T. silvicola* can be separated from the remaining three species in the genus (*T. brasiliensis*, *T. carrikeri*, and *T. schulzi*) by its larger size (forearm of the three smaller ranges from 33.3 to 48.4 mm; forearm of *T. silvicola* ranges from 50.0 to 59.3 mm), and longer, indented tragus (Genoways and Williams, 1984).

**GENERAL CHARACTERS.** *Tonatia silvicola* has round, long ears, wide wings, and a short tail, completely included in the uropatagium. The noseleaf is short but well developed, and as in a few other phyllostomids, the base if fused and indistinguishable from the upper lip. The V-shaped lower lip pads, shared with several other genera of phyllostomines (for example, *Macrotus* and *Micronycteris*), are covered with weakly developed granular warts. Hair color varies geographically from pale gray or brown to dark blackish tones. Hair on the back is long (about 8 mm) and dense. A large proportion of *T. silvicola* (82 of 103) from the northern half of the range have a white patch, that usually extends from the throat to the chest, but sometimes reaches the genital area. There is a large interfemoral membrane, the tail barely reaching its center. The proximal 50% of the forearm is hairy on both surfaces. Only the last phalanx of the thumb is free, the rest included in the propatagial membrane. Selected measurements of *T. silvicola* (in mm) are: length of forearm, 50.0 to 59.3; greatest length of skull, 26.4 to 30.4; condylobasal length, 22.2 to 24.8; zygomatic breadth, 12.7 to 14.7; postorbital constriction, 3.8 to 4.4; breadth of braincase, 10.1 to 11.2; length of maxillary toothrow, 8.9 to 10.4; breadth across upper molars, 8.1 to 9.6 (Genoways and Williams, 1984; Swanepoel and Genoways, 1977).

The skull of *T. silvicola* (Fig. 4) is strongly built, with massive cheek teeth and long canines. The internal upper incisors are at least three times as long as the external pair, and leave no space between the canines. The W-shaped lophs are evident when observing the large molars. The braincase is inflated and elongated, with a distinct projection of the lambdoid region backward. A strong sagittal crest starts in the low forehead. A conspicuous postorbital constriction is evident (Davis and Carter, 1978), even more apparent when comparing a skull of this species with one of *T. bidens*. Mass of *T. silvicola* ranges from 21 to 38 g. Statistically significant sexual dimorphism has been detected for *T. silvicola* in Suriname (Genoways and Williams, 1984) and in Brazil (Willig, 1983); males are larger than females in several measurements (in mm; means for males and females reported by Genoways and Williams (1984), followed by means for males and females reported by Willig (1983): greatest length of skull (28.9, 28.2; 27.8, 27.3); condylobasal length (23.8, 23.1; 24.3, 23.8); zygomatic breadth (14.0, 13.5; 13.7, 13.5); mastoidal breadth (14.1, 13.7; 13.5, 13.3). Brazilian males are heavier (33.9 versus 31.8 g) and have longer ears (29.6 versus 28.8 mm) than females (Willig, 1983).

**DISTRIBUTION.** *Tonatia silvicola* has a wide tropical distribution (Fig. 3), inhabiting zones of varied vegetation, from rainforest to drier areas, from Nicaragua to southern Brazil, Bolivia, and Paraguay in tropical South America to the eastern slope of the Andes, and one subspecies inhabits southwestern Ecuador and northwestern Perú. Altitudinally, the species has been recorded from sea level to at least 1,500 m (Davis and Carter, 1978; Genoways and Williams, 1984; Graham, 1983; Myers and Wetzel, 1979; Tuttle, 1970). No fossil records are known for *T. silvicola*.

**FORM AND FUNCTION.** *Tonatia silvicola* has the lowest wing aspect ratio among the phyllostomines (Smith and Starret, 1979), with remarkably short and broad wings. The metabolic rate of *T. silvicola* (around 2 cc $O_2/g^{-1}$ $h^{-1}$) is similar to that of other tropical insectivorous bats, but slightly lower than the closely related


FIG. 4. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tonatia silvicola* (USNM 361510) from Belem, Pará, Brazil. Greatest length of skull is 28.9 mm. Photographs courtesy of D. E. Wilson.

*T. bidens* (McNab, 1969). Temperature of *T. silvicola* dropped lower (from 38 to 31°C) than that of *T. bidens* when the environmental temperature was lowered (McNab, 1969).

Males of *T. silvicola* have an unusual endoplasmic reticulum in the submandibular salivary gland, unique among phyllostomids (Nagato et al., 1984). This suggests that the submandibular salivary gland, with the peculiar structure, probably produces a secretion involved with chemobehavioral recognition between males and females (Nagato et al., 1984), and that it also may act as a secondary isolating mechanism from the related *T. bidens* (Phillips and Tandler, 1987).

Sonograms of the echolocation calls of *T. silvicola* and of five other gleaning phyllostomines, showed a high degree of similarity among the calls (Belwood, 1989). Calls are <2 msec long, low amplitude and high frequency, and are accordingly, typical of a "high resolution, clutter-rejection pursuit strategy" (Simmons et al., 1979:19).

**ONTOGENY AND REPRODUCTION.** Litter size is one. *T. silvicola* probably follows a pattern that is at least diestrous; data from Fleming et al. (1972) and Bonaccorso (1979) showed at least two birth peaks, one near January and the other around July. Bonaccorso (1979) found evidence of postpartum estrus. Probably similar patterns are followed wherever forest seasonality allows continuous exploitation of resources. From Panama and northern South America, pregnant females have been reported during January, March, April, June and August, and lactating females from March, May and September (Bonaccorso, 1979; Fleming et al., 1972; Genoways and Williams, 1984; Thomas, 1972); specimens at the

U.S. National Museum include lactating females and juveniles from September and October. One lactating female was reported from Paraguay, in March (Myers and Wetzel, 1979). In the eastern lowlands of Perú, *T. silvicola* breeds both in the dry and the wet season, and pregnant females have been found from July through October, while juveniles have been observed in March, July, October and November (Graham, 1987).

**ECOLOGY.** The only published record of predation on *T. silvicola*, is that of man. The Nambiquara Indians of western Brazil hunted *T. silvicola* that were hanging from a branch close to a termite nest, and ate them (Setz and Sazima, 1987).

No endoparasites are known from this species. *T. silvicola* hosts at least one species of nycteribiid (*Basilia constricta*), and six species of streblids (*Pseudostrebla ribeiroi, Strebla kohlsi, Trichobius dybasi*, all known only from *T. silvicola*, plus *T. joblingi, T. parasiticus*, and *Mastoptera minuta*), and one species of tick (*Ornithodoros hasei*; Webb and Loomis, 1977). The habit of *Tonatia* to roost in hollow termite nests in small family groups may favor high densities in streblid populations, as the bats return to the same roost daily, reducing the risk of separation of host and parasite (Ubelaker, 1970).

*Tonatia silvicola* has been found in association with 41 other species of bats (Genoways and Williams, 1984). Only 30% of 47 adults captured in Brazil were males, showing a statistically significant inequality in sex ration (Willig, 1983).

Roosts of *T. silvicola* have been located inside hollow termite nests in mature forest in Perú (Tuttle, 1970), and in all instances the bats shared the roost with one or two *Phyllostomus hastatus*. Eighteen individuals were caught from inside a hollow tree in Perú (Tuttle, 1970). This species roosts in termite nests in Panama (Handley, 1966), and 29% of the *T. silvicola* from Venezuela were also found in termite nests in trees (Handley, 1976).

*Tonatia silvicola* is included in the "gleaning carnivore guild" that includes animalivorous bats that pluck prey off substrates (Bonaccorso, 1979). Bats of this species in Panama frequently fly through the groundstory level of the forest, while the related *T. bidens* flies in the subcanopy–canopy level, thus exploiting different vertical spaces. *T. silvicola* is common inside the forest, and is absent over creeks, being most active in the first 2 h after sunset (Bonaccorso, 1979).

*Tonatia silvicola* feeds on fruit and insects (Gardner, 1977). The stomachs of two bats from Costa Rica contained only plant remains (legume pollen and Apocynaceae [*Stemmadenia*]—Howell and Burch, 1974). Eleven bats from Panama had stomachs containing insects (Fleming et al., 1972), and fecal samples from Panama had remains of insects and whipscorpions (Arachnida—Bonaccorso, 1979). Orthopterans were found in 83% of fecal samples from Panama, and Coleoptera, Lepidoptera, and seeds accounted for <2% each (Belwood, 1989). Some overlap between diets of *T. silvicola* and *T. bidens* is evident from that study. In 48 fecal pellets of 17 *T. silvicola*, the following items were reported by decreasing relative abundance: Coleoptera, Pedipalpida, Homoptera, Orthoptera, Hemiptera, Diptera, fruit, and Hymenoptera (Humphrey et al., 1983). Again the diet greatly overlaps with that of *T. bidens*, the only major difference being that *T. bidens* takes spiders instead of whipscorpions. The proposed explanation involved a resource-partitioning mechanism, such as differential use of forest levels (Humphrey et al., 1983). Fecal pellets from one bat was 95% in volume Coleoptera, probably carabids (Whitaker and Findley, 1980). A *T. silvicola* from Manaus, Brazil, had bones and meat in the stomach (Reis and Peracchi, 1987).

**BEHAVIOR.** Roosting groups of *T. silvicola* range from 6 to 18 individuals (Fenton and Kunz, 1977; Tuttle, 1970). *T. silvicola* locates prey by the noise they produce. Mist nets baited with calling male katydids attracted nine *T. silvicola*, while no gleaning bats, *T. silvicola* or otherwise, were caught in nets baited with silent females (Belwood and Morris, 1987). Acoustical signals were also used in food resource partitioning between *T. silvicola* and a similar phyllostomine, *Trachops cirrhosus* (Tuttle et al., 1985). *T. silvicola* are attracted to insect calls, but not to frog calls; *T. cirrhosus* are attracted to frog calls, not to insect calls. When there are no frog calls both species are attracted to insect calls.

**GENETICS.** The karyotype of *T. silvicola* has a fundamental number of 60, a diploid number of 34, a submetacentric X chromosome, and an acrocentric Y (Honeycutt et al., 1980). The karyotype of *T. bidens* and *T. minuta* shows a large amount of evolutionary change, so that none of the arms of the proposed primitive karyotype are identifiable (Patton and Baker, 1978).

After examining allozymic characters of all but one (*T. evotis*) species of *Tonatia*, Arnold et al. (1983) concluded that *T. silvicola* is most closely related to *T. carrikeri*. An albumin-based phylogenetic tree constructed by Honeycutt and Sarich (1987*a*) yielded a close association between *T. silvicola* and *P. hastatus*, but in a consensus tree based on albumin immunology, chromosomes, and morphology, *Tonatia* joined a previous lineage formed by *Phyllostomus* and *Mimon*.

The condition of monophyly within the genera *Tonatia* and *Phyllostomus* based on albumin immunological distances placed *T. silvicola* in a three-way divergence, together with *T. bidens* and *T. schulzi* or *T. carrikeri*. *T. bidens* was the closest representative of the genus to *Phyllostomus* (Honeycutt and Sarich, 1987*b*).

**REMARKS.** The genus and species have undergone a considerable amount of nomenclatorial changes that have been summarized by Davis and Carter (1978) and Goodwin (1942). Recently more authors (for example, Gardner, 1976; Genoways and Williams, 1984) have agreed to place all the smaller forms of *Tonatia* (that is, *T. brasiliensis, T. minuta, T. nicaraguae*, and *T. venezuelae*) in the same species (*T. brasiliensis*). Additionally, two of the six recognized species were only recently described (*T. evotis* Davis and Carter, 1978, and *T. schulzi* Genoways and Williams, 1980).

The etymology of *Tonatia* is unknown. The specific epithet *evotis* refers to the large ears, and *silvicola* means "jungle dweller." Few authors have adopted the correct spelling of *silvicola*, derived from *Lophostoma silvicolum* D'Orbigny, 1836, but later modified to *sylvicola*, frequently used (incorrectly) in current literature. By Article 32 of the International Code of Zoological Nomenclature, the stem *silvicol-* is the correct spelling (Davis and Carter, 1978).

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