Submission procedures can be found at http://research.amnh.org/scipubs

Complete lists of all issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from:

American Museum of Natural History—Scientific Publications,
Central Park West at 79th St.,
New York, NY 10024.

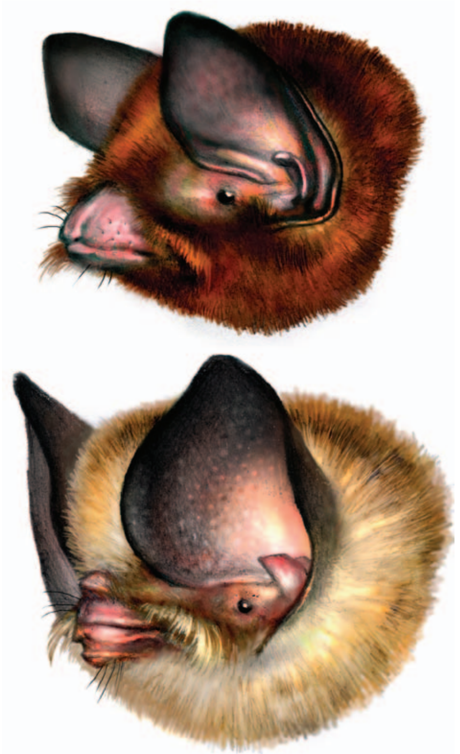
♾This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).

ON THE COVER: PORTRAITS OF TWO CUBAN FUNNEL-EARED BATS: *NYCTIELLUS LEPIDUS* (TOP), AND *CHILONATALUS MACER* (BOTTOM). WITH EIGHT SPECIES, THE WEST INDIES HAVE THE HIGHEST DIVERSITY OF FUNNEL-EARED BATS, TWO OF WHICH, THE CRITICALLY ENDANGERED *NATALUS PRIMUS* (CUBA) AND *NATALUS JAMAICENSIS* (JAMAICA), MAY SOON BECOME EXTINCT IN THE ABSENCE OF APPROPRIATE CONSERVATION EFFORTS.

TEJEDOR: FUNNEL-EARED BATS (CHIROPTERA: NATALIDAE) AMNH BULLETIN 353 2011

SYSTEMATICS OF FUNNEL-EARED BATS (CHIROPTERA: NATALIDAE)

ADRIAN TEJEDOR



BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

SYSTEMATICS OF FUNNEL-EARED BATS (CHIROPTERA: NATALIDAE)

ADRIAN TEJEDOR

Asociación para la Conservación de la Cuenca Amazónica
Oswaldo Baca 402
Magisterio, Cusco, Peru

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 353, 140 pp., 47 figures, 19 plates, 26 tables
Issued June 3, 2011

ISSN 0003-0090

CONTENTS

ABSTRACT

For much of the last third of the 20th century, the diversity of funnel-eared bats (family Natalidae) was underestimated. Although as many as four genera and 11 species were recognized by the mid 20th century, by the 1980s the family was traditionally listed as comprising a single genus of four or five species. In the past decade, the taxonomy of Natalidae has been updated by the discovery of new extant and fossil taxa, the rediscovery of taxa thought to be extinct, and the revalidation of old synonyms at the genus and species levels on the basis of new morphological and molecular evidence. Here, I provide a complete taxonomic revision of Natalidae based on the examination of all taxa described thus far within the family. Thirteen species are recognized here, including an extinct form. New diagnoses, descriptions, and illustrations are provided for each species, including summaries of published information on their natural history, discussions of their conservation status, and an illustrated identification key. The Natalidae appears to be an adaptively diverse clade of bats with distinct ecomorphs in terms of food acquisition, food processing, and mating systems.

INTRODUCTION

The systematic history of Natalidae has gone through three distinct stages common to most living groups (Patterson, 2001): (1) the stage of alpha taxonomy with numerous descriptions of species and genera; (2) the stage of revision and synonymization; and (3) the evaluation of interrelationships among taxonomic units (beta taxonomy), resulting in the revalidation of names previously treated as synonyms. As many as three extant genera, one subgenus, 12 species, and six subspecies were described in the family Natalidae between 1837 and 1971 (table 1). During the last third of the 20th century, however, only one genus and four species of Natalidae were recognized (table 2). The recognized diversity of the family is greatest at present, with four genera and 13 species, including an extinct form (table 2).

The first reference to a bat now placed in the family Natalidae was the description of *Vespertilio lepidus* by Gervais (1837) based on material collected in Cuba during the Compte de Castelnau scientific expedition to the New World tropics. The following year, Gray (1838) named a new genus and species, *Natalus stramineus*, based on a single specimen (Goodwin, 1959; Handley and Gardner, 1990), but gave no information about the material used, its geographic origin, or his reasons for choosing the generic name. In 1840, the taxon first described as *V. lepidus* was independently renamed *Vespertilio barbatus* by Gundlach (1840) and later assigned to the genus *Nyctiellus* by Gervais (1856). Two enigmatic taxa that have been considered synonyms of *Natalus* were also described during this time. One was *Spectrellum macrourum,* described by Gervais (1856) from Bahia, Brazil, and of which no material or illustrations remain. The second was *Vespertilio splendidus*, a taxon apparently referable to *Myotis* that was described by Wagner (1845) from the island of St. Thomas. The identity of *S. macrourum* and the reasons why *V. splendidus* has continued to be considered a synonym of *Natalus* are equally puzzling.

The first revision of Natalidae was made in the late 19th century by Dobson in his catalog of Chiroptera in the British Museum (1878). There, Dobson synonymized Gervais' *Nyctiellus* and *Spectrellum*, and Wagner's *V. splendidus* (with doubts) with Gray's *Natalus*. In addition, Dobson (1878: 342) included *Natalus* within Vespertilionidae, noting that the genus was "evidently the representative of [the Old World genus] *Kerivoula* in the New World," but that characters of the upper incisors allied it to the family Emballonuridae. Two years later, Dobson (1880) described an additional species of *Natalus* (*N. micropus*), a small form from Jamaica with unique dermal outgrowths on the muzzle.

A sudden increase in the recognized diversity of Natalidae took place during the turn of the 19th century and the first few decades of the 20th. During this time 11 new natalid taxa, most from the West Indies, were described, and new taxonomic arrangements were proposed. The most prolific bat taxonomist of this period was Gerrit S. Miller who established Natalidae as a distinct bat family

TABLE 1

Chronology of taxonomic descriptions of Natalidae by taxonomic level from genus to subspecies, including authors, known distribution at time of description, and current taxonomic status

Author	Genus	Subgenus	Species	Subspecies	Distribution	Current status
Gervais (1837)			*Vespertilio lepidus*		Cuba	distinct species
Gray (1838)	***Natalus***					distinct genus
Gray (1838)			***Natalus stramineus***		unknown	distinct species
Gervais (1856)	***Nyctiellus***					distinct genus
Dobson (1880)			*Natalus micropus*		Jamaica	distinct species
Miller (1898)		***Chilonatalus***				distinct genus
Miller (1898)			*Natalus (Chilonatalus) brevimanus*		Providencia	syn. of *C. m. micropus*
Miller (1900)			***Natalus tumidirostris***		Curacao	distinct species
Miller (1902)			***Natalus major***		Hispaniola	distinct species
Miller (1902)			***Natalus mexicanus***		Mexico	distinct species
Miller (1903)			***Chilonatalus tumidifrons***		Bahamas	distinct species
Miller (1906)	*Phodotes*					syn. of *Natalus*
Thomas (1910)				*Phodotes tumidirostris continentis*	Venezuela	ssp. of *N. tumidirostris*
Miller (1914)			***Chilonatalus macer***		Cuba	ssp. of C. *micropus*
Anthony (1919)			***Natalus primus***		Cuba	distinct species
Shamel (1926)			*Natalus dominicensis*		Dominica	syn. of *N. stramineus*
Dalquest and Hall (1949)				*Natalus mexicanus saturatus*	SE Mexico	syn. of *N. mexicanus*
Ruschi (1951)			***Natalus espiritosantensis***		SE Brazil	distinct species
Goodwin (1959)				*Natalus major jamaicensis*	Jamaica	distinct species
Goodwin (1959)				*Natalus stramineus natalensis*	NE Brazil	syn. of *N. espiritosantensis*
Goodwin (1959)				*Natalus tumidirostris haymani*	Trinidad	ssp. of *N. tumidirostris*
Linares (1971)				*Natalus stramineus tronchonii*	W Venezuela	syn. of *N. tumidirostris*
Morgan and Czaplewski (2003)	*Primonatalus*†					
Morgan and Czaplewski (2003)			***Primonatalus prattae***†		Florida	distinct species
Tejedor (2005)			***Natalus lanatus***		Mexico	distinct species

Genera and species level name combinations that are currently accepted are in **boldface**. † denotes an extinct taxon.

TABLE 2
Classifications of extant Natalidae

Miller, 1907	Dalquest, 1950	Goodwin, 1959	Hall, 1981
Natalidae	Natalidae		North American Natalidae
Genus *Natalus*	Genus *Natalus*	Genus Natalus	Genus *Natalus*
N. stramineus	Subgenus *Natalus*	*N. stramineus stramineus*	*N. stramineus stramineus*
N. mexicanus	*N. mexicanus mexicanus*	*N. stramineus natalensis*	*N. stramineus mexicanus*
N. major		*N. stramineus mexicanus*	*N. stramineus saturatus*
Genus Phodotes	*N. mexicanus saturatus*	*N. major major*	*N. stramineus major*
P. tumidirostris	*N. major*	*N. major jamaicensis*	*N. stramineus jamaicensis*
Genus *Chilonatalus*	*N. dominicensis*	*N. major primus*	*N. stramineus primus*
C. micropus	*N. primus*	*N. tumidirostris tumidirostris*	*N. micropus micropus*
C. brevimanus	*N. tumidirostris*	*N. tumidirostris continentis*	*N. micropus tumidifrons*
C. tumidifrons	Subgenus *Chilonatalus*	*N. tumidirostris haymani*	*N. micropus macer*
Genus *Nyctiellus*	*N. micropus*		Subgenus *Nyctiellus*
N. lepidus	*N. brevimanus*		*N. lepidus*
	N. macer		
	N. tumidifrons		
	Subgenus *Nyctiellus*		
	N. lepidus		

Koopman, 1994	Simmons, 2005	This study
Natalidae	Natalidae	Natalidae
Genus *Natalus*	Genus *Natalus*	Genus *Natalus*
Subgenus *Natalus*	*N. stramineus*	*N. stramineus*
N. stramineus stramineus	*N. major*	*N. major*
N. stramineus mexicanus	*N. jamaicensis*	*N. jamaicensis*
N. stramineus tronchoni	*N. primus*	*N. primus*
N. stramineus natalensis	*N. tumidirostris*	*N. tumidirostris*
N. stramineus espiritosantensis	Genus *Chilonatalus*	*N. espiritosantensis*
N. stramineus major	*C. micropus*	*N. mexicanus*
N. stramineus jamaicensis	*C. tumidifrons*	*N. lanatus*
N. tumidirostris tumidirostris	Genus *Nyctiellus*	Genus *Chilonatalus*
N. tumidirostris continentis	*N. lepidus*	*C. micropus*
Subgenus *Chilonatalus*		*C. tumidifrons*
N. micropus micropus		*C. macer*
N. micropus macer		Genus *Nyctiellus*
N. tumidifrons		*N. lepidus*
Subgenus *Nyctiellus*		Genus *Primonatalus*
N. lepidus		*P. prattae*

(originally including the genera *Natalus*, *Thyroptera*, *Furipterus*, and *Amorphochilus*; Miller, 1899), and described eight taxa. These included one subgenus (*Chilonatalus*, 1898, to include Dobson's *N. micropus*), one genus (*Phodotes*, 1906), and six new species: *Natalus* (*Chilonatalus*) *brevimanus*, 1898, from the island of Providencia, Colombia; *Natalus tumidirostris*, 1900 (later transferred to genus *Phodotes*; Miller, 1906), from Curaçao, Netherlands Antilles; *Natalus mexicanus*, 1902, from Mexico; *Natalus major*, 1902, from Hispaniola; *Chilonatalus tumidifrons*, 1903, from San Salvador Island, the Bahamas; and *Chilonatalus macer*, 1914, from Cuba. In additional works, Miller (1903) elevated *Chilonatalus* to genus level, restored the generic status of *Nyctiellus* (Miller, 1904), and moved the genera *Thyroptera*, *Furipterus*, and *Amorphochilus* from Natalidae to other bat families (Miller, 1907), ultimately recognizing four genera and eight species within Natalidae and giving it its essential modern form (table 2). Additional taxa described by other early 20th-century authors included a new subspecies from Venezuela (*Phodotes tumidirostris continentis* Thomas, 1910) and two insular species: *Natalus primus* Anthony, 1919, from Cuba (described from fossil remains and considered an extinct form), and *Natalus dominicensis* Shamel, 1926, from Dominica.

Taxonomic interest in the family Natalidae resurfaced in the second half of the 20th century, often with somewhat contradictory approaches: most authors reduced many former names by synonymy, yet often described new subspecies based on feeble evidence. Dalquest and Hall (1949), for example, defined a new subspecies of *Natalus mexicanus* (*N. m. saturatus*) from eastern Mexico on the basis of questionable size and pelage color differences, but Dalquest (1950) reduced all natalid genera (except *Phodotes* which he deemed indistinguishable from *Natalus*) to subgenera of *Natalus*. Goodwin (1959), in his revision of the subgenus *Natalus*, retained *N. major* as a distinct species but reduced *N. primus* to a subspecies of *N. major*, *N. mexicanus* to a subspecies of *N. stramineus*, and considered *N. dominicensis* indistinguishable from *N. stramineus stramineus*. Goodwin (1959) also described three additional subspecies: *Natalus major jamaicensis* (from Jamaica), *Natalus stramineus natalensis* (from Brazil), and *Natalus tumidirostris haymani* (from Trinidad). Of these, *N. tumidirostris haymani* was tenuously diagnosed by its slightly larger size compared to other *N. tumidirostris*, whereas *N. major jamaicensis* was diagnosed by a suite of unique morphological characters that made it very distinct from *N. major*, illustrating an inconsistent evaluation of the morphological evidence common in the polytypic species period.

South American authors joined the conservative trend of this period and some added new names to the list of subspecies of *Natalus stramineus*. In Brazil, Ruschi (1951) named several new bat species among which was *Myotis espiritosantensis*, which he later redescribed as *Natalus espiritosantensis* (Ruschi, 1970). Confirming the generic affinity, Pine and Ruschi (1976) reduced this taxon to a subspecies of *Natalus stramineus*. Cabrera (1957), in Argentina, suggested the recognition of only two species of *Natalus* (*N. stramineus* and *N. tumidirostris*) and raised doubts about the distinction of *Chilonatalus* from *Natalus* even at the subgenus level. In Venezuela, Linares (1971) described *N. stramineus tronchonii* from Sierra de Perijá on the basis of poorly cleaned skulls in which features of the palate used as diagnostic characters were partially obscured by remnant soft tissue. More importantly, Linares (1971) suggested that all forms of *Natalus* (subgenus *Natalus*) represented the single species *Natalus stramineus* (although he provisionally maintained *N. tumidirostris* as a valid name). This opinion was justified by the observation that all populations of *Natalus* (sensu stricto) showed an overall continuous increase in body size beginning with the smallest forms in Mexico, passing through intermediate forms in northern South America, the Lesser and Greater Antilles, and ending with the largest in Cuba. Linares' (1971) view was widely followed (e.g., by Varona, 1974; Silva-Taboada, 1979; Koopman, 1993, 1994). Koopman (1981, 1993, 1994), in addition to considering *N. stramineus* a species widespread throughout the Neotropics, retained *N. tumidirostris* as a distinct species. This, therefore, necessitated hypothesizing that *N. stramineus* and *N. tumidirostris* occurred as sympatric species in northern South America, a notion that has survived to the present (Dávalos, 2005; Simmons, 2005; see Note under *N. stramineus* in Systematic Account).

Working in the West Indies, Varona (1974) furthered the conservative trend of the period. First, he formalized Cabrera's (1957) doubts about the distinctiveness of *Chilonatalus* and did not list this name even as a subgenus. Also, he grouped all forms of *Chilonatalus* into the single species *Natalus micropus*. Varona's treatment was followed by Hall (1981), in a radical departure from his previous monograph (Hall and Kelson, 1959). Varona's (1974) and Hall's (1981) arrangements thus represented the climax of the conservative view regarding natalid diversity; Natalidae was seen as a small family of a single genus (*Natalus*) and four species: *Natalus* (*Nyctiellus*) *lepidus*; *Natalus* (*Natalus*) *stramineus*; *Natalus* (*Natalus*) *tumidirostris*; and *Natalus* (*Natalus*) *micropus*.

Although some conservative opinions have survived into recent years, the past three decades of natalid taxonomy has been dominated by a shift toward the revalidation of species previously considered synonyms. In 1982, Ottenwalder and Genoways argued for the separation of *Natalus* (= *Chilonatalus*) *tumidifrons* from *Natalus* (= *Chilonatalus*) *micropus*, on the basis of the smaller skull size of the latter. A few years later, Morgan (1989) offered ample evidence for the revalidation of *Nyctiellus* as a distinct genus and of *Natalus major* as a distinct species. In 2003, Morgan and Czaplewski described *Primonatalus prattae*, a fossil natalid from the Miocene of northern Florida, and argued strongly for the revalidation of *Chilonatalus* as a distinct genus. In addition, Tejedor et al. (2004) announced the rediscovery of a Cuban taxon, *Natalus primus*, previously thought extinct and long synonymized with *Natalus stramineus*. On the basis of morphological evidence, Tejedor et al. (2005b) revised the taxonomy of Greater Antillean *Natalus*, revalidating *N. primus* and elevating *Natalus jamaicensis* to the status of fully distinct species. The separation of *N. jamaicensis* from *N. major* was corroborated by Dávalos (2005) on the basis of gene sequences. In addition, Dávalos (2005) demonstrated a deep genetic divergence between *Chilonatalus* and *Natalus*, supporting the generic distinction of the former. Such sweep of old-name revalidations, however, was countered by Timm and Genoways (2003), and Genoways et al. (2005) who maintained that all greater Antillean *Natalus* are not distinct from *N. stramineus* at the species level, and retained *Chilonatalus* as a synonym of *Natalus*. Simmons (2005) nonetheless summarized the rise in recognized diversity of Natalidae listing it as comprising three genera and eight species (table 2).

Most recently, the systematics of Natalidae has continued to change through the description or revalidation of additional species. In 2005, Tejedor described *Natalus lanatus*, a species from Mexico that had remained undetected in museum collections for 140 years. Dávalos (2005), on the other hand, elevated the name *N. saturatus* to species level to designate the Mexican–Central American populations, which she found genetically different from *N. stramineus*. Finally, Tejedor (2006) revalidated *N. espiritosantensis* and *N. mexicanus* as species distinct from *N. stramineus*, but synonymized *N. saturatus* with *N. mexicanus*. This later revision, defined *N. tumidirostris* as the only species occurring in northern South America, a point of view sustained by Gardner (2008), and restricted *N. stramineus* to the Lesser Antilles. Neither of these changes was included in the latest worldwide list of Chiroptera (Simmons, 2005).

Below I provide a systematic revision encompassing all described forms of Natalidae including the fossil *Primonatalus prattae*. An undescribed Oligocene distal radius ascribed to Natalidae (Morgan and Czaplewski, 2003) and the Eocene fossils *Aegina*, *Chadronycteris*, *Chamtwaria*, *Honrovits*, and *Stehlinia*, excluded from Natalidae by Morgan and Czaplewski (2003) are not included in this account.

METHODS

SPECIMENS AND MEASUREMENTS: For this study I examined 3234 specimens of *Natalus* (including all 20 holotypes in the family). These specimens are housed in 26 museums, all of which are listed (including abbreviations) in appendix 1.

Morphological terminology follows Giannini et al. (2006) for the cranium, Smith (1972) and Morgan and Czaplewski (2003) for the postcranium, Freeman (1998) for the dentition, and Ridgway (1912) for pelage coloration. A total of 1137 specimens were measured for this study, of which eight were juveniles or young adults. Additional measurements were taken from Pedersen et al. (2003), López-González et al. (1998), Taddei and Uieda (2001), Silva-Taboada (1979), and Goodwin (1959). Length of forearm and length of tibia were measured from study skins, fluid-preserved specimens, and fresh specimens, whereas ear length was measured exclusively from fluid-preserved and fresh specimens. Given that measurements of length of tibia taken from fluid-preserved specimens have been found to be significantly larger on average than those taken from dry skins (Tejedor, 2005), means of length of tibia taken by those two measures are reported separately. Lineal measurements were taken with dial and digital calipers and are given in millimeters. Measurements of weight were taken from specimen tags and are given in grams. Lineal measurements are defined as follows:

Forearm length: Distance from the elbow to the distal end of the forearm including carpals, taken with the wing at least partially folded.

Ear length: Maximum distance between the ventral point of attachment of the pinna and the tip of the pinna.

Length of tibia: Distance from the proximal end of the tibia to the posterior base of the calcar (in dry specimens), and distance from the knee to the ankle with both knee and ankle bent to an angle of at least 90° (in fluid-preserved specimens).

Length of 3rd metacarpal: Distance from wrist to distal end of 3rd metacarpal, taken with the wing folded.

Length of 5th metacarpal: Distance from wrist to distal end of 5th metacarpal, taken with the wing folded.

Length of penis: Maximum distance from the caudal base to the tip of the penis, without stretching.

Length of natalid organ: Maximum distance from the rostral margin to the caudal margin of the natalid organ (in *Nyctiellus* and *Chilonatalus*) or from the dorsal point of flexion between rostrum and forehead to the caudal margin of the natalid organ (in *Natalus*), taken externally.

Greatest skull length: Maximum distance between the anteriormost point of the skull, including the incisors, and the posteriormost point of the occiput.

Zygomatic breadth: Greatest distance across the external margins of the zygomatic processes.

Braincase breadth: Greatest breadth of the globular part of the braincase, taken perpendicular to the skull's longitudinal axis.

Postorbital breadth: Least breadth across the postorbital constriction.

Breadth across molars: Greatest distance between the labial edges of the upper molar series.

Breadth across canines: Greatest distance between the labial edges of the cingula of the upper canines.

Maxillary toothrow length: Greatest crown length of the maxillary tooth row, measured from the anteriormost edge of the canine to the posteriormost edge of M3.

Mandibular toothrow length: Greatest crown length of the mandibular tooth row, measured from the anteriormost edge of the canine to the posteriormost edge of m3.

Mental length: Least distance from the mental foramen to the ventral margin of the dentary between the angular process and the condyle (used only for *Natalus primus*, a species for which numerous fossil specimens had incomplete mandibular tooth rows).

Depth of braincase: Distance between the basioccipito-palatal plane and the dorsalmost edge of the sagittal crest.

Cranial measurements (except mental length) are illustrated in figure 1.

In addition, to graphically represent interspecific variation in cranial shape, several indices were calculated: (1) relative breadth across canines = breadth across canines/ greatest skull length; (2) relative breadth across molars = breadth across molars/ maxillary toothrow length; (3) relative maxillary toothrow length = maxillary toothrow length/ greatest skull length; (4) relative breadth of postorbital constriction = postorbital breadth/zygomatic breadth.

ECOMORPHOLOGICAL ANALYSES: Ecomorphological traits were inferred from a combination of measurement data and field observations. Measurements of forearm length, length of tibia, and 3rd and 5th metacarpals were used as descriptors of flight surface shape. In all natalids, the uropatagium is roughly wedge shaped and its free margin extends from near the ankle to the tip of the tail; therefore, its extension depends mostly on the length of the legs and tail. For this reason, the length of the tibia was used as an indicator of the size of the uropatagium. Two indices were calculated to represent shape of flight surfaces: (1) shape of the wing tip (= length of 5th metacarpal/length of 3rd metacarpal) and (2) relative size of the uropatagium (= length of tibia/forearm length). In addition, two indices were calculated to represent relative size of organs related (or potentially related) to reproduction in males: (1) relative length of the penis (= length of penis/forearm length) and (2)

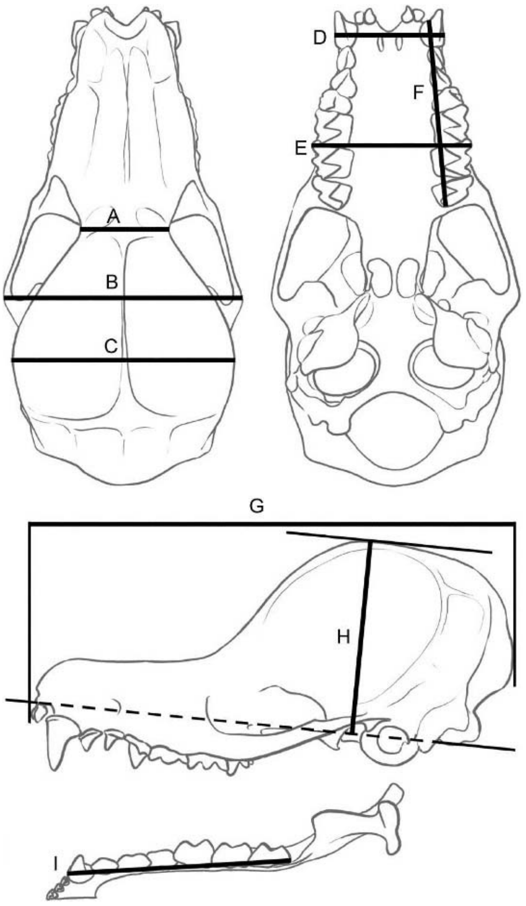


Fig. 1. Cranial dimensions measured in this study: **A,** postorbital breadth; **B,** zygomatic breadth; **C,** braincase breadth; **D,** breadth across canines; **E,** breadth across molars; **F,** maxillary toothrow length; **G,** greatest skull length; **H,** depth of skull; **I,** mandibular toothrow length.

relative length of the natalid organ (= length of natalid organ/forearm length). Forearm length was used to define three body size classes: (1) large (mean forearm length 43.5–49 mm), including *Natalus major*, *Natalus jamaicensis*, and *Natalus primus;* (2) medium (mean forearm length of 37–39 mm), including the remaining species of *Natalus;* and (3) small (mean forearm length of 29–34 mm), including *Nyctiellus* and *Chilonatalus*. Because of the outlying position of *Natalus primus* relative to other *Natalus* with respect to several ecomorphological traits, a distinction is made between *N. primus* and the remaining species of *Natalus,* which are hereinafter treated as the "*Natalus stramineus* group." Similarly, a distinction is made between *Chilonatalus micropus* and a *Chilonatalus* "*tumidifrons* group" (= *C. tumidifrons* + *C. macer*).

In figures, tables, and plates, species are abbreviated as follows: Cma, *Chilonatalus macer*; Cmi, *Chilonatalus micropus*; Ctu, *Chilonatalus tumidifrons*; Nes, *Natalus espiritosantensis*; Nja, *Natalus jamaicensis*; Nla, *Natalus lanatus*; Nma, *Natalus major*; Nme, *Natalus mexicanus*; Npr, *Natalus primus*; Ntu, *Natalus tumidirostris*; and Nst, *Natalus stramineus*.

Statistical Analyses: I used two-way ANOVAs to detect overall differences among species and populations (geographic subsets within a given species) and between sexes, as well as interaction effects between populations/species and sex. Where interaction effects were not found, one-way MANOVAs (performed over all variables simultaneously) were used to detect sexual differences within species. I also used one-way MANOVAs (performed over all variables simultaneously) to detect differences between two populations of one species within a single sex when only one sex was well represented and sexual differences in that species had been detected with previous ANOVAs. In species where simultaneous one-way MANOVAs were impractical due to unequal distribution of missing measurements, one-way ANOVAs were performed separately for each variable. Post hoc comparisons (Tukey tests for unequal sample sizes) tested for pairwise differences among species or populations. The significance level was set to $P = 0.05$ for the Tukey tests and the one-way MANOVAs in which tests were performed simultaneously over the sampling units. The significance level was set to $P = 0.01$ for all the two-way ANOVAs and the one-way ANOVAs in which multiple separate tests were performed over the same sampling units. I used canonical analyses to detect differences in body dimensions among species and among geographical samples within each species. All analyses were performed using STATISTICA 5.5 (StatSoft, Inc., 1995).

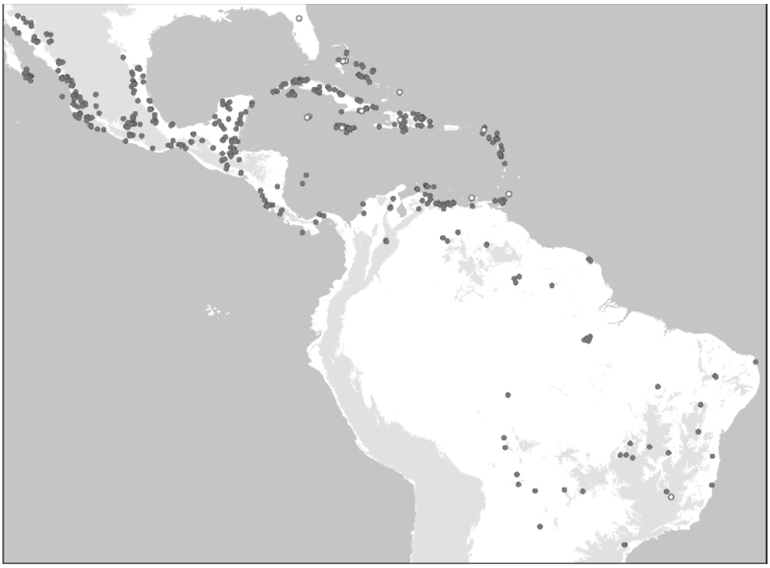


Fig. 2. Distribution of the family Natalidae. Solid dots indicate collection localities of extant specimens; open dots indicate collection localities of bone remains (e.g., fossils and subfossils) only. The distribution of Natalidae spans the intertropics of the New World, being notably absent from the western Amazon basin, Puerto Rico, and the southern Lesser Antilles. Natalids are more common in the northern Neotropics. Light gray shading shows land above 600 m.

SYSTEMATICS

Family Natalidae Miller, 1899

TYPE GENUS: *Natalus* Gray, 1838.

GEOGRAPHIC DISTRIBUTION: New World, from northern Mexico (Sonora and Baja California in the west and Tamaulipas in the east), through Central America (including several adjacent continental and oceanic islands), the West Indies (Greater and Lesser Antilles and the Bahamas), northern South America (northern Colombia, through Venezuela, and the Guianas, plus offshore Caribbean islands), eastern and central Brazil, to southern Brazil (São Paulo), eastern Bolivia and northeastern Paraguay; generally restricted to tropical environments (ranging from semiarid to wet) rich in caves, and below 2500 m (fig. 2; pls. 1–3).

DIAGNOSIS: Natalid organ present in males; funnel-shaped ears lacking a ridge or flap between lateral and ventral regions of pinna; ear ridges vestigial; lachrymal fossa present; long infraorbital canal, extending from P2 to M2; styliform process on rostral margin of ectotympanic; presence of cingular labial cusp on p4; lingual talonid crest of m3 straight; presence of protocone on P4; lack of upper molar ectocingulum; manubrium of sternum expanded laterally into platelike structure; long caudal vertebrae.

DESCRIPTION: Funnel-eared bats range in size from the very small *Nyctiellus lepidus* (2–3 g, forearm length 26.6–31.0 mm), one of the world's smallest bats, to the medium-sized *Natalus primus* (6.0–12.6 g, forearm length 46.1–51.2 mm). Funnel-eared bats are characterized by slender bodies, long extremities and tail, and wide wing membranes. The tail is usually longer than the head and body combined, and is entirely enclosed in an extensive, triangular or wedge-shaped uropatagium. The wing membranes are thin and translucent. The plagiopatagium inserts either at the ankle or at the tibia. The calcar is long and in most species extends along most of the free edge of the uropatagium. The body pelage is long, from lax to woolly, and ranges widely in coloration from pale buff to rich chestnut brown. Usually, ventral hairs are monocolored and dorsal hairs are bicolored with darker tips and lighter bases, with the exception of *N. lanatus*, in which both ventral and dorsal hairs have darker bases and lighter tips. The muzzle is long, slender, and dorsoventrally flattened. Natalids have a relatively simple facial anatomy, lacking, with the exception of the genus *Chilonatalus*, the dermal folds and excrescences typical of other tropical bat families (pl. 4). The dense pelage along the lateral margins of the upper lips gives these bats the appearance of having thick mustaches. The mustache hairs are curved ventrally and may direct airflow toward the mouth and ear, as has been suggested for the bat family Mormoopidae (Smith, 1972). The nostrils are usually oval shaped, ventrolaterally oriented, and open at the end of a dorsally prominent longitudinal nasal ridge at the margin of the upper lip. The lower lip is thickened and bears paired central pads incised by numerous diagonal grooves with the appearance of primate dermatoglyphs.

Males have a unique organ called the natalid organ on the dorsal surface of the muzzle. This organ is generally visible externally as a swollen mass, which can be as large as half the skull length in the genus *Chilonatalus* (pl. 5). The natalid organ secretes a translucent greenish, viscous liquid that may function in communication.

The ears are medium to large in size, with the pinna square shaped and expanded laterally to various degrees, in most species having the appearance of a funnel with a pointed apex. The ventral surface of the ears is relatively smooth; the typical ear ridges of bats are extremely reduced in size and restricted to a narrow area near the lateral margin of the distal pinna (pl. 5). The hair follicles on the ventral surface of the ear are relatively conspicuous. There is no cartilaginous ridge or flap between the lateral and ventral regions of the ear pinna. The tragus is small and twisted with a lanceolate tip. The eyes are very small, partly surrounded by the bases of the ears, and are partially hidden by the profuse facial pelage.

The skull is long and delicate, with a long, narrow, and dorsoventrally flattened rostrum (pls. 6–14). The braincase varies from moderately inflated to globular and is usually sharply elevated above the rostrum. The premaxilla is expanded dorsally and caudally to various degrees. The palatal branches of the premaxilla are fused along the ventral midline, leaving two small foramina and a slight rostral emargination. The infraorbital canal extends from P2 to M2, and opens caudally in a depression termed the *lachrymal fossa* (Morgan and Czaplewski, 2003). The ectotympanic is expanded rostrally into a styliform process. The condyloid and coronoid processes of the mandible are at nearly the same level above the alveolar plane. The angular process is long and has a dorsally or anterodorsally curved tip (pl. 15). The dental formula is 2/3, 1/1, 3/3, 3/3 = 38. There is a small gap between i3 and the lower canine. There is an accessory cusp on the labial cingulum of p4 of various degrees of development. The lingual talonid crest of m3 is straight. A protocone is present in P4 and the mesostyle of the upper molar series is elongated rostrocaudally forming an accessory crest termed a mesostylar crest (Morgan and Czaplewski, 2003; pl. 16).

The humerus is characterized by a distal articular surface displaced laterally relative to the longitudinal axis of the humerus, a broad, triangular-shaped epitrochlea, and tuberosities of similar size (pl. 17). The axial skeleton has various degrees of fusion between its constituting bones. The vertebrae C7 to T1 up to C7 to T6 are fused among them and with the ribs. The vertebrae from last thoracic to antepenultimate or penultimate lumbar are fused into a continuous, laterally compressed column with no evidence of sutures between elements. The sternum is expanded laterally into a platelike structure. The ribs are greatly expanded craniocaudally or fused entirely among them and with the sternum into a rigid thoracic bell-shaped structure (pl. 18). The tail vertebrae are greatly elongated.

KEY TO BATS OF THE FAMILY NATALIDAE

1 Free margin of uropatagium naked, lacking a fringe of hairs (fig. 3A); tibia less than half the length of the forearm; calcar occupying less than half the length of the free margin of uropatagium. . . . . *Nyctiellus lepidus*

— Free margin of uropatagium with a fringe of hairs (fig. 3B); tibia more than half the length of the forearm; calcar occupying more than half the length of the free margin of uropatagium 2

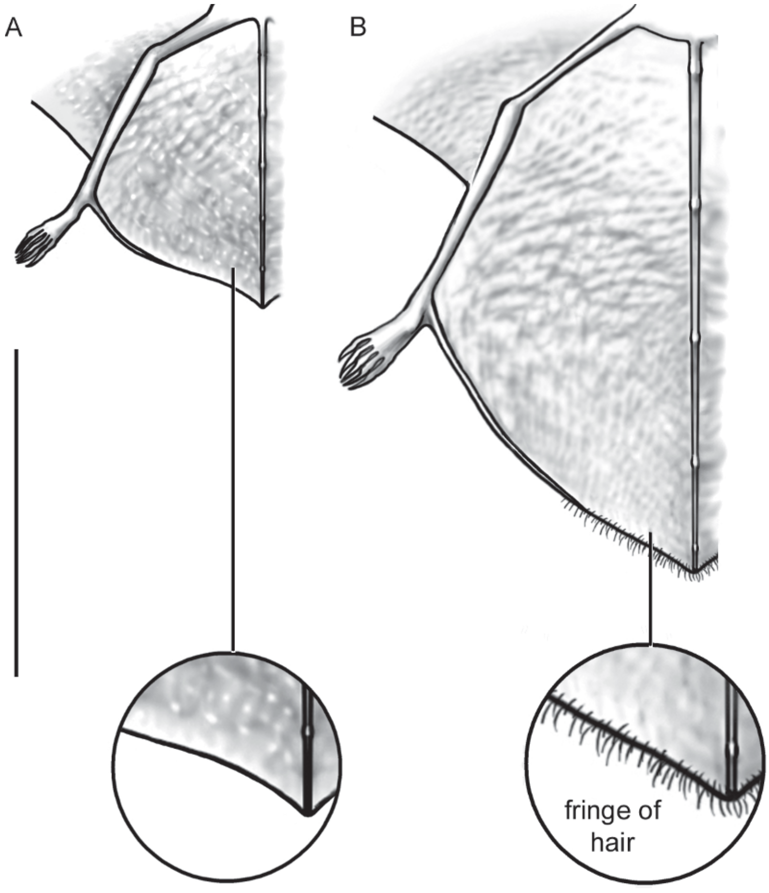


Fig. 3. Dorsal view of the left half of the uropatagium of two natalids: **A,** *Nyctiellus lepidus*, showing naked free margin of uropatagium; and **B,** *Chilonatalus macer*, showing fringe of hairs on free margin of uropatagium. Scale bar = 20 mm.

2 Muzzle showing a distinctive tubercle above nostrils and a small flap of skin below lower lip (fig. 4A) 3

— Muzzle smooth, lacking a tubercle above nostrils and a flap of skin below lower lip (fig 4B) 5

3 Tibia short, lateral margin of ear concave (fig. 5B); in males, penis long (3.6–6.5 mm) and natalid organ small and hemispheric (fig. 5B) . . . . *Chilonatalus micropus*

— Tibia long, lateral margin of ear straight (fig. 5A); in males, penis short (1–2.5 mm) and natalid organ large and elliptical (fig. 5A) 4

4 Greatest skull length 13.9–14.7 mm . . . . *Chilonatalus macer*

— Greatest skull length 15.0–16.0 mm . . . . *Chilonatalus tumidifrons*

5 Ungual hair tuft present (fig. 6A) . . . . *Natalus lanatus*

— Ungual hair tuft absent (fig. 6B). 6

6 Lateral margin of ear pinna straight . *Natalus primus*

— Lateral margin of ear pinna concave. 7

7 Medial margin of ear pinna straight (fig. 5B) 8

— Medial margin of ear pinna slightly to deeply concave (fig. 5C). 9

8 Maxilla concave dorsal to molars (fig. 7A); . . . . *Natalus jamaicensis*

— Maxilla convex dorsal to molars (fig. 7B); . . . . *Natalus major*

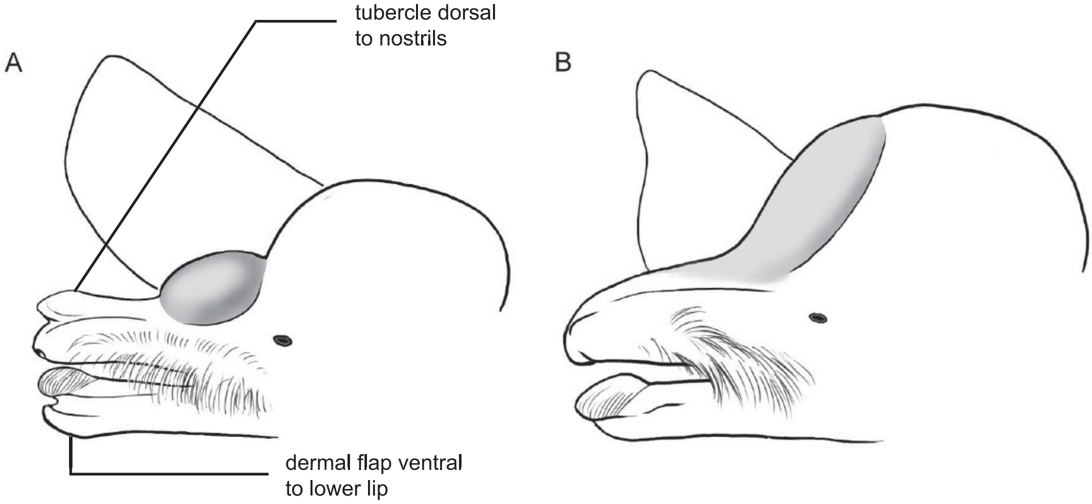


Fig. 4. Schematic lateral view of the heads of two natalids: **A,** *Chilonatalus micropus*, showing dermal outgrowths on the muzzle; and **B,** *Natalus tumidirostris*, showing lack of dermal outgrowths on the muzzle.

9 Caudal end of palate rostral to sphenorbital fissure (fig. 8A). . . . . . . *Natalus tumidirostris*

— Caudal end of palate caudal to sphenorbital fissure (fig. 8B) 10

10 Rostrum short and wide, breadth across molars 80%–85% of toothrow length . . . . *Natalus espiritosantensis*

— Rostrum long and narrow, breadth across molars 72%–81% of toothrow length 11

11 I1 rostral to I2 in ventral view (fig. 9A) . . . . *Natalus mexicanus*

— I1 at level with I2 in ventral view (fig. 9B). . . . . *Natalus stramineus*

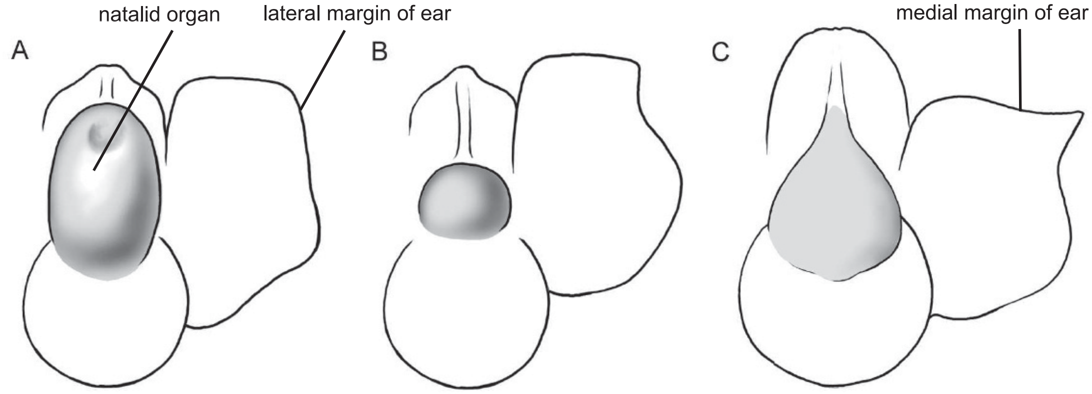


Fig. 5. Schematic dorsal view of the heads of three natalids: **A,** *Chilonatalus macer*, showing large, elliptical natalid organ and straight lateral and medial margins of ear; **B,** *Chilonatalus micropus*, showing small, hemispherical natalid organ, straight medial margin of ear, and concave lateral margin of ear; and **C,** *Natalus tumidirostris*, showing wedge-shaped natalid organ and concave medial and lateral margin of ear.

TABLE 3
Summary of diagnostic characters of four genera of Natalidae

	Nyctiellus	*Chilonatalus*	*Primonatalus*	*Natalus*
Forearm length	26.6–31.0	30.7–36.0	—	34.0–51.2
Length of tibia	12.3–14.0	14.7–20.3	—	16.0–29.1
Greatest skull length	12.5–14.0	13.5–16.0	—	15.0–19.9
Calcar	less than ½ the length of free edge of uropatagium	about ⅔ of free edge of uropatagium	—	slightly more than ½ the length of the free edge of uropatagium
Free edge of uropatagium	naked	with fringe of fine hairs	—	with fringe of fine hairs
Attachment of wing to tibia	at about the distal ¾ of tibia	from distal ⅔ to the proximal ⅓ of tibia	—	at distal 4/5 of tibia
Dermal outgrowths on muzzle	absent	present	—	absent
Mustaches	formed by highly parallel hairs	formed by highly parallel hairs	—	formed by disordered hairs
Distal third of ear pinna	narrow, huge notch	wide, small notch to no notch	—	wide, small notch to no notch
Ear folds	reduced, 7 or more	vestigial, 2–3	—	vestigial, 0–6
Natalid organ, dorsal view	square shaped, on dorsum of rostrum	hemispherical or spindle shaped, on dorsum of rostrum reaching forehead	—	elliptical or wedge shaped, on forehead
Anterior palatal emargination	very small	medium sized	—	medium sized
Base of zygomatic arch	deeper than crown height of last molar	about as deep as height of last molar crown	about as deep as height of last molar crown	about as deep as height of last molar crown
Braincase	uninflated	inflated to globular	—	inflated to globular
Basisphenoid pit	undivided by longitudinal ridge	divided in two by longitudinal ridge	—	divided in two by longitudinal ridge
Ectotympanic	large, covers periotic	small, periotic visible	—	small, periotic visible
Height of coronoid process	as high as condyloid	as high as condyloid	slightly higher than condyloid	slightly higher to as high as condyloid
Angular process	dorsally curved, with medial projection	dorsally curved, pointed	dorsally curved, with medial projection	anterodorsally curved and blunt
Crown of P2	extremely reduced	about as high as that of p3	—	about as high as that of p3
Ribs	broadly expanded	fused to each other	—	broadly expanded
Spinous process of humerus	higher than capitulum	higher than capitulum	as high as capitulum	as high as capitulum

SPECIES ACCOUNTS

Genus *Nyctiellus* Gervais, 1856

Nyctiellus Gervais, 1856: 84.Type species *Vespertilio lepidus* Gervais, 1837, by monotypy.
Natalus Dobson, 1878: 344. Part, not *Natalus* Gray, 1838.
Natalus (*Nyctiellus*): Dalquest, 1950: 443. Name combination.

DIAGNOSIS: Very small size; tibia shorter than half the length of the forearm; calcar occupying less than half the length of the free edge of uropatagium; free margin of uropatagium naked, lacking fringe of hairs; distal third of ear pinna relatively narrow, with seven or more ear ridges; ear tip rounded; funnellike form restricted to lateral and basal portions of ear pinna; free edge of uropatagium lacking fringe of hairs; natalid organ low, rather square shaped (with nearly parallel lateral margins) never reaching forehead; broad, deep rostrum; swollen maxilla;

TABLE 4
Diagnostic characters of species of the genus *Chilonatalus*

	micropus	*tumidifrons*	*macer*
Forearm length	30.7–35.1	31.7–36.0	32.1–33.8
Length of tibia	14.7–17.95	17.8–20.1	18.2–20.3
Length of penis	3.6–6.5	1.1–2.3	1.5–2.6
Length of natalid organ	2.1–4.3	3.6–8.5	2.4–7.7
Greatest skull length	13.5–14.7	15.0–15.95	13.8–14.9
Least postorbital breadth	relatively wide	relatively narrow	relatively wide
Lateral margin of ear	deeply notched	straight	straight
Attachment of wing to tibia	on distal ½ of tibia (at about ⅔ of its length, measured from knee to ankle	on proximal ½ of tibia (at about ⅓ of its length, measured from knee to ankle)	on proximal ½ of tibia (at about ⅓ of its length, measured from knee to ankle)
Braincase rise from rostrum, lateral view	abruptly, with a well defined angle dorsal to orbit	gently, with a shallow curving slope dorsal to orbit	gently, with a shallow curving slope dorsal to orbit
Ridge between basisphenoid furrows	wide	wide	narrow
Caudal margin of ascending ramus of mandible	forming an angle smaller than 90° with alveolar plane of dentary	forming a straight angle with alveolar plane of dentary	forming a straight angle with alveolar plane of dentary
Lateral sides of basisphenoid pits	widely diverging caudally	nearly parallel	nearly parallel
p2	not crowded	crowded	not crowded
Fusion between original elements of thoracic cage	complete but with visible suture lines	seamless ventrally	seamless ventrally

low braincase; slight cranial flexion, anterior portion of zygomatic arches wider (deeper) than twice the height of last molars; slight palatal emargination; basisphenoid pit deep and lacking longitudinal septum; ectotympanic large, covering most of the periotic; I2 inflected medially; reduced first premolars; molars cusps relatively thin and long, talonid broader than trigonid in lower molars; spinous process of humerus much higher than capitulum. A comparison of diagnostic characters between *Nyctiellus*, and other natalid genera is summarized in table 3.

ETYMOLOGY: From the latinized diminutive of *nyx,* Greek for "night."

CONTENTS: *N. lepidus* (type species) (Gervais, 1837).

Nyctiellus lepidus (Gervais, 1837)
Figure 10

Vespertilio lepidus Gervais, 1837: 253. No holotype bearing this name exists. The original specimen appears to have been relabeled as *Nyctiellus lepidus* when Gervais (1856) transferred *V. lepidus* to the genus *Nyctiellus*.

Vespertilio barbatus Gundlach, 1840: 356. Holotype unknown. Synonymized with *N. lepidus* by Gundlach in Peters (1861).

Nyctiellus lepidus: Gervais, 1856: 84. New combination.

Vespertilio (*Nyctiellus*) *lepidus*: Gundlach in Peters, 1861: 150. New combination.

Vespertilio (*Natalus*) *lepidus*: Gundlach, 1867: 252. New combination.

Natalus lepidus: Dobson, 1878: 344. New combination.

Natalus (*Natalus*) *lepidus*: Miller and Rehn, 1901: 274. New combination.

Natalus (*Nyctiellus*) *lepidus* Dalquest, 1950: 443. New combination.

HOLOTYPE: Holotype by monotypy, MNHN A.621, skin in alcohol with skull removed (skull lost), collected in Cuba (specific locality, date, and collector unknown). Skin in good condition, but highly bleached from long immersion in alcohol.

DISTRIBUTION: Cuba (including the Isle of Pines) and the Bahamas (Eleuthera, Cat, Great and Little Exuma, and Long; also, as a fossil, in Andros and New Providence; fig. 11).

TABLE 5
Diagnostic characters of species of the genus *Natalus*

	espiritosantensis	*jamaicensis*	*lanatus*	*major*	*mexicanus*	*primus*	*tumidirostris*	*stramineus*
Forearm length	37.0–42.1	44.0–47	35.4–38.6	41.1–45.0	34.0–40.6	46.1–51.2	36.1–41.5	37.2–40.5
Length of tibia	20.1–23.8	24.3–25.7	16.0–19.2	23.2–25.4	19.4–22.3	25.4–29.1	18.9–22.4	19.8–23.2
Greatest skull length	15.9–17.0	17.2–18.1	15.0–16.4	17.0–18.1	14.9–16.8	18.1–19.9	15.5–17.3	15.7–17.5
Breadth across canines	3.4–4.2	3.7–4.1	3.4–3.8	3.9–4.5	3.2–3.8	3.8–4.5	3.4–4.2	3.3–4.2
Maxillary tooth row	6.5–7.0	7.8–8.1	6.3–6.9	7.5–8.0	6.3–7.1	7.8–10.3	6.5–7.3	6.8–7.5
Medial margin of ear	deeply concave	straight	straight	straight	slightly concave	straight	deeply concave	slightly to deeply concave
Lateral margin of ear	deeply concave	deeply concave	deeply concave	deeply concave	deeply concave	straight	deeply concave	deeply concave
Number of ear folds	5–6	5–6	0–2	5–6	5–6	4	5–6	5–6
Ventral pelage	monocolored	monocolored	hair bases dark than tips	monocolored	monocolored	monocolored	monocolored	monocolored
Ungual tuft	absent	absent	present	absent	absent	absent	absent	absent
Premaxilla	not inflated	not inflated	not inflated	not inflated	not inflated	not inflated	not inflated	inflated
Maxilla dorsal to molars	convex, not inflated	concave	convex, not inflated	convex, not inflated	convex, not inflated	convex, not inflated	inflated	convex, not inflated
Postorbital region, dorsal view	sides widely diverging rostrally	sides nearly parallel	sides widely diverging rostrally	sides widely diverging rostrally	sides widely diverging rostrally	sides widely diverging rostrally	sides widely diverging rostrally	sides widely diverging rostrally
Palate between pterygoids	present	present	present	present	present	present	absent	present
Caudal margins of maxilla, ventral view	forming acute angle with longitudinal axis of skull	forming acute angle with longitudinal axis of skull	almost perpendicular to longitudinal axis of skull	forming acute angle with longitudinal axis of skull	forming acute angle with longitudinal axis of skull	almost perpendicular to longitudinal axis of skull	forming acute angle with longitudinal axis of skull	forming acute angle with longitudinal axis of skull
Basisphenoid pits	shallow	shallow	shallow	shallow	shallow	deep and steep sided	shallow	shallow
Caudal margin of mandible	perpendicular to alveolar plane	perpendicular to alveolar plane	perpendicular to alveolar plane	perpendicular to alveolar plane	perpendicular to alveolar plane	forming a 70° angle with alveolar plane	perpendicular to alveolar plane	perpendicular to alveolar plane
I1, ventral view	level with I2	level with I2	rostral to I2	level with I2	rostral to I2	rostral to I2	level with I2	level with I2
Mesostylar crest on m3	absent	absent	absent	absent	absent	present	absent	absent

Measurements: min.–max.

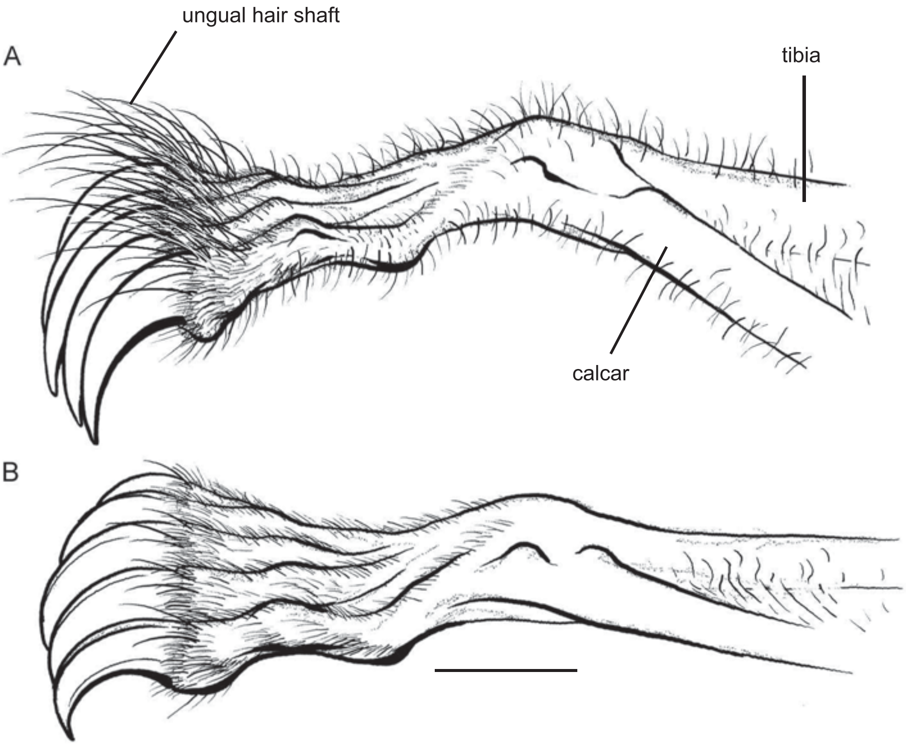


Fig. 6. Medial view of the feet in two species of *Natalus*: **A,** *Natalus lanatus*, showing ungual tufts; and **B,** *Natalus mexicanus*, showing no ungual tufts.

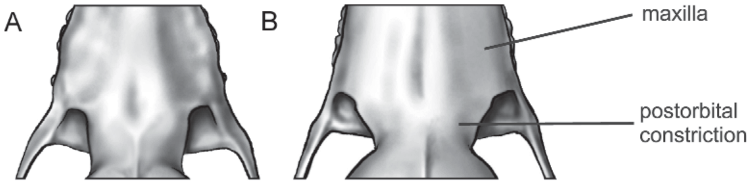


Fig. 7. Dorsal view of the postorbital region and base of the rostrum in two species of *Natalus*: **A,** *Natalus jamaicensis*, showing parallel sides of postorbital region and concave maxilla; **B,** *Natalus major*, showing sides of postorbital region diverging anteriorly and convex maxilla.

Fig. 8. Ventral view of the posterior palate in two species of *Natalus*: **A–B,** *Natalus tumidirostris*, showing caudal margin of palate (a) always rostral to sphenorbital fissure (b); and **C,** *Natalus espiritosantensis*, showing caudal margin of palate caudal to sphenorbital fissure.

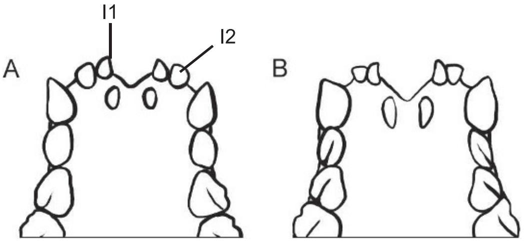


Fig. 9. Ventral view of the rostral end of the skull in two species of *Natalus*: **A,** *Natalus mexicanus*, showing I1 located rostral to I2; and **B,** *Natalus stramineus*, showing I1 at level with I2.

DIAGNOSIS: Same as for genus.

DESCRIPTION: Very small size (forearm length 26.6–31.0 mm; greatest skull length 12.5–14.0 mm; weight 2–3 g); muzzle broad and dorsoventrally flattened; nostrils nearly circular, opening ventrolaterally on a rounded skin pad on margin of upper lip; upper lip thin; lower lip thickened and indented in ventral margin, with numerous transversal grooves; natalid organ low, rather square shaped (with nearly parallel lateral margins) and never reaches forehead; ears relatively short (10.0–13.6 mm); ear pinna relatively narrow with rounded tip; 7 or more ear ridges along lateral margin of distal pinna; ventral region of ear pinna moderately expanded but funnellike; medial ear margin rigid, with longitudinal fold along ventral face; tragus short, wedge shaped, and contorted into funnellike structure; tibia (12.3–14.0 mm) shorter than half the length of the forearm; calcar long and thin, occupying less than half the length of the free edge of uropatagium; free margin of uropatagium naked, lacking fringe of hairs; wings relatively long and narrow, with 3rd metacarpal (23.8–26.6 mm) longer than 5th metacarpal (21.2–23.8 mm); pelage dense and lax; hairs long (4–6 mm); pelage color from grayish brown to reddish or orange brown; hairs bicolored, with tips darker than bases; contrast between tips and bases of hairs more marked dorsally than ventrally; dense mustachelike hair tufts along lateral margins of upper lip and on dorsum of muzzle; mustache along lateral margins of upper lip formed by dense, tough, parallel, and ventrally curved hairs; portion of mustache on dorsum of muzzle denser than that along upper lip; dorsum of natalid organ with a tuft of hairs; skull long with slight rostral flexion; rostrum broad and deep, with marked sulcus between nasals; slight palatal emargination; maxillaries swollen; braincase low, with well-developed sagittal crest; maxillary branch of zygomatic arch deeper than twice the height of crowns of last molars; pterygoids convergent; palate extending caudally to half the length of pterygoids; basisphenoid pit deep with steep sides; medial ridge along basisphenoid absent; ectotympanic large, covering most of the periotic; I2 inflected medially; reduced first premolars; molar cusps relatively thin and long; lower molars with talonid broader than trigonid; spinous process of humerus much higher than capitulum; thorax relatively long and narrow; ribs expanded craniocaudally; vertebrae C7 and T1 fused and fused to ribs; vertebrae T12–L4 fused entirely without vestige of sutures; vertebrae L5 and L6 free; caudal vertebrae 8 and 9 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: *Nyctiellus lepidus* is the smallest species in the family Natalidae and one of the smallest bats in the world (notably small bats include *Crasseonycteris thonglongyai*, 1.7–2.0 g; and *Pipistrellus nanulus*, 2.5 g; Hill and Smith, 1981). Among natalids, it is approached in body weight only by two species of *Chilonatalus* (*C. micropus*, and *C. macer*), but these have a forearm longer than 32.0 mm and in *Nyctiellus* the forearm is shorter than 31.0 mm. *Nyctiellus lepidus* can also be distinguished by its absolutely and relatively shorter tibia, which is shorter than half the length of its forearm. In all other genera of Natalidae the tibia is always longer than half the length of the forearm.

Externally, *N. lepidus* can be readily distinguished from all other natalids by its relatively narrow distal third of the ear pinna and by the naked free edge of the uropatagium. In all other natalids, the distal third of the ear pinna is wide (forming part of the funnel-shaped pinna that is typical of natalids) and there is a fringe of hairs along the free margin of the uropatagium. In addition, *N. lepidus* differs from species of *Chilonatalus* (the only natalids that could be confused with *Nyctiellus* because of their small size) by the

Fig. 10. Skull and mandible of *Nyctiellus lepidus* (AMNH 167133, male, Little Exuma, Bahamas). Scale bar = 10 mm.

lack of dermal outgrowths on the dorsum of rostrum and on the chin. In all species of *Chilonatalus*, the face shows distinctive dermal outgrowths.

The skull of *Nyctiellus* is well differentiated from that of all other natalids. Its braincase is not markedly inflated and shows a very high sagittal crest that is as high along its rostral half as it is along its caudal half. All other natalids have inflated or globular braincases and a much lower sagittal crest that is more prominent in its rostral half. In *N. lepidus*, the rostral branch of the zygomatic arch is relatively robust, being deeper (wider) than the height of the last molar. In all other natalids, on the other hand, the rostral base of the zygomatic arch is thin, being shallower (narrower) than the height of the last molar. In *N. lepidus*, the emargination between the two palatal branches of the premaxillary is narrow and the inner incisors (I1) almost touch each other along the midline, whereas in all other natalids the emargination is wider and the inner incisors are widely separated. *Nyctiellus lepidus* is also distinguishable from the remaining species of the family by its undivided basisphenoid pit, a structure always bisected by a longitudinal ridge in all

TABLE 6
Summary of measurements[a] of *Nyctiellus lepidus*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight[b]	68	2.4	(2.3–2.7)	–	68	2.3	(1.9–2.7)	–
Forearm length*	24	29.7	(28.1–31.0)	0.8	46	28.9	(26.6–31.0)	0.8
Length of tibia, dry	3	11.8	(11.4–12.2)	0.4	2		(11.4–12.1)	
Length of tibia	21	13.3	(12.3–14.0)	0.5	44	13.3	(12.4–14.0)	0.5
Length of 3rd metacarpal*	15	25.4	(24.3–26.6)	0.6	30	24.8	(23.8–25.9)	0.6
Length of 5th metacarpal	15	22.6	(21.5–23.7)	0.7	30	22.3	(21.2–23.8)	0.6
Length of ear	16	12.0	(10.0–13.0)	0.7	34	12.4	(10.6–13.6)	0.8
Length of penis	–	–	–	–	32	3.3	(1.9–4.3)	0.5
Length of natalid organ	–	–	–	–	29	3.5	(2.0–4.6)	0.5
Greatest skull length	4	12.9	(12.5–13.3)	0.4	21	13.2	(12.7–14.0)	0.3
Zygomatic breadth	2		(6.4–6.5)		20	6.4	(6.0–6.7)	0.2
Braincase breadth	4	5.6	(5.3–6.0)	0.3	21	5.5	(5.2–5.8)	0.2
Breadth across molars	5	4.8	(4.7–4.8)	0.0	21	4.8	(4.6–5.2)	0.1
Breadth across canines	5	3.2	(3.1–3.3)	0.1	21	3.3	(3.1–3.6)	0.1
Maxillary tooth row	5	5.2	(5.1–5.4)	0.1	21	5.3	(5.0–5.6)	0.1
Mandibular tooth row	5	5.4	(5.3–5.5)	0.1	18	5.4	(5.3–5.6)	0.1
Postorbital breadth	4	2.6	(2.5–2.6)	0.0	21	2.6	(2.3–2.8)	0.1
Depth of braincase	2		(4.2–4.5)		13	4.5	(4.3–5.4)	0.4

[a] Descriptive statistics of measurements for each sex. N = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

[b] Measurement taken from Silva-Taboada (1979), including specimens from Cuba only.

other natalids. In addition, the ectotympanic of *N. lepidus* is very large, almost covering the entire periotic, whereas in all other natalids the ectotympanic is smaller and a large portion of the periotic is visible.

Dentally, *N. lepidus* is easily distinguishable from all other natalids by the marked reduction in the first premolar both of the upper and lower dentition. In all other natalids the first premolar is of similar size to the remaining premolars.

VARIATION: Females have larger and longer wings than males (i.e., a longer forearm, $P < 0.05$, and a longer 3rd metacarpal, $P < 0.05$). Females from Cuba have longer skulls than males (Silva-Taboada, 1979).

Average forearm length in male *Nyctiellus lepidus* from the Bahamas was smaller than those from Cuba ($P < 0.05$; fig. 12), but the Bahamian males had broader and deeper skulls (larger mean of braincase breadth, postorbital breadth, and braincase depth; $P < 0.05$; fig. 12) and longer maxillary tooth row ($P < 0.05$; fig. 12). *N. lepidus* does not differ in size throughout Cuba and the Isle of Pines (Silva-Taboada, 1979), nor among islands of the Bahamas (within the sample analyzed here).

NATURAL HISTORY AND CONSERVATION: *Nyctiellus lepidus* is known from 63 localities (36 are day roosts), including one represented by bone remains only (fig. 11). Almost all known roost sites are caves except for one disused hotel cistern near Ferry, Exuma, Bahamas, which used to be permanently occupied by a colony of this species until its restoration in 2004 (K. Murray, in litt.). Caves occupied by *N. lepidus* vary widely in size (e.g., large, Cueva del Jagüey, Cuba, locality 155, with 1700 m of linear extension, Silva-Taboada, 1974; small, Cueva del Calabazar, Cuba, locality 142, less than 10 m, Tejedor et al., 2005a). *N. lepidus* selects caves or cave chambers that have high relative humidity (Silva-Taboada, 1979) where it is often found roosting in areas of low ceiling and near bodies of water. It is occasionally found in hot caves (temperature range 25°–40° C, sensu Silva-Taboada, 1977), but more

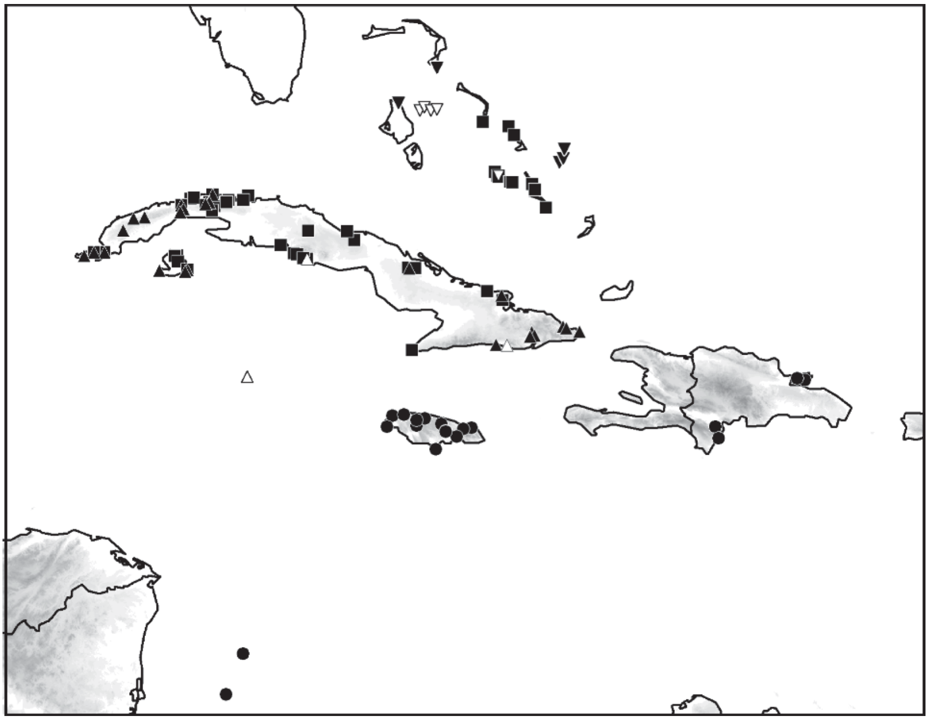


Fig. 11. Geographic distribution of *Nyctiellus lepidus* (squares), *Chilonatalus macer* (upright triangles), *C. micropus* (circles), and *C. tumidifrons* (upside down triangles). Open symbols indicate localities represented by bone remains only. Names of localities are listed in appendix 1. Gray shading on land indicates relief, with darknes increasing with altitude.

commonly roosts in caves with temperatures toward the low end of that range (Silva-Taboada, 1979). It has been found coexisting with 15 other bat species in the same cave (*Artibeus jamaicensis*, *Brachyphylla nana*, *Chilonatalus macer*, *Eptesicus fuscus*, *Erophylla sezekorni*, *Macrotus waterhousii*, *Mormoops blainvillei*, *Monophyllus redmani*, *Noctilio leporinus*, *Nyctinomops macrotis*, *Phyllonycteris poeyi*, *Pteronotus macleayi*, *Pteronotus parnellii*, *Pteronotus quadridens*, and *Tadarida brasiliensis*; Silva-Taboada, 1979), but seems to prefer caves or cave areas not occupied by groups of other species. Nonetheless, in Cueva del Calabazar, Pinar del Río, Cuba, it has been observed roosting in close association with *Chilonatalus macer* (Tejedor et al., 2005a). Within roosting groups, individuals hang widely spaced and are generally quiet, allowing human observers to approach closely (Silva-Taboada, 1979).

Nyctiellus lepidus is found from xeric (858 mm annual precipitation, Long Is., the Bahamas, locality 514) to mesic habitats (1763 mm annual precipitation, Guanayara, Cuba; locality 163) including scrub, semideciduous, and evergreen forest vegetations. In altitude, it ranges from sea level to 422 m.

Nyctiellus lepidus feeds on insects. Common food items in Cuba include leafhoppers (Cicadellidae and Fulgoridae), flies (Muscidae), termites (*Nasutitermes* sp.) plus moths (Lepidoptera) and hymenopterans (Silva-Taboada, 1979). In a 1969 study of food volume consumption by this species in Cueva Grande de Caguanes (locality 151), Cuba, females were able to carry up to near 30% of their body weight in terms of stomach contents, versus 22% in males. Also, females increased food consumption in summer (July) by 34% relative to winter (December), whereas this increase was only 8.9% for males. On average, young adults consumed

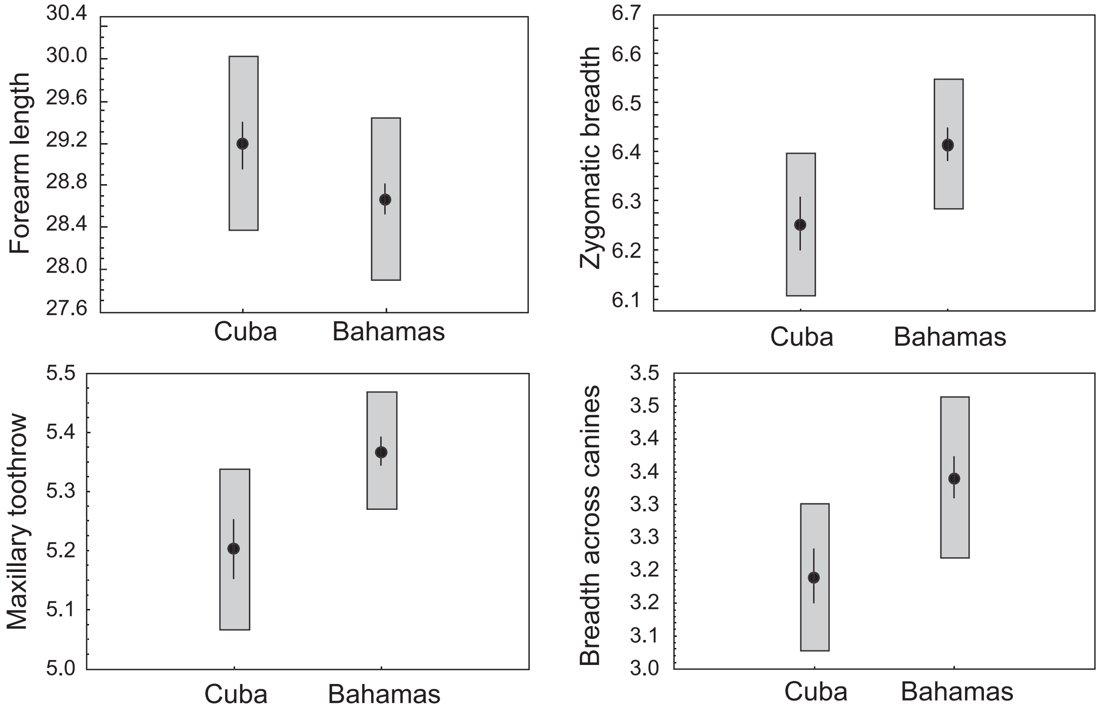


Fig. 12. Geographic variation of *Nyctiellus lepidus*. Cuba ($N = 17$) includes specimens from La Habana, Isla de la Juventud, and Granma. The Bahamas ($N = 37$) include specimens from Cat, Eleuthera, Little Exuma, Long. All specimens are male. Specimens from Cuba have slightly longer forearms but have narrower skulls and smaller rostra (Tukey, $P < 0.05$). Symbols: black dots, means; vertical gray bars, two standard deviations around the mean; vertical black line, two standard errors around the mean.

less food (about 15% of body weight) than did older adults (about 21%, Silva-Taboada, 1979).

Nyctiellus lepidus has a single annual estrus, and bears one pup per litter. In Cuba, where copulation may take place during winter (December to February), pregnant females have been found between March and July, and lactation extends from July to September, peaking in the latter month. Nonreproducing adult females are found throughout the year and subadults from both sexes are found from July to September (Silva-Taboada, 1979).

From July to September both sexes roost separately, with females gathering in large maternity colonies in the deepest parts of caves. Male-only groups form in more external areas of the caves or in neighboring caves where maternity colonies are not found. Nonreproductive females occasionally may be found within such groups of males. Allen and Sanborn (1937) noted that *N. lepidus* might also segregate sexually in July in the Bahamas. During foraging flights, females carry their pups, which average more than 35% the weight of their mothers.

Nyctiellus lepidus is an abundant species, and it is represented by at least 674 specimens in museum collections. Most specimens have been taken at only a few localities: Sheep Hill Cave, Cat, Bahamas (locality 501); Miller's Cave, Long, Bahamas (locality 512); Cueva de Las Tres Dolinas, Cuba (locality 149). Observed fluctuations in the size of colonies may be related to sexual segregation during the reproductive season.

Natural predators of the species are unknown. It is parasitized by trematodes (*Ochoterenatrema pricei*, *Limatulum solitarium*, *Urotrema scabridum*), nematodes (*Tricholeiperia* sp. *Physocephalus* sp., *Biacantha silvai*), mites (*Mesoperigliscurus nyctiellinus*, *Ornithodoros natalinus*, *Eutrombicula angulis-*

cuta, *Eutrombicula lipovskyana*), and streblids (*Trichobius wenzeli*; Milán and Stekol'nikov, 2004; Silva-Taboada, 1979).

Nightly, there are two foraging periods. The first begins around sunset (−8 min to +11 min) and extends for up to 45 minutes, the second is shorter and ends around sunrise (−8 min to +5 min). Males begin and end their foraging bouts before females, especially lactating ones, which carry their young in flight. Such short foraging bouts are associated with a massive exodus and return to the caves and probably with very small home ranges. Mark-recapture trials performed during foraging periods indicated that individuals were unable to return to their cave if released at distances greater than 2 km from the roost (Silva-Taboada, 1979). *Nyctiellus lepidus* flies very erratically and low within vegetation or over open pasture.

The body temperature of *Nyctiellus lepidus* has been observed to increase from 33.5° C to 35.2° C in association with a seasonal increase in ambient temperature from 24.7 (March) to 27.4 (May). This species is susceptible to rapid dehydration outside the roost, and has the highest rate of water loss from patagia among Cuban bats (other species of natalids were not examined; Silva-Taboada, 1979).

This species has been listed as least concern by the IUCN (2010) Its ability to form large colonies in very small caves or cavelike habitats and to forage over open pasture and secondary scrub suggest that it is a resilient species, unlikely to be threatened as long as its roost sites are left undisturbed.

Genus *Primonatalus* Morgan and Czaplewski, 2003

Primonatalus Morgan and Czaplewski, 2003: 733. Type species *Primontalaus prattae* Morgan and Czaplewski, 2003 by original designation.

DIAGNOSIS: Small size; distinct mandibular angle present; ventral margin of mandible nearly straight between p4 and mandibular angle; coronoid process slightly higher than condyloid, dorsally to alveolar plane of dentary; rostral margin of ascending ramus of mandible forming angle of about 70° with alveolar plane of dentary; pointed projection on margin of dentary between angular process and condyloid sometimes present; angular process spatulated with prominent medial projection; anterior rim of orbit nearly perpendicular to alveolar plane of maxilla; maxillary branch of zygomatic arch thin, nearly as deep as crown height of M2; p3 with labial cingulum distinctly indented between roots; occlusal outline of P4 with anterior indentation; mesostylar crests of M1 and M2 long and broadly curved (crescent shaped); mesostylar crest present on M3; capitulum of humerus large and bulbous; spinous process short and separated from capitulum by small notch. A comparison of diagnostic characters between *Primonatalus*, and other natalid genera is summarized in table 3.

ETYMOLOGY: From *primus*, Latin for "first," and *natalus*, type genus of the family Natalidae. The name indicates that it is the earliest known member of Natalidae.

CONTENTS: *P. prattae* (type species) Morgan and Czaplewski, 2003.

Primonatalus prattae Morgan and Czaplewski, 2003
Figure 13

HOLOTYPE: UF 108641, partial right dentary with m1–3, collected by A.E. Pratt in Thomas Farm, 12 km northeast of Bell, Gilchrist County, Florida (maped by Morgan and Czaplewski, 2003). Age of fossil deposit: early Miocene (early Hemingfordian North American land mammal age).

PARATYPES: UF 121145, ascending ramus of right dentary (fig. 13); UF 108647, edentulous partial left dentary with symphysis and alveoli for i1–p4; UF 108642, partial left dentary with p3 and alveoli for p2 and p4; UF 121136, right P4; UF108638, partial left maxilla with M1–2; UF 121139, right M3; UF 121141, periotic; UF 108650, distal half of left humerus.

DISTRIBUTION: Known only from the type locality.

DIAGNOSIS: Same as for genus.

DESCRIPTION: Small size (maximum width of distal humerus 2.8–2.9 mm, *N* = 4); distinct mandibular angle present and closer to level of coronoid than to level of condyloid; ventral margin of mandible almost straight between p4 and mandibular

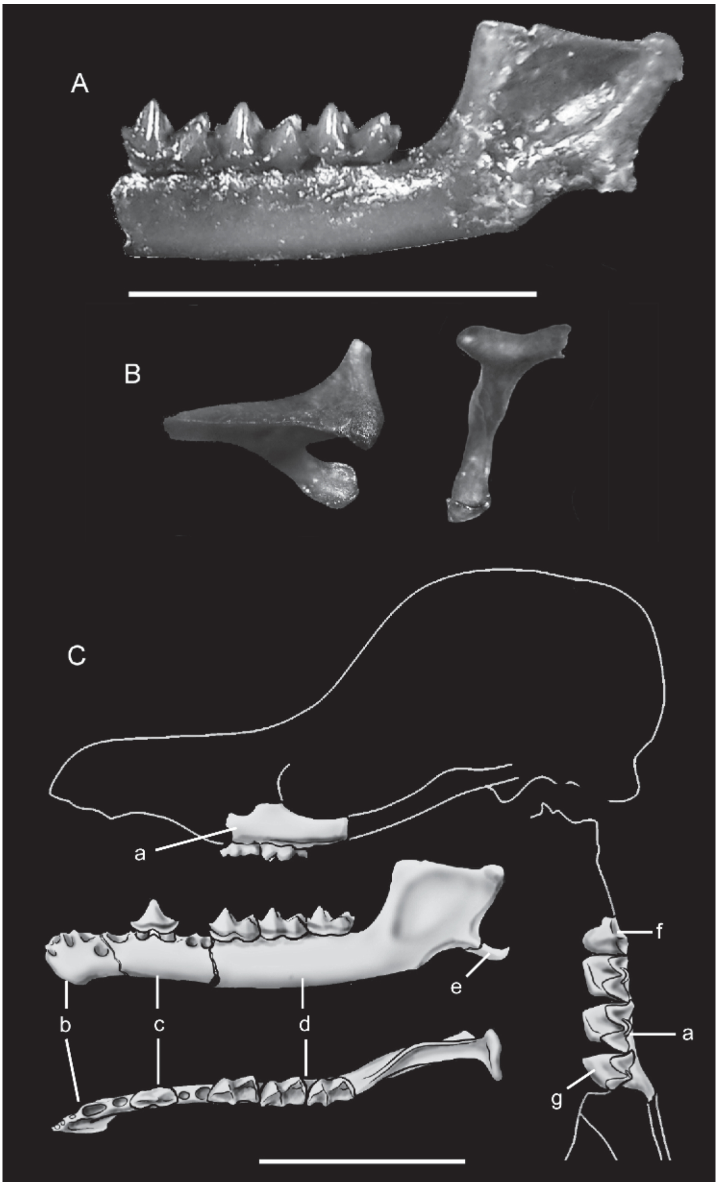


Fig. 13. **A,** Holotype of *Primonatalus prattae*, UF 10864, right dentary, image inverted. **B,** Right: dorsolateral view of right ascendant ramus of mandible with mandibular angle, UF 121145. Left: caudal view of right ascendant ramus of mandible with mandibular angle, UF 121145. **C,** Reconstruction of the skull and mandible of *Primonatalus prattae*. Specimens (a) UF 108638; (b) UF 108647 (not shown entirely); (c) UF 108642 (not shown entirely); (d) UF 108641 (holotype; right dentary, image inverted); (e) UF 121145 (not shown entirely; right mandibular angle, image inverted); (f) UF 121136 (right P4, image inverted); (g) UF 121139 (right M3, image inverted). Skull contour is conjectural. Scale bars = 5 mm.

angle; coronoid process slightly higher than condyloid above alveolar plane of dentary; rostral margin of ascending ramus of dentary forming angle of about 70° with alveolar plane of dentary; rounded projection on margin of dentary between angular process and condyloid sometimes present; angular process spatulated with prominent medial rounded projection; anterior rim of orbit nearly perpendicular to alveolar plane of maxilla; maxillary branch of zygomatic arc thin, nearly as deep as crown height of M2; maxilla apparently not inflated; i1 and i2 separated from i3 by small gap; occlusal outline of p3 long and constricted at level of cusp; p3 with labial cingulum distinctly indented between roots of tooth; mesostylar crests on M1 and M2 long and broadly curved; mesostylar crest present on M3 and longer along postparacrista; cingular cusp of P4 apparently short and broad; occlusal outline of P4 with anterolingual indentation; molars cusps relatively broad; spinous process of humerus much higher than capitulum; capitulum of humerus large and bulbous; spinous process short and trilobed, separated from capitulum by small notch.

COMPARISONS: *Primonatalus prattae* is known from a few fragmentary specimens, many of which are the only specimens known of their type. Therefore, for most characters, the morphological variation within this species cannot be evaluated at present. Nonetheless, the material at hand allows for distinguishing *P. prattae* unambiguously from other species of Natalidae, using a combination of unique and shared characters.

The only currently known diagnostic character unique to *Primonatalus prattae* is the apophysis of the angular process, which is characterized by a rounded medial projection that makes it broader than the shaft. In all other natalids, except *Nyctiellus lepidus*, the apophysis of the angular process is about as wide as the shaft and lacks a medial projection. The angular process of *Nyctiellus lepidus* is similar to that of *P. prattae,* but the medial projection in *N. lepidus* (which is absent in some individuals) is smaller than that of *P. prattae* and pointed. The lower dentition of *P. prattae* also differs from that of *Nyctiellus*. In *P. prattae*, the labial cingulum of p3 is indented between the roots of the tooth, whereas in *Nyctiellus* this cingulum is straight. Also, in *P. prattae*, the lower molar hypoconids diminish progressively in size from m1 to m3, whereas in *Nyctiellus* all hypoconids are of similar size. Finally, *P. prattae* differs from *Nyctiellus* in its broadly curved mesostylar crests of M2 and M3 (nearly straight in *Nyctiellus*), and its thin base of the zygomatic arch (thicker than 3/2 the height of the last molar in *Nyctiellus*, in lateral view).

The coronoid process of the holotype of *P. prattae* is slightly higher than the condyloid process above the alveolar plane of the dentary, a character it shares only with *Natalus primus* (although this character is polymorphic in the latter). All other species of Natalidae have a coronoid process that is slightly lower than or as high as the condyloid above the alveolar plane of the dentary. On the other hand, *P. prattae* differs from all species of the genus *Natalus* in that the base of its dentary bone ventral to molars is nearly straight (markedly curved in the genus *Natalus*). Also, it is distinguished from most species of *Natalus* in the presence of a mesostylar crest in M3, a feature absent in most representatives of *Natalus* (excluding *N. primus*). Finally, a large, bulbous capitulum and a short, triangular spinous process on the humerus distinguish *P. prattae* from the genera *Chilonatalus* and *Nyctiellus*, which have a smaller, somewhat cylindrical capitulum and a long and hooked spinous process. The size of the humerus, however, is most similar to that of the genus *Chilonatalus* (table 10).

NOTE: The characters that associate *P. prattae* with each of the three extant genera of Natalidae are all seen on separate specimens. The angular process is most similar to that of *Nyctiellus*, the dentary and lower and upper dentition are most similar to those of *Chilonatalus*, and the distal humerus is most similar to that of *Natalus*. This opens the question of whether *Primonatalus* is a chimera. The evidence, however, suggests otherwise. All natalid fossils from Thomas Farm were recovered from a single 3 m thick section of sediments of uniform taphonomy, indicating a similar age and origin of the fossils. Also, the size relationship among all *Primonatalus* specimens is similar to that among corresponding anatomical elements of extant natalid genera. Assuming similar body proportions between the Thomas Farm natalid fossils and extant natalids, it is reasonable to hypothesize that all fossils assigned to *Primonatalus* belong to a single taxon.

Genus *Chilonatalus* Miller, 1898

Natalus: Dobson, 1880: 443. Part, not *Natalus* Gray, 1838.

Natalus (*Chilonatalus*) Miller, 1898: 326. Type species *Natalus micropus* Dobson, 1880 by original designation.

Chilonatalus: Miller, 1903: 119. First use as a genus.

DIAGNOSIS: Dermal outgrowths on dorsum of rostrum and on chin, producing in profile a double-lipped aspect; ears large, without ear ridges; mustached formed by parallel hairs forming a compact row; plagiopatagium attaching at midtibia; rostrum long and slender, braincase globular and delicate, mandibular symphysis with long posteroventral projection; shaft of angular process long, slender, dorsally curved with a markedly hooked tip; labial cingular cusp of p4 long and pointed; ribs fused into a rigid thoracic bell. A comparison of diagnostic characters between *Chilonatalus*, and other natalid genera is summarized in table 3.

ETYMOLOGY: combination of the names of the genera *Natalus* and *Chilonycteris* (= *Pteronotus*), given by Miller (1898) in reference to the *Pteronotus*-like dermal outgrowths on the muzzle of this genus.

CONTENTS: *C. macer* Miller, 1914; *C. micropus* (type species) Dobson, 1880; *C. tumidifrons* Miller, 1906.

Chilonatalus macer Miller, 1914
Figure 14

Chilonatalus micropus: Miller, 1904: 340. Not *Natalus* (*Chilonatalus*) *micropus* Miller, 1898.

Chilonatalus macer Miller, 1914: 225. Type locality Baracoa, Guantánamo, Cuba.

Natalus (*Chilonatalus*) *macer*: Dalquest, 1950: 443. New combination.

Natalus micropus macer: Viña Bayés and Deas Díaz, 1970: 7. New combination.

HOLOTYPE: USNM 113724, adult female, skin in alcohol with skull removed, collected by W. Palmer on 6 February 1902, "in a cave" (identified by Silva-Taboada, 1979, as Cueva de la Majana), Baracoa, Cuba. The skin has the tail membrane and both hind legs disconnected from the body. The skull is complete but has been apparently slightly compressed transversally, so that the zygomatic arches are asymmetrically buckled.

DISTRIBUTION: Cuba, Isle of Pines, Grand Cayman (fossil only); fig. 11.

DIAGNOSIS: Forearm short (32.1–33.8 mm); tibia long (18.2–20.25 mm); penis short (1.5–1.9 mm); natalid organ long (2.35–7.7 mm); greatest skull length (13.8–14.5 mm); least postorbital breadth relatively narrow; lateral margin of ear straight; attachment of wing to tibia on the proximal half of the tibia (at about 1/3 of its length, measured from the knee); in lateral view, braincase uninflated and rising from rostrum as a gently curving slope dorsal to orbit; ridge between basisphenoid furrows wide; caudal margin of ascending ramus of mandible forming a straight angle with alveolar plane of dentary; lateral sides of basisphenoid pits nearly parallel; p2 not crowded; fusion between original elements of thoracic cage seamless ventrally. A comparison of diagnostic characters between *C. macer*, and other species of *Chilonatalus* is summarized in table 4.

DESCRIPTION: Small size (forearm length 32.1–33.8 mm; greatest skull length 14.2–14.9 mm; weight 2–4 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening ventrolaterally at the end of tubelike projections on margin of upper lip; upper lip slightly thickened; lower lip markedly thickened and constricted in dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; high dermal tubercle on dorsum of rostrum caudal to nostrils; tubercles of ramal vibrissae coalesced into transversal ridge ventral to lower lip; natalid organ very large (up to 1/2 of greatest length of skull), elliptical, and reaching crown of head; ears relatively long (12.7–16.4 mm); ear pinna very wide and funnel shaped; pinna with moderately pointed tip; lateral and medial margins of pinna straight; three very small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus markedly short, lanceolate, and twisted into helixlike structure; tibia (18.2–20.3 mm) longer than half the length of the forearm; calcar very long and thin, occupying about 2/3 of the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings

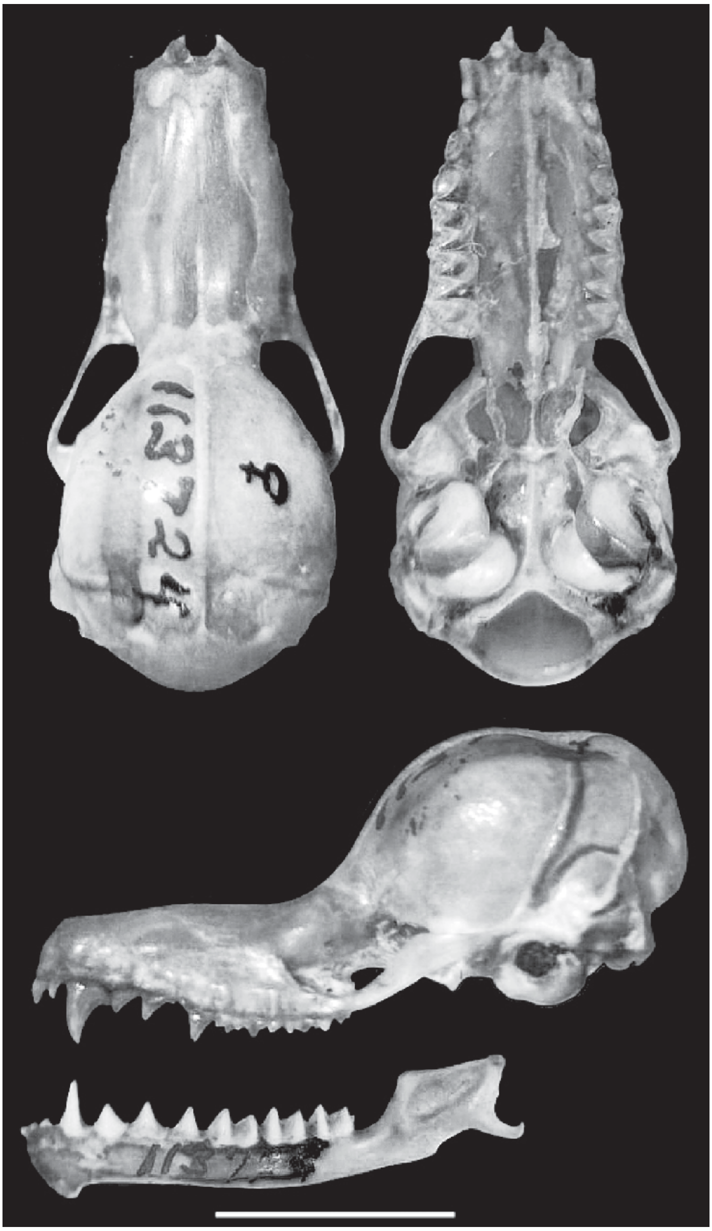


Fig. 14. Holotype of *Chilonatalus macer* (USNM 113724, female, Baracoa, Cuba). Scale bar = 5 mm.

relatively long and wide, with 3rd metacarpal (30.3–32.4 mm) longer than 5th metacarpal (27.9–30.5 mm); wings attach to tibia at proximal third of distance between knee and ankle; pelage dense and lax; hairs long (5–8 mm, dorsally; 3–7 mm, ventrally); pelage color from light brown to orange brown, lighter dorsally; hairs bicolored, with tips darker than bases; dense mustachelike hair tufts along lateral margins of upper lip; mustache formed by dense, tough, parallel, and ventrally curved hairs; natalid organ nearly naked; skull long and narrow with moderate rostral flexion; rostrum long and narrow, with marked sulcus between nasals; moderate palatal emargination; maxilla con-

TABLE 7
Summary of measurements[a] of *Chilonatalus macer*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight[b]	30	2.9	(2.6–3.2)	–	15	2.9	(2.6–3.3)	–
Forearm length	10	33.1	(32.1–33.8)	0.5	10	32.9	(32.3–33.4)	0.4
Length of tibia, dry	5	17.9	(17.2–18.3)	0.4	2	18.2	(18.0–18.4)	0.2
Length of tibia	5	18.9	(18.2–19.7)	0.7	8	19.4	(18.7–20.3)	0.6
Length of 3rd metacarpal	9	31.7	(30.9–32.4)	0.6	10	31.1	(30.3–31.9)	0.5
Length of 5th metacarpal	9	29.0	(28.2–30.5)	0.7	10	28.4	(27.9–29.0)	0.3
Length of ear	5	14.2	(12.7–16.4)	1.6	6	14.5	(13.2–15.4)	0.7
Length of penis		–	– –	–	8	1.8	(1.5–2.6)	0.3
Length of natalid organ		–	—	–	7	5.6	(2.4–7.7)	1.7
Greatest skull length	3	14.5	(14.3–14.6)	0.2	2	14.5	(14.2–14.9)	0.4
Zygomatic breadth	3	6.5	(6.5–6.6)	0.0	3	6.7	(6.6–6.7)	0.1
Braincase breadth	3	6.0	(5.8–6.1)	0.2	3	6.1	(6.0–6.2)	0.1
Breadth across molars	3	4.3	(4.1–4.6)	0.3	3	4.7	(4.6–4.7)	0.0
Breadth across canines	3	3.0	(2.9–3.2)	0.2	3	3.2	(3.2–3.3)	0.1
Maxillary tooth row	3	6.1	(5.9–6.2)	0.1	3	6.1	(5.9–6.3)	0.2
Mandibular tooth row	3	6.2	(6.1–6.3)	0.1	3	6.3	(6.2–6.5)	0.1
Postorbital breadth	3	2.7	(2.6–2.7)	0.1	3	2.9	(2.9–2.9)	0.0
Depth of braincase	3	5.0	(4.9–5.1)	0.1	1	5.1	(5.1–5.1)	–

[a] Descriptive statistics of measurements for each sex. *N* = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

[b] Measurement taken from Silva-Taboada (1979).

vex dorsal to molars; braincase greatly inflated, rising gently from rostrum; sagittal crest moderately developed; postorbital constriction relatively wide (42%–44% of zygomatic breadth); maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids convergent; palate extending caudally to half the length of pterygoids; basisphenoid pit deep and steep sided; longitudinal medial ridge on basisphenoid present; ectotympanic large, covering about half of the periotic; upper incisors long and pointed; occlusal profile of premolars long; upper premolars of similar size and not crowded; mesostylar crests on M1 and M2 long and broadly curved, mesostylar crest present on M3; cingular cusp of p4 long and pointed; molars cusps relatively broad; spinous process of humerus much higher than capitulum; thorax relatively short and wide; all ribs fused among each other and with sternum forming a single bell-shaped structure; vertebrae C7 to T7 fused among themselves and to ribs; vertebrae T11–L5 fused entirely without vestige of sutures; vertebrae L6 free; caudal vertebrae 4–7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: *Chilonatalus macer* is easily distinguishable from species of the genus *Natalus* and from *Nyctiellus lepidus* by generic-level diagnostic characters: presence of dermal outgrowths on dorsum of rostrum and on chin, producing a double-lipped aspect; presence of three ear ridges; mandibular symphysis with long posteroventral projection; shaft of angular process curved dorsally and with a markedly hooked tip; and labial cingular cusp of p4 long and pointed. In the genera *Natalus* and *Nyctiellus*, the face lacks dermal outgrows, the ear shows ridges in various numbers, the mandibular symphysis shows a short (or absent) posteroventral projection, the mandibular angle may be pointed (*Nyctiellus*) or blunt (*Natalus*); and the labial cingular cusp of p4 is short or very little developed.

From the other two species of *Chilonatalus*, *C. macer* can be separated using a combination of external and cranial characters. Externally, *Chilonatalus macer* differs from *C. micropus* in its straight lateral margin of the ear, the attachment of the wing on the proximal half of the tibia, a short penis (1.5–1.9 mm), a long tibia (18.2–20.25 mm), and a large, elliptical natalid organ (length of natalid organ 2.35–7.7 mm). *Chilonatalus micropus*, in contrast, is characterized by a concave lateral ear margin, a wing attaching to the tibia on its distal half, a long penis (3.6–6.5 mm), a short tibia (14.7–17.95 mm), and a small, hemispherical natalid organ (length of natalid organ 3.3–3.7 mm). Cranially, *C. macer* and *C. micropus* can be separated by the dorsal flexion point of the skull (with a well-defined angle in *C. micropus* and a gently curving slope in *C. macer*), the angle formed by the caudal margin of the ascending ramus of mandible with the alveolar plane of the dentary (straight in *C. macer* and about 70° in *C. micropus*), the lateral sides of the basisphenoid pits (nearly parallel in *C. macer* and widely diverging caudally in *C. micropus*), and by the fusion of the ribs with sternum (seamless in *C. macer* and retaining sutures in *C. micropus*).

Chilonatalus macer does not differ appreciably from *Chilonatalus tumidifrons* in external characters. The easiest way to separate both species is by skull size (greatest skull length 13.8–14.5 mm in *C. macer* and 15.15–15.95 mm in *C. tumidifrons*. Also, the two species differ in the relative width of the postorbital constriction (42%–44% of zygomatic breadth in C. *macer* and 38%–41% in C. *tumidifrons*), in the degree of crowding of P2 (not crowded in *C. macer* and crowded in *C. tumidifrons*), and in the relative width of the ridge between basioccipital furrows (narrow in *C. macer* and wide in *C. tumidifrons*).

VARIATION: In a sample of 12 males and 18 females the only measurement that showed sexual dimorphism in size was the length of the humerus (Silva-Taboada, 1974). The species shows no geographic variation between western and eastern Cuba or between Cuba and the Isle of Pines.

NATURAL HISTORY AND CONSERVATION: *Chilonatalus macer* is known from 33 localities (including two represented by bone remains only), of which 22 are day roosts, and 19 are caves. On three occasions it has been found roosting solitarily in highly unusual conditions: (1) inside a house for drying tobacco; (2) inside a camping tent, and (3) on a sugarcane sappling. These occurrences suggest that occasionally some individuals are unable to return to their permanent roosts before sunrise.

Chilonatalus macer roosts in warm and humid caves (six of these have been hot caves) but it has also been found solitarily in cooler and drier caves. These bats generally form groups of 30–50 individuals in protected areas of low ceilings, keeping a wide distance between individuals, which usually hang from a single foot. This species has been found coexisting in the same caves with 13 other bat species (*Artibeus jamaicensis*, *Brachyphylla nana*, *Eptesicus fuscus*, *Erophylla sezekorni*, *Macrotus waterhousii*, *Mormoops blainvillei*, *Monophyllus redmani*, *Natalus primus*, *Nyctiellus lepidus*, *Phyllonycteris poeyi*, *Pteronotus macleayi*, *Pteronotus parnellii*, and *Pteronotus quadridens*), but usually roosts separated from them (Silva-Taboada, 1979). Nonetheless, *C. macer* has been found in close association with other species on two occasions: (1) apparently solitarily, within a colony of *Pteronotus quadridens* (Cueva del los Majáes, Tejedor et al., 2005a); and (2) in a small group contiguous with a large colony of *Nyctiellus lepidus* (Cueva del Calabazar, Tejedor et al., 2005a).

Chilonatalus macer is commonly found in mesic habitats having up to 2521 mm of annual precipitation (Baracoa, Cuba; locality 152), but is occasionally found in xeric environments (e.g., Cueva de los Masones, locality 154; annual precipitation of 834 mm). It has been found from sea level up to 230 m (Cueva del Indio; locality 106).

Very little is known of the food habits of *C. macer*. In Cuba it has been found to feed mostly on moths (Lepidoptera) and occasionally on spiders. It can carry in its stomach up to 28.6% of its body weight (Silva-Taboada, 1979).

The reproductive pattern of *C. macer* is largely unknown. Two pregnant females found in May carried embryos measuring 10 mm in crown-rump length. Of two females taken in August, one was lactating and another postlactating. Reproductively inactive females have been found in January, March, and December (Silva-Taboada, 1979). In May, in Cueva La Barca, Pinar del Rio, Cuba, sexes have been found forming separate groups, with females roosting deep in a hot area of the cave and males occupying a cooler area near a small entrance, suggesting a pattern of sexual segregation similar to that of *N. lepidus*.

Chilonatalus macer is represented by at least 123 specimens in museum collections, most of which were collected at Cueva No. 2 Punta del Este, and Cueva del Promontorio, both in Isla de la Juventud, Cuba. Colonies are relatively small, containing from a few dozen to a few hundred bats.

Natural predators are not known. *Chilonatalus macer* is parasitized by the streblid *Trichobius frequens* (Silva-Taboada, 1979).

The foraging exodus of *C. macer* has been recorded to begin 14 min after sunset and to last for over 30 min. Individuals returning to their roosts have been taken late at night (23:00 hr) indicating that these bats were active for long periods throughout the night (Silva-Taboada, 1979). This species has an amazingly maneuverable flight. It is able to fly without hovering within reduced spaces (0.125 m^3) and is easily distinguishable inside caves by its rather rectilinear flight path and its very slow and shallow wing beat. Such slow, maneuverable flight, coupled with a small size, may enable this bat to forage in denser vegetation than most other Neotropical bats. It dehydrates and dies very rapidly if taken out of their caves during daytime.

It is is listed in IUCN's Red List of Threatened Species (IUCN, 2010) as near threatened under *Chilonatalus micropus*. With the recognition of this taxon as a Cuban endemic different from *Chilonatalus micropus*, the study of its population status merits attention to accurately evaluate its conservation needs. Given its habit of aggregating in relatively small numbers in isolated and sparsely distributed colonies, its future IUCN category may increase in threat level.

Chilonatalus micropus (Dobson, 1880)
Figure 15

Natalus micropus Dobson, 1880: 443. Type locality "Environs of Kingston, Jamaica."

Natalus (*Chilonatalus*) *brevimanus*: Miller, 1898: 328. Type locality "Old Providence island, Caribbean Sea," Colombia.

Chilonatalus micropus: Miller, 1907: 185. New combination.

Chilonatalus brevimanus: Miller, 1907: 185. New combination.

Natalus micropus brevimanus: Varona, 1974: 31. New combination.

Natalus micropus micropus: Varona, 1974: 32. Name combination.

HOLOTYPE: Holotype by monotypy, BMNH 80.12.14.1 collected in the "Environs of Kingston, Jamaica." Skull in good condition.

DISTRIBUTION: Hispaniola (Dominican Republic), Jamaica, San Andrés and Providencia islands (Colombia); fig. 11.

DIAGNOSIS: Forearm long (30.7–35.1 mm); tibia relatively short (14.7–17.95 mm); penis long (3.6–6.5 mm), natalid organ hemispherical and small (3.3–3.7 mm); least postorbital breadth relatively wide; lateral margin of ear deeply notched; wing attaches at the distal half of tibia (at about 2/3 of its length, measured from the knee); dorsal point of flexion between rostrum and braincase forming a well-defined angle dorsal to orbit; braincase globular and rising abruptly from rostrum; ridge between basisphenoid furrows wide, caudal margin of ascending ramus of mandible forming an angle smaller than 70° with alveolar plane of dentary; p2 not crowded; fusion between original elements of thoracic cage complete but with visible suture lines. A comparison of diagnostic characters between *C. micropus*, and other species of *Chilonatalus* is summarized in table 4.

DESCRIPTION: Small size (forearm length 30.7–35.1 mm; greatest skull length 13.5–14.7 mm; weight 2.6 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening ventrolaterally at the end of short, tubelike projections on margin of upper lip; upper lip slightly thickened; lower lip markedly thickened and constricted in dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; low dermal tubercle on dorsum of rostrum caudal to nostrils; tubercles of ramal vibrissae coalesced into transversal ridge ventral to lower lip; natalid organ

Fig. 15. Holotype of *Chilonatalus micropus* (BMNH 80.12.14.1, "environs of Kingston," Jamaica). Scale bar = 5 mm.

small and hemispherical, located at intersection between rostrum and braincase; ears relatively long (13.0–16.4 mm); ear pinna very wide and funnel shaped; pinna with moderately pointed tip; medial margin of pinna straight; lateral margin of pinna concave; three very small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus markedly short, lanceolate, and twisted into helixlike structure; tibia (14.7–17.9 mm) slightly shorter than half the length of the forearm; calcar

TABLE 8
Summary of measurements[a] of *Chilonatalus micropus*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min–Max.)	SD
Weight	1	3	– –	–	2	–	(2.6–5.0)	–
Forearm length*	34	33.8	(32.1–35.0)	0.8	56	33.2	(30.7–35.1)	0.9
Length of tibia, dry	3	15.8	(15.3–16.2)	0.5	6	15.8	(14.7–17.2)	1.0
Length of tibia	30	16.6	(15.1–17.9)	0.7	50	16.4	(14.7–17.8)	0.7
Length of 3rd metacarpal*	33	30.9	(28.9–33.5)	0.8	48	30.1	(25.5–31.9)	1.2
Length of 5th metacarpal*	33	28.2	(26.6–30.2)	0.9	47	27.4	(23.7–29.2)	1.1
Length of ear	14	14.7	(13.0–16.4)	1.0	23	14.8	(13.0–16.1)	0.9
Length of penis		–	– –	–	43	4.8	(3.6–6.5)	0.8
Length of natalid organ		–	– –	–	33	3.2	(2.1–4.3)	0.6
Greatest skull length	6	14.1	(13.9–14.2)	0.1	19	14.1	(13.5–14.7)	0.3
Zygomatic breadth	6	6.5	(6.3–6.7)	0.1	17	6.5	(6.2–6.8)	0.2
Braincase breadth	6	6.0	(5.8–6.2)	0.1	19	6.0	(5.7–6.5)	0.2
Breadth across molars	6	4.3	(4.1–4.4)	0.1	18	4.3	(3.8–4.5)	0.2
Breadth across canines	5	3.1	(3.0–3.2)	0.1	17	3.1	(2.8–3.4)	0.2
Maxillary tooth row	7	5.8	(5.7–5.9)	0.1	19	5.8	(5.6–6.0)	0.1
Mandibular tooth row	7	6.2	(6.0–6.3)	0.1	19	6.1	(5.8–6.3)	0.1
Postorbital breadth	7	2.7	(2.5–2.9)	0.1	19	2.8	(2.5–3.0)	0.1
Depth of braincase	6	5.0	(4.8–5.5)	0.2	17	5.1	(4.8–5.4)	0.2

[a] Descriptive statistics of measurements for each sex. *N* = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P \leq 0.05$) are followed by an asterisk (*).

very long and thin, occupying about 2/3 of the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively long and wide, with 3rd metacarpal (25.5–33.5 mm) longer than 5th metacarpal (23.7–30.2 mm); wings attach to tibia at about 2/3 the distance from knee to ankle; pelage dense and lax; hairs long (4–7 mm, dorsally; 3–6 mm, ventrally); pelage color from light grayish brown to yellowish or reddish brown, lighter dorsally; hairs bicolored, with tips darker than bases; dense mustachelike hair tufts along lateral margins of upper lip; mustache formed by dense, tough, parallel, and ventrally curved hairs; natalid organ nearly naked; skull long and narrow with moderate rostral flexion; rostrum long and narrow, with marked sulcus between nasals; moderate palatal emargination; maxilla concave dorsal to molars; braincase extremely inflated (globular), rising abruptly from rostrum; sagittal crest poorly developed; postorbital constriction relatively wide (41%–45% of zygomatic breadth); maxillary branch of zygomatic arch thin, as deep as the height of crowns of last molars; pterygoids convergent; palate extending caudally to half the length of pterygoids; basisphenoid pit deep and steep sided; longitudinal medial ridge on basisphenoid present; ectotympanic medium sized, covering about half of the periotic; upper incisors long and pointed; I1 similar in length to I2; occlusal profile of premolars long; upper premolars of similar size and not crowded; mesostylar crests on M1 and M2 long and broadly curved, mesostylar crest present on M3; cingular cusp of p4 long and pointed; molar cusps relatively broad; spinous process of humerus much higher than capitulum; thorax relatively short and wide; all ribs fused among each other and with sternum forming a single bell-shaped structure with sutures remaining among original elements; vertebrae C7 to T3 fused among themselves and to ribs; vertebrae T11–L5 fused entirely without vestige of sutures; vertebrae L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: From species of the genera *Natalus* and *Nyctiellus*, *Chilonatalus micropus*

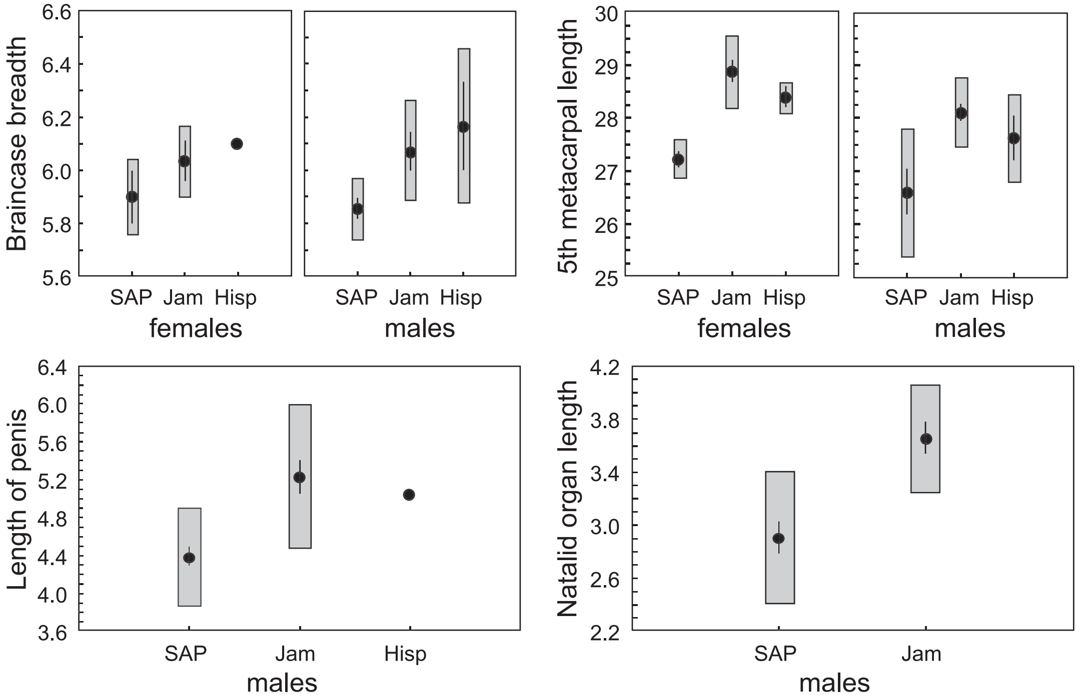


Fig. 16. Geographic variation of *Chilonatalus micropus*. SAP: San Andrés and Providencia islands, Colombia (12 females, 24 males); Jam: Jamaica (19 females, 29 males); Hisp: Hispaniola (2 females, 4 males). Mean braincase breadth of the sample from Hispaniola was larger but the difference was not statistically significant. The sample from Jamaica was larger in most external dimensions (Tukey, $P < 0.05$), most notably in length of 5th metacarpal, length of penis, and length of natalid organ. Symbols: black dots, means; vertical gray bars, two standard deviations around the mean; vertical black line, two standard errors around the mean.

can be distinguished on the basis of generic characters (see comparisons under account of *Chilonatalus macer*). From other species of *Chilonatalus* (i.e., *C. tumidifrons* and *C. macer*), *C. micropus* can be distinguished by several external and osteological characters. Externally, in *C. micropus*, the distal fourth of the ear is narrower than in the remaining species of *Chilonatalus*, leaving a concavity in the lateral margin of the pinna, which is absent in *C. macer* and *C. tumidirostris*. Also, the dermal tubercle above the nostrils is relatively low in *C. micropus*, whereas it is high and prominent in *C. tumidifrons* and *C. macer*. In *C. micropus*, the plagiopatagium attaches to the distal half of the tibia whereas in the other two species of *Chilonatalus* it attaches to the proximal half of the tibia. In addition, males of *C. micropus* have a relatively long penis (3.6–6.7 mm) and a small, hemispherical natalid organ, whereas males of *C. tumidifrons* and *C. macer* have a relatively short penis (penis length less than 2.5 mm) and a very large, elliptical natalid organ that in full development extends from the rostral tubercle to the crown.

Cranially, *C. micropus* is characterized by a globular braincase, which rises in a sharp angle from the rostrum. In *C. macer* and *C. tumidifrons* the braincase is relatively not as greatly inflated and rises from the rostrum in a gentler, sloping curve. Also, in *C. micropus* the caudal margin of the ascending ramus of the mandible is more concave and the shaft of the mandibular angle is thinner. In *C. tumidifrons* and *C. macer* the dorsal margin of the mandibular angle is deeper, rendering the caudal margin of the ascending ramus of the dentary less concave than in *C. micropus*.

In addition to the discrete characters mentioned above, *C. micropus* can be distinguished from *C. tumidifrons* on the basis of skull size alone (greatest skull length 13.5–14.7 mm in *C. micropus* and 15.15–15.95 mm in *C. tumidifrons*).

VARIATION: In *C. micropus*, females are larger than males in length of the forearm and 3rd and 5th metacarpals (Tukey, $P < 0.05$; table 8). Ottenwalder and Genoways (1982) showed that males are larger than females in depth of braincase and braincase breadth (the latter only true for Jamaican populations).

The inflation of the braincase decreases westward, with animals from Hispaniola having the most globular braincase within both the species and the family Natalidae (mean braincase breadth also follows this trend yet the differences were not statistically significant; $P > 0.01$; fig. 16). The depth of the rostrum, on the other hand, appears to decrease eastward with animals from Hispaniola having the most dorsoventrally flattened and slender rostra. Individuals from Jamaica were the largest in most external dimensions, with the exception of ear length ($P < 0.01$; fig. 16). In a larger sample, Ottenwalder and Genoways (1982) found the specimens from Old Providence to be the smallest (on average) in greatest skull length, breadth of braincase (males only) and maxillary tooth row (males only).

NATURAL HISTORY AND CONSERVATION: Species known from 21 localities of which eight have been day roosts, all of them caves. All caves known to harbor *C. micropus* are warm and humid, and at least five of these (Windsor, Oxford, Monarva, Los Patos, St. Clair) are medium-sized to large caves with hot sections (Fincham, 1997). In St. Clair cave, *C. micropus* was found in the warmest areas, where the air was saturated with water vapor and had high concentrations of hydrogen sulfide (Goodwin, 1970). It seems to favor protected areas inside caves such as high recesses (Osburn, 1865), wall chambers (Goodwin, 1970), or the underside of low ledges (Kerridge and Baker 1978), where it has been found roosting in loose clusters. Genoways et al. (2005), however, observed *C. micropus* roosting out in the main passageway of St. Clair Cave. It coexists in caves with nine other bats species (*Artibeus jamaicensis*, *Erophylla sezekorni*, *Monophyllus redmani*, *Mormoops blainvillei*, *Natalus jamaicensis*, *Phyllonycteris aphylla*, *Pteronotus macleayi*, *Pteronotus parnellii*, and *Pteronotus quadridens*). Osburn (1865; fide Genoways et al., 2005) observed *C. micropus* roosting separately from other species, but Goodwin (1970) found it in a mixed colony with *Natalus jamaicensis*, although he assumed the two species were segregated within the colony. When disturbed within caves, it retreats, flying near walls at about 1 m above the floor (Kerridge and Baker, 1978).

Chilonatalus micropus occurs most commonly in mesic environments receiving up to 2899 mm in annual precipitation (Port Antonio, Jamaica; locality 247), from sea level to 400 m in elevation (Mahogany Hall Cave, Jamaica; locality 244). Its food habits are unknown, but as for other representatives of Natalidae, *C. micropus* is most certainly insectivorous. The reproductive pattern is also little known. Samples of females taken in mid-July have contained 2.6% (Genoways et al., 2005) to 90% (Kerridge and Baker, 1978) lactating individuals. Fourteen females taken on 29 July seemed to be reproductively inactive (Genoways et al., 2005), suggesting that lactation may end during this month in Jamaica.

Chilonatalus micropus is represented by 335 museum specimens, with the largest samples having been taken in St. Clair cave (Jamaica), Cueva los Patos (Dominican Republic), and Old Providence Island. It is moderately gregarious at roosts, forming groups from 10–20 (Genoways et al., 2005) to several hundred individuals (Goodwin, 1970, Kerridge and Baker, 1978).

Nothing has been published on the activity patterns of *C. micropus*. In the Dominican Republic, one individual was netted at 20:00 hr apparently coming out of the upper entrance of Cueva los Patos, Barahona, 1.5 hours after the end of the exodus of six other bat species. A second individual was netted at 23:00, flying over a creek in Arroyo Chico, Samaná, Dominican Republic, indicating that the species is active until late at night.

Chilonatalus micropus flies very slowly and does not entangle in mistnets when caught in them. In an ecomorphological study, Obrist et al. (1993) predicted, based on dimensions of the ear pinna, that the echolocation calls of *C. micropus* probably consist of two harmonics in the 40–80 kHz range.

Chilonatalus micropus is listed in IUCN's Red List of Endangered Species (IUCN, 2010) as near threatened, but this classification included the Cuban *C. macer*, which seems to be a more common species. Yu and Dobson (2000) considered it "very rare," yet their conclusion was based on distribution and population data from Kerridge and Baker (1978), which stated that it was restricted to Jamaica. *Chilonatalus micropus* nonetheless appears to be more vulnerable than its current IUCN status indicates. The geographic range of this species is fragmented across four islands, two of which (San Andrés and Providencia) are very small, isolated, and with dense human populations. The only large population *C. micropus* in Jamaica is known from St. Clair Cave, where a resident population of feral cats is reported to feed on the cave's bats (McFarlane, 1986). On Hispaniola, where farmers traditionally engage in large-scale extraction of bat guano from caves, the only known roost site is Cueva Los Patos No. 2, a cave in the immediate vicinity of a small town. With such a limited known distribution and potential threats, the population status of this species warrants investigation to accurately assess its conservation needs.

Chilonatalus tumidifrons Miller, 1903
Figure 17

Chilonatalus tumidifrons Miller, 1903. Type locality "Watling Island" [= San Salvador Island], Bahamas.

Natalus (*Chilonatalus*) *tumidifrons*: Dalquest, 1950: 443. New combination.

Natalus micropus tumidifrons: Varona, 1974: 32. New combination.

Natalus tumidifrons: Ottenwalder and Genoways, 1982: 32. New combination.

HOLOTYPE: USNM 122024, adult male, skin in alcohol with skull removed, collected by J.H. Riley on 12 July 1903 in a cave near Sandy Point (locality 524 in appendix 1), San Salvador Island, the Bahamas. Skin and skull in good condition.

DISTRIBUTION: The Bahamas (Abaco, Andros, and San Salvador; also, as a fossil, in New Providence, Cat and Great Exuma); fig. 11.

DIAGNOSIS: Forearm short (31.7–36.0 mm) relative to skull length; length of tibia (17.8–20.05 mm); penis short (1.1–2.25 mm); natalid organ long (3.6–7.25 mm); skull long (15.15–15.95 mm) relative to forearm length; least postorbital breadth relatively narrow; lateral margin of ear straight; attachment of wing to tibia on the proximal half of the tibia (at about 1/3 of its length, measured from the knee); in lateral view, braincase rises from rostrum as a softly curving slope dorsal to orbit; ridge between basisphenoid furrows wide; caudal margin of ascending ramus of mandible forming a straight angle with alveolar plane of dentary; lateral sides of basisphenoid pits nearly parallel; p2 crowded; seamless fusion of ribs to sternum. A comparison of diagnostic characters between *C. tumidifrons*, and other species of *Chilonatalus* is summarized in table 4.

DESCRIPTION: Small size (forearm length 31.7–36.0 mm; greatest skull length 15.0–16.0 mm; weight 3–3.5 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening ventrolaterally at the end of tubelike projections on margin of upper lip; upper lip slightly thickened; lower lip markedly thickened and constricted on dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; high dermal tubercle on dorsum of rostrum caudal to nostrils; tubercles of ramal vibrissae coalesced into transversal ridge ventral to lower lip; natalid organ very large (up to 1/2 of greatest length of skull), spindle shaped, reaching crown of head; ears relatively long (14.7–17.2 mm); ear pinna very wide and funnel shaped; pinna with moderately pointed tip; lateral and medial margins of pinna straight; three very small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus markedly short, lanceolate, and twisted into helixlike structure; tibia (17.8–20.1 mm) longer than half the length of the forearm; calcar very long and thin, occupying about 2/3 of the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively long and wide, with 3rd metacarpal (30.3–32.4 mm) longer than 5th metacarpal

Fig. 17. Holotype of *Chilonatalus tumidifrons* (USNM 122024, male, San Salvador, the Bahamas). Scale bar = 5 mm.

(27.9–30.5 mm); wings attach to tibia at proximal third of distance between knee and ankle; pelage dense and lax; hairs long (5–9 mm, dorsally; 4–7 mm, ventrally); pelage color from light brown to orange brown, lighter dorsally; hairs bicolored, with tips darker than bases; dense mustachelike hair tufts along lateral margins of upper lip; mustache formed by dense, tough, parallel, and ventrally curved hairs; natalid organ nearly naked; skull long and narrow with moderate rostral flexion; rostrum long and narrow, with marked sulcus between nasals; moderate palatal emargination; maxilla

TABLE 9

Summary of measurements[a] of *Chilonatalus tumidifrons*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	4	3.0	(3.0–3.0)	0.0	4	3.1	(3.0–3.5)	0.3
Forearm length	13	34.4	(32.8–35.2)	0.7	40	33.8	(31.7–36.0)	0.9
Length of tibia, dry	8	17.4	(16.8–18.2)	0.5	7	17.4	(17.0–17.9)	0.3
Length of tibia	4	19.2	(18.5–19.7)	0.5	29	19.1	(17.8–20.1)	0.6
Length of 3rd metacarpal	6	32.1	(30.5–32.8)	0.9	30	31.9	(30.9–33.4)	0.6
Length of 5th metacarpal	5	30.1	(29.3–30.8)	0.6	30	29.5	(28.3–30.8)	0.6
Length of ear	4	15.6	(15.1–16.1)	0.5	18	15.7	(14.7–17.2)	0.8
Length of penis		–	– –	–	23	1.8	(1.1–2.3)	0.3
Length of natalid organ		–	– –	–	19	6.5	(3.6–8.5)	1.1
Greatest skull length	20	15.6	(15.0–16.0)	0.2	9	15.5	(15.2–15.6)	0.2
Zygomatic breadth	9	7.2	(7.1–7.4)	0.1	19	7.2	(7.1–7.4)	0.1
Braincase breadth	9	6.5	(6.2–6.9)	0.3	19	6.5	(6.3–6.8)	0.1
Breadth across molars	9	4.9	(4.8–5.1)	0.1	17	4.9	(4.7–5.1)	0.1
Breadth across canines	9	3.3	(3.2–3.4)	0.1	17	3.4	(3.2–3.6)	0.1
Maxillary tooth row	9	6.5	(6.4–6.7)	0.1	18	6.6	(6.3–6.8)	0.1
Mandibular tooth row	9	6.7	(6.5–6.9)	0.1	18	6.8	(6.4–7.0)	0.2
Postorbital breadth	9	2.9	(2.8–3.0)	0.1	19	2.9	(2.8–3.0)	0.1
Depth of braincase	9	5.5	(5.2–5.8)	0.2	17	5.6	(5.3–6.2)	0.3

[a] Descriptive statistics of measurements for each sex. N = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P \leq 0.05$) are followed by an asterisk (*).

convex dorsal to molars; braincase greatly inflated, rising gently from rostrum; sagittal crest moderately developed; postorbital constriction relatively narrow (38%–41% of zygomatic breadth); maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids convergent; palate extending caudally to half the length of pterygoids; basisphenoid pit deep and steep sided; longitudinal medial ridge on basisphenoid present; ectotympanic large, covering about half of the periotic; upper incisors long and pointed; occlusal profile of premolars long; upper premolars of similar size and crowded; mesostylar crests on M1 and M2 long and broadly curved, mesostylar crest present on M3; cingular cusp of p4 long and pointed; molars cusps relatively broad; spinous process of humerus much higher than capitulum; thorax relatively short and wide; all ribs fused together and with sternum forming a single bell-shaped structure; vertebrae C7 to T7 fused together and to ribs; vertebrae T11–L5 fused entirely without vestige of sutures; vertebrae L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: From species of the genera *Natalus* and *Nyctiellus*, *Chilonatalus tumidifrons* can be distinguished on the basis of generic level characters (for generic-level comparison between *Chilonatalus* and *Natalus* and *Nyctiellus* see account of *C. macer*). From *Chilonatalus micropus*, and *Chilonatalus macer*, *C. tumidifrons* can be distinguished using a combination of external and internal characters.

Externally, *Chilonatalus tumidifrons* differs from *C. micropus* in its straight lateral margin of the ear, the attachment of the wing on the proximal half of the tibia, a short penis (1.1–2.25 mm), a long tibia (17.8–20.05 mm), and a large, elliptical natalid organ (length of natalid organ 3.6–8.5 mm). *Chilonatalus micropus*, in contrast, is characterized by a deeply notched (concave) lateral ear margin, a wing attaching to the tibia on its distal half, a long penis (3.6–6.5 mm), a short tibia (14.7–17.95), and a small, hemispherical natalid organ (length of natalid organ 3.3–3.7). Cranially, *C. tumidifrons* and

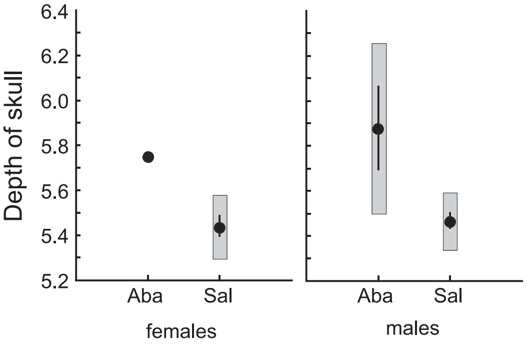


Fig. 18. Morphometric variation among two island populations of *Chilonatalus tumidifrons*. Islands: Aba = Abaco (1 female, 19 males); Sal = San Salvador (12 females, 20 males). On average, males from Abaco had significantly deeper braincases than males from San Salvador (Tukey, $P < 0.05$). Symbols: black dots, means; vertical gray bars, two standard deviations around the mean; vertical black line, two standard errors around the mean.

C. micropus can be separated by the dorsal flexion point of the skull (with a well-defined angle in *C. micropus* and a gently curving slope in *C. tumidifrons*), the angle formed by the caudal margin of the ascending ramus of mandible with the alveolar plane of the dentary (straight in *C. tumidifrons* and about 70° in *C. micropus*), the lateral sides of the basisphenoid pits (nearly parallel in *C. tumidifrons* and caudally divergent in *C. micropus*), and by the fusion of the ribs with sternum (without vestige of sutures in *C. tumidifrons* and retaining sutures in *C. micropus*).

Chilonatalus tumidifrons does not differ appreciably from *Chilonatalus macer* in external characters. The skull of *Chilonatalus tumidifrons* (greatest skull length 15.15–15.95 mm), however, is absolutely and proportionately (relative to forearm length) larger than that of *C. macer* (13.8–14.7 mm). Also, the two species differ in the relative width of the postorbital constriction (38%–41% of zygomatic breadth in *C. tumidirostris* and 42%–44% in *C. macer*), in the degree of crowding of P2 (crowded in *C. tumidifrons* and not crowded in *C. macer*), and in the relative width of the ridge between basicranial furrows (narrow in *C. tumidifrons* and wide in *C. macer*).

VARIATION: No significant sexual variation has been detected in the samples available of *C. tumidifrons* (Ottenwalder and Genoways, 1982). Specimens from Abaco had significantly deeper braincases (on average) than those from San Salvador ($P < 0.001$; fig. 18).

NATURAL HISTORY AND CONSERVATION: *Chilonatalus tumidifrons* is known from 20 localities (including 8 represented by bone remains only) of which eight are caves, this species' only known roost type. It has been found in caves both large and small where it often roosts above water, but also in drier areas. Individuals hang regularly spaced, and generally from a single foot (Miller, 1905). It has been found in caves with two other bat species (*Erophylla sezekorni* and *Macrotus waterhousii*; Andersen, 1994; Hall et al., 1998). When found sharing caves with *Erophylla*, *C. tumidifrons* occupies low areas often under shelves or ledges (Hall et al., 1998). Roost-site temperatures at one cave (locality 520) ranged from 22.8° to 24.2° C and in a second cave (locality 522) from 23.6 to 23.9° C. Roosting groups have been observed to switch roosting caves set on average 1 km apart, apparently on a daily basis. A colony of about 300 individuals in Abaco was observed to have abandoned a cave entirely, coinciding with the occupation of that cave by 100–200 *Erophylla* (Allen, 1905).

Chilonatalus tumidifrons is associated with deciduous forest habitats of moderate precipitation (1021–1288 mm annual precipitation) and occurs near sea level throughout its range. It is presumably insectivorous, but nothing has been published on the diet of this species.

Chilonatalus tumidifrons is known from at least 123 museum specimens. It has been found in groups ranging from less than 10 to over 500 individuals. The population of San Salvador Island could be relatively large given the high abundance of small, unsurveyed caves on the island that may potentially harbor colonies of this species (Hall et al., 1998). In Andros, *C. tumidifrons* is known from a single cave (Bat Cave) and although only four individuals were taken there, many individuals were observed to swarm out of the cave during a feeding exodus (Andersen, 1994). *Chilonatalus tumidifrons* has no known predators and reportedly is parasitized by the streblid *Trichobious wenzeli* (Hall et al., 1998).

The reproduction biology of *C. tumidifrons* is not known. Colonies apparently formed exclusively by males have been found in July (Allen, 1905), suggesting the sexual segregation pattern that occurs during the period of lactation in other species of the genus. Males have an extremely short penis (1.0–2.3 mm) relative to other natalids, but the possible implications of this trait in the reproduction and mating system of the species is unknown.

Foraging activity begins around sunset. At Crescent Top Cave (locality 520) emergence has been recorded to extend from 17:33 to 18:05 (January 1996) and from 17:44 to 18:10 (January 1997; Hall et al., 1998). Judging from its limb morphology, the flight of *C. tumidifrons* must be very slow, having been compared to that of a large moth (Miller, 1905).

Chilonatalus tumidifrons is listed as vulnerable in the IUCN's Red List of Threatened Species (IUCN, 2010). The extremely reduced range of this species, fragmented across three islands, is of concern. On Abaco and Andros this species is known from only two caves in each case. It seems most abundant in San Salvador, but further survey work is needed on that island to estimate its population size and conservation status (Hall et al., 1998).

Genus *Natalus* Gray, 1838

Natalus Gray, 1838: 496. Type species *Natalus stramineus* Gray, 1838, by monotypy.

Phodotes Miller, 1906: 85. Type species *Natalus tuminidirostris* Miller, 1900, by original designation.

DIAGNOSIS: Natalid organ wedge shaped and extending onto crown; plagiopatagium attaching above ankle, calcar extending throughout most of free edge of uropatagium; well-developed fringe of hairs along free edge of uropatagium; sagittal crest moderately high and most pronounced in its anterior half; angular process curved anterodorsally; apophysis of angular process rounded or quadrate; ventral margin of dentary curved ventral to molars; labial cingular cusp of p4 well developed but short; lesser trochanter in proximal view (aligning greater trochanter with shaft of femur) projects beyond head of femur away from axis of greater trochanter; larger axis of head of humerus oriented posteroventrally; lesser tuberosity almost as high as greater tuberosity and higher than head of humerus; head of humerus much larger than greater tuberosity; spinous process of humerus smaller than one half the radius of capitulum; capitulum swollen and wide at its midpoint;. A comparison of diagnostic characters between *Natalus*, and other natalid genera is summarized in table 3.

ETYMOLOGY: Gray (1838) did not give reasons for choosing the name *Natalus* (derived from Latin *natalis,* "of or relating to birth"), but Goodwin (1959) speculated that it was related to the unknown origin or "birthplace" of the taxon. Other authors have suggested that it derives from the neotenic aspect of the bat, as in the newborn (e.g., Gómez-Laverde, 1986).

CONTENTS: *Natalus espiritosantensis* (Ruschi), 1951; *N. jamaicensis* (Goodwin), 1959; *N. major* Miller, 1902; *N. mexicanus* Miller, 1902; *N. lanatus* Tejedor, 2005; *N. primus* Anthony, 1919; *N. stramineus* Gray, 1838; *N. tumidirostris* Miller, 1900.

Natalus espiritosantensis (Ruschi, 1951)
Figure 19

Natalus stramineus: Winge, 1893: 36. Not *Natalus stramineus* Gray, 1838.

Myotis espiritosantensis Ruschi, 1951: 7. Type locality "Gruta do Rio Itaúnas, no municipio de Conceição da Barra, no E.E. Santo," Brazil.

Natalus espiritosantensis: Ruschi, 1970: 5. New combination.

Natalus stramineus natalensis: Goodwin, 1959: 5. Type locality Natal, Rio Grande do Norte, Brazil; holotype USNM 242830.

Natalus stramineus espiritosantensis: Pine and Ruschi, 1976: 184. New combination.

Natalus stramineus macrourum: Gardner, 2008: 398. New combination.

HOLOTYPE: MBML 1801 male, skin in alcohol with skull extracted, collected by A. Ruschi in April 1953, Gruta Itaúnas (locality 37 in appendix 1), Conceicão da Barra, Espirito Santo, Brazil. The skull is missing the right petrosal, and the right pterygoid process (along with parts of the posterior

Fig. 19. Holotype of *Natalus espiritosantensis* (MBML 1801, male, Espirito Santo Brazil). Scale bar = 10 mm.

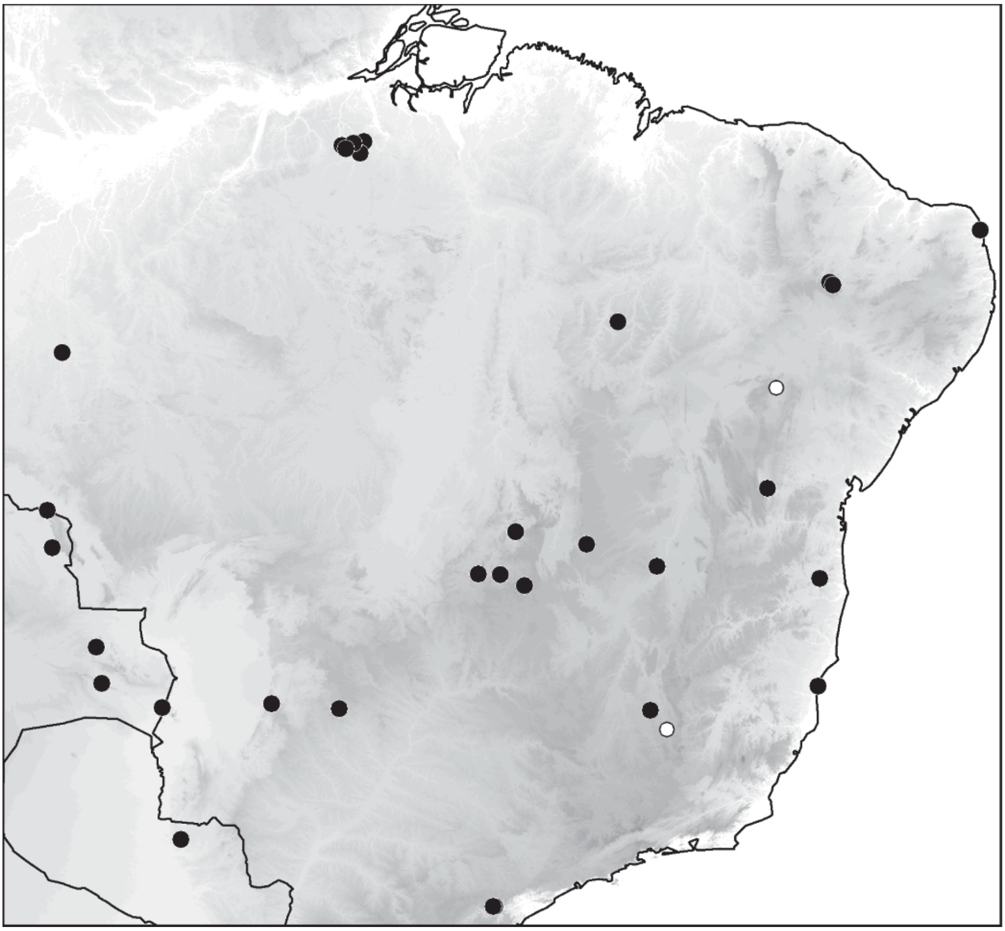


Fig. 20. Geographic distribution of *Natalus espiritosantensis*. Solid circles indicate localities where the species has been collected alive. Open circles indicate localities represented by bone remains only. Names of localities are listed in appendix 1. Gray shading on land indicates relief, with darknes increasing with altitude.

palate), but is otherwise complete. The skin is in fairly good condition but has the three right metacarpals broken as well as a few perforations in the wing membrane, and is moderately bleached by long immersion in alcohol.

DISTRIBUTION: South America south of the Amazon River in the countries of Brazil (Bahia, Ceará, Distrito Federal, Espirito Santo, Goiás, Mato Grosso do Sul, Mato Grosso, Minas Gerais, Pará, Piauí, Rio Grande do Norte, São Paulo), Bolivia, and Paraguay (fig. 20).

NOTE: In his recent review of South American natalids, Gardner (2008) assigned this taxon to *Natalus stramineus macrourum*. His decision stems from the description from Bahia, Brazil, of *Spectrellum macrourum* Gervais, 1856, and the subsequent allocation of this taxon to *Natalus* by Dobson (1878). Although the scant diagnostic characters of *S. macrourum* given by Gervais (1856) are reminiscent of the Natalidae, no specimens or illustrations of this taxon are known at present and Dobson did not argument its allocation to *Natalus*. In the absence of objective evidence that *S. macrourum* is indeed a natalid, it is preferable to name all South American *Natalus* south of the Amazon based on this taxon's oldest known holotype: *Myotis espiritosantensis*.

DIAGNOSIS: Medium size (forearm length 37.0–42.1 mm); maxillary toothrow length short (6.5–7.0 mm); medial margin of ear pinna deeply concave; lateral margin of ear pinna deeply notched; nostrils small, oval, opening ventrolaterally; ventral pelage monocolored; dorsal pelage bicolored, with hair bases lighter than tips; hair at base of claws short and inconspicuous or long and thin, never forming tufts; premaxilla not inflated, with premaxillary maxillary suture anterior to infraorbital foramen; maxilla convex but not inflated; postorbital region with sides widely diverging rostrally; palate ending caudally at 2/3 of the distance between M3 and tip of pterygoid process; caudal margins of maxillary bones forming an acute angle with longitudinal axis of skull; basisphenoid pit shallow; caudal margin of ascending ramus of dentary perpendicular to alveolar margin of dentary; I1 not visible in lateral view, being obscured by I2; mesostylar crest of M3 absent. A comparison of diagnostic characters between *N. espiritosantensis*, and other species of *Natalus* is summarized in table 5.

DESCRIPTION: Medium sized (forearm length 37.0–42.1 mm; greatest skull length 15.9–17.0 mm; weight 6 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening anteroventrally on shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along dorsal and ventral margin, with numerous transverse grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium sized and wedge shaped, extending from caudal base of rostrum to crown of head; ears medium sized (12.0–15.9 mm); ear pinna funnel shaped but distally thin; pinna with markedly pointed tip; medial and lateral margins of pinna deeply concave; five to six small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (20.1–23.8 mm) slightly longer than half the length of the forearm; calcar long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively broad, with 3rd metacarpal (35.1–39.6 mm) slightly longer than 5th metacarpal (34.7–39.1 mm); wings attach to tibia above ankle; pelage dense and lax; hairs long (8 mm, dorsally; 7 mm, ventrally); pelage usually darker dorsally than ventrally; pelage color from pale buff ventrally and light brown dorsally to bright yellowish brown both ventrally and dorsally (pl. 1); dorsal hairs bicolored, with tips darker than bases; ventral hairs usually monocolored; dense mustachelike hair tufts along lateral margins of upper lip and on dorsum of muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with thin hairs; skull long and relatively broad with moderate rostral flexion; rostrum wide and short, with sulcus between nasals almost imperceptible; moderate rostral palatal emargination; maxilla convex above molars; braincase inflated, rising abruptly from rostrum; sagittal crest moderately developed; postorbital constriction wide; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids nearly parallel; palate extending caudally to more than half the distance between bases and tips of pterygoids; basisphenoid pit shallow; longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors short and peglike; I2 obscuring I1 in lateral view; occlusal profile of premolars long; upper premolars of similar size; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molars cusps relatively broad; spinous process of humerus about as high as capitulum; thorax relatively short and wide; ribs markedly expanded craniocaudally and extensively in contact with one another; vertebrae C7 to T1 fused to each other and to ribs; vertebrae T12–L4 fused entirely without vestige of sutures; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: *Natalus espiritosantensis* is a medium sized *Natalus*. Its forearm is

TABLE 10
Range of diameter of distal humerus in fossil and extant Natalidae

	Diameter of distal humerus	
Species	*N*	Min.–Max.
Primonatalus prattae	4	2.8–2.9
Chilonatalus tumidifrons	14	2.9–3.1
Natalus tumidirostris	6	3.2–3.5
Natalus stramineus	7	3.3–3.5

smaller than those of the three greater Antillean species (*N. primus*, *N. major*, and *N. jamaicensis*) and larger on average than those of *N. mexicanus* and *N. lanatus*. It lacks external and cranial diagnostic features and must therefore be identified by a combination of characters and by geographic distribution. Externally, it is one of three species (the other two being *N. mexicanus* and *N. stramineus*) that combine a concave medial margin of the ear with small, elliptical, and ventrolaterally pointing nostrils. All greater Antillean *Natalus* and *N. lanatus* have a straight medial margin of the ear and can thus be distinguished from *N. espiritosantensis* by this trait alone.

Craniodentally, *N. espiritosantensis* can be distinguished from *Natalus jamaicensis* by the sides of its postorbital region, which are nearly parallel in *N. jamaicensis* and diverge anteriorly in *N. espiritosantensis*, in dorsal view. From *N. lanatus*, *N. espiritosantensis* differs in that the caudal margin of the palatal branches of the maxillae, in ventral view, form an acute angle with the midline of the skull, whereas in *N. lanatus* they form a nearly straight angle. *N. espiritosantensis* is distinguished from *N. primus* by its shallow basisphenoid pits, which are deep in *N. primus*. From *Natalus tumidirostris*, *N. espiritosantensis* differs in its convex yet uninflated maxilla (markedly inflated in *N. tumidirostris*) and in the caudal extension of the palate that reaches 2/3 of the distance between the caudal edge of M3 and the tip of the pterygoids (the palate ends caudally before reaching the sphenorbital fissure in *N. tumidirostris*). From *Natalus major* it differs in its smaller skull (greatest skull length is

TABLE 11
Summary of measurements[a] of *Natalus espiritosantensis*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min–Max.)	SD
Weight	3	6.0	(6.0–6.0)	0.0	2		(6.0–6.0)	
Forearm length	17	38.6	(37.2–40.4)	0.9	20	39.3	(37.0–42.1)	1.2
Length of tibia, dry	5	19.5	(18.6–20.1)	0.6	7	20.9	(19.4–22.8)	1.1
Length of tibia	8	21.3	(20.1–23.8)	1.4	9	21.9	(20.7–23.1)	0.9
Length of 3rd metacarpal	9	37.7	(35.1–39.6)	1.3	8	37.6	(35.8–39.1)	1.3
Length of 5th metacarpal	9	37.0	(35.3–39.1)	1.3	8	37.2	(34.7–38.5)	1.3
Length of ear	12	14.4	(12.0–15.9)	1.2	15	14.3	(12.0–15.7)	1.2
Length of penis		–	– –	–	6	4.5	(3.6–5.3)	0.6
Length of natalid organ		–	– –	–	6	7.2	(5.4–8.7)	1.4
Greatest skull length*	18	16.3	(15.9–17.0)	0.3	18	16.7	(16.2–17.0)	0.3
Zygomatic breadth*	17	8.5	(8.1–9.0)	0.2	18	8.7	(8.4–8.8)	0.1
Braincase breadth*	17	8.1	(7.9–8.3)	0.1	15	8.4	(8.0–8.6)	0.2
Breadth across molars*	18	5.5	(5.2–5.7)	0.1	18	5.6	(5.4–5.8)	0.1
Breadth across canines*	18	3.8	(3.5–4.0)	0.1	17	3.9	(3.6–4.2)	0.1
Maxillary tooth row*	18	6.6	(6.5–6.9)	0.1	16	6.8	(6.5–7.0)	0.1
Mandibular tooth row*	10	7.0	(6.8–7.3)	0.1	11	7.3	(7.1–7.5)	0.1
Postorbital breadth	18	3.2	(3.0–3.3)	0.1	16	3.2	(3.1–3.5)	0.1
Depth of braincase*	8	6.6	(6.4–6.8)	0.1	11	6.8	(6.5–7.1)	0.2

[a] Descriptive statistics of measurements for each sex. N = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

larger than 17.0 mm in *N. major* and smaller than 17.0 mm in *N. espiritosantensis*) and from *N. mexicanus* and *N. stramineus* in having a shorter and broader rostrum (breadth across molars ranges from 80%–85% of the length of the tooth row in N. espiritosantensis, and from 72%–81% in *N. mexicanus* and *N. stramineus*).

VARIATION: On average, males of *Natalus espiritosantensis* are larger than females in seven cranial dimensions (table 11), but females have longer mandibular tooth rows. Despite its vast geographic distribution, *Natalus espiritosantensis* is the least variable of the continental species of *Natalus*. Except for the smaller size (not statistically significant; one-way ANOVA, $P > 0.01$; fig. 21A) of individuals from northeast Brazil (Ceará, Rio Grande do Norte), no morphometric differences were apparent in the sample available for this species (fig. 21B).

NATURAL HISTORY AND CONSERVATION: This species is known from 36 localities (in 3 of these represented by bone remains only), of which 17 are caves. It has been captured in mistnets in 5 localities (3 in Ceará, Brazil, and 2 in Noel Kempff Mercado National Park, Bolivia). It roosts in caves opening both in sandstone and in limestone. The caves where *N. espiritosantensis* has been found are humid but not hot (22° C and 94% humidity, Cueva en Santiago de Chiquitos, Bolivia, locality 26; 25° C and 94% humidity, Cueva Concepcioncita, Bolivia, locality 27) and usually contain open bodies of water. It has been found coexisting in caves with 22 other bat species (*Anoura geoffroyi*, *Anoura caudifer*, *Artibeus planirostris*, *Carollia perspicillata*, *Chrotopterus auritus*, *Desmodus rotundus*, *Diphylla ecaudata*, *Glossophaga soricina*, *Lionycteris spurrelli*, *Lonchorhina aurita*, *Lonchophylla mordax*, *Macrophyllum macrophyllum*, *Micronycteris megalotis*, *Micronycteris* aff. *minuta*, *Phylloderma stenops*, *Pteronotus gymnonotus*, *Pteronotus parnellii*, *P. personatus*, *Pteropteryx macrotis*, *Pteropteryx kappleri*, *Tonatia saurophila*, *Tonatia bidens*; Gregorin and Mendes, 1999; Pine and Ruschi, 1976; Taddei and Uieda, 2001; Trajano and Gimenez, 1998; Trajano and Moreira, 1991). On one occasion *N. espiritosantensis* was found roosting solitarily at the edge of a compact cluster of *Carollia perspicillata* (Rodrigo Lopes Ferreira, in litt.).

TABLE 12

Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 5 geographic samples of *Natalus espiritosantensis*

Measurement	C 1	C 2
Greatest skull length	0.787	−1.600
Zygomatic breadth	−0.448	−0.122
Braincase breadth	−0.173	0.874
Breadth across molars	−0.951	−0.052
Breadth across canines	1.132	0.203
Maxillary tooth row	0.240	1.117
Eigen value	0.914	0.183
Percent explained	73.1	14.6

CVA scores are plotted in figure 25A.

Natalus espiritosantensis occurs from xeric habitats (e.g., caatinga, Itaeté, Brazil, 772 mm annual precipitation; locality 29) to moist habitats (Amazonian forest, Aripuaná, Brazil, 2119 mm annual precipitation; locality 50) and from sea level to middle elevations (1000 m, Brasilia, Brazil; locality 36). Nothing is known of the diet of this species.

Natalus espiritosantensis is the species of natalid with the widest geographic distribution, but is apparently rare over much of its large range. It is known from 73 museum specimens, most of which have been collected at two localities: Mato Grosso do Sul (Paranaiba, Rio Verde), and Poço Encantado, Itaeté, Bahia, both in Brazil. Colony sizes seem comparatively small, ranging from 5–10 individuals to about 50. It was one of the most common bats in two caves (Olhos D'agua, locality 45; Trajano and Gimenez, 1998; and in Caverna Planaltina, locality 53; Trajano and Moreira, 1991). Of two collections obtained in Paranaiba, Mato Grosso do Sul, Brazil, one taken in summer (28 January 1979) contained both males and females, whereas a second collection taken in early spring (3 November 79) was composed only of males, suggesting temporal sexual segregation.

Nothing is known of reproductive patterns in *N. espiritosantensis*. Apparently pregnant females (with greatly swollen abdomens) have been taken in Mato Grosso do Sul, Brazil, in summer (28 January 1979) and in late winter (7 September 1993).

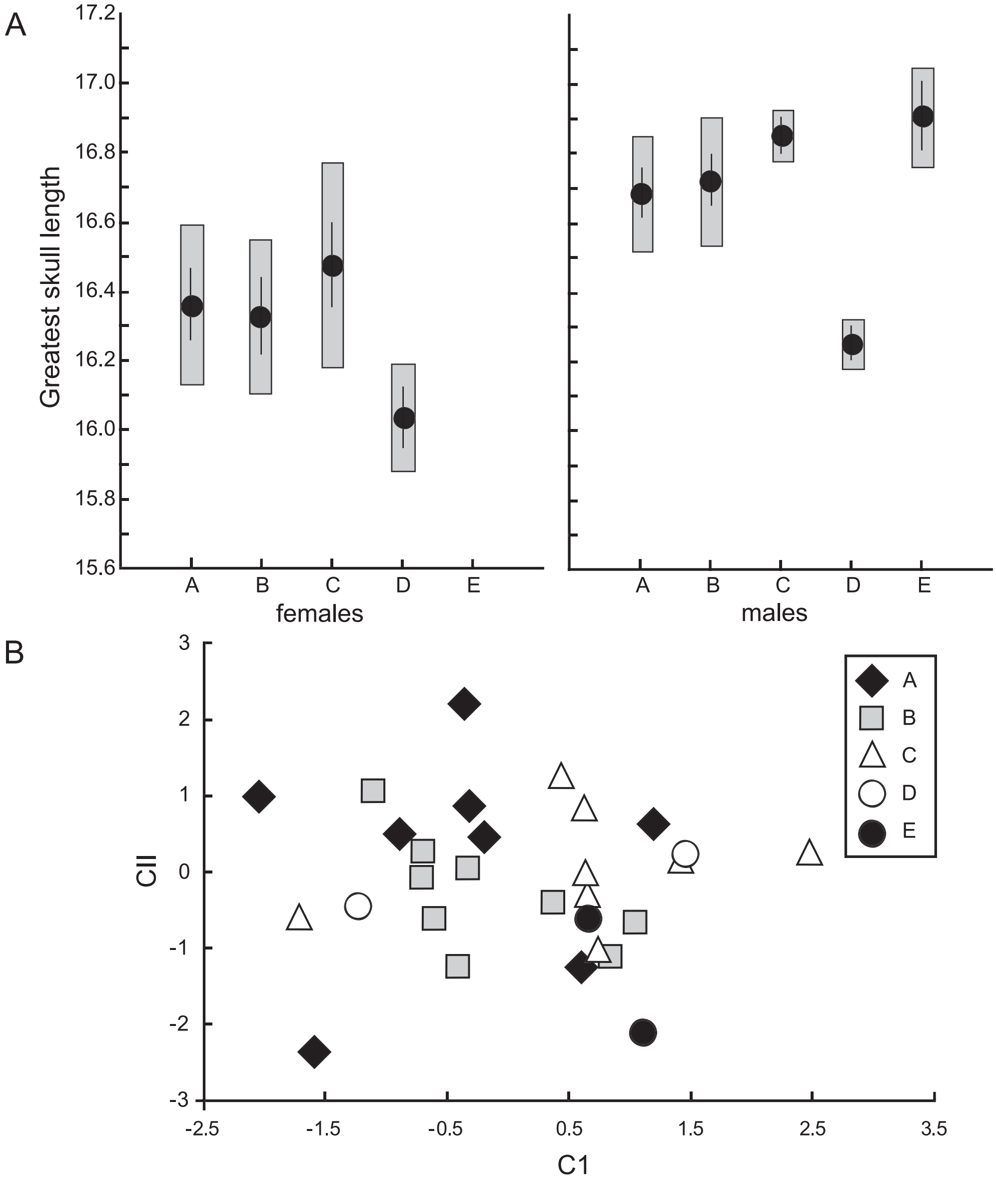


Fig. 21. **A,** Plot of means (black dots), two standard deviations around the mean (gray bars), and two standard errors of the mean (vertical black lines) of greatest skull length of *Natalus espiritosantensis* from five geographic areas: (A) Bolivia (5 females, 6 males); (B) SW Brazil [Mato Grosso do Sul], Paraguay (4 females, 6 males); (C) SE Brazil (Espirito Santo, Goiás, Minas Gerais, São Paulo; 7 females, 7 males); (D) NE Brazil (Ceará, Bahia, Rio Grande do Norte; 4 females, 2 males); (E) N Brazil (Pará; 2 males). Although the observed mean greatest skull length of males from NE Brazil was smaller, the difference was not statistically significant (MANOVA, $P > 0.01$). **B,** Plot of canonical scores for 6 cranial measurements of *N. espiritosantensis* from five geographic areas (same as above). Variable loadings are listed in table 12. The lack of morphometric separation between distant geographic units of *N. espiritosantensis* is congruent with the morphological homogeneity of the species (see text).

Natalus espiritosantensis is not listed in IUCN's Red List of Threatened Species (IUCN, 2010). It is an infrequently encountered species, and may be threatened by the practice of extermination of cave bat colonies that is widespread in Brazil. Large karst areas of southeast Brazil seem to have already suffered massive declines in populations of cave bat species. The vast geographic range of this species suggest that remote populations will escape intense human disturbance, but if bat extermination campaigns continue in the densely populated rural areas of Brazil, this bat may become extinct over a large part of its range.

Natalus jamaicensis (Goodwin, 1959)
Figure 22

Natalus major jamaicensis Goodwin, 1959: 9. Type locality "St. Clair, St. Catherine Parish, Jamaica, British West Indies."

Natalus stramineus jamaicensis: Linares, 1971: 83. New combination.

Natalus major: Morgan, 1989: 686. Part, not *Natalus major* Miller, 1902.

Natalus jamaicensis: Dávalos, 2005: 95. New combination.

HOLOTYPE: AMNH 182000, adult male, skull and skin in fluid, collected by C.B. Lewis in St. Clair Cave (locality 250 in appendix 1), St. Catherine Parish, Jamaica on 5 March 1954. The skull is complete and the skin is in good condition.

DISTRIBUTION: Jamaica, known to be extant at the type locality only (fig. 23).

DIAGNOSIS: A large representative of *Natalus* with a long forearm (44.1–44.8 mm) relative to its skull length (17.4–18.1 mm); medial margin of ear pinna straight; lateral margin of ear pinna deeply notched; nostrils small, oval, opening ventrolaterally; ventral pelage monocolored; dorsal pelage bicolored with hair bases lighter than tips; hair at base of claws short and inconspicuous or long and thin, never forming tufts; premaxilla not inflated, with maxilloincisive suture anterior to infraorbital foramen; maxilla above molars concave; palate ending caudally at 2/3 the distance between M3 and tip of pterygoid process; caudal margins of maxilla in ventral view forming an acute angle with longitudinal axis of skull; basisphenoid pit shallow; postorbital region narrow, with sides nearly parallel, in dorsal view; braincase rising abruptly from rostrum, with an angle greater than 60° between dorsal plane of rostrum and frontal plane of forehead; braincase rounded in dorsal profile, with breadth almost as great as length; postorbital constriction, its sides almost parallel; caudal margin of ascending ramus of mandible perpendicular to alveolar margin of dentary; I1 not visible in lateral view, being obscured by I2; mesostylar crest of M3 absent. A comparison of diagnostic characters between *N. jamaicensis* and other species of *Natalus* is summarized in table 5.

DESCRIPTION: Size large (forearm length 44.0–47.0 mm; greatest skull length 17.2–18.1 mm; weight 5.9–7.3 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening ventrolaterally on shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium size and elliptical, extending from caudal base of rostrum to crown of head; ears relatively long (15.3–19.1mm); ear pinna funnel shaped; pinna with markedly pointed tip; medial margin of pinna straight; lateral margin of pinna deeply concave; five to six small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (24.3–25.7 mm) slightly longer than half the length of the forearm; calcar long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively broad, with 3rd metacarpal (40.8–42.8 mm) slightly longer than 5th metacarpal (39.9–41.4 mm); wings attach to tibia above ankle; pelage dense and lax; hairs long (9–11 mm, dorsally; 6–7 mm, ventrally); pelage usually darker dorsally than ventrally; dorsal hairs bicolored, with tips darker than bases; ventral hairs usually slightly bicolored and rarely monocolored; pelage color from buff with tips sepia or ochraceous (tawny olive; pl.

Fig. 22. Holotype of *Natalus jamaicensis* (AMNH 182000, male, Jamaica). Scale bar = 10 mm. Photo: Mariko Kageyama, AMNH (see appendix for institutional abbreviations).

1); ventral hair bases are buff with tips pinkish buff; dense mustachelike hair tufts along lateral margins of upper lip and on dorsum of muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with thin hairs; skull long and relatively slender with moderate rostral flexion; rostrum long and slender, with sulcus between nasals short, shallow, and confined to point of flexion between rostrum and braincase; moderate rostral palatal emargination; maxilla concave dorsal to molars; braincase greatly inflated (globular), rising abruptly from rostrum; braincase in dorsal view nearly circular; sagittal crest well developed; postorbital

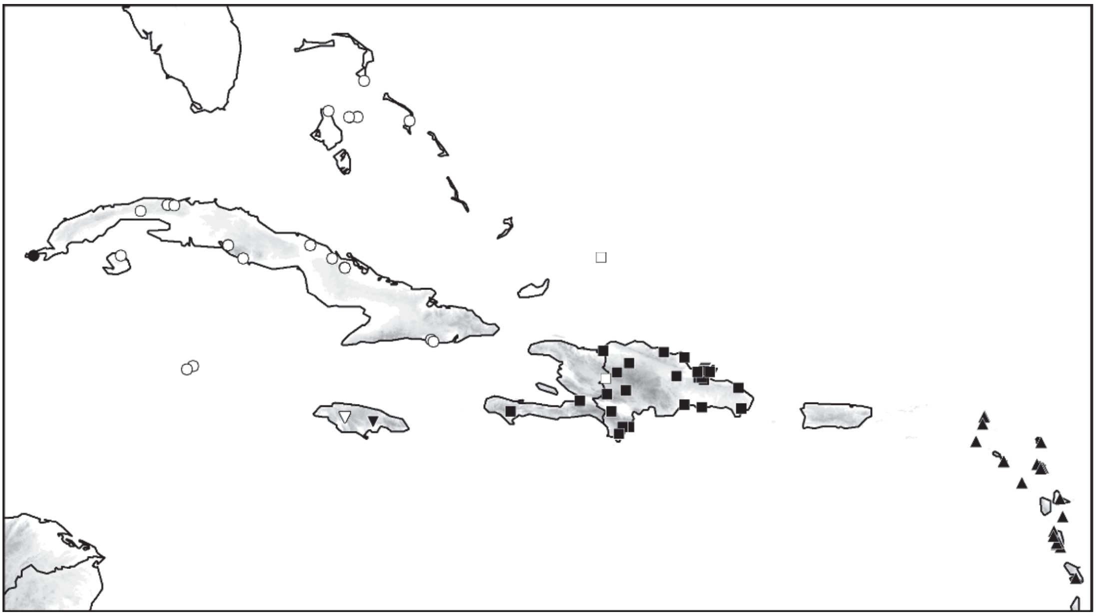


Fig. 23. Geographic distribution of *Natalus jamaicensis* (upside down triangles), *N. major* (squares), *N. primus* (circles), *and N. stramineus* (upright triangles). Open symbols indicate localities represented by bone remains only. Names of localities are listed in appendix 1. Gray shading on land indicates relief, with darknes increasing with altitude.

constriction narrow, its sides nearly parallel; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids nearly parallel; palate extending caudally to more than half the distance between bases and tips of pterygoids; basisphenoid pit shallow; longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors short and peglike; I2 obscuring I1 in lateral view; upper premolars slightly increasing in size from P2 to P4 and crowded; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molars cusps relatively broad; spinous process of humerus about as high as capitulum; thorax relatively short and wide; ribs markedly expanded craniocaudally and extensively in contact with one another; vertebrae C7 to T1 fused among themselves and to ribs; vertebrae T12–L4 fused entirely without vestige of sutures, forming a laterally compressed column; lumbar column relatively short and concave ventrally; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: The large body size (forearm length 44.0–47.0 mm) of *Natalus jamaicensis* readily separates this species from the continental and Lesser Antillean species of the genus *Natalus* (*Natalus stramineus*, forearm 36.9–41.9 mm; *Natalus tumidirostris*, forearm 35.0–42.0 mm; *Natalus mexicanus*, forearm 34.0–40.6 mm; and *Natalus lanatus*, forearm 35.4–38.6 mm), and from species of the genera *Nyctiellus* and *Chilonatalus*. *Natalus jamaicensis* is best distinguished from other greater Antillean *Natalus* (*N. primus* and *N. major*) by discrete cranial or external characters.

Cranially, *N. jamaicensis* is a very distinctive species. Its skull shows several modifications concomitant with its high degree of cranial flexion. First, in *N. jamaicensis* the frontal plane of the braincase raises very steeply from the rostrum, in an angle greater than 60°, a condition that is unique among species of the genus *Natalus*. Second, the braincase of *N. jamaicensis* is markedly

TABLE 13
Summary of measurements[a] of *Natalus jamaicensis*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	2		(6.8–7.3)		4	6.3	(5.9–6.7)	0.4
Forearm length	7	45.5	(44.6–47.0)	0.9	14	45.1	(44.0–47.0)	0.9
Length of tibia, dry	2		(22.1–24.0)		3	24.1	(23.8–24.4)	0.3
Length of tibia	3	25.0	(24.7–25.3)	0.3	7	24.8	(24.3–25.7)	0.5
Length of 3rd metacarpal	4	41.9	(41.1–42.8)	0.8	10	41.8	(40.8–42.8)	0.7
Length of 5th metacarpal	4	40.7	(40.0–41.1)	0.5	10	40.6	(39.9–41.4)	0.5
Length of ear	5	18.2	(17.8–19.1)	0.5	9	17.3	(15.3–18.3)	1.0
Length of penis		–	– –	–	6	3.5	(3.2–3.9)	0.2
Length of natalid organ		–	– –	–	2		(5.2–7.9)	
Greatest skull length	6	17.7	(17.2–18.1)	0.3	9	17.7	(17.4–18.0)	0.2
Zygomatic breadth	6	9.1	(8.7–9.5)	0.3	8	9.3	(9.1–9.5)	0.2
Braincase breadth	6	8.6	(8.4–8.7)	0.1	9	8.8	(8.6–9.0)	0.1
Breadth across molars	5	5.9	(5.8–6.1)	0.2	9	6.1	(5.9–6.2)	0.1
Breadth across canines*	5	3.8	(3.7–4.0)	0.1	8	4.0	(3.9–4.1)	0.1
Maxillary tooth row	4	7.9	(7.8–8.0)	0.1	8	7.9	(7.8–8.1)	0.1
Mandibular tooth row*	5	8.4	(8.2–8.5)	0.1	8	8.2	(8.2–8.3)	0.1
Postorbital breadth	5	2.9	(2.7–3.1)	0.1	9	2.8	(2.7–3.0)	0.1
Depth of braincase	4	7.4	(7.1–7.6)	0.2	8	7.5	(7.3–7.7)	0.1

[a] Descriptive statistics of measurements for each sex. N = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

inflated and almost as wide as long, and as a result has an almost circular profile in dorsal view. In all other species of *Natalus* the braincase is longer than wider and thus appears oval shaped. Third, the postorbital constriction of the skull of *N. jamaicensis* is proportionally narrower than in all other species of *Natalus*, with sides almost parallel in dorsal view, while in all other species of *Natalus* the sides of the postorbital constriction markedly diverge anteriorly. In addition, the rostrum of *N. jamaicensis* is flattened dorsally to a greater degree than in other species of *Natalus*, and shows a marked reduction of the sulcus between nasal bones, and a concave shape of the maxilla in the area dorsal to the molars. The concave maxilla is a readily observed character and is sufficient to diagnose *N. jamaicensis* because all other species of *Natalus* have markedly convex to markedly inflated maxillary bones.

Natalus jamaicensis is less well differentiated in external morphology, and no discrete external character has been found to distinguish it from *N. major*. It differs in its straight medial ear margin from most continental species of the genus (except *N. lanatus*), which have slightly to deeply concave medial ear margins. From *N. lanatus* it can be distinguished by the lack of hair tufts at the base of claws, which are present in *N. lanatus*. From *Natalus primus*, *N. jamaicensis* can be distinguished by its concave lateral margin of the ear pinna, which is straight in *N. primus*.

VARIATION: Secondary sexual dimorphism in *Natalus jamaicensis* was detected in two cranial measurements: breadth across canines and mandibular tooth row (table 12).

NATURAL HISTORY AND CONSERVATION: *Natalus jamaicensis* is known from just two localities, in only one of which (St. Clair Cave, St. Catherine) it is represented by an extant population. From the second locality, Wallingford Cave, St. Elizabeth, it is known by a single subfossil mandible. In St. Clair Cave, *N. jamaicensis* has been found at the entrance of a hot passage (Hoyt and Baker, 1980) through which runs a permanent stream and in a protected lateral recess 3.7 m above the floor of the hot passage (Goodwin, 1970). The bats usually hang from one foot and keep a distance between individuals of about 10 cm (Goodwin, 1970). A total of nine other bat species are found in St. Clair: *Artibeus jamaicensis, Chilonatalus micropus*, *Erophylla sezekorni*, *Monophyllus redmani*, *Mormoops blainvillei*, *Phyllonycteris aphylla*, *Pteronotus macleayi*, *Pteronotus parnellii*, and *Pteronotus quadridens* (Hoyt and Baker, 1980). Goodwin (1970) found *N. jamaicensis* in close association with *Chilonatalus micropus* but forming separate groups. Similarly, Hoyt and Baker (1980) noticed that these two species were spatially segregated with *N. jamaicensis* occupying the first 50 m of the hot passage and being replaced in deeper areas by a larger colony of *C. micropus*. St. Clair cave is located in an area of semideciduous forest (1472 mm annual precipitation) at 100 m above sea level.

In spite of occurring in a single cave, it has been extensively collected, being represented by at least 78 museum specimens. The size of St. Clair's colony appears to be very small. Observers have usually found it to be much less numerous than that of *C. micropus* (Hoy and Baker, 1980; Genoways et al., 2005). The only numeric estimate is that of Goodwin (1970) who reports only about 50 bats of this species in St. Clair. A total of 25 females taken in July and December did not show signs of reproductive activity (Goodwin, 1970).

Nothing is known of the diet and nocturnal activity of *N. jamaicensis*. As in other natalids this bat probably forages with slow flight in cluttered habitats. Its flight has been described as fluttery and mothlike (Goodwin, 1970). *Natalus jamaicensis* dehydrates very rapidly when taken outside the caves where they roost (Hoyt and Baker, 1980).

Natalus jamaicensis may be the most critically endangered species of all natalids and one of the world's mammals in greatest risk of extinction. Traditionally treated as *Natalus stramineus*, it was listed as critically endangered by the IUCN's (IUCN, 2010) until 2008. It was considered the rarest of Jamaican bats by Goodwin (1970) and McFarlane (1986) yet,alarmingly, it has been intensively collected, apparently being more common in museum collections than in the wild (see above). This species' only known roost site, St. Clair Cave, receives no form of official protection (Dávalos and Eriksson, 2003), and is thus open to unregulated human visitation. St. Clair Cave, in addition, has resident populations of feral domestic cats that feed on the bats (species not specified) and rats of the cave (McFarlane, 1997). A brief mistnet survey of St. Clair in December 2001 by Dávalos and Eriksson (2003) failed to detect this species. Immediate efforts are needed to understand this species' conservation requirements and to formulate a plan for its protection.

Natalus lanatus Tejedor, 2005
Figure 24

Natalus stramineus saturatus: Hall and Dalquest, 1963: 242. Part; specimen from Fortín, Veracruz, Mexico.

Natalus stramineus mexicanus: Anderson, 1972: 241. Part; two specimens from two localities in Chihuahua, Mexico.

Natalus stramineus: Rodríguez-Herrera, 2004: 125. Not *Natalus stramineus* Gray, 1838.

Natalus lanatus Tejedor, 2005: 1110. Type locality "6 miles SSE of Las Varas, Nayarit, Mexico."

HOLOTYPE: KU 39628, adult female, skin and skull, collected by J.R. Alcorn on 1 November 1950 (original field number JRA 13312) 6 miles SSE of Las Varas (locality 357 in appendix 1), Nayarit, Mexico. The skin is well preserved and the skull is complete.

PARATYPES: include an adult female (KU 39621) and an adult male (KU 39620), also collected by JRA at the same locality and date as the holotype.

DISTRIBUTION: Mexico (Chihuahua, Durango, Guerrero, Jalisco, Nayarit, Sinaloa, and Veracruz) and Costa Rica (fig. 25).

DIAGNOSIS: A small species of funnel-eared bat (forearm length 16.0–19.2 mm); legs considerably shorter than forearm; medial margin of ear straight; lateral margin of ear deeply notched; 0–1 folds on lateral margin of ear; nostrils small, opening ventrolaterally; bicolored ventral fur and bicolored or tricolored dorsal hairs; dorsal and ventral hairs always darker at the base than at the tips; pelage dense, woolly, and dull, grayish to ochraceous; ventral surface and more than half of dorsal surface of pinna profusely covered with hairs; legs and feet conspicuously hairy with tufts of long hairs projecting from bases of claws; rostrum shallow in lateral view; premaxilla not inflated; maxilloincisive suture anterior to infraorbital foramen; maxilla dorsal to molars convex, not inflated; sides of postorbital region in dorsal view widely diverging rostrally; palate between pterygoids ending caudally 2/3 of the distance between M3 and tip of pterygoid; posterior margins of maxilla almost perpendicular to longitudinal axis of skull, in ventral view; basisphenoid pit shallow; caudal margin of ascending ramus of mandible perpendicular to alveolar margin of dentary; I1 visible in lateral view, not obscured by I2; mesostylar crest on M3 absent. A comparison of diagnostic characters between *N. lanatus*, and other species of *Natalus* is summarized in table 5.

DESCRIPTION: Size small (forearm length 35.4–38.6 mm; greatest skull length 15.0–16.4 mm; weight 5.0–6.5 g); muzzle long and not particularly flattened dorsoventrally; nostrils narrowly elliptical, opening ventrolaterally to ventrally on very shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along dorsal and ventral margin; natalid organ medium size, elliptical and swollen, extending from caudal base of rostrum to crown of head; ears relatively short (12.0–15.6 mm); ear pinna funnel shaped and broad; pinna with moderately pointed tip; medial margin of pinna straight; lateral margin of pinna moderately concave; three to no small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (16.0–19.2 mm) shorter than half the length of the forearm; calcar long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with fringe of thin hairs; wings broad and relatively short, with 3rd metacarpal (31.2–33.9 mm) shorter than 5th metacarpal (33.2–35.5 mm); wings attach to tibia above ankle; pelage dense and woolly; hairs long (8–9 mm, dorsally; 7–8 mm, ventrally); pelage darker dorsally than ventrally; dorsal pelage color from gray (mouse gray) to ochraceous (tawny olive) (pl. 1); dorsal hairs bicolored or tricolored, with dark bases, light middle parts, and medium-dark tips; ventral pelage from gray to ochraceous but hairs markedly bicolored, with bases darker than tips; dense mustachelike hair tufts along lateral margins of upper lip and on dorsum of muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with long hairs; ventral face of ears covered with sparse wooly hairs; feet with marked ungual hair tufts at base of claws and fine covering of short erect hairs along tibia; skull long and relatively broad with moderate rostral flexion; rostrum conical, with wide base and tapering tip, with sulcus between nasals almost imperceptible; moderate rostral palatal emargination; maxilla convex above molars; braincase inflated, and elongated; sagittal crest well developed; postorbital constriction wide; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; caudal margin of palatal branch of maxilla nearly perpendicular to longitudinal axis of skull; pterygoids nearly parallel; palate extending caudally to more than half the distance between bases and tips of pterygoids; basisphenoid pit shallow; longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors long and pointed; I1 visible in lateral view, not being obscured by I2; occlusal profile of premolars long; upper premolars of similar size; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molar cusps relatively broad.

COMPARISONS: *Natalus lanatus* can be readily distinguished from all other known species of *Natalus* by its bicolored ventral pelage. The contrast among color bands in ventral pelage may be less noticeable in some individuals, but hair bases are always darker than tips. In all other species of *Natalus*, the ventral fur is monocolored (with the exception of *Natalus jamaicensis*, which has slightly lighter ventral hair tips, but the contrast in banding pattern is much less than in *N. lanatus*). *Natalus lanatus* can also be distinguished by its often tricolored dorsal hairs, which are always darker at the base than at the tips. In all other species of Natalidae the light and dark banding pattern of dorsal hairs, when present, is reversed, with the tips

Fig. 24. Holotype of *Natalus lanatus* (KU 39628, female, Nayarit, Mexico). Scale bar = 10 mm.

always darker than the bases. *Natalus lanatus* is also distinguishable from all other species in the genus by its hairier legs and feet, with conspicuous ungual tufts (fig. 6). In all other species of *Natalus* the legs are more sparsely haired and the tips of the toes usually lack long hairs (in cases where long hairs are present at the base of claws, they do not form

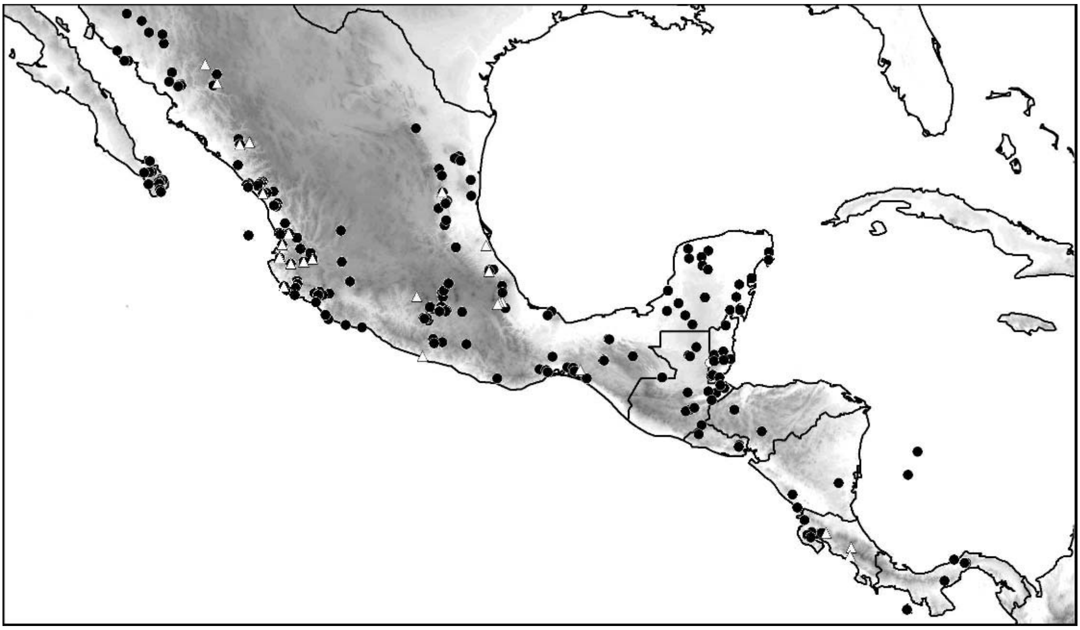


Fig. 25. Geographic distribution of *Natalus lanatus* (open triangles) and *N. mexicanus* (solid circles). Names of localities are listed in appendix 1. Some localities of *N. mexicanus* obtained from museum catalogues or the literature, especially those of the Mexico Basin and Veracruz highlands, may actually represent *Natalus lanatus* (see text). Gray shading on land indicates relief, with darknes increasing with altitude.

the dense tufts characteristic of *N. lanatus*). In some individuals of *N. lanatus*, however, the hair tufts at the base of claws may be thin, approaching the condition of the most thickly furred feet of other species of *Natalus*. Therefore, this character must be used in combination with ventral pelage and cranial characters for an accurate diagnosis of *N. lanatus*.

In addition to the characters mentioned above, *Natalus lanatus* differs from the sympatric *Natalus mexicanus* by its dense, woolly, dull, and often darker pelage, which does not show marked differences in overall darkness throughout the dorsum. The pelage of *N. mexicanus* is silkier and lax, and when grayish (as in juveniles and young adults), it shows a distinctive patch of dark-tipped hairs posterior to shoulders. From *N. mexicanus*, *N. lanatus* is also distinguishable by ear characters (only useful with fluid-preserved and fresh specimens). In *N. lanatus* the medial margin of the pinna is straight to slightly convex, and the apex of the pinna is relatively broad (the angle formed between the medial and lateral margins of the apex of the pinna in *N. lanatus* is about 90°). In *N. mexicanus*, the medial margin of the pinna is slightly concave, forming an angle smaller than 90° with the lateral margin of the pinna, giving the apex a more acutely pointed appearance. The ventral surface of the pinna in *N. lanatus* is also more densely haired and correspondingly shows a much denser packing of hair follicles than the pinna of *N. mexicanus*. With regard to body dimensions, the length of the tibia in *N. lanatus* averages almost 3 mm less than in *N. mexicanus*, and its overall leg length is considerably smaller than the forearm length. In *N. mexicanus*, the leg is about as long as or slightly longer than the forearm. Cranially, *N. lanatus* shows a longer and more anteriorly inflated braincase, and a better-developed sagittal crest than *N. mexicanus*. In addition, the skull of *N. lanatus* is slightly but significantly wider than that of *N. mexicanus*, as reflected by greater averages for zygomatic breadth, breadth across molars, and postorbital breadth. Conversely, the maxillary tooth

TABLE 14
Summary of measurements[a] of *Natalus lanatus*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	5	5.4	(5.0–6.0)	0.5	9	5.7	(5.0–6.5)	0.6
Forearm length	24	36.8	(35.4–38.6)	0.9	29	37.0	(35.4–38.3)	0.8
Length of tibia, dry	13	16.5	(15.9–17.3)	0.5	15	16.8	(15.5–18.4)	0.7
Length of tibia	11	17.8	(17.0–18.9)	0.6	15	18.3	(16.0–19.2)	0.8
Length of 3rd metacarpal	5	32.6	(31.2–33.9)	1.0	10	33.0	(32.0–33.8)	0.6
Length of 5th metacarpal	5	34.2	(33.2–35.5)	1.1	10	34.2	(33.2–34.9)	0.4
Length of ear	23	13.9	(13.0–15.3)	0.7	25	14.1	(12.0–15.6)	0.9
Length of penis		–	—	–	10	3.7	(3.1–4.4)	0.4
Length of natalid organ		–	—	–	8	4.3	(2.7–5.3)	0.9
Greatest skull length	13	15.8	(15.3–16.2)	0.3	14	16.0	(15.0–16.4)	0.4
Zygomatic breadth	13	8.1	(7.9–8.3)	0.1	14	8.2	(7.8–8.7)	0.2
Braincase breadth	13	7.7	(7.6–7.9)	0.1	14	7.9	(7.5–8.2)	0.2
Breadth across molars	13	5.4	(5.2–5.5)	0.1	14	5.4	(5.2–5.6)	0.1
Breadth across canines*	13	3.5	(3.4–3.6)	0.1	14	3.6	(3.5–3.8)	0.1
Maxillary tooth row	13	6.5	(6.3–6.8)	0.1	14	6.7	(6.4–6.9)	0.2
Mandibular tooth row	13	6.9	(6.7–7.2)	0.1	13	7.1	(6.9–7.4)	0.1
Postorbital breadth	13	3.2	(3.1–3.3)	0.1	14	3.2	(3.1–3.3)	0.1
Depth of braincase	13	6.3	(6.1–6.5)	0.1	13	6.4	(6.2–6.7)	0.1

[a] Descriptive statistics of measurements for each sex. *N* = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

row of *N. lanatus* is slightly shorter than that of *N. mexicanus*.

VARIATION: Males of *Natalus lanatus* have a slightly but significantly larger mean breadth across canines than females (table 14). Bats from the eastern versant of the Mexican highlands (Veracruz) have significantly longer forearms than bats from the western versant (Durango, Jalisco, Nayarit), and have wider skulls (zygomatic breadth, postorbital breadth, $P < 0.05$; fig. 26). A specimen of *N. lanatus* from Costa Rica (Río Savegre) is reported to be unusually large relative to *N. mexicanus* from that country, implying a larger size than in *N. lanatus* from Mexico (B. Rodríguez, personal commun.).

NATURAL HISTORY AND CONSERVATION: *Natalus lanatus* is known from 16 localities in Mexico and two in Costa Rica (B. Rodríguez and R.K. LaVal, personal commun.; fig. 25). In five of these localities it has been collected in a roost, of which four have been mines and one a cave. In at least three occasions it has been collected in mistnets (localities 70, 79, and 298). With further inspection of museum collections the number of collection localities of this species in Mexico and Central America will likely increase significantly. One specimen mistnetted in Río Macho, Costa Rica reported as *N. stramineus*, probably represents *N. lanatus* (see below).

At its roosts, *Natalus lanatus* has been found coexisting with *Balantiopteryx plicata*, *Carollia perspicillata*, *Desmodus rotundus*, *Glossophaga* sp., *Macrotus* sp., *Myotis thysanodes*, *Natalus mexicanus*, and *Pteronotus parnellii*. Large caves or mines are not known from some of the locations where it has been mistnetted (e.g., Rio Savegre, Monte Verde), suggesting that it may often use relatively small cavities as roosts.

The collection localities of *Natalus lanatus* differ considerably in climatic regimes, ranging from dry mountain subtropical habitats with marked seasonal variations in temperature and precipitation (e.g., La Bufa, Chihuahua; Anderson, 1972), through the zone of transition between pine/oak and tropical deciduous forests (Durango, C. López-González, field notes), to continuously moist

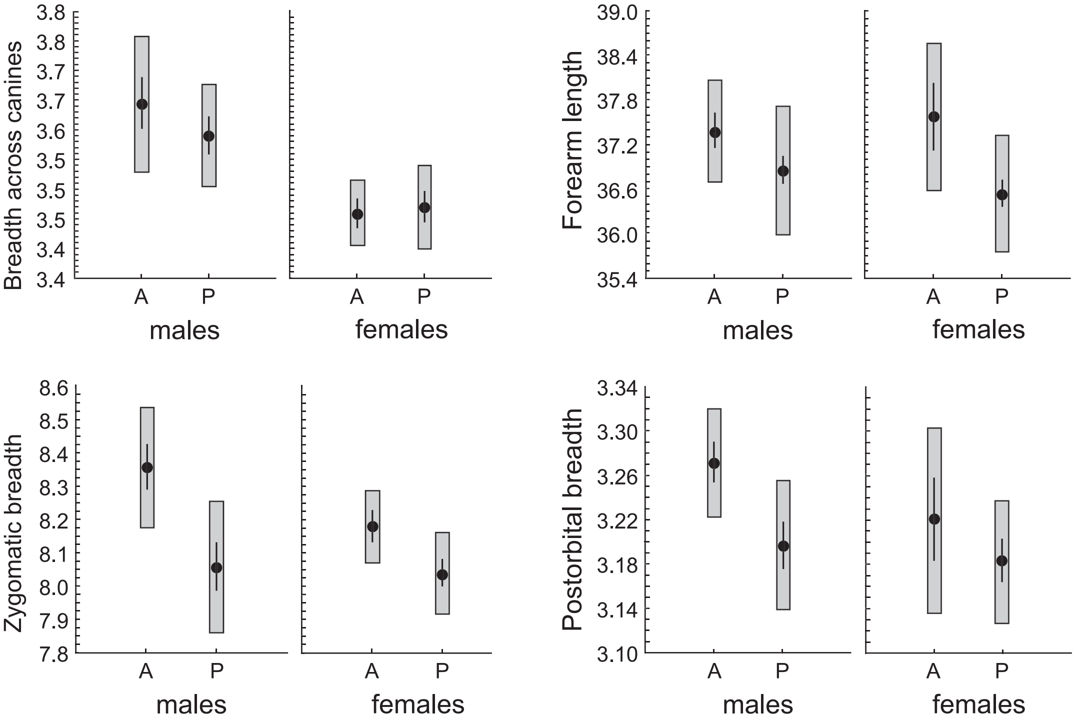


Fig. 26. Sexual and geographic variation in four cranial dimensions of *Natalus lanatus* from the Atlantic and Pacific versants of the Mexican highlands. Geographic areas: A = Atlantic (Veracruz; 8 males, 5 females); P = Pacific (Chihuahua, Durango, Jalisco, Nayarit; 18 males, 19 females). Symbols: black dots, means; vertical gray bars, two standard deviations around the mean; vertical black line, two standard errors around the mean. Females have narrower breadths across canines in both geographic areas (MANOVA, $P < 0.05$) whereas individuals (regardless of sex) from the Atlantic versant have longer forearms and wider skulls than individuals from the Pacific versant (Tukey, $P < 0.05$).

montane tropical forest (Orizaba, Veracruz; Hall and Dalquest, 1963). Most of the localities for which geographic coordinates are known with certainty correspond to middle elevations, ranging from 500 to 2000 m. The record from Río Macho, Costa Rica, a wet mountain forest habitat (1300 melevation, 2700 mm annual precipitation) without known caves, most likely corresponds to *N. lanatus* than to *N. mexicanus*, given that the latter species has been collected in Costa Rica exclusively in lowland areas with abundant caves.

Natalus lanatus is represented by at least 70 museum specimens. Given that it has been described only recently, many Mexican specimens of *N. lanatus* identified as *N. stramineus* (= *N. mexicanus*) probably remain in museum collections. This species may be less gregarious than other species of Natalidae. Although it has been collected in moderately large numbers at some localities (e.g., near Tuxpan, Veracruz, locality 445 in appendix 1; and in Ameca, Jalisco, locality 320), over half of the collection localities of this species are represented by a single museum specimen (appendix 1). In addition, it has been collected roosting solitarily in a cave occupied by a colony of *Carollia perspicillata* (Hall and Dalquest, 1963).

Nothing is known of the diet or activity patterns of *Natalus lanatus*, although it is possible that specimens of this taxon may have served as a basis for natural history accounts of *Natalus mexicanus* (e.g., Villa-R., 1966). As a representative of the genus *Natalus*, however, the new species is probably similar in its ecology to other species of the genus (e.g., *Natalus primus*, Tejedor et al., 2005b; and *Natalus tumidirostris*, Linares,

1998) in being a slow-flying insectivore that forages through low vegetation. The differences in morphology between *N. lanatus* and *N. mexicanus* (see section titled Ecomorphological Diversity), however, may reflect some ecological divergence between these two taxa, as it has been found for other closely related bat species (e.g., *Pipistrellus*, Barlow et al., 1997). Ecological studies of *N. lanatus*, with a focus on understanding its interaction with its sympatric close relative *N. mexicanus*, are highly needed.

Natalus lanatus is listed as least concern in the IUCN's Red List of Threatened Species (IUCN, 2010), but certainly more data is needed from this poorly known species before accurate conservation assessments can be undertaken.

Natalus major Miller, 1902
Figure 27

Natalus major Miller, 1902: 398. Type locality "near Savaneta, Santo Domingo," Dominican Republic.

Natalus stramineus major: Linares, 1971: 83. New combination.

HOLOTYPE: USNM 101395, adult male skull and skin in fluid, collected by W.M. Gabb between 1869 and 1871 "near Savaneta (locality 195 in appendix 1), Dominican Republic." The skull is complete (fig. 27) and the skin is in good condition.

DISTRIBUTION: Hispaniola, including the Dominican Republic and Haiti (fig. 23).

DIAGNOSIS: Forearm long (41.1–45.0), skull long relative to forearm, breadth across canines large (3.9–4.5), maxillary tooth row (7.5–8.0); medial ear margin straight; lateral ear margin deeply notched; nostrils small, opening ventrolaterally; ventral hairs monocolored; dorsal hairs bicolored, hair bases lighter than tips; hair at base of claws short and inconspicuous or long and thin, never forming tufts; maxilla dorsal to molars convex, not inflated; postorbital region with sides widely diverging rostrally; point of flexion between rostrum and braincase dorsal to the anterior edge of orbit; palate ending caudally 2/3 of the distance between M3 and tip of pterygoid; caudal margins of palatine wing of maxilla forming an acute angle with longitudinal axis of skull; basisphenoid pits shallow; caudal margin of ascending ramus of mandible perpendicular to alveolar plane of lower molars; I1 not visible in lateral view, obscured by I2; mesostylar crest on M3 absent. A comparison of diagnostic characters between *N. major*, and other species of *Natalus* is summarized in table 5.

DESCRIPTION: A large natalid (forearm length 41.1–45.0 mm; greatest skull length 17.0–18.1 mm; weight 5.5–10.0 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening anteroventrally on shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium size and elliptical, extending from caudal base of rostrum to crown of head; ears medium sized (13.0–18.9 mm); ear pinna funnel shaped with pointed tip; medial margin of pinna straight; lateral margin of pinna deeply concave; five to six small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (23.2–25.4 mm) slightly longer than half the length of the forearm; calcar long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings wide, with 3rd metacarpal (40.3–42.7 mm) slightly longer than 5th metacarpal (38.3–41.2 mm); wings attach to tibia above ankle; pelage dense and lax; hairs long (7 mm, dorsally and ventrally); pelage usually darker dorsally than ventrally; dorsal hairs bicolored, with tips darker than bases; ventral hairs monocolored; dorsal hair bases buff to drab with tips sepia to fuscous brown (pl. 1); ventral hairs creamy buff; dense mustachelike hair tufts along lateral margins of upper lip and across muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with thin hairs; skull long and relatively broad with moderate rostral flexion; rostrum short and broad, with moderate sulcus between nasals; moderate rostral palatal emargination; maxilla convex dorsal

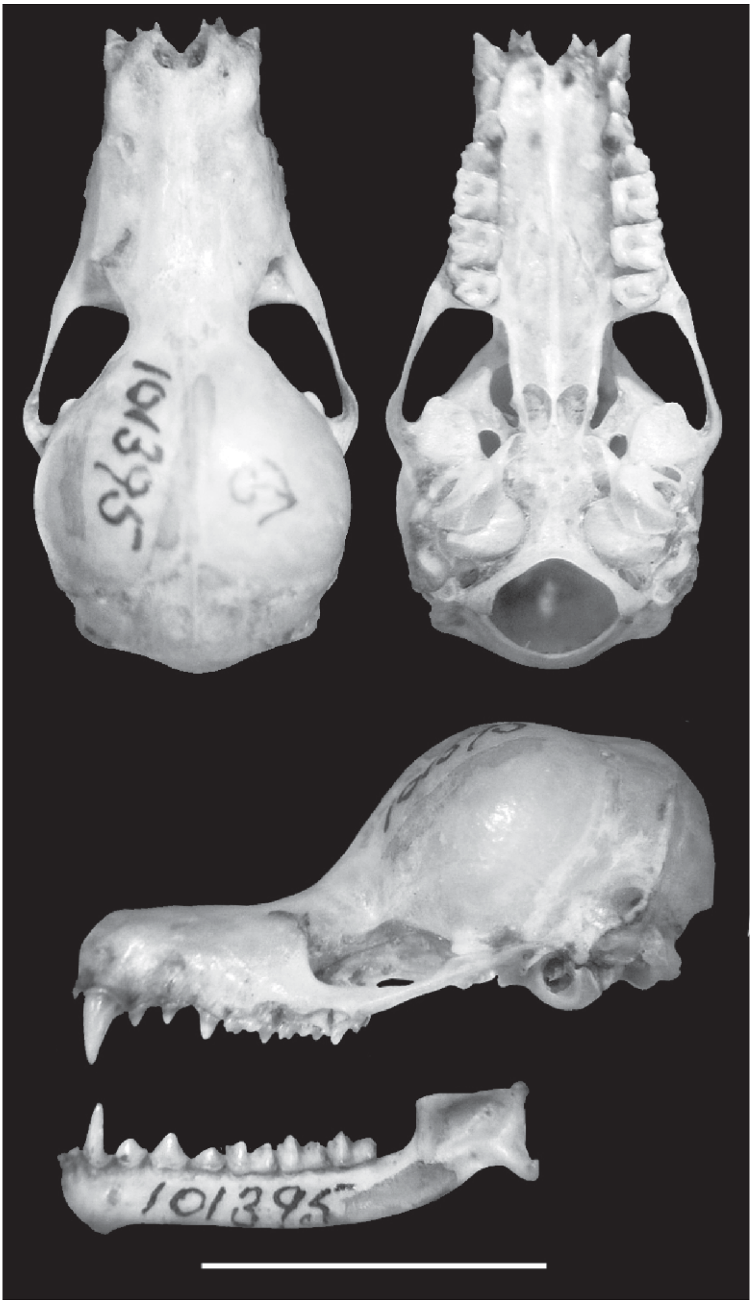


Fig. 27. Holotype of *Natalus major* (USNM 101395, male, Hispaniola [Dominican Republic]). Scale bar = 10 mm.

to molars; braincase greatly inflated, rising gently from rostrum; braincase elliptical in dorsal view; sagittal crest well developed; postorbital constriction wide, its sides diverging rostrally; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids nearly parallel; palate extending caudally to more than half the distance between bases and tips of pterygoids; basisphenoid pit shallow;

longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors short and peglike; I2 obscuring I1 in lateral view; upper premolars slightly increasing in size from P2 to P4 and crowded; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molars cusps relatively broad; spinous process of humerus about as high as capitulum; thorax relatively short and wide; ribs markedly expanded craniocaudally and extensively in contact with one another; vertebrae C7 to T1 fused and fused to ribs; vertebrae T12–L4 fused into a laterally compressed column without vestige of sutures; lumbar column relatively long and not particularly concave ventrally; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: Unique morphological features are not apparent in *Natalus major*. It, therefore, must be distinguished from other species of Natalidae by a combination of shared diagnostic characters. From species of the genera *Chilonatalus* and *Nyctiellus*, *Natalus major* is distinguished by its large size (forearm length > 41.1 mm) and by generic-level characters (table 3).

Natalus major can be easily distinguished from continental and Lesser Antillean species of *Natalus* on the basis of its larger forearm length and its straight medial ear margin. *Natalus mexicanus* has a slightly concave medial ear margin and its forearm is shorter than 40.0 mm. Only very large individuals of *N. stramineus*, *N. tumidirostris*, and *N. espiritosantensis* reach the forearm length of the smallest individuals of *N. major*, yet in the first three species, the medial ear margin is concave. *Natalus lanatus*, on the other hand, has a straight medial ear margin, but its forearm is shorter than 38.0 mm.

From *Natalus primus*, *N. major* can be distinguished by size, ear, and cranial characters. Relative to *N. major*, *N. primus* has a larger forearm (more than 46.0 mm; the forearm is shorter than 45.0 mm in *N. major*), has a straight lateral ear margin (concave or notched in *N. major*), and is characterized by deep basisphenoid pits (shallow in *N. major*), the presence of a mesostylar crest on M3 (absent in *N. major*), and an elongated premaxillary region (reflected in a laterally visible gap between I2 and the upper canine and a rostrally projecting I1; in *N. major* neither the gap between I2 and the upper canine, and I1 are visible in lateral view).

Of all natalids, *Natalus major* is most similar to *Natalus jamaicensis* in size and external characters, but can be easily distinguished by its wide postorbital region with sides widely diverging anteriorly, whereas the postorbital region in *N. jamaicensis* is narrow and with sides nearly parallel. The maxilla of *N. major* is convex dorsal to the molars, whereas that of *N. jamaicensis* is concave. Also, the braincase of *N. major* is oval in dorsal profile (with length greater than the greatest breadth) and does not rise abruptly from the rostrum (in an angle smaller than 55°), whereas that of *N. jamaicensis* is nearly circular in dorsal profile (with length similar to greatest breadth) and rises abruptly from the rostrum in an angle greater than 60°.

VARIATION: On average, males of *Natalus major* are significantly larger than females in length of tibia (Tukey; $P < 0.05$) and breadth across canines (Tukey; $P = 0.05$; table 15). Geographic variation is not apparent in this species. Most individuals have been collected in neighboring localities of the northwest of Hispaniola and other localities on the island are represented by only one or a few individuals.

Young adults with silky, grayish pelage have smaller zygomatic breadths even though the remaining cranial dimensions are similar to that of full adults. A specimen from Haiti (KU 150721), which Timm and Genoways (2003) speculated could belong to a separate subspecies because of its smaller dimensions and coloration, appears to be a young adult.

NATURAL HISTORY: *Natalus major* is known from 30 localities (including two represented by fossil remains only) of which at least 10 have been roost sites, nine of them caves and one a large hollow tree (Timm and Genoways, 2003). The caves where *N. major* has been found range from small to very large, are always humid, and often contain hot chambers and bodies of water. Most of these caves have a phreatic origin, with wide chambers and constricted entrances, but some are also fluvial caves characterized by

TABLE 15

Summary of measurements[a] of *Natalus major*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	4	6.7	(5.5–7.6)	1.1	9	7.5	(6.0–10.0)	1.3
Forearm length	11	43.5	(41.1–44.8)	1.0	22	43.4	(42.0–45.0)	0.9
Length of tibia, dry	2	21.4	(21.3–21.4)	0.1	7	22.7	(21.9–23.8)	0.7
Length of tibia*	8	23.6	(23.2–24.3)	0.4	14	24.2	(23.3–25.4)	0.7
Length of 3rd metacarpal	7	41.3	(40.3–42.3)	0.8	12	41.6	(40.5–42.7)	0.7
Length of 5th metacarpal	7	40.1	(38.3–41.2)	0.9	12	40.3	(38.9–40.9)	0.6
Length of ear	9	16.1	(14.0–18.9)	1.5	20	16.0	(13.0–17.9)	1.2
Length of penis		–	—	–	12	4.5	(3.6–5.8)	0.7
Length of natalid organ		–	—	–	9	7.0	(5.4–8.3)	0.9
Greatest skull length	2	17.3	(17.0–17.6)	0.4	11	17.7	(17.3–18.1)	0.2
Zygomatic breadth	2	9.4	(9.3–9.4)	0.1	11	9.5	(9.3–9.6)	0.1
Braincase breadth	2	8.7	(8.6–8.7)	0.1	11	8.8	(8.6–9.0)	0.1
Breadth across molars	2	6.3	(6.1–6.4)	0.2	12	6.3	(6.1–6.4)	0.1
Breadth across canines*	2	4.1	(4.1–4.1)	0.0	10	4.3	(4.1–4.4)	0.1
Maxillary tooth row	2	7.7	(7.6–7.7)	0.1	12	7.8	(7.6–8.0)	0.1
Mandibular tooth row	1	8.1	—	–	8	8.2	(8.0–8.4)	0.1
Postorbital breadth	2	3.4	(3.3–3.4)	0.1	12	3.4	(3.2–3.5)	0.1
Depth of braincase	1	7.2	—	–	7	7.1	(6.9–7.3)	0.2

[a] Descriptive statistics of measurements for each sex. N = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

linear passages. One was a sea cave with its floor partially inundated by the tide. *N. major* roosts in loose groups of less than 10 to more than 50 individuals, occupying areas of low ceilings (including solution cavities) or cave walls. Individuals hang from one or both feet, without body contact with the substrate or among themselves, and keeping a distance between individuals of about 10 cm (pl. 19-A). Occasionally, pairs of individuals are found hanging back to back. *Natalus major* can coexist at roosts with 10 other bat species (*Artibeus jamaicensis*, *Brachyphylla nana*, *Chilonatalus micropus*, *Erophylla bombifrons*, *Macrotus waterhousii*, *Monophyllus redmani*, *Mormoops blainvillei*, *Phyllonycteris poeyi*, *Pteronotus quadridens*, and *Pteronotus parnellii*), but it has never been found in multispecies groups. It usually tolerates disturbance for long periods and can occasionally be caught by hand while roosting, but this happens only when a colony has not been disturbed for a long time. On second and third visits to a cave the bats are usually alert and the groups move to alternative roosting sites within the cave at the slightest disturbance (e.g., the beam of a flashlight). When retreating from disturbance, the bats fly close to the floor and walls of the caves (pl. 9-B).

Natalus major is found from semiarid lowlands of thorn scrub (Pepillo Salcedo, Dominican Republic, 883 mm annual precipitation; locality 187) to degraded wet forest (Camp Perrin, Haiti, 2841 mm annual precipitation) and from sea level to about 1000 m (locality 182). Little is known of the diet or reproduction in this species. Young adults have been found in late October, indicating that parturition and lactation probably take place from July to September, as in *Natalus mexicanus*. *Natalus major* is the most common of Greater Antillean *Natalus*, being represented by 105 museum specimens, most of which have been captured in the northeast of the Dominican Republic. Roosting colonies may reach a few hundred individuals.

Natalus major begins its foraging activity shortly after sunset. One individual was mistnetted at 15:39, at least 4 km away from any known cave where the species roosted. A

TABLE 16
Summary of measurements[a] of *Natalus mexicanus*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	42	5.2	(3.5–7.0)	0.8	41	5.4	(3.9–8.0)	0.9
Forearm length	139	37.6	(34.0–40.4)	1.0	166	37.8	(35.1–40.6)	1.0
Length of tibia, dry*	74	18.9	(16.3–21.8)	1.0	104	19.5	(16.2–21.9)	0.9
Length of tibia	44	20.5	(18.7–21.8)	0.6	38	20.7	(19.4–22.3)	0.7
Length of 3rd metacarpal	25	35.5	(34.2–37.4)	0.9	33	35.4	(33.4–37.3)	1.0
Length of 5th metacarpal	25	34.8	(33.1–37.2)	0.9	33	35.1	(33.5–36.7)	0.8
Length of ear	85	14.4	(12.0–17.0)	0.9	85	14.5	(12.0–17.0)	0.9
Length of penis		–	– –	–	22	3.9	(3.0–4.9)	0.5
Length of natalid organ		–	– –	–	5	6.5	(5.3–7.3)	0.8
Greatest skull length*	98	15.7	(14.9–16.3)	0.3	130	16.0	(15.3–16.8)	0.3
Zygomatic breadth	93	7.9	(7.4–8.4)	0.2	127	8.0	(7.5–8.5)	0.2
Braincase breadth*	98	7.6	(6.9–8.0)	0.2	129	7.7	(7.2–8.3)	0.2
Breadth across molars*	98	5.2	(4.8–5.6)	0.2	130	5.3	(4.9–5.7)	0.1
Breadth across canines*	97	3.5	(3.1–3.7)	0.1	127	3.6	(3.2–3.9)	0.1
Maxillary tooth row *	98	6.7	(6.4–7.1)	0.2	131	6.8	(6.3–7.2)	0.2
Mandibular tooth row*	76	7.1	(6.6–7.5)	0.2	97	7.2	(6.7–7.6)	0.2
Postorbital breadth	98	3.1	(2.8–3.4)	0.1	130	3.1	(2.8–3.4)	0.1
Depth of braincase*	76	6.2	(5.5–6.7)	0.2	97	6.4	(5.9–6.9)	0.2

[a] Descriptive statistics of measurements for each sex. *N* = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P \leq 0.05$) are followed by an asterisk (*).

second individual was mistnetted well after dark entering a cave not used by the species as a day roost, suggesting that night roosts may be used at least occasionally. It has a very slow and maneuverable flight and dehydrates quickly if taken outside the cave during daytime.

Natalus major is listed asnear threatened in IUCN's Red list of Threatened Species (IUCN, 2010). Yu and Dobson (2000) considered this species "very rare," yet their conclusion was based on distribution and ecological data from Hoyt and Baker (1980), who listed the type localities of *N. major major and N. major jamcensis* as the only localities of *N. major* (sensu lato), and based their natural history account on *N. jamaicensis*. Even though it is represented by relatively few specimens compared to continental species (e.g., *N. tumidirostris* and *N. mexicanus*), it seems ubiquitous throughout Hispaniola (particularly in the moist northeast) and is one of the most frequently encountered bats in the island's caves. Given that a significant proportion of the many caves that may remain unsurveyed in Hispaniola's protected karstic areas (e.g., Parque Nacional Jaragua and Parque Nacional los Haitises) probably harbor this species, *N. major* may be more accurately regarded as of least concern for conservation. Nonetheless, considering that this species is restricted to Hispaniola, adequate population assessments should be undertaken to evaluate its potential conservation needs.

Natalus mexicanus Miller, 1902
Figure 28

Natalus mexicanus Miller, 1902: 399. Type locality "Santa Anita, lower California, Mexico."

Natalus mexicanus saturatus: Dalquest and Hall, 1949: 153. Type locality "3 kilometers east of San Andres Tuxtla, 1000 feet elevation, Veracruz, Mexico."

Natalus stramineus mexicanus: Goodwin, 1959: 6. Part, new combination.

Natalus stramineus saturatus: Goodwin, 1959: 7. Part, new combination.

Natalus saturatus: Dávalos, 2005: 100. New combination.

HOLOTYPE: USNM 96496, adult female, skin in alcohol with skull extracted, collected

Fig. 28. Holotype of *Natalus mexicanus* (USNM 96496, Baja California Sur, Mexico). Scale bar = 10 mm.

TABLE 17

Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 9 geographic samples of *Natalus mexicanus*

Measurement	C I	C II
Greatest skull length	−0.016	0.106
Zygomatic breadth	−0.096	0.354
Braincase breadth	0.938	−0.201
Breadth across molars	0.454	0.549
Breadth across canines	−0.804	−0.421
Maxillary tooth row	0.005	0.987
Postorbital tooth row	0.484	−0.210
Depth of skull	0.058	−0.607
Eigen value	1.045	0.716
Percent explained	45.5	31.7

CVA scores are plotted in figure 38B.

by J.F. Abbot in August 1897, at Santa Anita (locality 266 in appendix 1), Baja California Sur, Mexico. The skin is in good condition. The skull has the braincase caved in and cracked on its left side but otherwise is in good condition.

DISTRIBUTION: Southern North America and Central America in the countries of Mexico (Baja California Sur, Campeche, Chiapas, Chihuahua, Colima, Distrito Federal, Durango, Guerrero, Hidalgo, Jalisco, Mexico, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz, Yucatán, Zacatecas), Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, and Panama, including several offshore continental or oceanic islands (María Magdalena and Cozumel, Mexico; Coiba, Panama; San Andrés and Old Providence, Colombia); fig. 25.

DIAGNOSIS: Size small (forearm length 34.0–40.6 mm); medial margin of ear slightly concave; lateral margin of ear deeply notched; premaxilla not inflated with maxilloincisive suture rostral to infraorbital foramen; maxilla convex but not inflated dorsal to molars; palate ending caudally about 2/3 of the distance between the caudal margin of M3 and the tip of the pterygoid process; ventral hairs monocolored; dorsal hairs monocolored or bicolored with bases lighter than tips; toes lacking conspicuous tufts of hair at base of claws; caudal margins of the maxillary bones forming an acute angle with midline of skull; basisphenoid pit double and shallow; postorbital region with sides widely diverging rostrally, in dorsal view; caudal margin of ascending ramus of dentary perpendicular to alveolar plane of dentary; I1 slightly projected rostrally and visible in lateral view, not being obscured by I2; mesostylar crest of M3 absent. A comparison of diagnostic characters between *N. mexicanus*, and other species of *Natalus* is summarized in table 5.

DESCRIPTION: Small to medium natalid (forearm length 34.0–40.6 mm; greatest skull length 14.9–16.8 mm; weight 3.5–8.0 g); muzzle long and dorsoventrally flattened; nostrils elliptical; opening ventrolaterally, sometimes at the end of tubelike projections, on shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium size and elliptical, extending from caudal base of rostrum to crown of head; ears medium sized (12.0–17.0 mm); ear pinna funnel shaped but distally thin, with markedly pointed tip, medial margin slightly concave, and lateral margin deeply concave; five to six small ear ridges along lateral margin of distal pinna; ventral region of pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (18.7–22.3 mm) slightly longer than half the length of the forearm; calcar long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively broad, with 3rd metacarpal (33.4–37.3 mm) similar in size to 5th metacarpal (33.1–37.2 mm); wings attach to tibia above ankle; pelage dense and lax; hairs long (8 mm, dorsally; 7 mm, ventrally); pelage usually darker dorsally than ventrally; pelage color from almost white ventrally and very light yellow brown dorsally to bright orange brown and chestnut brown both ventrally and dorsally (pl. 1); dorsal hairs bicolored, with tips darker than bases; ventral hairs usually monocolored; dense mustachelike hair tufts along lateral margins of upper lip and on dorsum of muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with thin hairs; skull long and narrow with moderate rostral flexion; rostrum narrow, with shallow sulcus between nasals; maxilla dorsal to molars; braincase inflated, rising gently from rostrum; sagittal crest moderately developed; postorbital constriction narrow; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; caudal margin of palatal branch of maxilla forming an acute angle with longitudinal axis of skull; pterygoids nearly parallel; palate extending caudally to half the distance between bases and tips of pterygoids; basisphenoid pit shallow; longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors short and peglike; I1 visible in lateral view, not being obscured by I2; occlusal profile of premolars long; upper premolars slightly increasing in size from P2 to P4; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molars cusps relatively broad; spinous process of humerus about as high as capitulum; thorax relatively short and wide; ribs markedly expanded craniocaudally and extensively in contact with one another; vertebrae C7 to T1 fused among themselves and to ribs; vertebrae T12–L4 fused entirely without vestige of sutures; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: *Natalus mexicanus* is one of the two smallest species in the genus *Natalus,* the other being *N. lanatus*. Its forearm is shorter than those of all insular (*N. primus*, *N. major*, *N. jamaicensis*, and *N. stramineus*) and South American (*N. tumidirostris* and *N. espiritosantensis*) representatives of the genus. The only distinct diagnostic external character of *N. mexicanus* is the shape of the medial margin of the ear, which is slightly concave, and seems intermediate in shape between the straight medial margin of *N. lanatus*, *N. primus*, *N. major*, and *N. jamaicensis*, and the markedly concave medial margin of *N. tumidirostris*, *N. espiritosantensis*, and *N. stramineus*. In addition, most *N. mexicanus* can be distinguished from *N. tumidirostris* by the large and nearly circular nostrils in this species versus small and elliptical nostrils in *N. mexicanus*. This trait, however, can be variable in *N. tumidirostris* (see Comparisons under the account of that species) and should thus be used in combination with other traits for a confident diagnosis of *N. mexicanus*. For a comparison of external morphology between *N. mexicanus* and its sympatric species *N. lanatus*, see Comparison under the account of the latter species.

Craniodentally, *N. mexicanus* is diagnosed by a combination of characters; therefore, identification must be done by elimination of species with which it may be confused. From the greater Antillean species *N. mexicanus* can be distinguished by forearm length (less than 40.6 mm in *N. mexicanus*, greater than 41.1 mm in Greater Antillean species). From *N. stramineus* it is distinguished by the position of its first incisors. In *N. mexicanus*, I1 is rostral to I2 in ventral view and in *N. stramineus* I1 is at the level of I2, so that it is not visible in lateral view. From *N. tumidirostris* it differs in its convex yet uninflated premaxilla (markedly inflated in *N. tumidirostris*) and in the caudal extension of the palate, which reaches 2/3 of the distance between the caudal edge of M3 and the tip of the pterygoids (the palate ands caudally at M3 or M2 in *N. tumidirostris*). Relative to *N. espiritosantensis*, *N. mexicanus* has a more slender skull and a longer tooth row, yet there are overlaps in measurements, therefore an appropriate differentiation of both species should be based also on external characters and geographic distribution. From *Natalus lanatus*, its sympatric species, *N. mexicanus* is distinguished by a deeper and less tapering rostrum in lateral view, more robust dentition, especially incisors and canines, caudal margins of maxillary bones, in ventral view, forming an acute angle with midline of skull, less globular braincase, and smaller sphenorbital fissure.

VARIATION: Males of *N. mexicanus* are slightly, yet significantly, larger than females in eight external and cranial measurements (table 15).

Size variation in *N. mexicanus* is due mostly to variation within populations rather than to variation among populations. None-

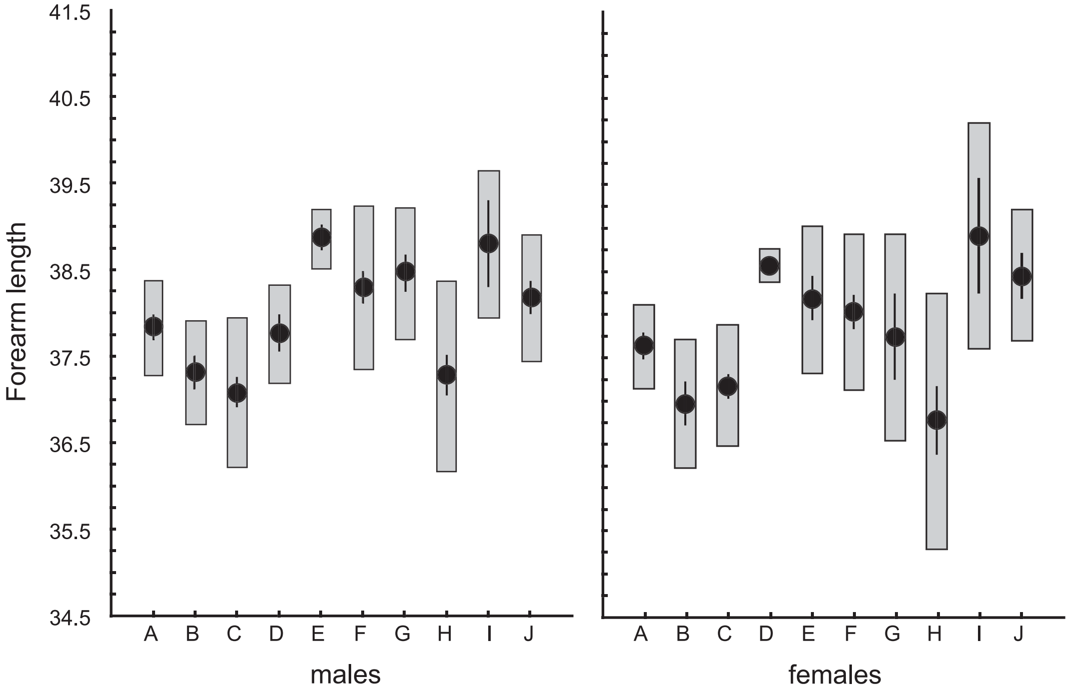


Fig. 29. **A,** Plot of means (black dots), two standard deviations around the mean (gray bars), and two standard errors of the mean (vertical black lines) of forearm length of *Natalus mexicanus* from 10 geographic areas: A = N Peninsular Mexico (Baja California Sur; 16 males, 18 females; B = NW Mexico (Chihuahua, Sonora; 11 males, 12 females); C = W Mexico (Durango, Jalisco, Nayarit, Sinaloa; 29 males, 32 females); D = South Central Mexico (Guerrero, Morelos, Puebla; 8 males, 7 females); E = NE Mexico (Tamaulipas; 6 males, 11 females); F = Isthmic Mexico (Veracruz, Oaxaca; 30 males, 22 females); G = N Central America (Chiapas, Guatemala; 12 males, 6 females); H = Yucatan (Belize, Campeche, Guatemala [Petén], Quintana Roo, Yucatán; 30 males, 18 females); I = San Andrés and Providencia Isl., Colombia (3 males, 4 females); J = Southern Central America (Panama; 16 males, 9 females). Individuals from Isthmic Mexico, San Andrés and Providencia, and S Central America are significantly larger than those from the Yucatan, and W and NW Mexico (one-way ANOVA, $P < 0.01$).

theless, individuals from eastern Mexico (Tamaulipas to Chiapas) and Central America (Guatemala, Colombia [San Andrés and Providencia], and Panama) average larger in forearm length (fig. 29A) than individuals from western Mexico (Jalisco to Sonora and Baja California). This trend, however, is not uniform, because individuals from the Yucatan average smallest and those from the Isthmus of Tehuantepec average largest in most measurements. Differences in body proportions are slight, but specimens from Panama are notable in having a relatively shorter and wider rostrum (fig. 29).

Natalus mexicanus exhibits the widest color variation of any natalid, but most is individual rather than geographic. Some individuals from the Isthmus of Tehuantepec (Los Tuxtlas, Veracruz, and Tehuantepec, Oaxaca) have the darkest pelage of any natalid, being rich chestnut brown dorsally, and slightly lighter ventrally. Some individuals from Baja California, conversely, are extremely pale, being pale buff dorsally and almost pure white ventrally. Most populations, however, exhibit color variants that range from buff to bright orange brown and yellow, and it is likely that the apparent lack of color variants within any one population is mostly due to small sample size.

NATURAL HISTORY AND CONSERVATION: *N. mexicanus* is known from 253 localities, in 85 of which this species has been taken at roost sites (63 are reported as caves, 21 as

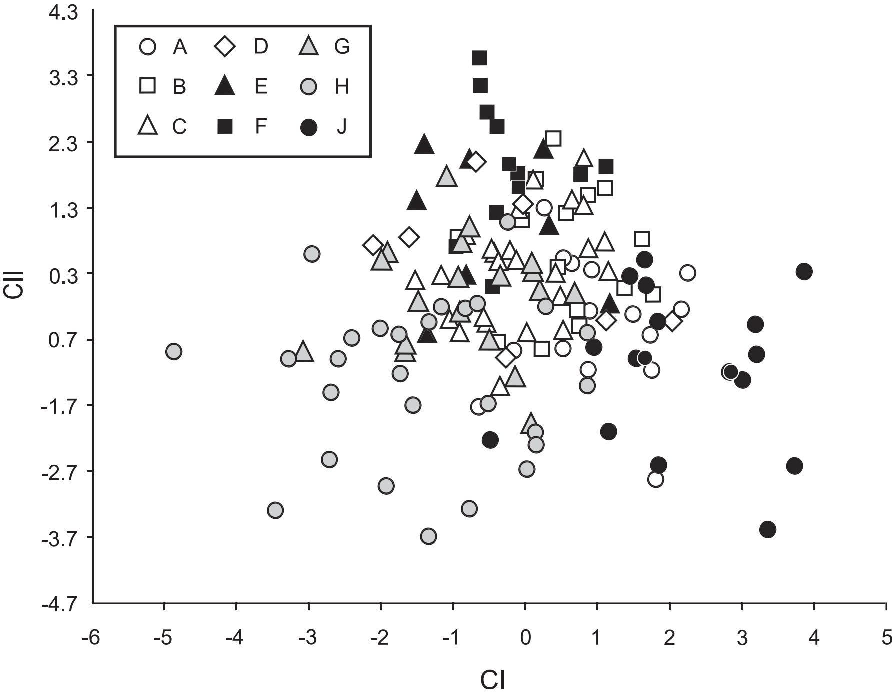


Fig. 29 (*continued*). **B,** Plot of canonical scores for seven cranial measurements of *N. mexicanus* from nine geographic areas (same as above, San Andrés and Providencia not included). Variable loadings are listed in table 17. Three most divergent groups are distinguished: (1) individuals from the Yucatan characterized by overall small skulls; (2) individuals from Isthmic Mexico, characterized by large skulls and long rostra; and (3) individuals from Panama, characterized by large skulls and short rostra.

mines, two were hollow trees, and one was a drainage pipe under a road [Moreno, 1996]). Some reported localities for this species are represented by specimens not examined in this work; therefore may include misidentified specimens of *Natalus lanatus*.

Natalus mexicanus roosts in caves ranging from very large in linear extension (e.g., more than 10 km in linear extension, Gruta de Cacahuamilpa, Guerrero), to very small (e.g., less than 10 m, Cueva Chica, Baja California). Several individuals collected in Progreso, Guatemala, were taken from behind an overhanging rock where they roosted under full daylight together with a group of *Glossophaga* sp. (Goodwin, 1934). *N. mexicanus* is generally found in warm and humid caves, but avoids the warmest portions of such refuges; in a cave in Veracruz Hall and Dalquest (1963) observed it roosting in a relatively cool area at the entrance of a hot passage occupied by large colonies of *Pteronotus personatus* and *Pteronotus davyi*. Temperatures measured in *N. mexicanus* roosts have ranged between 17° and 27° C (Ávila-Flores and Medellín, 2004; Mitchell, 1965; personal obs.). The relative humidity of roost sites has been reported to range from 74% to 99% (Ávila-Flores and Medellín, 2004; Mitchell, 1965, McNab, 1969). On one occasion, I found the relative humidity of a roost as low as 54% (deep end of Cueva Chica, Baja California), but the bats caught there might have been displaced from a more sheltered (and perhaps more humid) location where the largest colony was found, due to disturbance created by human visitors. George G. Goodwin (personal commun. in Mitchell, 1965; as *N. stramineus saturatus*) mentioned that two groups of three to five individuals of *N. mexicanus* had been found in San Antonio, Oaxaca, roosting during the day in hollow trees in a limestone/karst area with thorn scrub vegetation.

Natalus mexicanus has been found coexisting in caves with 32 other bat species (*Artibeus hirsutus*, *Artibeus jamaicensis*, *Arti-*

beus lituratus, *Balantiopteryx io*, *Balantiopteryx plicata*, *Carollia brevicauda*, *Choeronycteris mexicana*, *Desmodus rotundus*, *Diaemus youngi*, *Diphylla ecaudata*, *Glossophaga soricina*, *Glyphonycteris sylvestris*, *Leptonycteris nivalis*, *Leptonycteris yerbabuenae*, *Lonchorhina aurita*, *Macrotus californicus*, *Macrotus waterhousii*, *Micronycteris megalotis*, *Mimon cozumelae*, *Mormoops megalophylla*, *Myotis peninsularis*, *Myotis thysanodes*, *Myotis velifer*, *Myotis keaysi*, *Myotis nigricans*, *Plecotus townsendi*, *Pteronotus davyi*, *Pteronotus gymnonotus*, *Pteronotus parnellii*, *Pteronotus personatus*, *Pteropteryx macrotis*, *Tadarida brasiliensis*; Arita, 1997). Still, it generally roosts separated from other species (Mitchell, 1965). While roosting, *N. mexicanus* hangs in loose aggregations from the walls of caves and tunnels and less frequently from ceilings, keeping a regular distance (of about 10 cm) between individuals (Mitchell, 1965). In the roost, individuals can be extremely quiet, allowing themselves to be hand-caught, or can fly away at the least indication of human presence (Hall and Dalquest, 1963; Mitchell, 1965). It has been found in caves on a variety of rock types, including limestone, volcanic rock, and loose sandstone. Groups of *N. mexicanus* appear to move between alternative caves. Hall and Dalquest (1963) noted that the number of individuals in a ''lava cave'' near San Andres Tuxtla, Mexico, changed on a daily basis, reaching a low of two bats on 2 January 1948, and a high of about 300 on 10 January 1948. Also, the population in Mina Armolillo, Sonora, decreased from about 1000 bats during November 1963–April 1964 to about 200 bats during June–July. During the later period, individuals banded in February in Mina Armolillo were found roosting in Mina Yeger (about 3 km south of Mina Armolillo), which never harbored *N. mexicanus* from August to March, and in Mina La Aduana (less than 1 km apart from Mina Yeger), which harbored a permanent colony of *N. mexicanus* that increased in size from June to July 1964. The emigration from Mina Armolillo coincided with late pregnancy, and lactation of *N. mexicanus* and with a marked increase in numbers of *Leptonycteris* sp. (identified as *L. nivalis* in the original account) and *Glossophaga soricina* in that mine (Mitchell, 1965).

Using niche models based on collection localities of the state of Michoacán, Wang et al. (2003) predicted that *N. mexicanus* would be found in tropical deciduous and semideciduous forests characterized by a 22°–26° C mean annual temperature and 800–1500 mm annual precipitation. In the rest of its range, however, the habitats of this species vary from desert scrub (Pescadero, Baja California, Mexico, 156 mm annual precipitation; locality 265) to degraded rain forest (Teapa, Tabasco, Mexico, above 3800 mm annual precipitation; locality 426). Also, it occurs in a wide variety of altitudes, ranging from sea level to 2300 m (Tlalpan, Mexico; locality 294). It is possible, however, that some of the high elevation localities of *N. mexicanus* may actually represent records of *N. lanatus*.

Although it is surely insectivorous, nothing is known of the diet of *N. mexicanus*. The reproductive pattern of a colony of *N. mexicanus* inhabiting Mina Armolillo, Sonora, was studied by Mitchell (1965) between 1964 and 1965. His study showed that *N. mexicanus* is monoestrous and bears a single pup per year. The gestation period was found to be very long, with copula and fertilization probably taking place during December or early January (when the males are at the height of spermatogenesis and the females begin to show implantation) and parturition around late July. In males, from June to October the testes were barely visible even upon dissection. Beginning in October, the testes increased in size from about 1.5 mm in length to slightly over 2.0 mm by the end of January, with a corresponding increase in seminal sperm counts.

All pregnant females examined by Mitchell (1965) between January and August always carried a single embryo exclusively in the left horn of the uterus. Between January and April the embryo showed little growth, although both anterior and posterior limb buds were well formed by the end of this period. The weight of the embryos increased from 0.01 g in early April to 0.3 g in late May, by which time the limbs (forearm = 5 mm) and wing membranes were well formed. From this point on, the weight and forearm length of the embryos underwent an exponential increase, which ended about

20 days after birth for weight and 40 days after birth for forearm length. At birth, which took place between 12–20 July, newborns weighed 1.45–1.75 g and their forearms measured 11.0–16.0 mm. The fastest growth took place immediately after birth until weights leveled off at 2.8–4.4 g (about a 145% increase from birth weight) and forearm lengths at 34–35 mm (about a 185% increase from forearm length at birth). The end of the growth spurt in forearm length coincided with the onset of flight, which took place around late August. After the onset of flight, the weight of the young increased slowly but steadily until the observations ended on 26 February, by which time the bats had reached 5.7–6.2 g, nearly equalling the weight of the adults (5.7–6.6 g). During this period, forearm length increased more slowly than weight, but also attaining a range (35–38 mm) near that of adults (36–39 mm).

The *N. mexicanus* of Mina Armolillo were born naked and with eyes closed. Lightly haired young with eyes open were not seen until 7 August, about two weeks after birth. By 24 August, when the young were first observed to fly actively, their pelage had grown longer and was deep (or darkish) mouse gray on the tips and smoke gray basally. By 27 November, the pelage had grown even longer and was lighter in overall color, with hair tips drab and hair bases pale smoke gray. Two months later (26 February), body hairs of the subadults were still drab at the tips but had become even lighter basally (light grayish olive).

In Mina Armolillo, on 20 July, about 50 newborn *N. mexicanus* were found in a cluster on the wall, about 1 m from the floor and much closer to the entrance (about 18 m) than the areas where adults roosted (40–75 m away from the entrance). Three or four adult females, which were nursing their young within the cluster, flew away carrying the newborn bats with them when the cluster was approached by human observers. The cluster was formed by mixed haired and naked young, evidently of different ages. When the most advanced young were able to fly, they left the cluster and hung separately in its vicinity. These young still nursed, but some began to consume insects. Neither sex of *N. mexicanus* seems sexually mature in the first year.

Natalus mexicanus is the natalid most common in collections, being represented by at least 2491 museum specimens. The number of specimens per locality is more evenly distributed relative to that of other species. Colony sizes of *N. mexicaus* can be moderately large (e.g., about 1000 individuals, Mina Armolillo, Sonora), but are generally formed by only a few hundred bats (Alvarez, 1963; Hall and Dalquest, 1963), and some bats are occasionally found roosting solitarily (Cueva de Agua Caliente, Izabal).

The lyre snake *Trimorphodon biscutatus* has been reported to prey on *N. mexicanus* in Chamela (Sánchez-Hernández and Ramirez-Bautista, 1992). The fungus *Histoplasma capsulatum* was isolated from internal organs of two out of five *Natalus* from Morelos (Taylor et al., 1999). Lunaschi (2002) reported the trematode *Ochoterenatrema labda* (Digenea: Lecithodendriidae) as a parasite of this species.

Nocturnal emergence begins at about 30 min after sunset (Reid, 1997). Mitchell observed the *N. mexicanus* of Mina Armolillo begin their foraging 10–15 min before total darkness, with emergence lasting about 10 min. On 27 January 1964 only one bat remained in the mine immediately after the colony's emergence. The bats began returning to the cave 2 hours after emergence and continued entering and leaving the cave for the remainder of the night. Before emergence, most individuals were hanging near the entrance of the mine in a restless state, and when disturbed some flew out of the mine and hung in the vegetation outside until it became dark (Mitchell, 1965). During their foraging activity, *N. mexicanus* visits sources of drinking water (e.g., a swimming pool near Mina Armolillo; Mitchell, 1965).

The flight of *N. mexicanus* is slow and very maneuverable. Only a few bats were caught in two nets set over a swimming pool in Alamos, Sonora, even though many bats were observed drinking water from the pool (Mitchell, 1965). Even when some bats hit the net, they rarely became entangled and were able to fly off.

The echolocation calls of *N. mexicanus* have been described as very weak (low intensity) and hard to detect unless the bat is <0.5 m from the microphone. The search

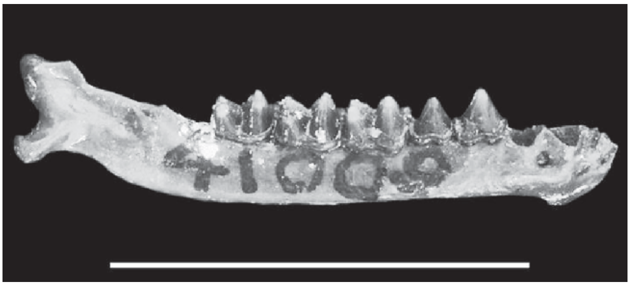


Fig. 30. Holotype of *Natalus primus* (AMNH 41009, fossil right dentary, image inverted). Scale bar = 10 mm. Photo: Mariko Kageyama, AMNH (see appendix for institutional abbreviations).

calls consist of short (about 2 ms) FM sweeps with most energy in the second harmonic at 100–130 kHz, but with occasional emphasis on the fundamental frequency. They are emitted at short and variable intervals and with a low duty cycle (Rydell et al., 2002). Miller (2004) stated that current echolocation call detection techniques are unsuited for detecting the low-intensity calls of *N. mexicanus* during foraging.

Natalus mexicanus is very susceptible to dehydration. Bats taken from the humid interior of Mina Armolillo (84% relative humidity) to the exterior (65% relative humidity) died within an hour, even though sheltered from the sun (Mitchell, 1965). Shaldach (in Nowak 1994) reported torpid *N. mexicanus* (indentified as *N. stramineus*) in a cave in Tamaulipas, in an oak forest area, with an outside temperature of 12° C.

Natalus mexicanus is listed as least concern in the IUCN Red List of Threatened Species (IUCN, 2010) "]. Even though its separation from *Natalus stramineus* implies a marked range reduction for *N. mexicanus*, its abundance and large number of known localities indicate that its current IUCN status is correct.

Natalus primus Anthony, 1919
Figures 30, 31

Natalus primus Anthony, 1919: 642. Type locality "Daiquirí," Santiago de Cuba, Cuba.

Natalus major primus: Goodwin, 1959: 10. New combination.

Natalus stramineus primus Varona, 1974: 33. New combination.

Natalus major: Tejedor et al., 2004: 153. Not *Natalus major* Miller, 1902.

HOLOTYPE: AMNH 41009, a fossil right dentary (fig. 30), collected by H.E. Anthony in 1917, Cueva de Los Indios (locality 28 in the appendix), Daiquirí, Santiago de Cuba, Cuba. The holotype is missing the coronoid process plus the incisors, canine, and first premolar, and is stained dark brown. (A second right dentary, designated by Anthony as a topotype, is in the vial with the holotype. It is complete, but lacks almost all teeth except p4 and m1).

DISTRIBUTION: Cuba, Isle of Pines, the Bahamas (Abaco, Andros, New Providence, and Eleuthera), and Grand Cayman. There is only one locality (Cueva La Barca, Cuba; Tejedor et al., 2004) where live *N. primus* has been found and 14 localities where the species is represented by fossils (fig. 23).

DIAGNOSIS: Largest living species in the genus *Natalus* (forearm length 46.1–51.2 mm, greatest skull length 18.1–19.9 mm); rostrum long; point of flexion between rostrum and braincase slightly caudal to rostral edge of orbit; medial and lateral ear margin straight; nostrils small, opening ventrolaterally; ventral hairs monocolored; dorsal hairs bicolored, hair bases lighter than tips; hairs at base of claws short and inconspicuous or long and thin, never forming tufts; premaxilla not inflated; maxilloincisive suture anterior to infraorbital foramen; maxilla dorsal to molars convex, not inflated; postorbital region with sides widely diverging rostrally; caudal margin of palate at 1/2 of the distance between M3 and tip of pterygoid; caudal margin of maxilla behind M3 nearly at right angle to longitudinal axis of skull; basisphenoid pits deep and steep sided; caudal margin

Fig. 31. Skull and mandible of *Natalus primus* (dorsal and lateral views plus mandible: AT 1, Pinar del Río, Cuba; ventral view: AT2, Pinar del Río, Cuba). Scale bar = 5 mm.

of dentary forming a 70° angle with alveolar margin of lower molars; I1 visible in lateral view, not obscured by I2; mesostylar crest present on M3. Diagnostic characters contrasting *N. primus* with other species of *Natalus* are summarized in table 5.

DESCRIPTION: Size large (forearm length 46.1–51.2 mm; greatest skull length 18.1–19.9 mm; weight 6–12.6 g); muzzle very long and dorsoventrally flattened; nostrils elliptical, opening ventrolaterally at the end of short tubelike projections on shallow depression on margin of upper lip; upper and lower lips markedly thickened; lower lip markedly constricted at midline, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; ears long (20.2–21.2 mm); ear pinna very wide and funnel shaped, with moderately pointed tip; lateral and medial margins of pinna straight; four very small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus markedly short, lanceolate, and twisted into helixlike structure; tibia (25.4–29.1 mm) longer than half the length of the forearm; calcar very long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively long and wide, with 3rd metacarpal (43.2–49.0 mm) much longer than 5th metacarpal (40.0–44.8 mm); wings attach to tibia above ankle; pelage dense and lax; hairs long (8–9 mm) both dorsally and ventrally; hairs bicolored, with tips darker than bases; pelage color from drab with fuscous tips to buff with tips sepia; dense mustachelike hair tufts along lateral margins of upper lip; mustache formed by dense, lax, irregular, and ventrally curved hairs; skull long and narrow with moderate rostral flexion; rostrum long and narrow, with marked sulcus between nasals; moderate rostral palatal emargination; maxilla convex dorsal to molars; braincase greatly inflated, rising gently from rostrum; sagittal crest moderately developed; postorbital constriction narrow relative to skull length; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids slightly convergent; palate extending caudally to half the length of pterygoids; basisphenoid pit deep and steep sided; longitudinal medial ridge on basisphenoid present; ectotympanic large, covering about half of the periotic; upper incisors long, pointed, and slightly hooked; premolars markedly long in occlusal profile; upper premolars of similar size and not crowded; mesostylar crests on M1 and M2 long and broadly curved, mesostylar crest present on M3; cingular cusp of p4 short and broad; molars cusps relatively broad; spinous process of humerus about as high capitulum; thorax relatively short and wide; ribs greatly expanded craniocaudally with extensive contact among themselves; vertebrae C7 to T1 fused among themselves and to ribs; vertebrae T12–L4 fused entirely without vestige of sutures; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: *Natalus primus* is the largest of all extant *Natalus*, and overlaps only in range of forearm length with *N. jamaicensis*. *N. primus* can, therefore, be distinguished by size alone from most species in the family Natalidae, including those of the genera *Chilonatalus* and *Nyctiellus*. In addition to overall body size, *N. primus* differs from the genera *Chilonatalus* and *Nyctiellus* in generic level characters (table 3).

Externally, *N. primus* is unique within the genus *Natalus* in having a straight lateral ear margin, which gives the ear pinna a rather square shape with a broad tip. In all other *Natalus*, the lateral ear margin is concave or notched and the ear tip is much more pointed.

Cranially, *Natalus primus* is unlike any other species of *Natalus* in that its basisphenoid pits are very deep and steep sided (as in the genus *Chilonatalus*), while in the remaining species of the genus the basisphenoid pits are shallow. Also, in *N. primus*, the rostrum appears proportionately longer, relative to skull length, than in all other species of *Natalus*. This overall greater length of the rostrum in *N. primus* is the result of (1) the rostral elongation of the premaxilla, with an anterior projection of the incisors, and (2) the position of the dorsal point of flexion of the skull, which, in lateral view, lies caudal to the anterior edge of the orbit. In all other species of *Natalus*, the premaxilla is not markedly elongated, so that the incisors are at or near the level of the canines, and the dorsal point of flexion of the skull, in lateral view, lies dorsal to the anterior edge of the orbit. Finally, in *N. primus*, the posterior edge of the ascending ramus of the mandible forms an angle of about 70° with the alveolar plane of the lower molars, and usually shows a small rounded projection between the base of the angular process and the condyloid process. In all other species of *Natalus*, the caudal margin of the ascending ramus of the mandible is nearly perpendicular to the alveolar plane of the lower molars and the rounded process between the base of the angular process and the condyloid process is always absent.

VARIATION: On average, males of *N. primus* are heavier and have a longer tibia

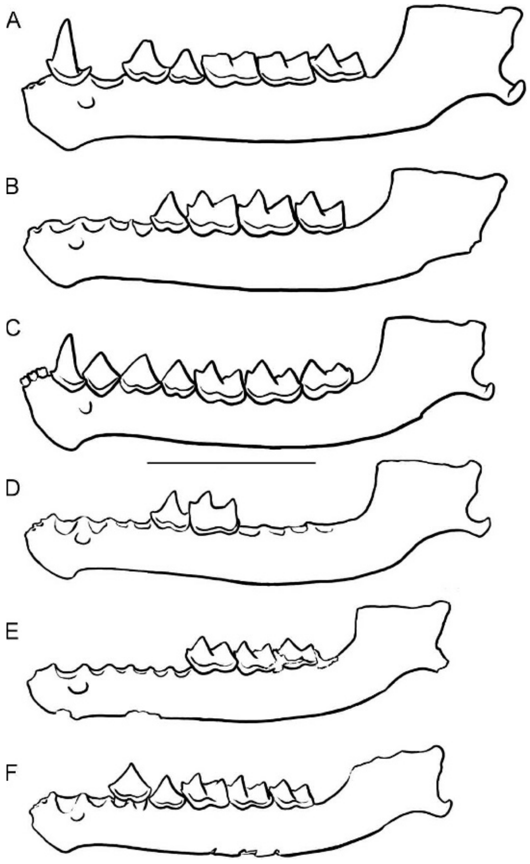


Fig. 32. Morphological variation among extant and fossil populations of *Natalus primus*. Populations: A = Abaco; B = Eleuthera; C = Cuba (extant); D = Cuba (fossil, topotype of *N. primus*); E, F = Grand Cayman.

and a larger skull than females (Tukey; $P < 0.05$).

Tejedor et al. (2004) reported that the extant population from Cueva La Barca was significantly smaller in four cranial dimensions than a fossil sample (attributed to late Pleistocene; Silva-Taboada, 1974) from Central Cuba, but could not distinguish whether the difference was due to chronological or geographic variation. Comparison with fossil material (also attributed to late Pleistocene; Morgan, 1989, 1994) from the Bahamas and the Cayman islands indicates significant geographic differences among the three island groups (table 17, fig. 32). The *N. primus* from the Bahamas are largest, with little overlap in range of mental length with the sample of fossils from Cuba, and no overlap with the extant sample. The sample from Grand Cayman is the smallest and does not overlap in range with any of the Cuban samples, which are of intermediate size. In addition, the caudal margin of one dentary from Grand Cayman does not form an angle of about 70° with the alveolar plane of the dentary, a diagnostic trait of *N. primus*, but is rather perpendicular to the alveolar plane of the mandible. These differences suggest that *N. primus* as recognized here may represent a complex of allopatric species rather than a single widespread taxon. Future fossil finds in the Bahamas and Cayman Islands should help test this hypothesis.

NATURAL HISTORY AND CONSERVATION: *Natalus primus* is known from 22 localities but is known in the flesh from only one: Cueva La Barca (locality 130 in the appendix), Pinar del Río, Cuba, a large cave comprising several warm and humid chambers (including a hot chamber) and one permanent pond. In Cueva La Barca, *N. primus* occupies rather well-ventilated areas of the warm chambers, roosting almost exclusively along the east walls, which are more sinuous than the west walls and are farther from entrances. Roosting groups contain a few dozen to a few hundred bats. Individual bats hang from one or both feet without ventral contact with the substrate and regularly spaced from each other, keeping a distance between themselves of about 10 cm. The roosting groups scatter on the lower parts of walls, at about 1 m from the floor, and occasionally on the low roofs of wall niches. Specific roosting spots were regularly occupied by similarly sized groups of *N. primus* in all visits to the cave, indicating that seasonal migrations out of Cueva La Barca are unlikely.

Ten other bats (*Phyllonycteris poeyi*, *Pteronotus quadridens*, *Pteronotus macleayi*, *Pteronotus parnellii*, *Mormoops blainvillei*, *Brachyphylla nana*, *Erophylla sezekorni*, *Monophyllus redmani*, *Artibeus jamaicensis*, and *Chilonatalus macer*) roost together with *Natalus primus* in Cueva La Barca, yet none were ever observed in mixed groups. Groups of *N. primus* sometimes roost adjacent to groups of *M. blainvillei* (which also appear to favor the cave's walls as roosting areas).

TABLE 18
Summary of measurements[a] of *Natalus primus*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight*	24	8.4	(6.0–10.1)	1.0	26	9.8	(7.8–12.6)	1.2
Forearm length	25	48.5	(47.0–50.1)	0.8	26	48.8	(46.1–51.2)	1.2
Length of tibia*	25	26.4	(25.4–27.1)	0.6	26	27.3	(26.0–29.1)	0.8
Length of 3rd metacarpal	24	46.2	(43.2–48.5)	1.2	26	46.5	(44.8–49.0)	1.2
Length of 5th metacarpal	24	41.9	(40.0–43.9)	1.1	26	42.5	(41.0–44.8)	1.0
Length of ear	2	20.9	(20.6–21.2)	0.4	1	20.2	– –	–
Length of penis		–	– –	–	1	3.0	– –	–
Greatest skull length*	19	18.8	(18.1–19.5)	0.4	18	19.2	(18.5–19.9)	0.4
Zygomatic breadth*	13	9.3	(9.1–9.5)	0.1	13	9.6	(9.2–10.0)	0.2
Braincase breadth	13	8.4	(8.1–8.7)	0.2	14	8.5	(8.3–8.7)	0.1
Breadth across molars	11	6.7	(6.3–7.0)	0.2	12	6.7	(6.5–6.9)	0.2
Breadth across canines	17	4.1	(3.8–4.2)	0.1	16	4.2	(4.0–4.5)	0.1
Maxillary tooth row	6	8.6	(8.4–8.8)	0.1	6	8.8	(8.6–9.0)	0.1
Mandibular tooth row	12	9.2	(7.8–10.3)	0.7	11	9.1	(8.7–9.8)	0.4
Postorbital breadth	20	3.3	(3.0–3.4)	0.1	18	3.4	(3.2–3.5)	0.1
Depth of braincase	2	7.4	(7.3–7.5)	0.1		–	– –	–

[a] Descriptive statistics of measurements for each sex. *N* = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P \leq 0.05$) are followed by an asterisk (*).

Captive *N. primus* individuals are aggressive and frequently attack bats of other species, even of larger size, if confined together in a small enclosure.

In general, individuals of *N. primus* remain active while roosting during the day, taking flight at the slightest sign of disturbance (human steps, distant glare from a flashlight), but usually some individuals allow the extreme close proximity of the observer for a few seconds. If disturbance (e.g., artificial illumination) persists for some minutes, all bats move to alternative roosting areas of the same chambers, joining the groups that may already be present there. When moving to other areas inside the cave, the bats invariably fly extremely close to the walls and about 1 m from the floor, forming a highly distinctive, continuous stream of bats along the wall. No *N. primus* was ever captured with a butterfly net more than 2 m away from any cave wall. Cueva la Barca is located in an area of nearly undisturbed semideciduous forest of moderate precipitation (1402 mm), near sea level.

Analysis of stomach contents obtained at dawn on 23 July 1993 revealed that the bats had consumed insects belonging to eight orders. The most commonly represented groups were: Lepidoptera, Orthoptera (Gryllidae), and Coleoptera. The remaining orders (represented by single cases) were Hymenoptera (Formicidae), Neuroptera, Diptera, Homoptera, and Hemiptera.

The reproductive activity of *N. primus* is largely unknown. Three females collected on 1 May 1992 were pregnant, each holding a single large embryo. At midday, on 17 April

TABLE 19
Variation in mental length among extant and extinct populations of *Natalus primus*

	N	Mean	(Min.–Max.)	SD
Cueva extant[a]	34*	12.0	(11.6–12.6)	0.2
Cuba fossil[b]	50	12.4	(12.1–12.8)	–
Bahamas[c]	8*	13.0	(12.6–13.6)	0.4
Grand Cayman	3*	10.9	(10.7–11.0)	0.2

[a] Specimens from Cueva La Barca

[b] Data from Silva-Taboada (1979)

[c] Includes specimens from Abaco, Andros, and Eleuthera

[*] Means that are significantly different (one-way ANOVA, $P < 0.01$)

1993, most *N. primus* groups were observed to have abandoned their usual roosting areas in Cueva La Barca and moved to the entrance of the hot chamber. Most of the *N. primus* groups observed in this unusual location were composed of what appeared to be copulating pairs, which were much more easily approached by humans than isolated bats. The long period of pregnancy reported for other species of Natalidae (e.g., *Nyctiellus*, Silva-Taboada, 1979; *Natalus mexicanus*, Mitchell, 1965), however, indicates that such pairing between individuals of *N. primus* may represent a behavior other than copulation.

With 58 museum specimens, *N. primus* is relatively well represented in collections despite being known from a single extant colony. On July 1993, visual estimates indicated that a few thousand *Natalus primus* inhabited Cueva La Barca. Observations made as recently as August 2001 suggest that this bat remains common in the cave (F. Balseiro, personal commun.). It may be an occasional prey of owls, as suggested by fossil remains of this species found in an early Holocene deposit accumulated at least partially through the feeding activity of the barn owl (*Tyto alba*; Jimenez-Vázquez et al., 2005).

The flight of *Natalus primus* is extremely slow and highly maneuverable. Several individuals released during the day in the forest outside the cave entrance showed a greater tendency and ability to fly through highly cluttered understory vegetation than most other species (except *Chilonatalus macer*) present in Cueva La Barca. Given the slow flight of this bat and its high rate of dehydration outside the cave (as judged by the rapid increase in brittleness of patagia of handled animals) it is probable that its foraging range is relatively small. On two occasions (April and July 1993) the species was not seen inside the cave between 22:00 and 24:00 hr and animals collected early in the morning on 23 July 1993 had full stomachs indicating that foraging may extend until daybreak. The permanent pool of Cueva La Barca might serve as source of drinking water for *N. primus*. The echolocation calls of *N. primus* are unknown, but it produces weak and high-pitched audible sounds when held in the hand.

Natalus primus is a critically endangered bat (IUCN 2006). The only known extant population of *N. primus* (i.e., that of Cueva La Barca) appears to be a relict of what was a widespread species that ranged throughout most of Cuba, the Bahamas, and the Cayman Islands. This dramatic reduction in range appears to have begun in the late Pleistocene and to have extended into the late Holocene (Silva-Taboada, 1974, Tejedor et al., 2004), suggesting a population decline that may have continued until the present. Cueva La Barca is thus far protected from human disturbance by its remoteness in Guanahacabibes Peninsula, but it may soon become more accessible as Cuba opens its remote areas to tourism (Díaz-Brisquet and Pérez-López, 2000). Although 1992 estimates indicated a relatively large population of *Natalus primus* (Tejedor et al., 2004), its current population trend is unknown and should be evaluated to adequately formulate conservation plans for this species.

Natalus stramineus Gray, 1838

Figure 33

Natalus stramineus Gray, 1838: 496. Original description based on unspecified material of unknown geographic origin deposited at the BMNH. Handley and Gardner (1990) deduced that this taxon's description must have been based on the specimen numbered BMNH 70.2324.

Natalus dominicensis Shamel, 1926: 67. Subjective synonym. Original description based on material (USNM 113605) from the island of Dominica.

HOLOTYPE: Holotype by monotypy, BMNH 70.2324, adult male in alcohol with skull removed; collector and collection locality unknown. The skull lacks parts of the left temporal but is otherwise complete. The skin is in good condition although both tibiae and 15 finger bones are broken.

DISTRIBUTION: Islands of the Lesser Antilles north of the St. Lucia Channel: Anguilla, Antigua, Barbuda, Dominica, Guadeloupe, Marie Galante, Martinique, Montserrat, Nevis, Saba, and St. Maarten (skeletal remains only; fig. 23).

NOTE: The name *Natalus stramineus* has been historically applied to populations of the genus *Natalus* from virtually the entire

Fig. 33. Holotype of *Natalus stramineus* (BMNH 70.2324, male, collection locality unknown).

Neotropics. The original description of *Natalus stramineus* (Gray, 1838), however, gives no indication of the geographic origin of the holotype, leading to widespread confusion concerning the nomenclature, and geographic and taxonomic limits of species of *Natalus*. The type locality of *N. stramineus* was listed as Brazil for about a century (Cabrera, 1957; Carter and Dolan, 1978; Dobson, 1878). Despite claims that the type locality was in the Lesser Antilles (Goodwin, 1959; Handley and Gardner, 1990), opinions that it could actually be in Brazil persisted (Taddei and Uieda, 2001). This conflict was compounded by the fact that *N. stramineus* was assumed to range throughout South America, and to be sympatric with *N. tumidirostris* to the north of the Amazon (Dávalos, 2005; Koopman, 1981; Simmons, 2005; Soriano and Ochoa, 1997). Recently, Tejedor (2006), on the basis of the inflated premaxilla of the holotype of *N. stramineus*, confirmed that the type locality of this species is in the northern Lesser Antilles (although the specific island remains uncertain) and showed that *N. tumidirostris* is the only taxon that occurs in South America north of the Amazon.

DIAGNOSIS: Medium-sized representative of genus *Natalus* (forearm length 37.2–40.0 mm, breadth across canines (3.8–4.2 mm) large in relationship to skull length; maxillary tooth row (6.8–7.5 mm) medial margin of ear deeply concave; lateral margin of ear deeply notched, 5–6 folds on lateral margin of ear; nostrils small, opening ventrolaterally; ventral hairs monocolored; dorsal hairs bicolored, hair bases lighter than tips, hair at base of claws short and inconspicuous or long and thin, never forming tufts; premaxilla inflated, with a lateral profile nearly forming a straight angle between rostral plane of premaxilla and dorsal plane of nasals; maxilloincisive suture dorsal to infraorbital foramen, maxilla dorsal to molars convex, not inflated; sides of postorbital region widely diverging rostrally, in dorsal view; palate between pterygoids ending caudally at two thirds of the distance between M3 and tip of pterygoid; posterior margins of maxilla, in ventral view, forming an oblique angle with longitudinal axis of skull; basisphenoid pits shallow; caudal margin of ascending ramus of mandible perpendicular to alveolar margin of dentary; I1 not visible in lateral view, obscured by I2; mesostylar crest on M3 absent. A comparison of diagnostic characters between *N. stramineus*, and other species of *Natalus* is summarized in table 5.

DESCRIPTION: Medium-sized natalid (forearm length 36.9–41.9 mm; greatest skull length 15.7–17.5 mm; weight 4.6–5.3 g); muzzle long and dorsoventrally flattened; nostrils elliptical, opening ventrolaterally on shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along midline, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium size and elliptical, extending from caudal base of rostrum to crown of head; ears relatively long (14.6–17.5 mm); ear pinna funnel shaped but distally thin; pinna with markedly pointed tip; medial margin of pinna slightly to deeply concave; lateral margins of pinna deeply concave; five to six small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (19.8–23.2 mm) slightly longer than half the length of the forearm; calcar long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively long and pointed, with 3rd metacarpal (33.8–38.1 mm) longer than 5th metacarpal (33.3–37.0 mm); wings attach to tibia above ankle; pelage dense, lax, and slightly woolly; hairs long (8–9 mm, dorsally; 6–7 mm, ventrally); dorsal hairs slightly bicolored, with bases lighter than tips; ventral hairs monocolored; dorsal hairs smoke gray with wood brown tips to amber or orange brown with medium brown tips (pl. 1); ventral hairs pale smoke gray or pinkish buff to light amber-chestnut or orange brown; dense mustachelike hair tufts along lateral margins of upper lip and on dorsum of muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with thin hairs; skull long and relatively broad with moderate rostral flexion; rostrum wide and short, with sulcus between nasals shallow; moderate rostral palatal emargination; premaxilla moderately to markedly inflated; maxilloincisive suture slightly to markedly displaced caudally, sometimes dorsal to infraorbital foramen, in lateral view; maxilla convex above molars; braincase moderately inflated, rising gently from rostrum; sagittal crest moderately developed; postorbital constriction wide; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids nearly parallel; palate extending caudally to more than half the distance between bases and tips of pterygoids; basisphenoid pit shallow; longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors short and peglike; I2 obscuring I1 in lateral view; occlusal profile of premolars long; upper premolars of similar size; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molars cusps relatively broad; spinous process of humerus about as high as capitulum; thorax relatively short and wide; ribs markedly expanded craniocaudally and extensively in contact with one another; vertebrae C7 to T1 fused among themselves and to ribs; vertebrae T12–L4 fused entirely without vestige of sutures; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: The inflation of the premaxilla and the associated caudal displacement of the maxilloincisive suture is sufficient to distinguish *N. stramineus* from other species of *Natalus* as herein restricted. In most specimens of *N. stramineus* from the northern Lesser Antilles, the maxilloincisive suture is dorsal to the infraorbital foramen, whereas in specimens from the central Lesser Antilles and in all other species of *Natalus* this suture is located more anteriorly, at about 1/3 of the distance between the infraorbital foramen and the anteriormost margin of the premaxilla (plates 8, 14; table 1). Also, in specimens with an inflated premaxilla, in lateral view, the anterior and dorsal planes of the premaxilla form a nearly right angle in *N. stramineus*, whereas in all other *Natalus* this angle is obtuse, particularly so in *N. tumidirostris*. Specimens of *N. stramineus* that lack the inflated premaxilla can be distinguished from other species of *Natalus* by a combination of characters including size, discrete traits, and cranial proportions.

On the basis of body size alone, *Natalus stramineus* can be distinguished from the large Greater Antillean species *N. primus*, *N. major*, and *N. jamaicensis*. The observed range of forearm length in *N. stramineus* (37.2–41.9 mm) overlaps only slightly with that of *N. major* (41.1–45.0 mm, $P < 0.01$; table 1), the smallest of the Greater Antillean species. On the other hand, *N. stramineus* is slightly larger than the North American *Natalus lanatus*, and the North and Central American *N. mexicanus* (table 2), but from these species, *N. stramineus* is more easily distinguished by external and cranial characters. Whereas in *N. stramineus* the medial ear margin is concave (usually as much as the lateral ear margin), in *N. lanatus* it is straight. In addition, *N. lanatus* has shorter legs (length of tibia in fresh or fluid-preserved specimens, 16.2–19.2 mm) than *N. stramineus* (length of tibia 19.8–21.5 mm, $P < 0.01$). From *N. mexicanus*, *N. stramineus* can be distinguished by its upper incisors, which are at the same level in ventral view, whereas in *N. mexicanus* the caudal base of I1 is rostral to the caudal base of I2.

Natalus stramineus is most similar in size and external characters to the South American *N. tumidirostris* and *N. espiritosantensis*. From *N. tumidirostris*, *N. stramineus* can be separated by its small, oval, and ventrolaterally oriented nostrils (larger, usually circular, and more anteriorly facing in *N. tumidirostris*) and by a palate extended caudally between the pterygoids (the palate is emarginated in *N. tumidirostris*). Relative to *N. stramineus*, *N. espiritosantensis* has a more robust, shorter rostrum (reflected in its shorter maxillary tooth row, $P < 0.01$; table 5).

VARIATION: The sample of *Natalus stramineus* examined for this study showed significant sexual, geographic, and individual variation. Males were significantly larger than females in two external and four cranial dimensions (MANOVA, $P < 0.05$; table 20). Canonical variate analyses between four geographic samples (Anguilla, Antigua + Barbuda, Saba + Montserrat, Dominica), using four external and seven cranial dimensions, indicate that the sample from Dominica is morphometrically distinct from that of the remaining islands, in particular with longer 3rd metacarpals (fig. 34A) and narrower breadths across canines (fig. 34B). The three available skins from Anguilla are grayish brown (smoke gray at base and wood brown at tips, with an overall drab appearance), whereas those from the remainder of the range have a reddish amber brown to tawny olive brown pelage.

The morphology of the rostrum showed both geographic and individual variation. The inflation of the premaxilla that characterizes the holotype of *N. stramineus* was present in all specimens from Anguilla, Barbuda, and Antigua, and in one female from Saba and another from Montserrat. Two adult females and one adult male from Saba, however, lacked this trait, being indistinguishable, at least cranially, from specimens from Guadeloupe and Dominica.

TABLE 20

Summary of measurements[a] of *Natalus stramineus*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	4	4.9	(4.6–5.3)	0.3	3	5.0	(4.9–5.2)	0.2
Forearm length	26	38.9	(36.9–41.2)	1.1	39	39.5	(37.8–41.9)	0.9
Length of tibia, dry*	6	19.2	(18.8–19.8)	0.4	8	20.1	(18.3–21.7)	1.1
Length of tibia*	21	20.9	(19.8–22.0)	0.8	23	21.7	(20.8–23.2)	0.6
Length of 3rd metacarpal	18	36.5	(33.8–38.1)	1.1	20	36.9	(35.5–37.9)	0.8
Length of 5th metacarpal*	18	35.2	(33.3–36.7)	0.8	20	35.9	(35.1–37.0)	0.5
Length of ear	12	16.0	(14.6–17.5)	0.7	15	16.0	(14.7–17.5)	0.8
Length of penis		–	– –	–	20	3.2	(2.4–4.2)	0.5
Length of natalid organ		–	– –	–	14	6.7	(5.2–7.8)	0.9
Greatest skull length	13	16.3	(15.7–17.5)	0.5	24	16.7	(15.9–17.2)	0.3
Zygomatic breadth*	14	8.3	(7.9–8.8)	0.2	24	8.5	(7.9–8.9)	0.2
Braincase breadth	13	7.8	(7.6–8.4)	0.2	23	8.0	(7.8–8.3)	0.1
Breadth across molars*	14	5.4	(5.1–5.6)	0.2	24	5.6	(5.0–5.9)	0.2
Breadth across canines*	14	3.7	(3.5–4.1)	0.2	23	3.9	(3.3–4.2)	0.2
Maxillary tooth row	14	7.0	(6.8–7.5)	0.2	24	7.3	(6.9–7.5)	0.2
Mandibular tooth row	14	7.5	(7.3–7.8)	0.2	17	7.6	(7.2–7.8)	0.1
Postorbital breadth	14	3.1	(3.0–3.3)	0.1	24	3.2	(3.0–3.4)	0.1
Depth of braincase*	8	6.4	(6.2–6.7)	0.2	17	6.6	(6.4–6.8)	0.1

[a] Descriptive statistics of measurements for each sex. N = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

NATURAL HISTORY AND CONSERVATION: *Natalus stramineus* is known from 35 localities (including three represented only by bone remains), 15 of which have been caves. It is found both in the volcanic inner-arc islands (Saba, Nevis, Montserrat, Dominica, and Martinique) and in the limestone outer-arc islands (Anguilla, St. Maarten, Barbuda, Antigua, Guadeloupe (Grande-Terre), Marie Galante; Baker et al., 1978; Genoways et al., 2001; Pedersen et al., 2003, in press). In Dominica, in addition, it has been taken in a brick tunnel (Genoways et al., 2001). On Nevis, it has been found in a small, humid cave (3 m wide by 6 m high) that is not permanently occupied throughout the year (Pedersen et al., 2003). In Dominica, it has been found coexisting with several thousand *Pteronotus davyi* in a narrow cave opening on a sandy cliff (Genoways et al., 2001).

Natalus stramineus occurs from sea level to middle elevations and in habitats ranging from relatively dry (e.g., Barbuda, 925 mm annual precipitation; locality 7) to rain forest (e.g., Sylvania, Dominica, 3232 mm; locality 171) and from sea level to 473 m (locality 171).

Although its diet has never been studied, *N. stramineus* is surely insectivorous, as are other representatives of Natalidae (e.g., *Nyctiellus lepidus*, Silva-Taboada, 1979; *Natalus primus*, Tejedor et al., 2004).

It is known from 114 museum specimens, most of which are from the islands of Dominica (77), Barbuda (12), and Saba (8), where it seems to be a common bat. The records from Marie Galante, and Martinique, the last of which is known from a mention in A. Schwartz's research notes (Timm and Genoways, 2003), are based on a single specimen each.

Little is known of reproductive activity in *N. stramineus* but it may be concentrated earlier in the year than in other species of *Natalus* from the West Indies. Females taken in April in Dominica included lactating, nonpregnant, and pregnant individuals, yet a sample from July was composed entirely of nonreproductive females (Genoways et al.,

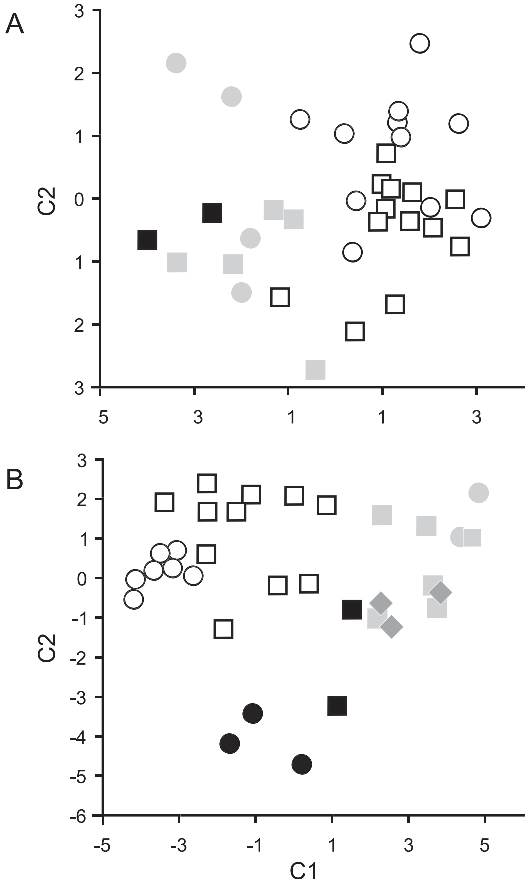


Fig. 34. Canonical variates analyses (CVA) scores for external (A) and cranial (B) measurements of populations of *Natalus stramineus* from 6 Lesser Antillean islands: (●) Antigua + Barbuda, females; (■) Antigua + Barbuda, males; (◆) Anguilla, males; (●) Montserrat + Saba, females; (■) Montserrat + Saba, males; (○) Guadeloupe, females; (□) Guadeloupe, males. Axes are scaled relative to their eigenvalues. The first canonical axes can be interpreted as a measure of the length of the 3rd metacarpal (A) and of breadth across canines (B; table 21).

2001). *N. stramineus* is parasitized by the streblid *Trichobius caecus* (Genoways et al., 2001).

In an ecomorphological study, Jennings et al. (2004) stated that *N. stramineus stramineus* can fly very slowly in clutter and that it hunts by slow hawking and/or by gleaning. They found that *N. stramineus* produced multiharmonic FM echolocation calls with most energy in the second harmonic. The greatest energy of the fundamental frequency was centered around 60 kHz, and that of the second harmonic at 90–100 kHz. The duty cycle was intermediate (Jennings et al., 2004).

TABLE 21

Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 4 geographic samples of *Natalus stramineus*

Measurement	C I	CII
External		
Forearm length	−1.646	0.227
Length of tibia	0.382	−0.881
Length of 3rd metacarpal	1.825	0.524
Length of 5th metacarpal	−0.289	−0.762
Eigenvalues	3.997	0.598
Cranial		
Greatest skull length	−0.340	0.228
Zygomatic breadth	−0.806	0.447
Braincase breadth	0.748	0.477
Breadth across molars	−0.197	0.485
Breadth across canines	1.101	−1.339
Maxillary tooth row	0.886	0.723
Postorbital width	−0.670	−0.149
Eigenvalues	8.938	2.976

CVA scores are plotted in figure 49.

Natalus stramineus is listed as least concern in the current global red list of threatened species (IUCN, 2010) However, its small, naturally fragmented geographic range, and its apparent requirement for humid caves, point to a limited availability of suitable habitat and therefore to a vulnerable status. The species seems, nonetheless, locally common in at least four islands (Antigua, Barbuda, Dominica and Saba; Genoways et al., 2001; S.C. Pedersen, personal commun.), and future surveys may increase the number of islands where it is known to occur. On Nevis, it has been encountered less frequently, with the single specimen in museum collections from that island having been killed accidentally by a ceiling fan (Pedersen et al., 2003). In Martinique, it is also known from a single individual (Timm and Genoways, 2003), and in St. Maarten, it has been recorded exclusively from a skull and partial skeleton found in a cave (Genoways et al., 2007). In Montserrat, an island where bat populations have been severely affected by recent volcanic eruptions (Pedersen, 2003), the only known population of *N. stramineus* occurs in Aymers Ghaut (S.C. Pedersen, in litt.), one of the island's valleys most vulnerable to devastating pyroclastic flows and lahars (Baker, 1985). If *N. stramineus* does not occur in other, undiscovered sites on Montserrat, its long-term survival on that island seems highly uncertain.

Natalus tumidirostris Miller, 1900
Figure 35

Natalus tumidirostris Miller, 1900: 160. Type locality "Hatto, Curaçao, Netherlands Antilles."

Phodotes tumidirostris: Miller, 1906: 85. New combination.

Phodotes tumidirostris continentis Thomas, 1910: 513. Type locality "San Esteban, Carabobo, Venezuela"; holotype, BMNH 5.11/12.25.

Natalus tumidirostris tumidirostris (part): Goodwin, 1959: 11. New combination.

Natalus tumidirostris continentis (part): Goodwin, 1959: 11. New combination.

Natalus tumidirostris haymani: Goodwin, 1959: 12. Type locality "Mt. Tamana, Trinidad, Trinidad and Tobago"; holotype, AMNH 176590.

Natalus stramineus tronchonii: Linares, 1971: 81. Type locality "Cueva de los Gavilanes, Rio Guasare, Zulia, Venezuela"; holotype, MBUCV 1578.

Natalus stramineus: Linares, 1998: 515. Not *Natalus stramineus* Gray, 1838.

HOLOTYPE: USNM 102106, adult male, skin in alcohol with skull removed, collected by L.J. Guthrie on 5 January 1900, in Hatto [=Hato] (locality 467 in appendix 1), Curacao, Netherlands Antilles. Both the skin and skull are in good condition but the skin color has faded due to long immersion in alcohol.

DISTRIBUTION: Mainland South America north of the Amazon River in the countries of Colombia, Venezuela, Guyana, Suriname, and French Guiana, and also on the islands of Trinidad, Tobago, Margarita, Curaçao, and Bonaire. Although to date it has not been reported from Brazil it very likely occurs there given that three collection localities (two in Guyana and one in Suriname) lie less than 15 km from the border with that country (fig. 36).

DIAGNOSIS: Size medium (forearm length 35.0–42.0mm), medial margin of ear pinna deeply concave; lateral margin of ear pinna deeply notched; nostrils usually large, opening anteriorly; maxilla above molars convex and markedly inflated; palate ending caudally always rostral to optic canal; ventral pelage monocolored; dorsal pelage monocolored or, if bicolored, hair bases lighter than tips; hair at base of claws short and inconspicuous or long and thin, never forming tufts; caudal margins of maxilla in ventral view forming an acute angle with longitudinal axis of skull; basisphenoid pit shallow; postorbital region with sides widely diverging rostrally, in dorsal view; caudal margin of ascending ramus of mandible perpendicular to alveolar margin of dentary; I1 not visible in lateral view, being obscured by I2; mesostylar crest of M3 absent. A comparison of diagnostic characters between *N. tumidirostris*, and other species of *Natalus* is summarized in table 5.

DESCRIPTION: Size medium (forearm length 35.0–42.0 mm; greatest skull length 15.5–17.3 mm; weight 4.3–8.9 g); muzzle long and dorsoventrally flattened; nostrils often wide and nearly circular, rarely elliptical; opening anteriorly on shallow depression on margin of upper lip; upper lip thickened; lower lip markedly thickened and constricted along dorsal and ventral margin, with numerous transversal grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium size and elliptical, extending from caudal base of rostrum to crown of head; ears medium sized (13.0–16.4 mm); ear pinna funnel shaped but distally thin; pinna with markedly pointed tip; medial and lateral margins of pinna deeply concave; five to six small ear ridges along lateral margin of distal pinna; ventral region of ear pinna greatly expanded, covering the eye and tragus in lateral view; medial ear margin thin and flexible; tragus short, lanceolate, and twisted into helixlike structure; tibia (18.9–22.4 mm) slightly longer than half the length of the forearm; calcar very long and thin, occupying about half the length of the free edge of uropatagium; free margin of uropatagium with sparse fringe of thin hairs; wings relatively broad, with 3rd metacarpal (33.7–38.7 mm) slightly longer than 5th metacarpal (30.4–38.3 mm); wings attach to tibia above ankle; pelage dense and lax; hairs long (7–9 mm, dorsally; 6–7 mm,

Fig. 35. Holotype of *Natalus tumidirostris* (USNM 102106, male, Curaçao). Scale bar = 10 mm.

ventrally); pelage usually darker dorsally than ventrally; pelage color from almost white ventrally and very light brown dorsally to bright orange brown both ventrally and dorsally (pl. 1); dorsal hairs bicolored, with tips darker than bases; ventral hairs usually monocolored; dense mustachelike hair tufts along lateral margins of upper lip and across

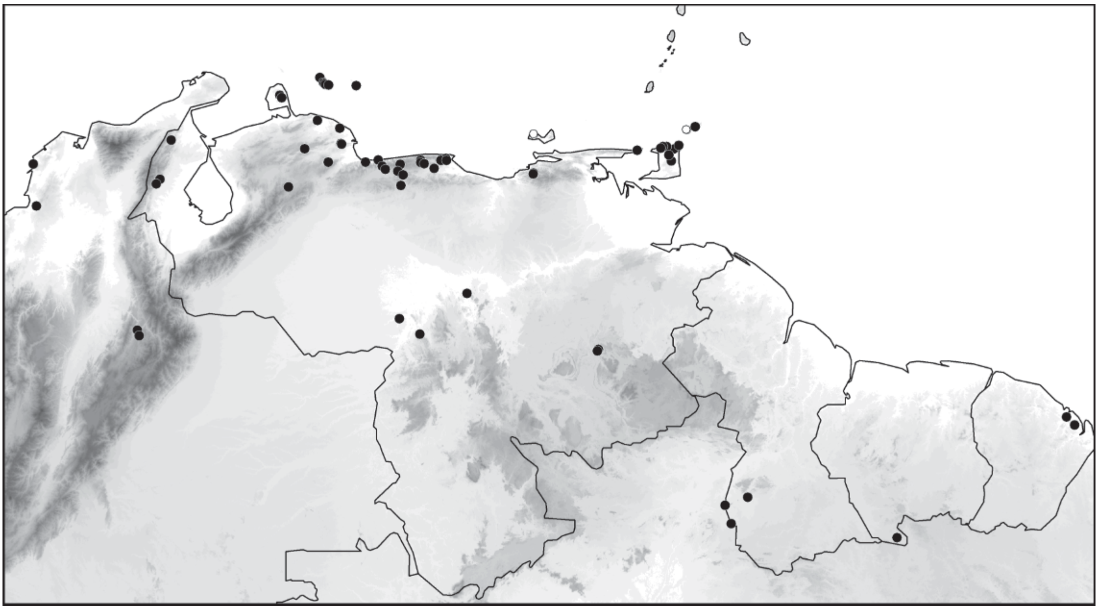


Fig. 36. Geographic distribution of *Natalus tumidirostris.* Solid circles indicate localities where the species has been collected alive. Open symbols indicate localities represented by bone remains only. Names of localities are listed in appendix 1. Gray shading on land indicates relief, with darknes increasing with altitude.

muzzle; mustache formed by dense, lax, irregularly arranged, and ventrally curved hairs; natalid organ covered with thin hairs; skull long and relatively broad with moderate rostral flexion; rostrum wide, with sulcus between nasals almost imperceptible; moderate rostral palatal emargination; maxilla inflated, obscuring molars in dorsal view; braincase inflated, rising abruptly from rostrum; sagittal crest moderately developed; postorbital constriction wide; maxillary branch of zygomatic arch thin, less deep than twice the height of crowns of last molars; pterygoids nearly parallel; palate extending caudally to level of M2 or M3; basisphenoid pit shallow; longitudinal medial ridge on basisphenoid present; ectotympanic small, covering less than half of periotic; upper incisors short and peglike; I2 obscuring I1 in lateral view; occlusal profile of premolars long; upper premolars of similar size; mesostylar crests on M1 and M2 short and straight, mesostylar crest absent on M3; cingular cusp of p4 medium sized and broad; molars cusps relatively broad; spinous process of humerus about as high as capitulum; thorax relatively short and wide; ribs markedly expanded craniocaudally and extensively in contact with one another; vertebrae C7 to T1 fused among themselves and to ribs; vertebrae T12–L4 fused entirely without vestige of sutures; vertebrae L5 and L6 free; caudal vertebrae 4 to 7 longer than distance from ischium to iliac crest of sacrum.

COMPARISONS: Fenestration of the palate is more extensive in *N. tumidirostris* than in any other species of *Natalus*. All palatal fenestrae, the interpterygoid and the intermolar, are very large and can coalesce with each other in various ways creating three main patterns: (1) all fenestrae separate, caudal edge of palate nearly at level with the caudal margin of M3 (common in individuals from Colombia); (2) intermolar fenestrae coalesced and separate from interpterygoid fenestrae, caudal edge of palate nearly at level with caudal margin of M3 (common in individuals from Sierra de Perijá); (3) all fenestrae coalesced forming deep palatal emarginations that reach caudal margin of M1 (common in individuals from the center and east of the species' range).

Occasionally, the degree of coalescence of the fenestrae is not symmetrical within a single individual, creating a combination of any two of the patterns mentioned above. In *N. tumidirostris*, thus, the caudal edge of the palate lies at the caudal margin of M1 or M3 whereas in all other species of *Natalus* the caudal margin of the palate lies at 1/2–2/3 of the way between the caudal margin of M3 and the tip of the pterygoid processes. Also, in all other species of *Natalus*, the intermolar palatal fenestrae, if present, are usually small and only rarely coalesce.

In *Natalus tumidirostris*, the maxillae are conspicuously inflated (although less so in individuals from Colombia and western Venezuela) and in dorsal aspect may hide the molars from view. In all other *Natalus* the labial margins of the molars are visible in dorsal view. In most specimens of *N. tumidirostris*, in lateral aspect, the rostral surface of the premaxilla forms a shallow (obtuse) angle with the dorsal surface of the nasals, whereas in all other species of *Natalus* this angle is less obtuse (even straight, in *N. stramineus*). Also in lateral view, the dorsal surface of the nasals of *N. tumidirostris* is more parallel with the alveolar margin of the maxilla than in other species of *Natalus*, making the rostrum of this species appear relatively deeper anteriorly. In all other species of *Natalus*, especially in *N. lanatus* and *N. primus*, the rostrum tapers anteriorly more markedly.

Externally, *Natalus tumidirostris* can be distinguished from *N. mexicanus*, *N. lanatus*, *N. primus*, *N. major*, and *N. jamaicensis* by its concave medial margin of the ear. In *N. tumidirostris*, the medial margin of the ear pinna is almost as concave as the lateral margin, so that the ear tip appears acutely pointed. In the remaining aforementioned species, the medial margin of the ear pinna is straight to very slightly concave, so that the ear tip appears less acutely pointed. In most cases, *N. tumidirostris* can be distinguished from other species of the genus by the shape and size of its nostrils. The nostrils of *N. tumidirostris* tend to be as large as the external nasal septum, circular, and forwardly oriented. The nostrils of other species of *Natalus* are always smaller than the external nasal septum, elliptical, and usually oriented ventrolaterally. In some individuals of *N. tumidirostris* (as is common in Sierra de Perijá and on the island of Trinidad), however, these traits are less noticeable and the nostrils are similar in shape as in other species of the genus; thus, the shape of the nostrils should be used in combination with other traits, especially cranial ones, for a confident diagnosis of *N. tumidirostris*.

Natalus tumidirostris has a longer forearm and skull than *N. mexicanus* and *N. lanatus*. It is, however, smaller than the three Greater Antillean species *N. primus*, *N. major,* and *N. jamaicensis*. *N. tumidirostris* overlaps widely in size with two other species of the genus: *N. espiritosantensis* and *N. stramineus*. Nonetheless, its toothrow length is larger than that of *N. espiritosantensis*. From *N. stramineus*, *N. tumidirostris* is best identified on the basis of qualitative characters only.

VARIATION: Gómez-Laverde (1986) reported that young adults (individuals with fused epiphyses and silky grayish pelage) from Cueva de Macaregua, Colombia, had a mean zygomatic breadth significantly smaller than that of (older) adults with brownish or yellowish pelage.

Pelage color varies widely in *Natalus tumidirostris*. Some specimens from Cueva Ricardo Zuloaga, state of Miranda, Venezuela, are bright orange brown, whereas most individuals from Paraguaná peninsula are extremely pale, being pale buff dorsally and pale cream to white ventrally. The palest individuals from Paraguaná, in addition, show an extreme lack of skin melanin, having entirely light pink faces and ears. Several color variants are usually present in a single population, and it seems that the apparent lack of variants within a population is due primarily to small sample size.

Male *Natalus tumidirostris* are larger than females in 10 of 14 measurements ($P < 0.05$; table 22). Females from Colombia, however, had a longer forearm than males from Colombia, offsetting the species-wide sexual difference in this trait (interaction effect $P < 0.05$).

Natalus tumidirostris is the most geographically variable of the four continental species of *Natalus*. Four populations (Perijá, Paraguaná, Curaçao-Bonaire, and Trinidad) showed no overlap in a canonical variate

TABLE 22
Summary of measurements[a] of *Natalus tumidirostris*

	Females				Males			
	N	Mean	(Min.–Max.)	SD	*N*	Mean	(Min.–Max.)	SD
Weight	29	6.4	(4.5–8.9)	1.1	28	6.3	(4.3–8.6)	1.0
Forearm length*	94	38.7	(36.1–41.5)	1.1	146	38.8	(35.0–42.0)	1.4
Length of tibia, dry*	25	18.9	(17.3–20.0)	0.7	28	19.7	(17.6–22.0)	1.1
Length of tibia*	34	20.3	(18.9–21.9)	0.8	59	20.8	(18.9–22.4)	0.8
Length of 3rd metacarpal	23	36.2	(34.5–37.9)	1.1	39	36.2	(33.7–38.7)	1.2
Length of 5th metacarpal	23	35.3	(30.4–37.2)	1.4	39	35.5	(33.2–38.3)	1.3
Length of ear	57	14.9	(13.0–17.3)	1.1	79	14.9	(13.0–17.2)	0.9
Length of penis		–	– –	–	34	3.5	(2.4–4.9)	0.6
Length of natalid organ		–	– –	–		–	– –	–
Greatest skull length*	67	16.5	(15.5–17.2)	0.3	105	16.7	(15.5–17.3)	0.4
Zygomatic breadth*	66	8.3	(7.7–8.8)	0.2	101	8.4	(7.7–9.0)	0.2
Braincase breadth*	69	8.0	(7.4–8.4)	0.2	103	8.1	(7.3–8.7)	0.2
Breadth across molars*	71	5.5	(5.0–6.0)	0.2	105	5.5	(5.1–5.9)	0.2
Breadth across canines*	69	3.8	(3.4–4.1)	0.2	101	3.9	(3.3–4.2)	0.2
Maxillary tooth row *	73	7.0	(6.5–7.2)	0.2	103	7.1	(6.7–7.4)	0.2
Mandibular tooth row*	63	7.4	(6.8–7.7)	0.2	89	7.5	(6.9–7.8)	0.2
Postorbital breadth	66	3.4	(3.2–3.6)	0.1	106	3.4	(3.0–4.0)	0.2
Depth of braincase*	36	6.5	(6.1–7.2)	0.2	62	6.7	(6.2–7.2)	0.2

[a] Descriptive statistics of measurements for each sex. *N* = sample size; SD = standard deviation. Weight is given in g; all other measurements are given in mm. See text for description of measurement methods. Measurements significantly different between sexes ($P < 0.05$) are followed by an asterisk (*).

analysis based on one external (forearm length) and seven skull measurements. Specimens from Colombia, the coastal ranges of northern Venezuela, Venezuelan Guiana, and Trinidad are the largest in both external and internal measurements, whereas populations from Perijá, and Curaçao-Bonaire were the smallest. Specimens from Paraguaná were characterized by a relatively short forearm but a relatively large skull ($P < 0.05$, fig. 37).

Inflation of the maxilla is less marked in animals from the western part of the range (Colombia, Perijá). Similarly, fenestration of the palate is less extensive in specimens from the western part of their range, especially in animals from Sierra de Perijá (pl. 7).

NOTE: The population from Perijá was originally described as a subspecies of *N. stramineus* (*N. s. tronchonii*) by Linares (1971) mainly on the basis of a supposedly unique pattern of palatal fenestration. Upon examining the skull of the holotype of *N. s. tronchonii*, I found that it had been incompletely cleaned and that the remaining soft tissue obscured a pattern of palatal fenestration similar to that of specimens of *N. tumidirostris* from Colombia.

NATURAL HISTORY AND CONSERVATION: *Natalus tumidirostris* is known from 64 localities, including two represented by bone remains only. In 33 of the collection localities it has been found at day roosts, almost all being caves (30) and mines (2), except for a group of three individuals found roosting in a hollow rubber tree near Tamana caves (Goodwin and Greenhall, 1961). *Natalus tumidirostris* has been found in caves varying from medium (e.g., Cueva Pararille; De Bellard Pietri, 1969) to large size (e.g., Ricardo Zuloaga, De Bellard Pietri, 1969), although it also probably occupies caves of smaller sizes. As in other species of *Natalus*, *N. tumidirostris* roosts in caves that are warm and humid, but avoids the warmest areas within the caves. In a study performed in Cueva del Guano and Cueva Piedra Honda (listed as "Cueva Barra Honda"), Paraguaná, Venezuela, *N. tumidirostris* selected roost sites of about 30° C but moved to warmer (33° C) or cooler (28° C) spots when

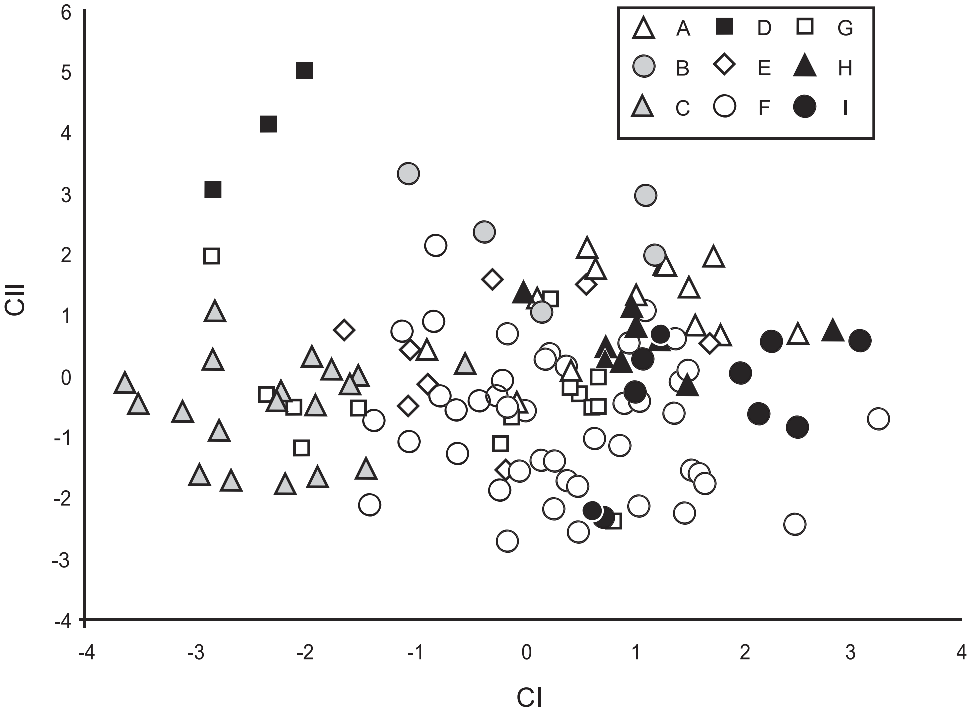


Fig. 37. Plot of canonical scores of forearm length and six cranial variables of *Natalus tumidirostris* from nine geographic areas: A = Colombia; B = Perijá (Zulia); C = Paraguaná; D = Curaçao; E = Continental Falcón; F = Coastal Cordillera; G = Guyana Shield (Bolívar); H = Sucre; I = Trinidad. Variable loadings are shown in table 23. Four areas contain morphometrically divergent populations: (1) Curaçao, characterized by bats of overall small size; (2) Paraguaná, characterized by bats with short forearms and large skulls; (3) Perijá, Characterized by bats with long forearms and small skulls; and (4) Trinidad, characterized by bats with overall large body size.

disturbed (Genoud et al., 1990). Some of the caves inhabited by *N. tumidirostris* may contain high levels of ammonia (e.g., Cueva Ricardo Zuloaga). Most caves known to harbor *N. tumidirostris* are formed in limestone. Linares and Löbig-A. (1973) mentioned that *N. tumidirostris* shifts roosting caves throughout the year.

Roosts of *Natalus* are unknown in the Guyana Shield (southern Venezuela, the Guianas, and extreme northern Brazil), and all 12 records of the genus from this area correspond to captures with mistnets. In the Guyana shield, however, other cave-dwelling bats (i.e., mormoopids, *Lonchorhina*) have been found in caves formed by the accumulation of large boulders around the eroding Precambrian granite inselbergs that dominate the Guianan landscape. It is therefore likely that on the Guianan shield *Natalus tumidirostris* also roosts in these types of caves.

Natalus tumidirostris has been found sharing roosts with 10 other bat species (*Pteronotus parnellii*, *Pteronotus gymnonotus*, *Pteronotus personatus*, *Mormoops megalophylla*, *Leptonycteris curasaoe*, *Phyllostomus hastatus*, *Carollia perspicillata*, *Artibeus jamaicensis*, *Desmodus rotundus*, *Myotis keaysi*) and roosts in closest association to *Carollia perspicillata* with which it often forms mixed groups, as in Macaregua (Gómez-Laverde, 1986) and Cueva las Animas. Within roosting groups individuals hang widely spaced and are generally quiet, sometimes allowing themselves to be caught by hand. Occasionally, when large multispecies groups of bats abandon certain areas of a given cave due to the presence of visitors, individuals of *N.*

TABLE 23

Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 9 geographic samples of *Natalus tumidirostris*

Measurement	C I	C II
Forearm length	1.142	0.437
Greatest skull length	−1.081	−0.074
Zygomatic breadth	−0.192	−0.337
Braincase breadth	0.285	0.050
Breadth across molars	−0.604	−0.557
Breadth across canines	0.345	−0.786
Maxillary tooth row	0.447	−0.075
Postorbital tooth row	−0.106	−0.053
Depth of skull	−0.650	0.351
Eigen value	2.638	1.888
Percent explained	48.0	34.3

CVA scores are plotted in figure 45.

tumidirostris are the last to leave their roosting spots. Nonetheless, it has been observed to become more alert while roosting when a cave is repeatedly visited by humans (Gómez-Laverde, 1986). It generally roosts in low areas of walls, but it is occasionally found hanging from high (3–5 m) ceilings.

Natalus tumidirostris has been found in habitats ranging from dry cactus scrub (Bonaire, 464 mm annual precipitation; locality 465) to wet forest (Camp Patawa, French Guiana), but most commonly it is found in areas of deciduous to semideciduous forest. It occurs from sea level to middle elevations (e.g., Cueva Macaregua, Colombia, 1400 m; locality 67).

Natalus tumidirostris feeds on insects, and is reported by Linares (1998) to consume mostly Lepidoptera and Diptera. It seems to have a single annual estrus, and bears only one pup per year. The timing of the reproductive activity varies slightly among localities. In northern Venezuela, 13 (65%) out of 20 females collected between 16–30 April 2004 were pregnant. In the only well-known Colombian population, however, birth takes place before late March (Gómez-Laverde, 1986). Throughout lactation, juveniles have been found to aggregate in compact clusters in cave ceilings during the daytime. Gómez-Laverde (1986) described the development during four months of one such groups in Cueva Macaregua, Colombia. In this cave, in late March, hairless neonatal individuals were found aggregated in a compact cluster on the cave ceiling, in association with a few adult females, which flew away after being disturbed. By mid-April, this group had consolidated into a large mass of many juveniles that occupied a 1 × 1.5 m of substrate. By the end of the month, these juveniles had appreciably grown, were already haired, and some were able to fly. In early June, the cluster had disappeared and, in its stead, there were many dispersed, adult-sized, and gray-colored individuals, all capable of full flight. The following year the cluster of juveniles was much reduced in size, reaching a maximum of only about 200 individuals, and was in a different location. It was not determined, however, whether this change reflected an overall smaller number of births or a change in the distribution of the newborns within the cave. In an incident in Macaregua, a piece of cave ceiling fell to the floor with about 10 nonflying pups still clinging to it; in spite of the accidental change in location, the pups continued to be fed, since observations made 15 days after the initial one revealed that they had grown appreciably and were still on the piece of fallen ceiling. A photograph taken in Cueva Ricardo Zuloaga, Venezuela, in an unspecified date, documents a similar cluster-forming behavior of newborn *N. tumidirostris* (Carreño, 1998). Sex ratios appear widely skewed in some caves (e.g., an all male colony in Cueva del Guano in April, 2004) suggesting a pattern of sexual segregation similar to that of other natalids.

Natalus tumidirostris is an abundant species known from at least 961 museum specimens, 74% of which having been collected in just three localities: Cueva Macaregua, Colombia; Cueva Ricardo Zuloaga, Venezuela; and Tamana Caves, Trinidad. It appears most densely distributed along northernVenezuela. Natural predators are not known, but at least in Cueva del Guano, Paraguaná, they could be occasional victims of giant centipedes (*Scolopendra gigantea*, which is reported to actively hunt bats in this cave; Molinari et al., 2005). One of the few known specimens from French Guiana, was caught by a domestic cat that brought it into a house (Charles-Dominique et al., 2001). Parasites of this species include *Tricholeiperia* *trinidadensis* (Nematoda, Molineidae; Gibbons and Omah-Maharaj, 1991) and the bacterium *Borrelia* (Marinkelle and Grosse, 1968).

Harp trap surveys in Cueva Macaregua (Cadena, 1974) indicate that nightly foraging begins relatively early at around sunset. The same study reported continuous activity of bats leaving and entering the cave until 22:00, when observations were stopped. Occasionally there was a peak in the number bats leaving the cave about half an hour after sunset.

The flight of *Natalus tumidirostris* is slow and very maneuverable, as in other species of the genus. If on the ground, *N. tumidirostris* seems unable to crawl, but can initiate flight vertically with strong downward thrusts of the wings (Riskin et al., 2005).

As in other species of natalids, *Natalus tumidirostris* dies quickly (in fewer than 20 hr) of starvation and/or dehydration when kept in captivity. Its basal metabolic rate (1.54 ml O_2/ghr) is very low (30% below expected value) relative to that of other Neotropical insectivorous bats of similar body mass. Such a low basal metabolic rate may help this bat reduce its risk of starvation and water loss when roosting in warm caves and when foraging in dry habitats (Genoud et al., 1990). *Natalus tumidirostris* seems able to survive lower temperatures than other small Neotropical bats due to its relatively low thermal conductance (0.41 ml O_2/ghr °C), which is probably afforded by its long and lax hair (Genoud et al., 1990). The thermoneutral zone of *N. tumidirostris* was determined to lie between 28° and 35° C, and this bat is able to maintain a stable body temperature of about 32° C within ambient temperature values ranging between 28° and 20° C, falling into torpor when the ambient temperature decreases below 20° C. It seems, however, unable to survive ambient temperatures below 10° C for longer than 2 hours (Genoud et al., 1990).

Natalus tumidirostris is a species of least concern in IUCN's Red List of Threatened Species (IUCN, 20102010). In northern Venezuela it seems a ubiquitous and locally abundant bat and therefore not threatened. Petit (1996) considered it to be threatened in Curaçao, with an islandwide population count of just 50–60 bats. The colony of Hato Cave, the source of the holotype of the species, has disappeared and the cave has been turned into a tourist attraction. Whitout appropriate management, this unique island population might become extinct.

ECOMORPHOLOGICAL DIVERSITY

Until recently, traditional taxonomists (with the notable exception of G.S. Miller) had failed to detect the subtle yet significant morphological variation that is present among members of the family Natalidae. As a consequence, intriguing patterns of morphological diversity within this group have been overlooked. Armed with a deeper understanding of the diversity of the family, these patterns can now be explored. Here, I examine morphology in an ecological context, and discuss their possible functional value.

Natalids show a range of body sizes (2 g in *Nyctiellus lepidus* to 12 g in *Natalus primus*) and variations in morphology that are remarkable for a bat family of relatively low diversity (4 genera, 13 species). The anatomical modifications of some natalids represent extremes of morphological differentiation among New World bats, including the great extension of the flight membranes and the acquisition of accessory molar crests. In addition, one natalid genus, *Chilonatalus*, shows one of the greatest ranges in penis length within Chiroptera, as well as considerable variation in the size of the natalid organ, a glandular cephalic structure unique to Natalidae. These morphological phenomena have rarely been described, much less discussed in light of the ecology of the group.

In this section, available information on natalid ecology is used to address questions on the morphological diversification of the family. Three main questions are addressed in this section: (1) do different natalid species correspond to different ecomorphs of flight and feeding morphology? (2) is the structure of natalid faunas influenced by competition? (3) is genital morphology sexually selected in Natalidae?

FLIGHT MORPHOLOGY: The relative size and shape (aerodynamic design) of flight surfaces (wings plus uropatagium) is highly

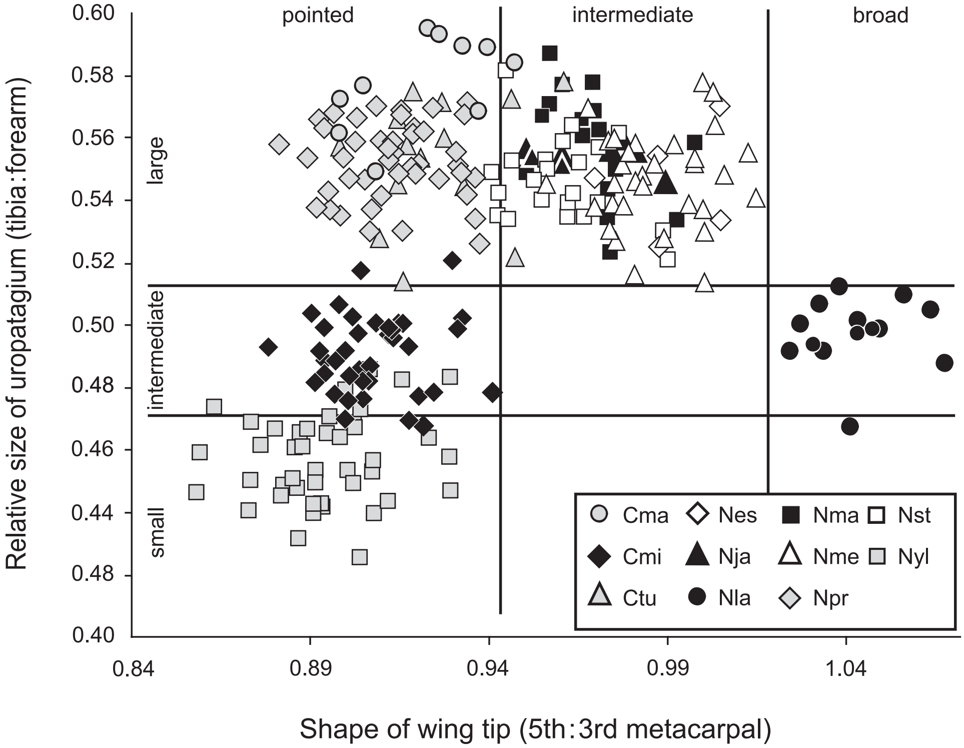


Fig. 38. Plot of wing-tip shape index vs. relative size of the uropatagium in 11 species of Natalidae. Five different ecomorphs are formed by the intersection of these two indices. The genus *Natalus* is the most diverse in flight morphology, with most species clustering in the intermediate wing tip and large uropatagium ecomorph and two outliers: (1) *Natalus primus*, which clusters with two species of *Chilonatalus*, and (2) *Natalus lanatus*, whose broad wing tip is unique among natalids.

variable among bats and has a profound influence on their ecology. Bats with pointed wing tips and narrow flight surfaces (high aspect ratio, defined as the ratio of the length to the width of a wing) fly fast, have little maneuverability, and exploit food resources in open spaces. Bats with broad wing tips and broad flight surfaces (low aspect ratio) tend to fly more slowly, have high maneuverability, and exploit food resources in cluttered habitats (i.e., within vegetation, McKenzie et al, 1995; Norberg and Rayner, 1987; Norberg, 1998; Stockwell, 2001). The maneuverability and flight speed of bats is significantly influenced by the size of the uropatagium, which represents a caudal extension of the flight membranes that is used in steering and adds aerodynamic drag. Bats with a large uropatagium tend to have higher flight maneuverability and to fly more slowly than bats with a small uropatagium (Lawlor, 1973; Norberg, 1995).

Because of their wide wings and large uropatagia, natalids represent an extreme strategy among bats for slow, maneuverable flight (Jennings et al., 2004; Norberg, 1998). Still, even within Natalidae there is significant variation in two measures of flight-surface design, the shape of the wing tip and the size of the uropatagium. With regard to wing-tip shape, natalids seem to comprise three distinct groups: (1) bats with relatively narrow wing tips (*Nyctiellus*, *Chilonatalus*, and *Natalus primus*); (2) bats with broad wing tips (*Natalus lanatus*); and (3) bats with wing tips of intermediate width (remaining members of genus *Natalus*; figs. 38, 39). With regard to size of the uropatagium, natalids also fall into three categories: (1) bats with small uropatagia

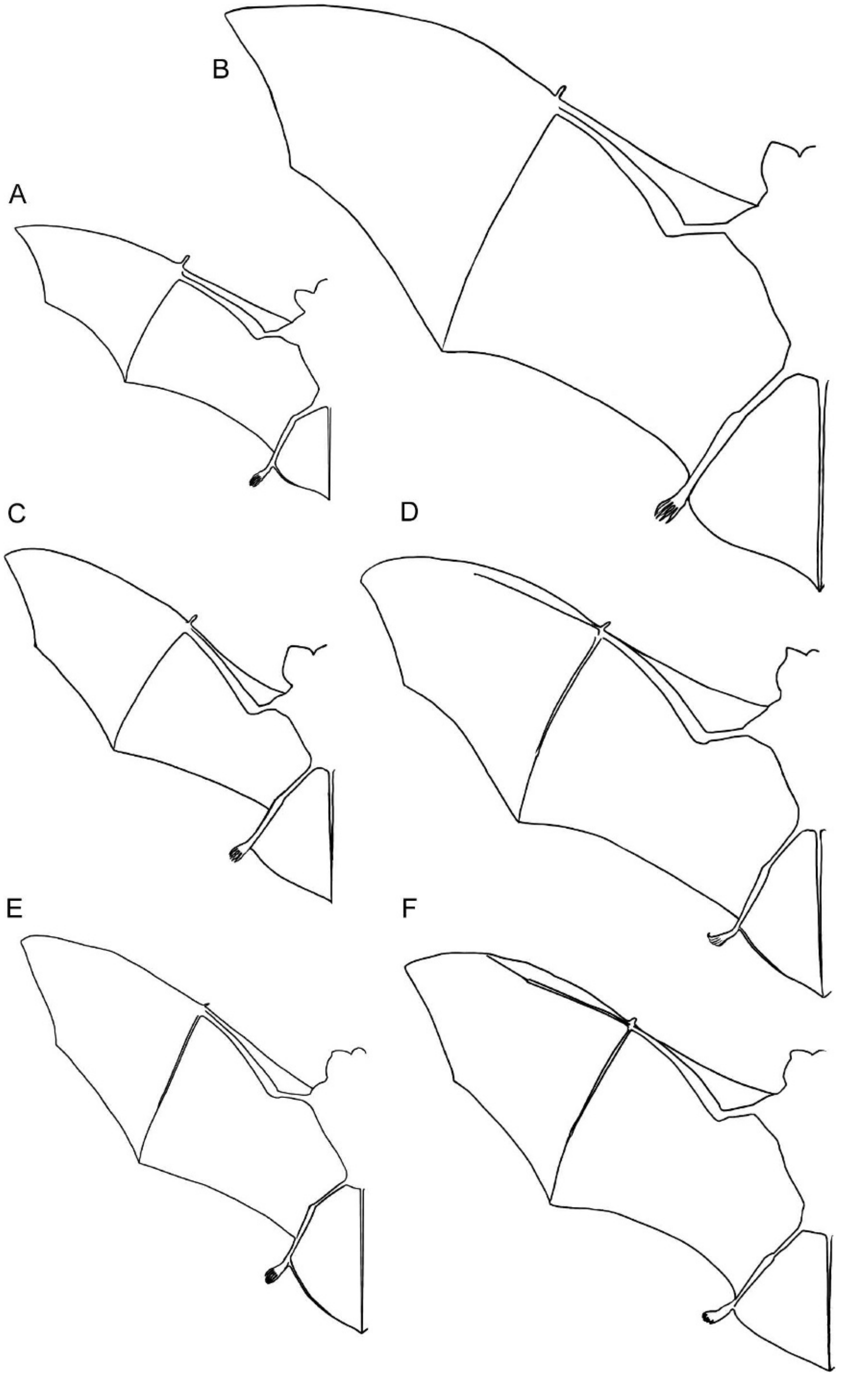


Fig. 39. Wing outlines of six species of Natalidae: **A,** *Nyctiellus lepidus* (modified from Silva-Taboada, 1979); **B,** *Natalus primus*; **C,** *Chilonatalus macer* (modified from Silva-Taboada, 1979); **D,** *Natalus major*; **E,** *Chilonatalus micropus*; **F,** *Natalus lanatus. Nyctiellus lepidus* has the narrowest wing of all natalids.

TABLE 24
Distribution and ecomorphs of Natalidae

		Flight ecomorph		Feeding ecomorph		
Distribution	Taxon	Shape of wing tip	Size of uropatagium	Skull	Mesostylar crests	Body-size ecomorph
Florida	Ppr	—	—	—	long	—
Bahamas	Nyl	pointed	small	broad	short	small
	Ctu	pointed	large	narrow	long	small
Cuba	Nyl	pointed	small	broad	short	small
	Cma	pointed	large	narrow	long	small
	Npr	pointed	large	narrow	long	large
Jamaica	Cmi	pointed	intermediate	narrow	long	small
	Nja	intermediate	large	broad	short	large
Hispaniola	Cmi	pointed	intermediate	narrow	long	small
	Nma	intermediate	large	broad	short	large
Lesser Antilles	Nst	intermediate	large	broad	short	intermediate
Mexico and	Nme	intermediate	large	broad	short	intermediate
Central America	Nla	rounded	intermediate	broad	short	intermediate
South America north of Amazon River	Ntu	intermediate	large	broad	short	intermediate
South America south of Amazon river	Nes	intermediate	large	broad	short	intermediate

(*Nyctiellus*); (2) bats with large uropatagia (*Natalus*, *Chilonatalus tumidifrons*, and *C. macer*); and (3) bats with intermediate-sized uropatagia (*Chilonatalus micropus*, *Natalus lanatus*; figs. 38, 39).

Principles of bat-wing aerodynamics predict that natalids with narrow wing tips and small uropatagia will fly faster and with less maneuverability than natalids with broad wings and large uropatagia. Although natural history information that might corroborate these predictions is scant and vague, field observations seem to make a distinction between the flight of most natalids and that of *Nyctiellus lepidus*. With the exception of *Nyctiellus lepidus*, the flight of most species of Natalidae has been described as slow, very maneuverable, and even mothlike (Goodwin, 1970; Jennings et al., 2004; Miller, 1905; Tejedor et al., 2004, 2005; the term "agile" given by some authors [e.g., Mitchell, 1965] is understood here to mean maneuverable). The flight of *Nyctiellus lepidus*, on the other hand, is relatively fast (Silva-Taboada, 1979).

Despite the difficulty of interpreting the flight morphology of natalids in the absence of behavioral data, the differences found among genera and species are notable and suggest the existence of five distinct ecomorphs. Sympatric species normally belong to separate ecomorphs (table 24). In this regard, the outlying position of *N. lanatus* is remarkable given that its sympatry with *N. mexicanus* represents the only known case of coexistence of two natalid species of the same genus. In only one case (*Chilonatalus macer* and *Natalus primus*) is the same ecomorph shared by two sympatric species.

MOLARIFORM DENTITION: Among bats, natalids show a particularly marked rostrocaudal elongation of the mesostyle of the upper molars. These modified molar cusps have been termed mesostylar crests by Morgan and Czaplewski (2003: fig. 4; pl. 16). Bat genera from other families, including *Thyroptera* (Thyropteridae), *Furipterus* (Furipteridae), and *Kerivoula* (Vespertilionidae) also show mesostylar crests, usually with a slightly different orientation and a lesser degree of development. Within Natalidae, the development of mesostylar crests is greatest in *Primonatalus*, *Chilonatalus*, and *Natalus primus*. In these taxa, the mesostylar crests are high, long, and broadly curved,

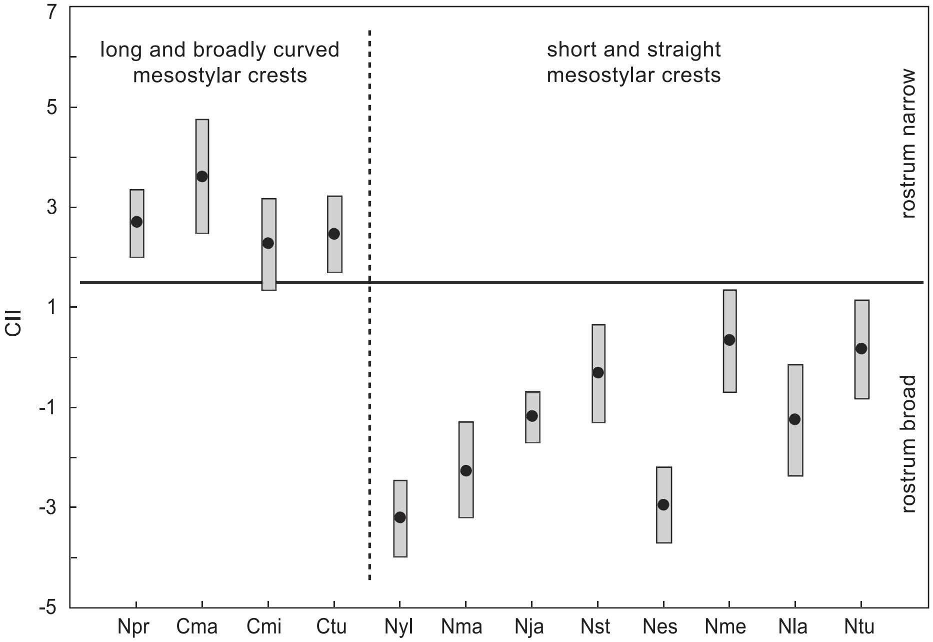


Fig. 40. Plot of scores of the second canonical root obtained by canonical variates analysis of seven cranial dimensions from 12 species of Natalidae. CII is an axis of rostrum shape, being most influenced by maxillary tooth row (table 2). Black dots are score means and gray bars represent two standard deviations around the mean. Species toward the positive side of the axis have long, narrow rostra, whereas species toward the negative side have relatively short, broad rostra. Long and broadly curved mesostylar crests occur only in species with long, narrow rostra.

occupying more than a third of the labial side of the occlusal surface of the upper molars. In *Nyctiellus* and the remaining species of the genus *Natalus*, the mesostylar crests are straight and relatively short (occupying less than 1/3 of the labial side of the occlusal surface of the upper molars). In addition, most members of *Natalus* (except *N. primus*) lack a mesostylar crest on M3.

Long, sharp edges on molar crests appear within several predatory mammalian lineages (e.g., carnivorans: Butler, 1946; insectivorans and microchiropterans: Strait, 1993). The dilambdodont tooth of insectivorous bats, bearing multiple shearing crests on the W-shaped ectoloph, is a classic example (Koopman and MacIntyre, 1980). These structures are thought to be optimal for shearing relatively soft food items as opposed to grinding coarser food, and are more highly developed in animals that specialize in eating boneless muscle (Evans and Sanson, 2003) and/or soft-bodied insects (Strait, 1993). Among insectivorous bats, the consumption of soft food items is also directly reflected in the shape of the skull. Bats with short, broad rostra can deliver stronger bites and are thought to specialize on eating hard-shelled insects (e.g., beetles), whereas bats with long, narrow rostra deliver weaker bites and consume soft-bodied insects (e.g., moths; Freeman, 1979).

The mesostylar crests of natalids represent additional shearing crests to the already well-developed dilambdodont teeth of these bats. Also, natalids show the greatest elongation of the rostrum among all insectivorous bats. This combination of traits suggests that natalids select soft food items. Moreover, the variation observed within the family in the development of the mesostylar crests seems to be associated with variation in the elongation of the rostrum.

Two main natalid groups are defined by rostral geometry: (1) bats with longer, narrower rostra (*Chilonatalus* and *Natalus*

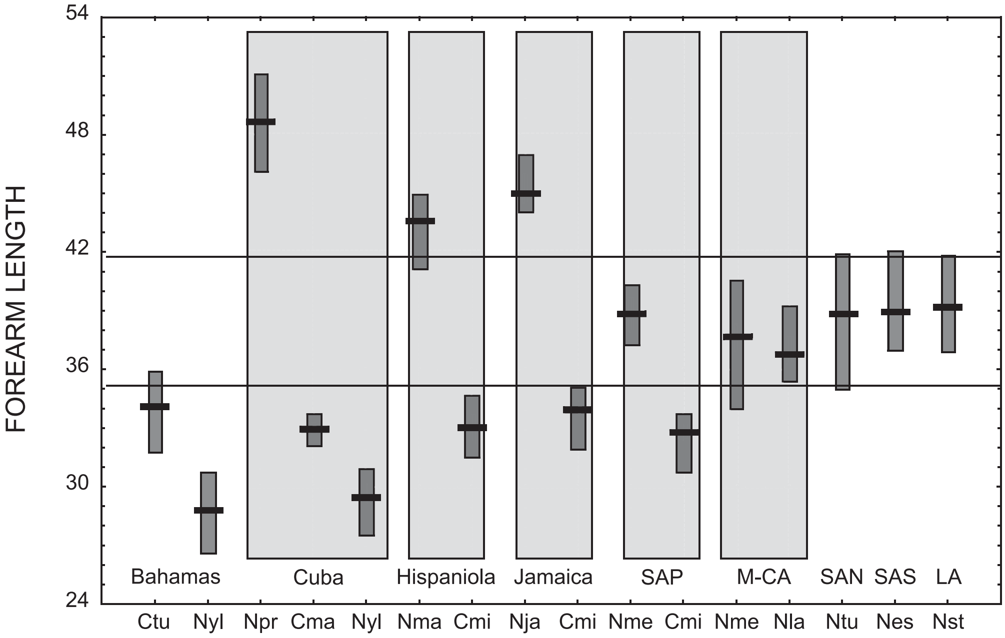


Fig. 41. Variation of forearm length in Natalidae in relation to geographic distribution. Vertical gray bars represent the observed range of variation per species per region and the horizontal black line represents the median. Large gray rectangles frame populations that occur in sympatry. Sample sizes: Bahamas (Ctu, 53; Nyl, 45); Cuba (Npr, 51; Cma, 20; Nyl 24); Hispaniola (Nma, 34; Cmi, 6); Jamaica (Nja, 21; Cmi, 48); SAP = San Andrés and Providencia islands, Colombia (Nme, 7; Cmi, 36); M-CA = Mexico–Central America (Nme, 298; Nla, 33); SAN = South America N of the Amazon (230); SAS = South America S of the Amazon (37); LA = lesser Antilles (65). There is no overlap in forearm length neither among genera nor among insular populations that occur in sympatry. Representatives of the composite fauna of San Andrés and Providencia islands (i.e., the West Indian derived *C. micropus*, and the continental derived *N. mexicanus*) show the least amount of difference in forearm length among sympatric members of these two genera.

primus); and (2) bats with shorter, wider rostra (*Nyctiellus* and the remaining species of *Natalus*; fig. 40). Only species with long, narrow rostra show long and broadly curved mesostylar crests. Although the potential functional association of these two traits seems highly influenced by phylogeny (all species with long rostra and more shearing teeth descend from relatively basal nodes), it does indicate the existence of different natalid ecomorphs with relation to skull shape and molariform dentition. This variation probably reflects significant trophic niche differentiation among natalids.

Dietary data that could test this hypothesis is scant but hints at niche partitioning within Natalidae. The most complete dietary study of a natalid, *Nyctiellus lepidus* (a broad-skulled species) reported a preponderance of insects of medium hardness (Homoptera, Diptera, and Hymenoptera; Silva-Taboada, 1979). By contrast, accounts of the diet of narrow-skulled species mention a marked predominance of moths (*Chilonatalus macer;* Silva-Taboada, 1979) or moths and small crickets (*Natalus primus*; Tejedor et al., 2004).

As in the design of flight morphology, the putative ecomorphs of the feeding apparatus are partitioned among sympatric species with the exception of *Natalus primus* and *Chilonatalus macer*, which share the long rostrum/long mesostylar crest ecomorph (table 24). A second sympatric species pair, *N. mexicanus* and *N. lanatus*, also fall within the same ecomorph.

BODY SIZE: For a small family, Natalidae has a wide variation of body sizes. The largest member of the family, *Natalus primus*,

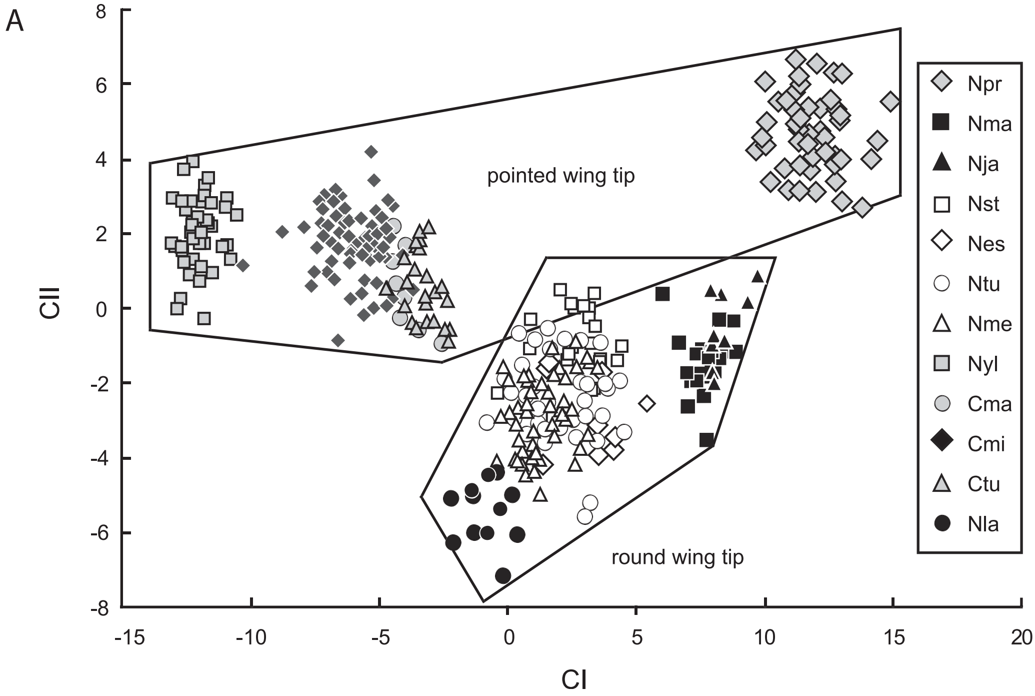


Fig. 42. **A,** Canonical analysis axis scores for four limb measurements of 12 species of Natalidae. Loading contributions of variables to each axis is shown in table 3. CI is an axis of body size and CII is an axis of wing-tip shape, with bats on the positive side of the axis having more pointed tips. Scores of canonical analyses are shown in table 25.

is five times heavier and has almost twice the forearm length of *Nyctiellus lepidus*, the smallest natalid and one of the smallest bats in the world. Body sizes in Natalidae have a strong taxonomic component, with medium to large body sizes occurring only in the genus *Natalus* and small body sizes in *Chilonatalus* and *Nyctiellus*.

The distribution of body size in Natalidae appears to be related to sympatry among species (fig. 41). In three of the five natalid faunas with sympatric species there is a wide difference between the largest and smallest member of the assemblage. At present, the fauna of the Bahamas is unique within the West Indies in that it is composed of allopatric taxa (*N. lepidus* and *C. tumidifrons* occur on different islands) and lacks a large species. During the last Pleistocene glaciation, however, the fauna of the Bahamas was similar to that of Cuba, having three sympatric species, and including an even larger-bodied representative of Cuba's recent *Natalus primus* (Morgan, 1989, 2001).

Differences in body size among closely related insular species are traditionally explained by two nonexclusive mechanisms: species assortment and/or character displacement. Species assortment states that only species with divergent morphology can successfully colonize and coexist on an island (Grant and Abbot, 1980), whereas character displacement is defined as the divergence in morphology between species after the onset of sympatry as a result of selection due to competition (Brown and Wilson, 1956). Rigorous demonstration of either mechanism requires proof of competition for resources and a genetic (rather than environmental) base for the observed morphological variation (Schluter, 2000). Nonetheless, preliminary explanations seek support in the pattern of distribution and phylogenetic history of the taxa in question. The characteristic evidence for species assortment is that members of each size class are closest relatives. That for character displacement is that taxa that occur both allopatrically and sympatrically are

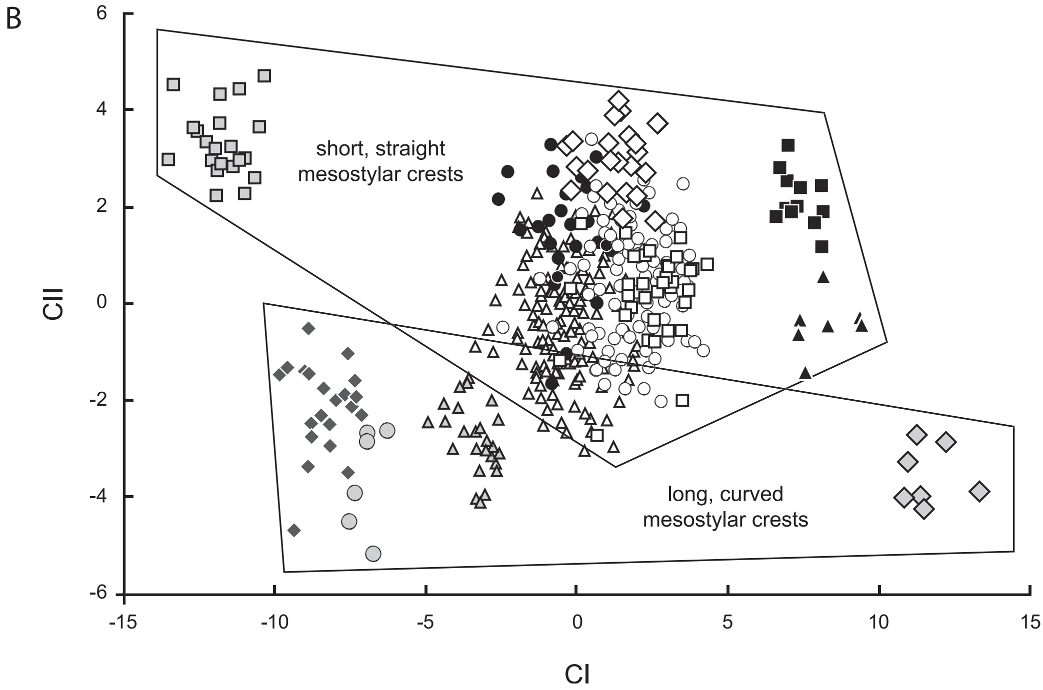


Fig. 42 (*continued*). **B,** Canonical analysis axis scores for seven skull measurements of 12 species of Natalidae. Loading contributions of variables to each axis is shown in table 2. C I is an axis of body size and C II is an axis of rostrum shape, with bats on the negative side of the axis having longer, narrower rostra. *Natalus primus*, which shares many ecomorphological traits with *Chilonatalus*, is widely separated from them in ecomorphological space when body size is taken into account. Scores of canonical analyses are shown in table 26.

more divergent between themselves when they occur sympatrically than when they occur allopatrically (Losos, 1990).

Both patterns are present in Natalidae. The consistent generic difference in body size between *Natalus* (always large) and *Chilonatalus* (always small) in all islands where small and large natalids are found sympatrically is compatible with species assortment. By contrast, a unidirectional change in body size of the large (*Natalus*) and small (*Chilonatalus micropus*) natalids on the islands of Hispaniola, Jamaica, San Andrés, and Providencia, suggests character displacement. In Jamaica, where the largest *Natalus* (*N. jamaicensis*) of those islands occurs, *C. micropus* reaches its maximal body size, whereas in Hispaniola, where the smaller *N. major* occurs, *C. micropus* is also smaller (fig. 41). In San Andrés and Providencia, moreover, a member of the Antillean fauna (*Chilonatalus*) coexists with a medium-sized member of the continental fauna (*N. mexicanus*). In these two islands, *N. mexicanus* appears to have reached its largest body size and C. *micropus* its smallest, in agreement with the predictions of character displacement. Although the size difference between *C. micropus* and *N. mexicanus* on San Andrés and Providencia is much smaller than that between *C. micropus* and greater Antillean *Natalus*, the lack of differentiation in discrete characters of the insular *N. mexicanus* relative to that of the mainland (they are recognized as a single species) suggests that interaction between these two taxa is relatively recent and that the difference observed, if due to size divergence, may be only incipient.

Independently of the preponderance of one or the other mechanism in structuring natalid assemblages, two extreme cases, one of exaggerated size difference (between *N. primus* and *C. macer* in Cuba) and a second of lack of difference (between *N. mexicanus*

TABLE 25

Loadings of the first two canonical axes of a canonical variates analyses (CVA) performed with 4 external variables of Natalidae

Measurement	C I	C II
Forearm length	0.133	0.604
Length of tibia	0.352	0.034
Length of 3rd metacarpal	0.196	1.361
Length of 5th metacarpal	0.466	−1.850
Eigen value	47.940	7.410
Percent explained	83.333	13.217

CVA scores are plotted in figure 42A.

TABLE 26

Loadings of the first two canonical axes of a canonical variates analyses (CVA) performed with 7 cranial variables of Natalidae

Measurement	C I	C II
Greatest skull length	0.183	−0.312
Zygomatic breadth	0.684	0.648
Braincase breadth	0.084	0.069
Breadth across molars	0.020	0.629
Breadth across canines	−0.453	0.332
Maxillary tooth row	0.595	−0.799
Postorbital breadth	−0.032	−0.316
Eigen value	14.494	1.689
Percent explained	74.103	10.468

CVA scores are plotted in figure 42B.

and *N. lanatus* in Mexico) suggest that competition and the evolution of body size are related in Natalidae. The large difference in forearm size between *N. primus* and *C. macer* may be related to the fact that these species share a similar morphospace. *Natalus primus* is unique in its genus in that it resembles *Chilonatalus* in its relatively long wing tip, large uropatagium, long rostrum, and high development of mesostylar crests of the upper molars. It is possible that the greater morphological similarity between *N. primus* and *Chilonatalus* has forced *N. primus* to become disproportionately larger to avoid competition. If body size is taken into account as an additional ecomorphological component, the pair *N. primus*/*C. macer* splits into clearly distinct groups in both wing shape and skull shape morphospaces (fig. 42 A, B).

The pair *N. lanatus* and *N. mexicanus* represent an opposite case. These two species are very similar in forearm length but have different flight morphology. Also, even though they both belong to the relatively wide-rostrum/short mesostylar crest ecomorph, they fall in opposite extremes of that ecomorph in the cranial shape ordination (fig. 42B). Separation into different flight and food-processing ecomorphs may thus be sufficient to partition resources between these two species, relaxing competition and the selective pressure to diverge in size. Nonetheless, as suggested before, it is possible that these two species may show some habitat segregation both in altitude and in roost selection, and that competition in this species pair may actually be minimal in nature.

GENITAL MORPHOLOGY: The relative length of the penis (length of the penis/forearm length) is markedly variable among natalids. Three classes of penis length relative to body size can be distinguished in Natalidae: (1) penis long (*C. micropus*); (2) penis intermediate (*Natalus* and *Nyctiellus*); and (3) penis short (*C. macer* and *C. tumidifrons*; fig. 43). The mean relative penis length of *C. tumidifrons* (5.4% of forearm length) is more than 10 standard deviations shorter than that of *C. micropus* (14.6% of forearm length; figs. 43, 44).

Genital morphology has been shown to be associated with mating strategies and with the likelihood that females will mate with multiple males (Hosken and Stockely, 2004). In species with promiscuous females, sperm competition is intense and males are selected for production of large amounts of sperm (i.e., larger testes), for a deeper delivery of the ejaculate (i.e., longer penises), and for prolonged intromissions, all of which will increase the probability of inseminating females (Arnqvist, 1998). Trends like these have been documented in primates (Dixson, 1987; Harcourt et al., 1981; Verrell, 1992), carnivores (Dixson, 1995), birds (Briskie and Montgomery, 1997; Møller, 1988), flies (Hosken and Ward, 2001), and butterflies (Gage, 1994).

The positive association between intensity of sperm competition and testis size found in a wide range of taxa has been confirmed in bats (Hosken, 1997, 1998; Wilkinson and McCracken, 2003). Investigations of the

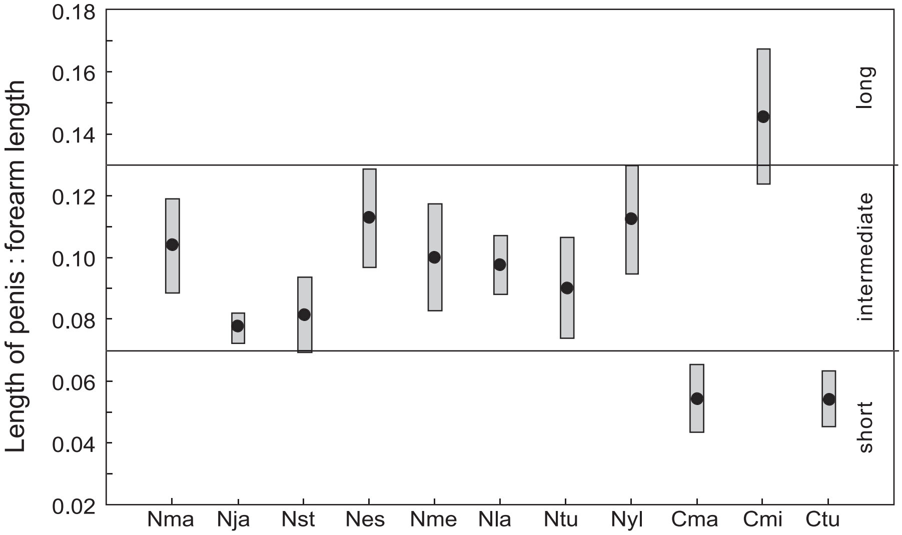


Fig. 43. Distribution of relative penis length in 11 species of Natalidae. Black dots are means and vertical gray bars are two standard deviations around the mean. Most natalids have an intermediate-length penis but the genus *Chilonatalus* includes species with short or long penises.

relationship of penis morphology to mating system in bats, however, have been inconclusive. In a study including 163 species of 12 bat families, significant positive correlations were found among relative baculum length, relative testis size, and mating system (Hosken et al., 2001). The relationships did not hold, however, after correction for phylogenetic history. The authors, therefore, speculated that other factors unrelated to sexual selection could influence baculum length, including aspects of female tract morphology and the size of the uropatagium, the last seen as a physical obstacle during copulation.

Natalids are an interesting group in which to explore genital evolution in bats given their significant variation in penis length and relative size of the uropatagium. Comparisons of penis length with length of the tibia (a correlate of size of the uropatagium in Natalidae, see Methods) showed no family-wide correlation (fig. 45). Stronger trends, however, were detected within two species groups that differ in the relative size of the natalid organ: (1) bats with large natalid organs, reaching 13%–26% the length of the forearm; and (2) bats with small natalid organs, reaching 6%–16%. Interestingly, across Natalidae, relative penis length does appear to be negatively associated with relative length of the natalid organ (fig. 46).

The natalid organ, a unique synapomorphy of Natalidae (Simmons, 1998), is a presumed exocrine gland that is present in the forehead of adult males only (Dalquest, 1950; Goodwin, 1959). The size and shape of the natalid organ varies widely among natalid genera (fig. 47; pl. 5), reaching its maximum development (8.5 mm; 53% of the skull length) in *C. tumidifrons*. Although the function of the natalid organ is unknown, its exclusive presence in males suggests it has a sexual function. When manipulated, living males of the genus *Natalus* sometimes secrete a drop of an oily, translucent green liquid through a pore on the anterodorsal surface of the natalid organ. This secretion does not dissolve in alcohol, as individuals with hardened amber-colored droplets are occasionally found among specimens preserved in fluid. It is possible that secretions from the natalid organ function as a social signal in male-female and/or male-male interactions. The apparent negative association of the size of this organ with male genital size strengthens the hypothesis that both penis length and natalid organ are sexually selected in natalids.

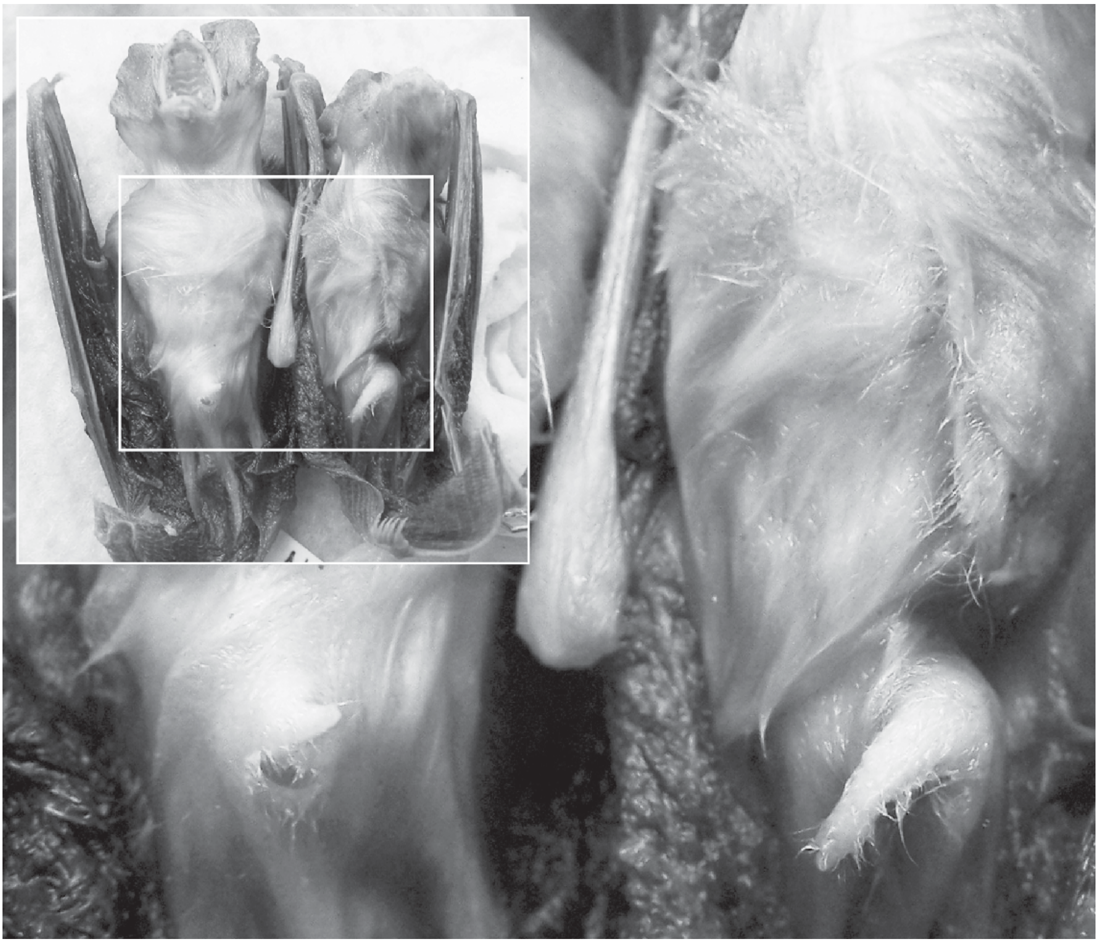


Fig. 44. Ventral view of males of two species of *Chilonatalus* (left, *C. tumidifrons*; right, *C. micropus*) showing longer penis in *C. micropus*.

The presence of opposite evolutionary trends in genital size within *Chilonatalus* is remarkable, and suggests significant differences in mating system among species of this genus. The long penis of *C. micropus* might be related to high levels of sperm competition in this species, perhaps entailed by high levels of female promiscuity. Conversely, the extremely short penis of *C. tumidifrons* and *C. macer*, together with the extreme development of their natalid organ suggest a different strategy. In these two species sperm competition could be reduced by an influence of this gland in social communication. It is possible that individuals with some extreme quality of the natalid organ or its production may have more exclusive access to females, as may occur among harem-keeping or lekking species with exaggerated secondary sexual dimorphism (Andersson, 1994). These intriguing hypotheses remain to be tested with behavioral data.

ACKNOWLEDGMENTS

This work is part of a Ph.D. thesis completed through the joint program of the American Museum of Natural History (AMNH) and the City University of New York. It benefited greatly from the guidance and appraisal of my Ph.D. thesis advisor, Nancy B. Simmons, and of my dissertation

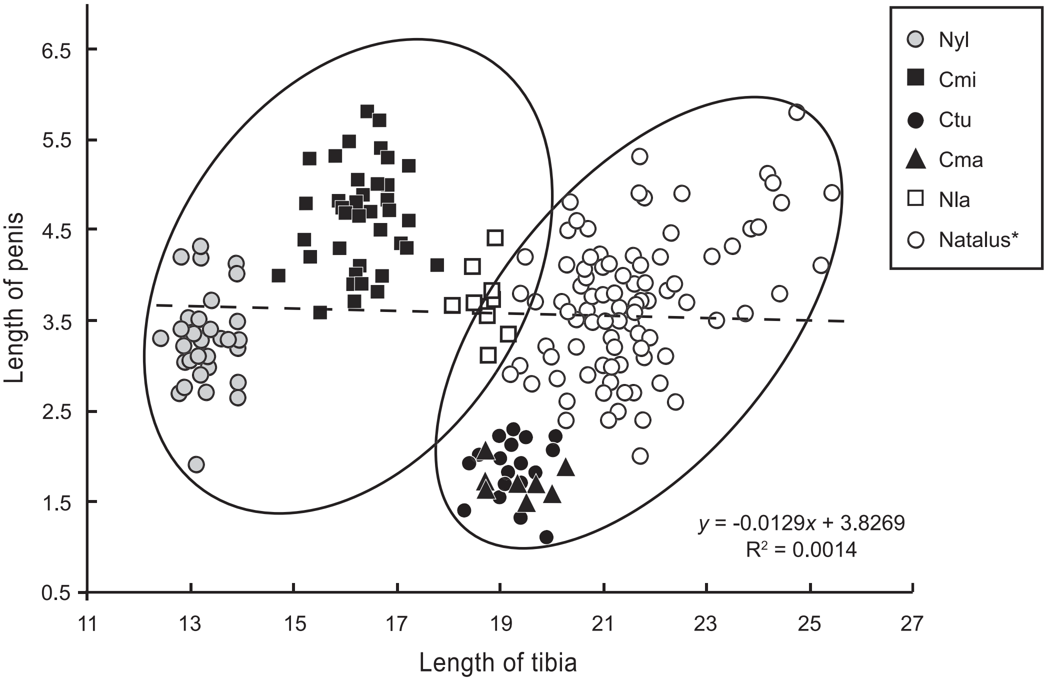


Fig. 45. Relationship of penis length with length of the tibia in Natalidae. Familywide, penis length is not correlated with length of the tibia. Natalids, however, cluster into two groups that differ in the relative size of their natalid organ. *Includes four species of *Natalus*.

committee members, Christopher Raxworthy, Robert F. Rockwell, Robert S. Voss, and John H. Wahlert. It is based on work funded by the National Science Foundation under grant no. 0407950. It received generous support from the AMNH and from the Graduate Center of the City University of New York under a Magnet Fellowship. Fieldwork and travel to museums was supported by an Ernst Mayr Travel Award of the Museum of Comparative Zoology, Harvard University, the Theodore Roosevelt Memorial Grant of the American Museum of Natural History, the American Society of Mammalogists Grants-in-aid Program, the Sue Rosenberg Zalk Student Grant (Graduate Center, CUNY), and an Exploration Grant from the Explorer's Club.

Visits to museums abroad were graciously hosted and arranged by Richard Harbord and Paula Jenkins (BMNH; see appendix 1 for museum acronyms), Fernando A. Cervantes and Julieta Vargas (CNMA), Renato Gregorin (DZSJRP), Javier Sánchez (EBRG), Belkis Rivas (FLS), William Stanley and Michi Schulenberg (FMNH), Thor Holmes (KU), Marlene Hoffman and Helio de Q.B. Fernandes (MBML), Judith Chupasko and Mark Omura (MCZ), Robert Asher and Irene Thomas (MFN), Norka Rocha (MNK), Gilberto Silva-Taboada (MNHN), Mario de Vivo (MZUSP), Gary S. Morgan (NMMNH), Candace McCaffery (UF), Pascual Soriano (ULA), Linda Gordon, Helen Kafka, Jeremy Jacobs, and David Schmidt (USNM). Loaned tissue was provided by Annie Tibbels, Robert Baker, and Peter Larsen.

For their direct participation in fieldwork and/or arranging collecting permits and logistics I am grateful to Aidee Vargas (Bolivia), Rodrigo Redondo and Maria Olimpia Lopes (Brazil), Carlos Mancina and Valeria Tavares (Cuba), Johanset Orihuela, Kevin Murray, Gabriela Nuñez, Isaías Olmo, Miqueas Hilario, Nelson García Marcano, and Renato Rímoli (Dominican Republic), Celia López González, Gabriel

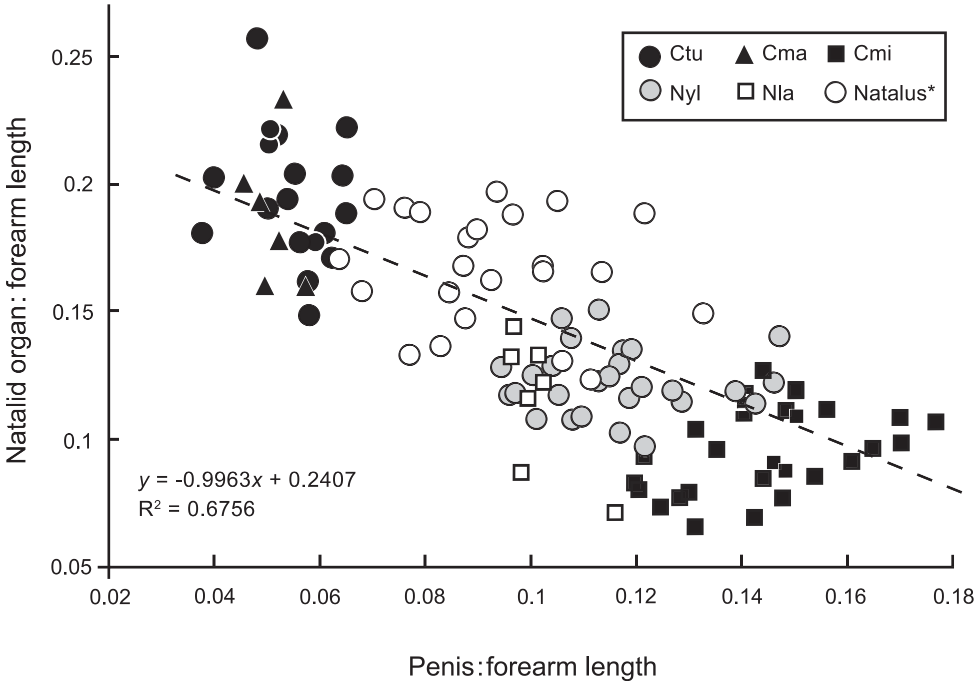


Fig. 46. Plot of relative penis length vs. relative length of the natalid organ in seven species of Natalidae. The relative length of the penis is negatively correlated with the relative length of the natalid organ. *Includes four species of *Natalus*.

Villegas, and Gabriela Nuñez (Mexico), and Ascanio Rincón, Jafet Nassar, and Jose Reyes (Venezuela).

The staff of the AMNH's Department of Mammalogy and its library, including Patricia Brunauer, Neil Duncan, Mary deJong, Mariko Kageyama, Darrin Lunde, Richard Monk, Chris Norris, Ruth O'Leary, Erica Pannen, and Eileen Westwig, provided invaluable help with paperwork, specimen loans and preparation, and location of rare publications. Alfred L. Gardner and Gary S. Morgan carefully read a previous version of the manuscript and offered suggestions that improved it significantly. The meticulous reviews of Mary Knight and Robert S. Voss, AMNH Scientific Publications, of the later versions of the manuscript have been decisive in ensuring its highest quality in print.

During dissertation years, friends and colleagues at the AMNH and abroad made work more productive and life more pleasurable by stimulating discussion, sharing information and photos, and by offering hospitality and companionship. They are Alexandra Bezerra, Annika Keeley, Ana Luz Porcekanzki, Bernal Rodríguez, Brian W. Keeley, David Flores, Elisa Bonaccorso, Enrique Peñalver, Francisco Rocha, Gabriela Nuñez, Gilberto Silva-Taboada, Ilya Temkin, J.M. Guayasamín, Janet Castro, Jose G. Tello, the late Justine Salton, Lara Lopardo, Liliana Dávalos, Louise Crawley, Luis Aguirre, Luis Orioni, Marcela Gómez-Laverde, Marcelo Weksler, Megan Cevasco, Milena Rodríguez, Neusa Rocha, Norberto P. Giannini, Patricia Brito, Pere Bover, Rachel Rocha, Robert P. Anderson, Roberto Keller, Sara Bertelli, Ted Fleming, and Valeria Tavares.

This study on funnel-eared bats ultimately owes most to my biological ancestors: Sylvia Gutierrez (mother), Oscar Tejedor Jr. (father), Oscar Tejedor Sr. (paternal grandfather), and Sylvia Valliciergo (maternal grandmother), who taught me to look at nature with admiration and reason.

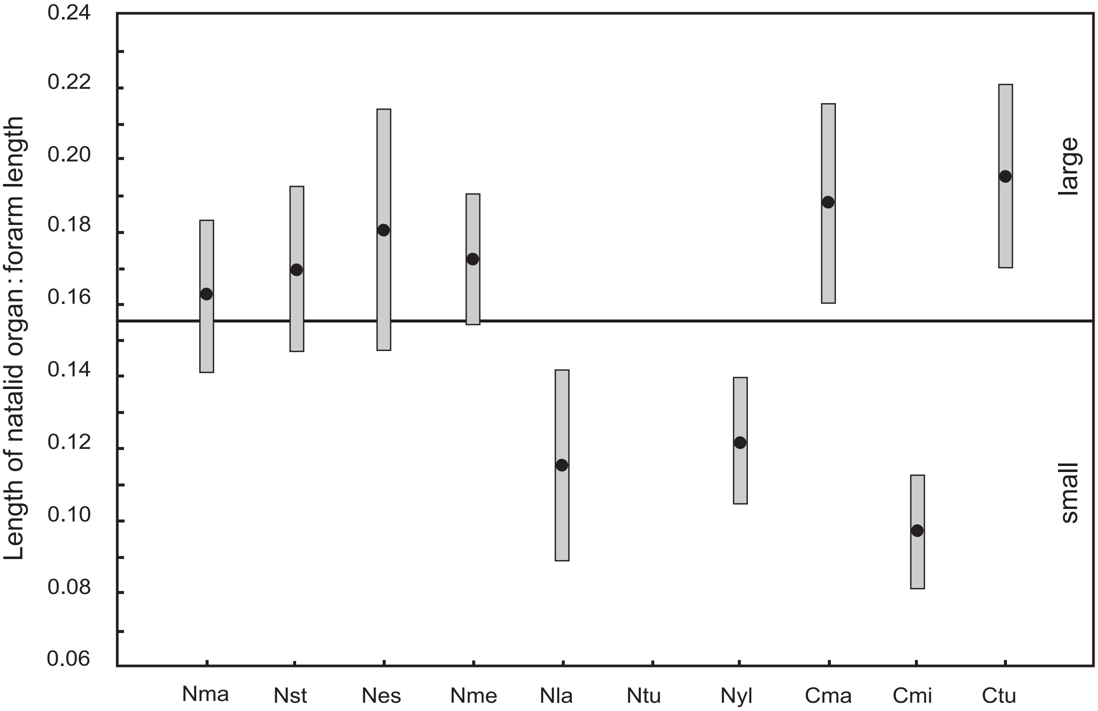


Fig. 47. Distribution of relative size of the natalid organ in 10 species of Natalidae. Two groups of species can be distinguished with relation to relative size of the natalid organ: one, containing species with a relatively large natalid organ and a second containing species with a relatively small natalid organ.

REFERENCES

Allen, G.M. 1905. Notes on Bahama bats. Proceedings of the Biological Society of Washington 18: 65–71.

Allen, G.M., and C.C. Sanborn. 1937. Notes on bats from the Bahamas. Journal of Mammalogy 18: 226–228.

Álvarez, T. 1963. The recent mammals of Tamaulipas, México. University of Kansas Publications of the Museum of Natural History 14: 363–473.

Andersen, K.W. 1994. On the status of bats on Andros and San Salvador island, Bahamas. *In* L.B. Kass (editor), Proceedings of the 5th Symposium on the Natural History of the Bahamas: 1–4. San Salvador, Bahamas: Bahamian Field Station.

Anderson, S. 1972. Mammals of Chihuahua: taxonomy and distribution. Bulletin of the American Museum of Natural History 148 (2): 149–410.

Andersson, M. 1994. Sexual selection. Princeton, NJ: Princeton University Press.

Anthony, H.E. 1919. Mammals collected in eastern Cuba in 1917, with descriptions of two new species. Bulletin of the American Museum of Natural History 41 (20): 625–643.

Arita, H. 1997. Murciélagos cavernícolas de México. Cave list distributed by the author.

Arnqvist, G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. Nature 393: 784–786.

Ávila-Flores, R., and R.A. Medellín. 2004. Ecological, taxonomic, and physiological correlates of cave use by Mexican bats. Journal of Mammalogy 85: 675–687.

Baker, P.E. 1985. Volcanic hazards on St. Kitts and Montserrat, West Indies. Journal of the Geological Society 142: 279–295.

Baker, R.H., and J.K. Greer. 1962. Mammals of the Mexican state of Durango. Publication of the Museum Michigan State University Biological Series 2: 29–154.

Baker, R.J., H.H. Genoways, and J.D. Patton. 1978. Bats of Guadeloupe. Occasional Papers of the Museum of Texas Tech University 50: 1–16.

Barlow, K.E., G. Jones, and E.M. Barratt. 1997. Can skull morphology be used to predict ecological relationships between bat species? A test using two cryptic species of pipistrelle. Proceedings of the Royal Society of London 264: 1695–1700.

Briskie, J.V., and R. Montgomery. 1997. Sexual selection and the intromittent organ of birds. Journal of Avian Biology 28: 73–86.

Broadbooks, H.E. 1961. The funnel-eared bat in Sonora. Journal of Mammalogy 42: 403.

Brown, W.L.J., and E.O. Wilson. 1956. Character displacement. Systematic Zoology 5: 49–64.

Brunet, A.K., and R.A. Medellín. 2001. The species-area relationship in bat assemblages of tropical caves. Journal of Mammalogy 82: 1114–1122.

Butler, P.M. 1946. The evolution of carnassial dentitions in the Mammalia. Proceedings of the Zoological Society of London 116: 198–220.

Caballero, E. 1942a. Descripción de *Parallintoshius tadaridae* n. sp. (Nematoda: Trichostrongylidae) de los murciélagos de México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 13: 105–109.

Caballero, E. 1942b. Tremátodos de los murciélagos de México. III. Descripción de *Urotrema scabridum* Braun, 1900, y posición sistemática de las especies norteamericanas de este género. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 13: 641–648.

Cabrera, A. 1957. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino des Ciencias Naturales ‘‘Bernardino Rivadavia’’ 4: 1–308.

Cadena, A. 1974. Estudio de una población del murciélago *Natalus tumidirostris* en la cueva de Macaregua-San Gil. Informe Técnico Comité de Investigaciones, Universidad de los Andes.

Carreño, R. 1998. Colonia con infantes del murciélago *Natalus stramineus* en la cueva Ricardo Zuloaga. Boletín de la Sociedad Venezolana de Espeleología 32: Cover photo.

Carter, D.C., and P.G. Dolan. 1978. Catalogue of type specimens of Neotropical bats in selected European museums. Special Publication, Museum Texas Tech University 15: 1–138.

Ceballos, G., and C. Galindo. 1984. Mamíferos silvestres de la Cuenca de México. México DF: LIMUSA–Instituto de Ecología.

Cervantes, F.A., J.N. Ramírez-Vite, S. Ramirez-Vite, and C. Ballesteros. 2004. New records of mammals from Hidalgo and Guerrero, Mexico. Southwestern Naturalist 49: 122–124.

Charles-Dominique, P., A. Brosset, and S. Jouard. 2001. Les chauves-souris de Guyane. Paris: Muséum National d'Histoire Naturelle.

Corbet, G.B., and J.E. Hill. 1986. A world list of mammalian species. 2nd ed. London: British Museum (Natural History).

Czaplewski, N.J., and C. Cartelle. 1998. Pleistocene bats from cave deposits in Bahia, Brazil. Journal of Mammalogy 79: 784–803.

Dalquest, W.W. 1950. The genera of the chiropteran family Natalidae. Journal of Mammalogy 31: 436–443.

Dalquest, W.W., and E.R. Hall. 1949. A new subspecies of funnel-eared bat (*Natalus mexicanus*) from eastern Mexico. Proceedings of the Biological Society of Washington 62: 153–154.

Dávalos, L.M. 2005. Molecular phylogeny of funnel-eared bats (Chiroptera: Natalidae), with notes on biogeography and conservation. Molecular Phylogenetics and Evolution 37: 91–103.

Dávalos, L.M., and R. Eriksson. 2003. New and noteworthy records from ten Jamaican bat caves. Caribbean Journal of Science 39: 140–144.

Davis, W.D., and D.C. Carter. 1962. Notes on Central American bats with description of a new species of *Mormoops*. Southwestern Naturalist 7: 64–74.

De Bellard Pietri, E. 1969. Atlas espeleológico de Venezuela. Boletín de la Academia de Ciencias Físicas Matemáticas y Naturales (Caracas) 29: 21–106.

Díaz-Brisquets, S., and J.F. Pérez-López. 2000. Conquering nature: the environmental legacy of socialism in Cuba. Pittsburgh: Pittsburgh University Press.

Dixson, A.F. 1987. Observations on the evolution of the genitalia and copulatory behaviour in male primates. Journal of Zoology (London) 213: 423–443.

Dixson, A.F. 1995. Baculum length and copulatory behaviour in carnivores and pinnipeds (grand order Ferae). Journal of Zoology (London) 235: 67–76.

Dobson, G.E. 1878. Catalogue of the Chiroptera in the collection of the British Museum. London: British Museum of Natural History.

Dobson, G.E. 1880. Description of a new species of the genus Natalus (Vespertilionidae from Jamaica. Proceedings of the Scientific Meetings of the Zoological Society of London, 443–444.

Eshelman, R.E., and G.S. Morgan. 1985. Tobagan Recent mammals, fossil vertebrates, and their zoogeographical implications. National Geographic Society Research Reports 21: 137–143.

Estrada, A., and R. Coates-Estrada. 2001. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. Journal of Tropical Ecology 17: 627–646.

Evans, A.R., and Sanson, G.D. 2003. The tooth of perfection: functional and spatial constraints on mammalian tooth shape. Biological Journal of the Linnean Society 78: 173–191.

Fincham, A.G. 1997. Jamaica underground: the caves, sinkholes and underground rivers of the island. Kingston: University of West Indies Press.

Fracasso, M.P.A., and L.O. Salles. 2005. Diversity of Quaternary bats from Serra da Mesa (State of Goias, Brazil). Zootaxa 817: 1–19.

Freeman, P.W. 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. Journal of Mammalogy 60: 467–479.

Freeman, P.W. 1998. Form, function, and evolution in skulls and teeth of bats. *In* T.H. Kunz and P.A. Racey (editors), Bat biology and conservation: 140–156. Washington, DC: Smithsonian Institution Press.

Gage, M.J.G. 1994. Associations between body size, mating pattern, testis size and sperm lengths across butterflies. Proceedings of the Royal Society of London B Biological Sciences 258: 247–254.

Gardner, A.L. 2008. Genus *Natalus* Gray 1838. *In* A.L. Gardneer (editor), Mammals of South America: 397–399. Chicago: University of Chicago Press.

Genoud, M., F.J. Bonaccorso, and A. Arends. 1990. Rate of metabolism and temperature regulation in two small tropical insectivorous bats (*Peropteryx macrotis* and *Natalus tumidirostris*). Comparative Biochemistry and Physiology 97: 229–234.

Genoways, H.H., R.J. Baker, J.W. Bickham, and C.J. Phillips. 2005. Bats of Jamaica. Special Publications, Museum of Texas Tech University 48: 1–155.

Genoways, H.H., S.C. Pedersen, P.A. Larsen, G.G. Kwiecinski, and J.J. Huebschman. 2007. Bats of Saint Martin, French West Indies/Sint Maarten, Netherlands Antilles. Mastozoología Neotropical 14: 169–188.

Genoways, H.H., R.M. Timm, R.J. Baker, C.J. Phillips, and D.A. Schlitter. 2001. Bats of the West Indian island of Dominica: natural history, areography, and trophic structure. Special Publications, Museum of Texas Tech University 43: 1–43.

Gervais, P. 1837. Sur les animaux mamifères des Antilles. L'Institut, Paris 5 (218): 253–254.

Gervais, P. 1856. Deuxièmemémoire. Documents zoologiques pour servir a la monographie des chéiroptères Sud-Américains In Mammifères, ed. P. Gervais, 25–88. In Animaux nouveaux ou rares recueillis pendant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para; exécutée par ordre du gouvernement français pendant les années 1843 a 1847, sous la direction du comte Francis de Castelnau, ed. F. de Castelnau. Paris: P. Bertrand, 1: 1–116.

Giannini, N.P., J.R. Wible, and N.B. Simmons. 2006. On the cranial osteology of Chiroptera. I. *Pteropus* (Megachiroptera: Pteropodidae). Bulletin of the American Museum of Natural History 295: 1–134.

Gibbons, L.M., and I. Omah-Maharaj. 1991. *Tricholeiperia trinidadensis* n. sp. (Nematoda, Molineidae) from *Natalus tumidirostris haymani* (Microchiroptera, Natalidae) in Trinidad. Systematic Parasitology 20: 149–154.

Gómez-Laverde, M. 1986. Morfología y cariología de una población de *Natalus tumidirostris* (Chiroptera: Natalidae). Undergraduate thesis, Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia.

Goodwin, G.G. 1934. Mammals collected by A.W. Anthony in Guatemala, 1924–1928. Bulletin of the American Museum of Natural History 68: 1–60.

Goodwin, G.G. 1959. Bats of the subgenus *Natalus*. American Museum Novitates 1977: 1–22.

Goodwin, G.G. 1969. Mammals from the state of Oaxaca, Mexico, in the American Museum of Natural History. Bulletin of the American Museum of Natural History 141 (1): 1–270.

Goodwin, G.G., and A.M. Greenhall. 1961. A review of the bats of Trinidad and Tobago: descriptions, rabies infections, and ecology. Bulletin of the American Museum of Natural History 122 (3): 187–302.

Goodwin, R.E. 1970. The ecology of Jamaican bats. Journal of Mammalogy 51: 571–579.

Grant, P.R., and I. Abbot. 1980. Interspecific competition, island biogeography and null hypotheses. Evolution 34: 322–341.

Gray, J.E. 1838. A revision of the genera of bats (Vespertilionidae) and the description of some new genera and species. Magazine of Zoology and Botany 2: 483–505.

Gregorin, R., and L.F. Mendes. 1999. Sobre quirópteros (Emballonuridae, Phyllostomidae, Natalidae) de duas cavernas da Chapada Diamantina, Bahia, Brasil. Iheringia Série Zoologica 86: 121–124.

Gundlach, J. 1840. Beschreibung von vier auf Cuba gefangenen Fledermäusen. Weigmann's Archiv Naturgeshichte 6: 356–358.

Gundlach, J. 1866(1867). Revista y catálogo de los mamíferos cubanos. Anales de la Sociedad Española de Historia Natural 1: 231–258.

Hall, E.R. 1981. The mammals of North America. Vol. 1. 2nd ed. New York: John Wiley.

Hall, E.R., and K.R. Kelson. 1959. The mammals of North America. Vol. 1. New York: Ronald Press.

Hall, E.R., and W.W. Dalquest. 1963. The mammals of Veracruz. University of Kansas Publications, Museum of Natural History 14: 165–362.

Hall, J.S., C.W. Stihler, and P.L. Dougherty. 1998. Bat populations on San Salvador and New Providence islands. Bahamas Journal of Science 5: 22–27.

Handley, C.O., Jr., and A.L. Gardner. 1990. The holotype of *Natalus stramineus* Gray (Mammalia: Chiroptera: Natalidae). Proceedings of the Biological Society of Washington 103: 966–972.

Harcourt, A.H., P.H. Harvey, S.G. Larson, and R.V. Short. 1981. Testis weight, body weight and breeding system in primates. Nature 293: 55–57.

Hijmans, R., L. Guarino, A. Jarvis, and R. O'Brien. 2006. DIVA-GIS 4.5. Internet resource (available from http://www.diva-gis.org/).

Hill, J.E., and S.E. Smith. 1981. *Craseonycteris thonglongyai*. Mammalian Species 160: 1–4.

Hosken, D.J. 1997. Sperm competition in bats. Proceedings of the Royal Society of London B Biological Sciences 264: 385–392.

Hosken, D.J. 1998. Testis mass in megachiropteran bats varies in accordance with sperm competition theory. Behavioral Ecology and Sociobiology 44: 169–177.

Hosken, D.J., and P. Stockley. 2004. Sexual selection and genital evolution. Trends in Ecology and Evolution 19: 87–93.

Hosken, D.J., and P.I. Ward. 2001. Experimental evidence for testis size evolution via sperm competition. Ecology Letters 4: 10–13.

Hosken, D.J., K.E. Jones, K. Chipperfield, and A. Dixson. 2001. Is the bat os penis sexually selected? Behavioral Ecology and Sociobiology 50: 450–460.

Hoyt, R.A., and R.J. Baker. 1980. *Natalus major*. Mammalian Species 130: 1–3.

IUCN (International Union for Conservation of Nature and Natural Resources) 2010.2. 2010. IUCN red list of threatened species. Internet resource (http://www.iucnredlist.org), accessed 16 December 2010.

Jennings, N.V., S. Parsons, K.E. Barlow, and M.R. Gannon. 2004. Echolocation calls and wing morphology of bats from the West Indies. Acta Chiropterologica 6 (1): 75–90.

Jiménez-Vázquez, O., M.M. Condis, and E. García-Cancio. 2005. Vertebrados post-glaciales en un residuario fósil de *Tyto alba scopoli* (Aves: Tytonidae) en el occidente de Cuba. Revista Mexicana de Mastozoología 9: 80–101.

Kerridge, D.C., and R.J. Baker. 1978. *Natalus micropus*. Mammalian Species 114: 1–3.

Koopman, K.F. 1981. Biogeography of the bats of South America. *In* M.A. Mares and H.H. Genoways (editors), Mammalian biology in South America. The Pymatuning Symposia in Ecology: 273–302. Pennsylvania: University of Pittsburgh Pymatuning Laboratory of Ecology Special Publication Series.

Koopman, K.F. 1993. Order Chiroptera. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, a taxonomic and geographic reference, 2nd ed.: 137–242. Washington DC: Smithsonian Institution.

Koopman, K.F. 1994. Chiroptera: systematics. *In* J. Niethammer, H. Schliemann, and D. Stark (editors), Handbuch der Zoologie, Vol. VIII, Mammalia, Part 60, 1–217. Berlin: Walter de Gruyter.

Koopman, K.F., and G.T. MacIntyre. 1980. Phylogenetic analysis of chiropteran dentition. *In* D.E. Wilson and A.L. Gardner (editors), Proceedings of the Fifth International Bat Research Conference, 279–288. Lubbock: Texas Tech Press.

Koopman, K.F., and R. Ruibal. 1955. Cave-fossil vertebrates from Camaguey, Cuba. Breviora 46: 1–8.

Koopman, K.F., and E.E. Williams. 1951. Fossil chiroptera collected by H.E. Anthony in Jamaica, 1919–1920. American Museum Novitates 1519: 1–29.

Koopman, K.F., M.K. Hecht, and E. Lidecky-Janacek. 1957. Notes on the mammals of the Bahamas with special reference to bats. Journal of Mammalogy 38: 164–174.

LaVal, R.K., and T.J. Lewis. 1988. *Natalus stramineus* killed by katydid. Bat Research News 29: 1–2.

Lawlor, T.E. 1973. Aerodynamic characteristics of some Neotropical bats. Journal of Mammalogy 54: 71–78.

Linares, O.J. 1971. A new subspecies of funnel-eared bat (*Natalus stramineus*) from western Venezuela. Bulletin of the Southern California Academy of Sciences 70: 81–84.

Linares, O.J. 1998. Mamíferos de Venezuela. Caracas: Sociedad Conservacionista Audubon de Venezuela.

Linares, O.J., and I. Löbig-A. 1973. El cariotipo del murciélago cavernícola *Natalus tumidirostris*, del norte de Venezuela, y observaciones sobre las afinidades de esta especie con *N. stramineus* (Chiroptera: Natalidae). Boletín de la Sociedad Venezolana de Espeleología 4: 89–95.

López González, C., S.J. Presley, R.D. Owen, M.R. Willig, and I. Gamarra de Fox. 1998. Noteworthy records of bats from Paraguay. Mastozoologia Neotropical 5: 41–45.

Losos, J.B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. Evolution 44: 558–569.

Lukens, P.W., Jr., and W.B. Davis. 1957. Bats of the Mexican state of Guerrero. Journal of Mammalogy 38: 1–14.

Lunaschi, L. 2002. Redescripción y comentarios taxonómicos sobre *Ochoterenatrema labda* (Digenea: Lecithodendriidae), parásito de quirópteros en México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 73: 11–18.

Marinkelle, C.J., and E.S. Grosse. 1968. Species of *Borrelia* from a Colombian bat (*Natalus tumidirostris*). Nature 218 (140): 487.

McFarlane, D.A. 1986. Cave bats in Jamaica. Oryx 20: 27–30.

McFarlane, D.A. 1997. Cave vertebrates. *In* A.G. Fincham (editor), Jamaica underground: the caves, sinkholes and underground rivers of the island, 57–62. Kingston: University of the West Indies Press.

McKenzie, N.L., A.C. Gunnell, M. Yani, and M.R. Williams. 1995. Correspondence between flight morphology and foraging ecology in some Palaeotropical bats. Australian Journal of Zoology 43: 241–257.

McNab, B.K. 1969. The economics of temperature regulation in Neotropical bats. Comparative Biochemistry and Physiology 31: 227–268.

Milán, D., and A.A. Stekol'nikov. 2004. Chigger mites of the genus Eutrombicula Ewing, 1938 (Acari: Trombiculidae) from Cuba, with the description of three new species. Folia Parasitologica 51: 359–36.

Miller, B.W. 2004. Acoustic surveys and non-phyllostomid Neotropical bats: how effective are they? *In* R.M. Brigham, E.K.V. Kalko, G. Jones, S. Parsons, and H.J.G.A. Limpens (editors), Bat echolocation research: tools, techniques and analysis, 58–63. Austin, TX: Bat Conservation International.

Miller, G.S., Jr. 1898. Descriptions of five new phyllostome bats. Proceedings of the Academy of Natural Sciences of Philadelphia 50: 326–337.

Miller, G.S., Jr. 1899. History and characters of the family Natalidae. Bulletin of the American Museum of Natural History 12 (18): 245–253.

Miller, G.S., Jr. 1900. A second collection of bats from the island of Curaçao. Proceedings of the Biological Society of Washington 13: 159–162.

Miller, G.S., Jr. 1902. Twenty new American bats. Proceedings of the Academy of Natural Sciences of Philadelphia 54: 389–412.

Miller, G.S., Jr. 1903. A new nataline bat from the Bahamas. Proceedings of the Biological Society of Washington 16: 119–120.

Miller, G.S., Jr. 1904. Notes on bats collected by William Palmer in Cuba. Proceedings of the United States National Museum 27: 337–348.

Miller, G.S., Jr. 1905. Mammals of the Bahama Islands. *In* G.B. Shattuck (editor), The Bahama Islands, 373–384. New York: Macmillan.

Miller, G.S., Jr. 1906. Twelve new genera of bats. Proceedings of the Biological Society of Washington 19: 83–85.

Miller, G.S., Jr. 1907. The families and genera of bats. Bulletin of the United States National Museum 57: 1–282.

Miller, G.S., Jr. 1914. A new bat from Cuba. Proceedings of the Biological Society of Washington 27: 225–226.

Miller, G.S., Jr, and J.A.G. Rehn. 1901. Systematic results of the study of North American land mammals to the close of the year 1900. Proceedings of the Boston Society of Natural History 30: 1–352.

Mitchell, G.C. 1965. A natural history study of the funnel-eared bat *Natalus stramineus*. Unpublished M.Sc. thesis, University of Arizona.

Mok, W.Y., D.E. Wilson, L.A. Lacey, and R.C.C. Luizao. 1982. Lista atualizada de quirópteros da Amazônia Brasileira. Acta Amazonica 12 (4): 817–823.

Molinari, J., E.E. Gutiérrez, A.A. de Ascenção, J.M. Nassar, A. Arends, and R.J. Márquez. 2005. Predation by giant centipedes, *Scolopendra gigantea*, on three species of bats in a Venezuelan cave. Caribbean Journal of Science 41: 340–346.

Møller, A.P. 1988Testis size ejaculate quality and sperm competition in birds. Biological Journal of the Linnaean Society 33: 273–283.

Moreno, A. 1996. Murciélagos de Nuevo León. Monterrey, México: Impresora Monterrey.

Morgan, G.S. 1989. Fossil Chiroptera and Rodentia from the Bahamas, and the historical biogeography of the Bahamian mammal fauna. *In* C.A. Woods (editor), Biogeography of the West Indies: past, present and future: 685–740. Gainesville, FL: Sandhill Crane Press.

Morgan, G.S. 1994. Late Quaternary fossil vertebrates from the Cayman Islands. *In* M.A. Brunt and J.E. Davies (editors), The Cayman Islands: natural history and biogeography, 465–580. Dordrecht: Kluwer Academic Publishers.

Morgan, G.S. 2001. Patterns of extinction in West Indian bats. *In* C.A. Woods and F.E. Sergile (editors), Biogeography of the West Indies: patterns and perspectives, 369–406. Boca Raton, FL: CRC Press.

Morgan, G.S., and N.J. Czaplewski. 2003. A new bat (Chiroptera: Natalidae) from the early Miocene of Florida, with comments on natalid phylogeny. Journal of Mammalogy 84: 729–752.

Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. Functional Ecology 9: 48–54.

Norberg, U.M. 1998. Morphological adaptations for flight in bats. *In* T.H. Kunz and P.A. Racey (editors), Bat biology and conservation, 93–108.

Washington, DC: Smithsonian Institution Press.

Norberg, U.M., and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B Biological Sciences 316: 337–419.

Nowak, R.M. 1994. Walker's bats of the world. Baltimore, MD: Johns Hopkins University Press.

Obrist, M.K., M.B. Fenton, J.L. Eger, and P.A. Schlegel, P.A. 1993. What ears do for bats: a comparative study of pinna sound pressure transformation in Chiroptera. Journal of Experimental Biology 180: 119–152.

Ochoa-G, J., C. Molina, and S. Giner. 1993. Inventario y estudio comunitario de los mamíferos del Parque Nacional Canaima, con una lista de las especies registradas para la Guayana Venezolana. Acta Científica Venezolana (Ecología) 44: 245–262.

Osburn, W. 1865. Notes on the Chiroptera of Jamaica. Proceedings of the Zoological Society of London, 61–85.

Ottenwalder, J., and H. Genoways. 1982. Systematic review of the Antillean bats of the *Natalus micropus*-complex. Annals of Carnegie Museum 51: 17–36.

Patterson, B.D. 2001. Fathoming tropical biodiversity: the continuing discovery of Neotropical mammals. Diversity and Distributions 7: 191–196.

Pedersen, S. 2003. Earth, wind, and fire: the story of the fruit bats of Montserrat. Natural History 112: 20–24.

Pedersen, S., P.A. Larsen, H.H. Genoways, M.N. Morton, K.C. Lindsay, and J. Cindric. 2007. Bats of Barbuda, northern Lesser Antilles. Occasional Papers, Museum of Texas Tech University 271: 1–19.

Pedersen, S.C., H.H. Genoways, and P. Larsen. 2006. Bats of Antigua, northern Lesser Antilles. Occasional Papers, Museum of Texas Tech University 249: 1–17.

Pedersen, S., H.H. Genoways, M.N. Morton, J.W. Johnson, and S.E. Courts. 2003. Bats from Nevis, northern Lesser Antilles. Acta Chiropterologica 5: 251–267.

Peters, W. 1861. Übersicht der von Hrn. Dr. Gundlach beobachteten Flederthiere auf Cuba. Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1861: 817–818.

Petit, S. 1996. The status of bats on Curaçao. Biological Conservation 77: 27–31.

Pine, R.H., and A. Ruschi. 1976. Concerning certain bats described and recorded from Espirito Santo, Brazil. Anales del Instituto de Biologia Universidad Nacional Autónoma de Mexico Serie Zoológica 47: 183–196.

Pozo de La Tijera, C., and J.E. Escobedo-Cabrera. 1999. Mamíferos terrestres de la Reserva de la Biosfera de Sian Ka'an, Quintana Roo, México. Revista de Biología Tropical 47: 251–262.

Ramírez-Pulido, J., M.C. Britton, A. Perdomo, and A. Castro. 1986. Guía de los mamíferos de México. Referencias hasta 1983. México, DF: Universidad Autónoma Metropolitana, Unidad Iztapalapa.

Reid, F.A. 1997. A field guide to the mammals of Central America and southeast Mexico. New York: Oxford University Press.

Riba-Hernández, P. 1996. Notas sobre los murciélagos de la estación biológica Río Macho, Costa Rica. Brenesia 45–46: 183–186.

Ridgway, R. 1912. Color standards and color nomenclature. Washington, DC: Published by the author.

Riskin, D.K., J.E.A. Bertram, and J.W. Hermanson. 2005. Testing the hindlimb-strength hypothesis: non-aerial locomotion by Chiroptera is not constrained by the dimensions of the femur or tibia. Journal of Experimental Biology 208: 1309–1319.

Rodríguez-Herrera, B. 2004. Ampliaciones de ámbito y registro de nuevas localidades de especies de mamíferos en Costa Rica. Brenesia 61: 125–126.

Ronquist, F. 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. Systematic Biology 46: 193–201.

Ruschi, A. 1951. Morcegos do estado do Espirito Santo. Família Vespertilionidae, chave analítica para os gêneros e espécies representadas no E. Santo. Descrição de *Myotis nigricans nigricans* e *Myotis espiritosantensis* n. sp. e algumas observações a seu respeito. Boletim do Museo de Biologia Profesor Mello-Leitão 4: 1–11.

Ruschi, A. 1970. Morcegos do estado do Espirito Santo. Chaves analíticas e artificiais para a determinação das famílias, gêneros, espécies e subespécies dos morcegos represetados no E.E. Santo, descrição de uma nova especie da Família Natalidae Miller, 1899 da região do Rio Itaunas, em Conceição da Barra e Rio Mucurí ao sul da Bahia: *Natalus espiritosantensis* n. sp. Boletim do Museo de Biologia Profesor Mello-Leitão 43: 1–11.

Rydell, J., H.T. Arita, M. Santos, and J. Granados. 2002. Acoustic identification of insectivorous bats (order Chiroptera) of Yucatan, Mexico. Journal of Zoology (London) 257: 27–36.

Sánchez-Hernández, C., and A. Ramírez-Bautista. 1992. *Trimorphodon biscutatus* (lyre snake). Prey. Herpetological Review 23: 121.

Schluter, D. 2000. Ecological character displacement in adaptive radiation. American Naturalist 156: S4–S16.

Shamel, H.H. 1926. A new bat from Dominica. Proceedings of the Biological Society of Washington 41: 67–68.

Silva-Taboada, G. 1974. Fossil Chiroptera from cave deposits in central Cuba, with descriptions of two new species and the first West Indian record of *Mormoops megalophylla*. Acta Zoologica Cracoviensia 19: 33–73.

Silva-Taboada, G. 1977. Algunos aspectos de la selección de hábitat en el murciélago *Phyllonycteris poeyi* Gundlach en Peters, 1861 (Mammalia: Chiroptera). Poeyana 168: 1–10.

Silva-Taboada, G. 1979. Los murciélagos de Cuba. La Habana: Editorial Academia.

Simmons, N.B. 1998. A reappraisal of interfamilial relationships of bats. *In* T.H. Kunz and P.A. Racey (editors), Bat Biology and Conservation: 3–26. Washington, D.C.: Smithsonian Institution Press.

Simmons, N.B. 2005. Order Chiroptera. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference, 312–529. Baltimore, MD: Johns Hopkins University Press.

Smith, J.D. 1972. Systematics of the chiropteran family Mormoopidae. Miscellaneous Publication, University of Kansas Museum of Natural History 56: 1–132.

Sorba, G.C., A. Horvath, Z. Korsos, R. Vidal-Lopez, and A. Munoz-Alonso. 2004. Results of the collecting trips of the Hungarian Natural History Museum in Chiapas, Mexico, in 2000–2001: Mammalia, Reptilia, Amphibia. Annales Historico-Naturales Musei Nationalis Ungarici 96: 321–334.

Soriano, P., and J. Ochoa G. 1997. Lista actualizada de los mamíferos de Venezuela. *In* E. La Marca (editor), Vertebrados actuales y fósiles de Venezuela, 203–227, Serie Catálogo Zoológico de Venezuela, Fundacite Mérida.

StatSoft, Inc. 1995. STATISTICA (data analysis software system), version 5. Tulsa, OK: StatSoft, Inc.

Stockwell, E.F. 2001. Morphology and flight manoeuvrability in New World leaf-nosed bats (Chiroptera: Phyllostomidae). Journal of Zoology 254: 505–514.

Strait, S.G. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. Journal of Mammalogy 74: 391–402.

Taddei, V.A., and W. Uieda. 2001. Distribution and morphometrics of *Natalus stramineus* from South America (Chiroptera, Natalidae). Iheringia Série Zoologica 91: 123–132.

Taylor, M.L., et al. (1999). Environmental conditions favoring bat infection with *Histoplasma capsulatum* in Mexican shelters. American Journal of Tropical Medicine and Hygiene 61: 914–919.

Tejedor, A. 2005. A new funnel-eared bat (Natalidae: *Natalus*) from Mexico. Journal of Mammalogy 86: 1109–1120.

Tejedor, A. 2006. The type locality of *Natalus stramineus* (Chiroptera: Natalidae): implications for the taxonomy and biogeography of the genus *Natalus*. Acta Chiropterologica 8: 361–380.

Tejedor, A., G. Silva-Taboada, and D. Rodríguez-Hernández. 2004. Discovery of extant *Natalus major* (Chiroptera: Natalidae) in Cuba. Mammalian Biology 69: 153–162.

Tejedor, A., V.daC. Tavares, and D. Rodríguez-Hernandez. 2005a. New records of hot-cave bats from Cuba and the Dominican Republic. Boletín de la Sociedad Venezolana de Espeleología 39: 10–15.

Tejedor, A., V.daC. Tavares, and G. Silva-Taboada. 2005b. A revision of extant Greater Antillean bats of the genus *Natalus* (Chiroptera: Natalidae). American Museum Novitates 3493: 1–22.

Thomas, O. 1910. New mammals from tropical South America. Annals and Magazine of Natural History (8) 7: 513–517.

Timm, R.M., and H.H. Genoways. 2003. Mammals of the Albert Schwartz collection: biological and historical information. Scientific Papers, University of Kansas Natural History Museum 29: 1–47.

Trajano, E., and E.A. Gimenez. 1998. Bat community in a cave from eastern Brazil, including a new record of *Lionycteris* (Phyllostomidae, Glossophaginae). Studies on Neotropical Fauna and Environment 33: 69–75.

Trajano, E., and J.R.A. Moreira. 1991. Estudo da fauna de cavernas da Província Espeleológica Arenítica Altamira-Itaituba, Pará. Revista Brasileira de Biologia 51 (1): 13–29.

Varona, L.S. 1974. Catálogo de los mamíferos vivientes y extinguidos de las Antillas. La Habana: Editorial Academia.

Verrell, P.A. 1992. Primate penile morphologies and social systems: further evidence for an association. Folia Primatologica 59: 114–120.

Villa-R, B. 1966. Los murciélagos de México. México: Universidad Nacional Autónoma de México.

Viña Bayés, N., and D. Deas Díaz. 1970. Estudio meteorológico de la Caverna de los Majáes, Siboney, Caney, Oriente. Academia de Ciencias de Cuba Serie Espeleología y Carsología 24: 1–11.

Wagner, A. 1845. Diagnosen einiger neuen Arten von Nagern und Handflügern. Archiv fur Naturgeshichte München Akademisches 11: 145–149.

Wang, H.G., R.D. Owen, C. Sanchez-Hernandez, and M.de L. Romero-Almaraz. 2003. Ecological characterization of bat species distributions in Michoacan, Mexico, using a geographic information system. Global Ecology and Biogeography 12: 65–85.

Watkins, L.C., J.K. Jones, Jr, and H.H. Genoways. 1972. Bats of Jalisco, Mexico. Special Publications, Museum of Texas Tech University 1: 1–44.

Wilkinson, G.S., and G.F. McCracken. 2003. Bats and balls: sexual selection and sperm competition in the Chiroptera. *In* T.H. Kunz and M.B. Fenton (editors), Bat ecology, 128–155. Chicago: University of Chicago Press.

Willig, M.R. 1983. Composition, microgeographic variation, and sexual dimorphism in Caatingas and Cerrado bat communities from northeast Brazil. Bulletin of Carnegie Museum of Natural History 23: 1–131.

Winge, H. 1893. Jordfundne og nulevende Flagermus (Chiroptera) fra Lagoa Santa, Minas Gerais, Brasilien. Med udsigt over Flagermusenes undbyrdes Slaegstkab. E Museo Lundii 2: 1–92.

Yu, J., and F.S. Dobson. 2000. Seven forms of rarity in mammals. Journal of Biogeography 27: 131–139.

APPENDIX 1

Gazetteer and Specimens Examined

A comprehensive list of localities where Natalidae have been collected or observed is provided below. Localities were obtained from museum catalogs, published sources, and personal communications and observations. Geographic coordinates of localities were obtained from museum catalogs, specimen labels, published sources, and Internet-based geographic databases (Fallingrain, Geonames, Google-Earth). Altitude data was obtained using DIVA-GIS 5.4 (Hijmans et al., 2006). Localities supported by voucher specimens include specimen numbers by species. Species are abbreviated as follows: Cma, *Chilonatalus macer*; Cmi, *Chilonatalus micropus*, Ctu, *Chilonatalus tumidifrons*, Nes, *Natalus espiritosantensis*; Nja, *Natalus jamaicensis*; Nla, *Natalus lanatus*; Nma, *Natalus major*; Nme, *Natalus mexicanus*; Npr, *Natalus primus*; Ntu, *Natalus tumidirostris*; Nst, *Natalus stramineus*; Nyl, *Nyctiellus lepidus*; and Ppr, *Primonatalus prattae*. Localities represented by bone remains only list species abbreviations followed by an asterix [*]. A count of specimens follows the species abbreviation if the species are represented at that locality by voucher specimens other than bone remains only. Localities obtained from the literature include a citation following the species abbreviation. Countries, provinces, and specific localities are listed alphabetically. Locality numbers correspond with locality points shown in the distribution map(s) of each species. Institutional abbreviations (in bold, institutions from which all specimens of Natalidae were directly examined or, marked with an asterix [*], institutions from which a sample of their Natalidae collection was examined through specimen loans): **AMNH** — American Museum of Natural History, New York, USA; **BMNH** — The Natural History Museum (British Museum of Natural History), London, UK; CAS — California Academy of Sciences, San Francisco, USA; CM — Carnegie Museum, Pittsburgh, USA; **CNMA**—Colección Nacional de Mamíferos, Universidad Autónoma de México, Mexico, Mexico; **CRD** — Colección Regional Durango, Instituto Politécnico Nacional Unidad Durango, Durango, Mexico; **CZUFMG**—Zoology collection, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; **DZSJRP** — Department of Zoology, Universidade Estadual Paulista, São José do Rio Preto, Brazil; **EBRG** — Estación Biológica Rancho Grande, Maracay, Venezuela; **FMNH** — Field Museum of Natural History, Chicago, USA; **LACM*** — Los Angeles County Museum, Los Angeles, USA; **KU**, University of Kansas Natural History Museum, Lawrence, Kansas, USA; **MBML** — Museu de Biologia Professor Mello-Leitao; Santa Teresa, Brazil; **MBUCV** — Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela; **MCZ** — Museum of Comparative Zoology, Harvard University, Cambridge, USA; **MFN** — Museum für Naturkunde der Humboldt Universität, Berlin, Germany; **MHNLS** — Museo de Historia Natural La Salle, Fundación La Salle, Caracas, Venezuela; **MNHN** — Museum National d'Histoire Naturelle, Paris, France; **MNHNc** — Museo Nacional de Historia Natural, Havana, Cuba; **MNK** — Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia; **MSB**— Museum of Southwestern Biology, Albuquerque, USA; MVZ — Museum of Vertebrate Zoology, University of California at Berkeley, Berkeley, USA; **MZUSP** — Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; **NNM** — National Museum of Natural History, Leiden, The Netherlands; PSM — James R. Slater Museum, Tacoma, USA; **ROM***—Royal Ontario Museum, Toronto, Canada; SDNHM — San Diego Natural History Museum, San Diego, USA; **TTU (TK)***— Museum of Texas Tech University, Lubbock, USA; UMMZ — University of Michigan Museum of Zoology, Ann Harbor, USA; UCR—Universidad de Costa Rica, San José, Costa Rica; **UF** — Florida Museum of Natural History, Gainesville, Florida, USA; **ULA** — Colección de Zoología, Universidad de los Andes, Mérida, Venezuela; **USNM** — National Museum of Natural History (Smithsonian), Washington DC, USA; UWBM — Burke Museum, University of Washington, Seattle, USA.

ANGUILLA

Anguilla

1. North Side estate (18.2166, −63.0500, 27 m). **Nst** (2): AMNH 72368, 72369.
2. Cave at head of Katouche Bay North Hill Village (18.2000, −63.0666, 8 m) **Nst** (1): USNM 544834.

ANTIGUA AND BARBUDA

Antigua

3. Bat Cave at UHSA St. John's, St. John (17.1166, −61.85, 6 m). **Nst** (S.C. Pedersen, personal commun.).
4. Montpelier Cave, 1.2 Km E, 0.2 Km S, St. Philips (17.0433, −61.7144, 67 m). **Nst** (3): TTU 101719–101721.
5. Christian Valley, St. Paul (17.0333, −61.75, 21 m). **Nst** (S.C. Pedersen, personal commun.).
6. English Harbor, St. Paul (17.0166, −61.7666). **Nst** (4): MCZ 17469–17472.

Barbuda

7. Dark Cave (17.6238, −61.7533, 27 m). **Nst** (12): TTU 101723–101729, 101738–101742.
8. Bryants Cave. **Nst** (S.C. Pedersen, personal commun.).
9. Cave 1. **Nst***: UF 3366, 24019–24023.
10. Cave 2. **Nst***: UF 2812.
11. Indian Cave. **Nst** (S.C. Pedersen, personal commun.).
12. New Cave. **Nst** (S.C. Pedersen, personal commun.).

BELIZE

Cayo District

13. Sibun Camp, Military Bldg along Sibun R (17.0830, −88.6500, 302m). **Nme** (1): FMNH 58480.
14. Augustine (16.9666, −88.9833, 483 m). **Nme** (10): Cm 91907–91916.

15. Las Cuevas Research Station Belmopan (16.7333, −88.9833, 592 m). **Nme** (1): BMNH 2003.201.
16. Cebada Cave (16.6515, −89.1639, 490 m). **Nme*** (Czaplewski et al., 2003).

Orange Walk District*

17. Richmond Hill, 8.9 Km SSW Orange Walk Town (18.0666, −88.5500, 8 m). **Nme** (1): CM 91917.

Stann Creek

18. Kendal at Sittee River, Dunker Ranch (16.8000, −88.3670, 30 m). **Nme** (1): FMNH 58479.
19. Cockscomb Basin (16.7666, −88.6166, 305 m). **Nme** (2): USNM 583063, 583064.

Toledo District

20. 1.2 Km E Aguacate Village (16.1622, −89.0938, 53 m). **Nme** (4): CM 90567–90569.
21. Blue Creek Village, 1 Km upstream From Village (16.1977, −89.0422, 40 m). **Nme** (1): MSB 53573.
22. Cave, S Cerro Hill, Vista Hermosa Ranch, Carib (16.1166, −88.7833, 16 m). **Nme** (14): FMNH 121072–12085.

BOLIVIA
Santa Cruz

23. Flor de Oro, (−13.5508, −61.0600, 179 m). **Nes** (1): MNK 1927 (male).
24. Los Fierros, (−14.5861, −60.9200, 199 m). **Nes** (1): MNK 3199 (male).
25. Cueva Concesión Minera Don Mario, San Juán de Chiquitos (−17.3386, −59.7000, 337m). **Nes** (5): MNK 2070–2074.
26. Cave, Santiago de Chiquitos (−18.3441, −59.5500, 847 m). **Nes** (2): A.Vargas collection numbers *Natalus* 1–2.
27. Cueva Concepcioncita, Motacucito, Puerto Suárez (−19.0171, −57.8700, 199 m). **Nes** (1): SJRP 14507.

BRAZIL
Bahia

28. Toca da Boa Vista, Laje dos Negros, Campo Formoso (−10.1625, −40.8600, 554 m). **Nes*** (2): MCL 10201, 10237.
29. Poço Encantado, Itaetê. MZUSP (−12.9447, −41.11, 385 m). **Nes** (14): MZUSP 29054–29066, 29499.
30. Gruta Toca dos Morcegos (−15.4500, −39.6500, 209 m). **Nes** (1): MBML 1965.
31. Gruta California, Pau Brasil (−15.45 −39.65, 209 m). **Nes** (R. Lopes Ferreira, personal commun.).

Ceará

32. 9 Km S Crato, Floresta Nacional Araripe (−7.2288, −39.3800, 419 m). **Nes** (1): CM 100753.
33. Chapada do Araripe, Crato (−7.2288, −39.3800, 419 m). **Nes** (Willig, 1983).
34. Floresta Nacional Araripe, Crato (−7.2288, −39.38, 419 m). **Nes** (1): USNM 555711.
35. Barbalha, Serra do Araripe, Arajara (−7.3166, −39.2800, 456 m) **Nes** (1): USNM 536442.

Distrito Federal

36. Gruta da Saúva, Sobradinho (−15.6333, −47.8300, 1079 m). **Nes** (Tadei and Uieda, 2001).

Espirito Santo

37. "Gruta do rio Itaúnas," Itaúnas, Conceição da Barra (−18.4222, −39.71, 3 m). **Nes** (3): MBML 1801 (holotype), 1802, 1803.

Goiás

38. Fazenda São Domingos. **Nes** (1): UNB1022
39. Fazenda Pé da Serra. **Nes** (1): UNB 921
40. Serra da Mesa. **Nes*** (Fracasso and Salles, 2005).
41. Colinas do Sul (−14.1494, −48.08, 526 m). **Nes** (Taddei and Uieda, 2001).
42. Gruta de Porcos, Mambaí (−14.4930, −46.11, 727 m). **Nes** (1): CZUFMG *Natalus* 1.
43. Lapa do Fuzil, Goianésia (−15.3269, −49.12, 647 m). **Nes** (Taddei and Uieda, 2001).
44. Padre Bernardo (−15.3333, −48.5677, 666 m). **Nes** (Taddei and Uieda, 2001).

Mato Grosso

45. Aripuanã (−9.1833, −60.6333, 143 m). **Nes** (Mok et al., 1982).

Mato Grosso do Sul

46. Rio Verde de Mato Grosso (−18.9166, −54.8333, 327 m). **Nes** (5): SJRP 16748–16752.
47. Paranaíba (=Paraíso) (−19.05, −52.9666, 612 m). **Nes** (24): SJRP 12116–12118, 12120, 12122, 12124, 12125, 12127–12129, 12249, 12251, 12252, 12254–12257, 12261, 12263–12266, 12268, 12269.

Minas Gerais

48. Caverna Olhos D'Agua, Itacarambí (−15.1127, −44.1691, 515 m). **Nes** (Trajano, 1998).
59. Furna Misteriosa, Sete Lagoas (−19.0925, −44.3497, 859 m). **Nes** (E.C. Moreira, personal commun.).
50. Lagoa Santa (−19.6333, −43.8833, 801 m). **Nes*** (Winge, 1893).

Pará

51. Medicilândia (−3.446, −52.889, 105 m). **Nes** (Taddei and Uieda, 2001).
52. Caverna do Tatajuba, Altamira, 17 km S by road (−3.3344, −52.2802, 158 m). **Nes** (1): USNM 549504.
53. Caverna Planaltina (−3.3750, −52.5717, 230 m). **Nes** (Trajano and Moreira, 1989).
54. Caverna do Limoeiro (−3.5388, −52.7853, 224 m). **Nes** (Trajano and Moreira, 1989).
55. Cachoeira Espelho, Rio Xingú (−3.65, −52.3833, 108 m). **Nes** (1): MZUSP 21360.

Piauí

56. São João do Piauí (−8.3333, −45.25, 508 m). **Nes** (Taddei and Uieda, 2001).

Rio Grande do Norte

57. Natal (−5.7833, −35.2166, 5 m). **Nes** (4): USNM 245517, 242828–242830.

São Paulo

58. Caverna Gurutuva, Iporanga (−24.5333, −48.65, 546 m). **Nes** (1): MZUSP 12073.
59. Caverna Santana, Iporanga (−24.5333, −48.7, 472 m). **Nes** (1): MZUSP 13228.

CAYMAN ISLANDS

Grand Cayman

60. Dolphin Cave (19.3516, −81.1263, 7 m). **Npr***: UF (Morgan, 1994).
61. Bodden Cave, Bodden Town (19.2787, −81.2664, 6 m). **Npr***: UF (Morgan, 1994). **Cma***: UF (Morgan, 1994)

COLOMBIA

Bolívar

62. Cartagena (10.3997, −75.5144, 34 m). **Ntu** (1): USNM.

Isla Providencia

63. Unspecified (13.352, −81.3698). **Cmi** (56): AMNH 1647; FMNH 15087, 15088; USNM 15804–15805, 15807–15823, 15825–15827, 15829–15858, 15860. **Nme** (1): MCZ 28203.

Isla San Andrés

64. Cave near South end (12.4824, −81.7303, m). **Cmi** (6): LACM 38872–38877. **Nme** (22): LACM 038850–038871.
65. Room and Hall Cave, May's Cliff. **Nme** (7): LACM 028872–028878.

Santander

66. Cueva del Nitro, N San Gil (9.4536, −75.4428, 55 m). **Ntu** (2): AMNH 183854, 183855.
67. Macaregua Cave, 14 Km N of Sangil (6.6742, −73.1778, 1462 m). **Ntu** (178): FMNH 72125–72129, 72290–72296; KU 125086–125091 ROM 53688–53697, 69654–69698, 43988; MBUCV 2335–2345, 1865–1869, USNM 433370–433375, 445849–445928, 588322, 588323.
68. North of San Gil. **Ntu** (15): ROM 45532, 45104–45108, 45231–45237; FMNH 65637, 65638.

Sucre

69. Tolu Viejo (9.453611, −75.44278, 55 m). **Ntu** (5): ROM 45238–45242.

COSTA RICA

Alajuela

70. Monteverde (10.3, −84.8, 1517 m). **Nla** (LaVal and Lewis, 1988).

Cartago

71. Río Macho (9.7667, −83.85, 1306 m). **Nla** (Riba-Hernández, 1996).

Guanacaste

72. Santa Rosa National Park (10.7863, −85.6047, 205 m). **Nme** (2): USNM 563306, UCR 1851.
73. Palo Verde (= 2 Km S, 12 Km E Bolsón), 6 M (10.3444, −85.3383, 7 M). **Nme** (11): KU 158310; USNM 506598, 563306; MMNH 14103, UCR 1961, 1995; MNCR 186, 736–739.
74. Mina Tres Hermanos, Cueva Calcárea, Abangares, (10.3, −84.96, 317 m). **Nme** (1): CNMA 5124.
75. Hacienda Solimar, Abangares, (10.275, −85.1333, 12 m). **Nme** (1): UCR 1989.
76. Curiol de Santa Rosa = Curiol (10.2333, −85.5, 340 m). **Nme** (3): LACM 024742, 024759, 024760.
77. Cueva La Trampa, Parque Nacional Barra Honda (10.15, −85.3667, 103 m). **Nme** (1): USNM 543423.
78. Cueva Nicoa, Parque Nacional Barra Honda (10.15, −85.3667, 103 m). **Nme** (5): USNM 543420–543422, UCR 885.

Puntarenas

79. Cuenca Río Savegre. **Nla** (Rodríguez-Herrera, 2004).

CUBA

Camagüey

80. Cueva de los Portales de Pinto, Jaronú (21.8, −77.95, 23 m). **Npr*** (Koopman and Ruibal, 1955).
81. Cueva del Jaguey, Cerro Limones (21.6130, −77.8269, 212 m). **Nyl** (Silva-Taboada, 1979).
82. Cueva Bonita, Cairije (21.6, −77.6666, 35 m). **Nyl** (30): IES 1.3303–1.3332.
83. Cueva de la Tripa, Cairije (21.6, −77.6666, 35 m). **Nyl** (15): IES 1.3359–1.3273.
84. Cueva del Círculo, Cairije (21.6, −77.6666, 35 m). **Npr*** (Silva-Taboada, 1979). **Nyl*** (Silva-Taboada, 1979).
85. Cueva Pichardo, Cerro Tuabaquey (21.5988, −77.7983, 135 m). **Cma** (Silva-Taboada, 1979).
86. Cueva Bonita, Sierra de Cubitas, **Nyl** (6): ROM 63176–63181.

Ciego de Ávila

87. Cuevas de Boquerones, Mabuya, Moron (22.1975, −78.9775, 51 m). **Nyl** (Silva-Taboada, 1979).

Cienfuegos

88. Cueva de la Macha, Soledad (22.1166, −80.3166, 59 m). **Npr*** (Goodwin, 1959).
89. Cueva de la Luz, Juraguá (22.0988, −80.5563, 14 m). **Nyl** (Silva-Taboada, 1979).
90. Punta de San Juan, San Juan, (21.9202, −80.2683, 21 m). **Nyl** (Silva-Taboada, 1979).
91. Gruta de Yaguanabo, Yaguanabo (21.89194, −80.195, 92 m). **Nyl**(3): IES 1.3419, 1.3420, 1.3235.

Ciudad de La Habana

92. Cueva de Doña Juana (no longer existing), Almendares (23.09, −82.4827, 5 m). **Nyl** (28): AMNH 61169–61190; MCZ 17493–17498.
93. La Habana (23.11444, −82.41167, 35 m). **Nyl**(9): FMNH 34057; MCZ 17127, 17129–17134; USNM 300528.

Granma

94. Entre rocas grandes, Cabo Cruz (19.85, −77.73333, 4 m). **Nyl** (Gundlach, 1866).
95. Faro de Cabo Cruz, Cabo Cruz (19.85, −77.73333, 4 m). **Nyl** (1): MCZ 12544; (Barbour, 1945).

Guantánamo

96. Baracoa, Baracoa (20.35, −74.5, 14 m). **Cma** (3): AMNH 61191; MCZ 11667, 16662.
97. Cueva de La Majana, Güiniao (20.3166, −74.4333, 53 m). **Cma** (2): AMNH 42710; USNM 113724 (holotype).
98. Cueva de La Patana, Maisí (20.24944, −74.15, 12 m). **Cma** (3): IES 1.3156–1.3158.

99. Cave above power plant at Guaso, Guaso (20.2316, −75.1683, 117 m). **Cma** (6): USNM 300522–300527; (Silva-Taboada, 1979).
100. El Yarey, Río Seco, Yateras (20.1652, −75.1080, 59 m). **Cma** (1): USNM 300521 female.
101. Guantánamo (20.1452, −75.2061, 51 m). **Cma** (Silva-Taboada, 1979).

Holguín

102. Gibara, Gibara (21.10972, −76.13167, 7 m). **Nyl** (Silva-Taboada, 1979).
103. Cueva del Hoyito, Cuatrocientas Rosas, Mulas, Banes (20.91667, −75.8, 28 m). **Nyl** (Silva-Taboada, 1979).

Isla de la Juventud

104. Nueva Gerona (21.8833, −82.8, 14 m). **Nyl** (1): USNM 103898.
105. Cueva de la Cantera, Sierra de Colombo, Sierra de Caballos (21.8727, −82.7766, 39 m). **Nyl** (5): IES 1.3369–1.3374.
106. Cueva de los Lagos, Sierra de Caballos (21.8727, −82.7766, 39 m). **Nyl** (34): AMNH 186982, 186983; FMNH 93686, 93687; IES 1.3376–1.3385, 1.3244–1.3263.
107. Cueva del Abuelo, Sierra de Caballos (21.8666, −82.7666, 17 m). **Npr*** (Silva-Taboada, 1979).
108. Cueva del Agua, Sierra de Casas (21.8580, −82.8211, 96 m). **Nyl** (Silva-Taboada, 1979).
109. Eastern base of Sierra de Casas, Sierra de Casas (21.8580, −82.8211, 96 m). **Nyl** (8): KU 150708–150711, 151181–151184.
110. Gruta Grande de Santa Isabel, Santa Fe. (21.7422, −82.755, 27 m). **Nyl** (Silva-Taboada, 1979).
111. Cueva de la Casimba, Punta del Este (21.5625, −82.5586, 16 m). **Nyl** (1): IES 1.3375; **Cma** (5): IES 1.3182–1.3186.
112. Cueva del Promontorio = Cueva de Cayamas, Punta del Este (21.5625, −82.55861, 16 m). **Cma** (25): ROM 38800–38805; IES 1.3187–1.3203, 1.3205, 1.3206.
113. Cueva No. 2 de Punta del Este, Punta del Este, (21.5625, −82.5586, 16 m). **Cma** (27): IES 1.3129–1.3155.
114. Furnia de Punta del Este, Punta del Este (21.5625, −82.55861, 16 m). **Nyl** (Silva-Taboada, 1979).
115. Cueva de Los Murciélagos, Punta Pedernales (21.5783, −83.1697, 16 m). **Cma** (8): IES1.3208–1.3215.
116. Cueva de Punta Brava, Punta Brava, (21.5258, −82.6044, 12 m). **Cma** (8): AMNH 186978–186981; FMNH 93682–93685.

La Habana

117. Cueva del Jaguey, Boca de Jaruco (23.1752, −82.0111, 8 m). **Nyl** (Silva-Taboada, 1979).
118. Cueva del Majá, Santa Cruz del Norte (23.1752, −82.0111, 8 m). **Cma** (Silva-Taboada, 1979).
119. Cueva del Indio, La Jaula (23.01667, −82.08333, 233 m). **Nyl** (2): IES 1.3416, 1.3417. **Cma** (1): IES 1.3161.
120. Camoa, Jamaica (22.97917, −82.17028, 134 m). **Cma** (Silva-Taboada 1979).
121. Cueva de Cotilla, Cotilla, San José de las Lajas (22.96139, −82.15111, 138 m). **Nyl** (8): IES 1.3350–1.3357.
122. Cueva de William Palmer, San José, Guanajay (22.95, −82.68333, 124 m). **Nyl** (54): KU 151185–151193, 152351–152356; ROM 38806–38811, 78779, 78780; IES 1.3387, 1.3388, 1.3274, 1.3275–1.3302. **Cma** (3): IES 1.3160, 1.3204, 1.3178.
123. Cueva del Mudo, Cuarto, Catalina de Güines (22.92694, −81.97722, 89 m). **Nyl** (Silva-Taboada, 1979).
124. Cuevas Blancas, Aguacate, Quivicán (22.885, −82.32111, 126 m). **Npr*** (Jiménez et al., 2006).
125. Ceiba del Agua (22.87722, −82.64139, 89 m). **Cma** (1): AMNH 176161.
126. Cueva del Túnel, Yarey, La Salud (22.87139, −82.42389, 62 m). **Nyl*** (Silva-Taboada, 1979).
127. Finca Aston, Cañas (22.80694, −82.70944, 36 m). **Cma** (1): IES 1.3207.
128. Cueva de Paredones. **Cma** (Silva-Taboada, 1979).
129. Cueva de Sandoval. **Cma** (1): IES 1.781.
130. Güines (22.83611, −82.02805, 66 m). **Nyl** (Silva-Taboada, 1979).
131. Cueva San Javier. **Nyl** (2): USNM 300529, 300530.

Matanzas

132. Varadero (23.1536, −81.2513, 2 m). **Nyl** (Silva-Taboada, 1979).
133. Camarioca (23.0608, −81.3569, 38 m). **Nyl** (Silva-Taboada, 1979).
134. Cueva de Pluma, Seboruco, Corral Nuevo (23.0588, −81.6738, 63 m). **Nyl** (Silva-Taboada, 1979).
135. Cueva del Palenque (23.0188, −81.7163, 113 m). **Nyl** (Silva-Taboada, 1979); **Npr*** (J. Orihuela, personal commun.).
136. Cueva de la Eloísa, Bellamar (23.01667, −81.55, 55 m). **Npr*** (Silva-Taboada, 1979). **Nyl*** (Silva-Taboada, 1979).
137. Cueva del Gato, Bellamar (23.01667, −81.55, 55 m). **Npr*** (J. Orihuela, personal commun.).
138. Cueva de Santa Catalina, Camarioca. **Nyl** (1): IES 1.3386. **Cma** (1): CNMA 39848.

Pinar del Río

139. Cueva de Los Majáes, Galalón (22.6922, −83.47, 153 m). **Cma** (Tejedor et al., 2006).
140. Cueva del Indio, Viñales (22.6694, −83.7075, 153 m). **Cma** (5): AMNH 176160; KU 152357–152360.
141. Valle de Pica Pica, Sumidero (22.41583, −83.92667, 116 m). **Cma** (Silva-Taboada, 1979).
142. Cueva del Calabazar, Vallecito (21.94528, −84.33194, 8 m). **Nyl** (Tejedor et al., 2005a). **Cma** (Tejedor et al., 2005a).
143. El Veral (40 Km W of El Cayuco), Guanahacabibes (21.9419, −84.5583, 23 m). **Nyl** (2): KU 150712; IES 1.793. **Cma** (1): IES 1.4877.
144. Cueva del Chelao, Leña, Consolación. **Nyl** (Silva-Taboada, 1979).
145. Cueva La Barca, Guanahacabibes (21.8694, −84.7622, 16 m). **Cma** (Tejedor et al., 2005a). **Npr** (58): MNHN 1–51 G. Silva-Taboada filed

numbers; UF 26810 (female); IES 1.5557–1.5559, 1.5582–1.5584.
146. Unspecified locality. **Cma** (1): MCZ 11646.

Sancti Spíritus

147. Cueva de Colón, Cayo Caguanes (22.3902, −79.1230, 5 m). **Nyl** (2): IES 1.3389, 1.3418.
148. Cueva de Humboldt, Cayo Caguanes (22.3902, −79.1230, 5 m). **Nyl** (Silva-Taboada, 1979).
149. Cueva de las Tres Dolinas, Cayo Caguanes (22.3902, −79.1230, 5 m). **Nyl** (112): IES 1.3390–1.3415, 1.3421–1.3487, 1.3216–1.3234.
150. Cueva de Ramos, Cayo Caguanes (22.3902, −79.1230, 5 m). **Nyl** (Silva-Taboada, 1979).
151. Cueva Grande de Caguanes, Cayo Caguanes (22.39028, −79.12306, 5 m). **Nyl** (1): IES 1.3358.
152. Cueva Sandalio Noda, Cayo Caguanes (22.39028, −79.12306, 5 m). **Nyl** (Silva-Taboada, 1979).
153. Lomas de Judas, Yaguajay (22.1, −78.45, 211 m). **Npr*** (Silva-Taboada, 1979).
154. Cueva de los Masones, Trinidad (21.8, −79.9833, 51 m). **Nyl** (25): IES 1.3236–1.3243, 1.3333–1.3349. **Cma** (Silva-Taboada, 1979). **Npr***: ROM 59133–59135; (Silva-Taboada 1974).
155. Cueva del Jagüey, Trinidad (21.8, −79.9833, 51 m). **Nyl** (Silva-Taboada, 1979). **Cma** (Silva-Taboada, 1979). **Npr*** (Silva-Taboada, 1979).
156. Sierra de Jatibonico. **Nyl** (1): AMNH 32685.
157. Cueva de Guanayara, Guanayara (21.8142, −80.0736, 422 m). **Nyl** (Silva-Taboada, 1979).

Santiago de Cuba

158. Santiago de Cuba (21.02472, −75.82194, 227 m). **Cma** (19): IES 1.3159, 1.3162–1.3177, 1.3179, 1.3180.
159. Cueva del Tesoro, Mar Verde (19.9675, −75.9363, 18 m). **Cma** (1): IES 1.3181.
160. Cueva de la Cantera, Siboney (19.95, −75.7). **Cma** (Silva-Taboada, 1979). **Npr*** (Silva-Taboada, 1979).
161. Cueva de Los Majáes, Siboney (19.95, −75.7). **Cma** (Silva-Taboada, 1979).
162. Cueva de Los Indios, Daiquirí (19.91667, −75.65). **Npr***: AMNH 41009 (holotype).

Villa Clara

163. Gavilán, Santa Clara (22.4, −79.9666, 133 m). **Nyl** (2): UMMZ 105766, 105767.

DOMINICA

St. George

164. Trafalgar Falls (in mistnet) (15.3166, −61.35, 225 m). **Nst** (11): KU 104920–104930.
165. 6 Miles NE Roseau (15.3, −61.3833, 73 m). **Nst** (1): KU 150726.
166. Roseau (15.3, −61.4). **Nst** (21): USNM 62850, 113185, 113596–113604, 113605 (holotype), 113606–113614.

St. John

167. 0.5 mi N Toucari (15.6166, −61.4666, 2 m). **Nst** (25): TTU 31457–31481.
168. Tanetane (Cave above Douglas Bay, and brick tunnel (15.6, −61.4666). **Nst** (10): USNM 361906–361910, 362100–362104.

St. Patrick

169. Berekua (15.2333, −61.3166, 164 m). **Nst** (1): ROM 69411.
170. Corona = Mourne Couronne (15.3966, −61.3694, 465 m). **Nst** (1): AMNH 237393.

St. Paul

171. Sylvania (15.3666, −61.3666, 473 m). **Nst** (1): AMNH 237394.
172. Springfield (15.35, −61.36667, 400 m). **Nst** (1): TTU 31486.
173. Massacre sea cave (15.33333, −61.4, 7 m). **Nst** (3): CM 111878–111880.

St. Peter

174. Cave below highway, 1.1 km S Colihaut (15.4854, −61.4619, 12 m). **Nst** (1): CM 112376.
175. Unspecified locality. **Nst** (1): MCZ 17781.

DOMINICAN REPUBLIC

Barahona

176. Cabral, 3 mi S of (18.2097, −71.2425, 172 m). **Cmi** (1): PSM 11566.
177. Cueva Los Patos No. 1 and No. 2, Los patos (17.9666, −71.1666, 9 m). **Cmi** (39): AMNH (AT 158, male); PSM 25873, 11063, 11562–11565, 11567–11597, 14736. **Nma** (8): AMNH 97590, AT 149 (field number); PSM 11045, 11551–11555.
178. Maniel Viejo (17.9666, −71.3166, 278 m). **Nma** (1): AMNH 97589.
179. Oviedo (17.80111, −71.40167, 37 m). **Nma** (1): MCZ 50055.

Distrito Nacional

180. Santo Domingo (Ciudad Trujillo) (18.4666, −69.9, 16 m). **Nma** (3): UF 5517; MCZ 20659, 50055.

Elías Piña

181. Nalga de Maco (19.2055, −71.4444, 820 m). **Nma** (K. Christenson, personal commun.).
182. Cerro de San Francisco, Bánica (19.0666, −71.7, 282 m). **Nma***: UF (without number); (Morgan, 2001).
183. Rancho La Guardia, Hondo Valle (18.7166, −71.6666, 1020 m). **Nma** (4): MCZ 52462–52465.

Hato Mayor

184. Cueva Vangel (19.0851, −69.5766). **Nma** (3): AMNH (AT 172, 173, 176)..
185. Cueva de Cristian (19.0333, −69.4481, 92 m). **Nma** (2): AMNH (AT 181, 182).
186. Cueva de Johnny (19.0881, −69.5, −4 m). **Nma** (1): AMNH (AT 177).

Independencia

187. Puerto Escondido, 9.9 km S (north slope Sierra de Bahoruco) (18.3166, −71.5666, 414 m). **Nma** (1): USNM 542274.

La Altagracia

188. Las Lagunas de Nisibón (18.85, −68.6666, 38 m). **Nma** (4): PSM 11539–11541, 12624.
189. Boca de Yuma (18.3833, −68.6, 3 m). **Nma** (N. García Marcano, personal commun.).

María Trinidad Sánchez

190. Cueva de Murciélagos (= Cueva de Chelo), La Entrada (19.55, −69.9 m). **Nma** (18): AMNH 238148, 238149, 275480, 275481, 275485, 275487, 275488); PSM 11061, 11062, 11542–11550.

Montecristi

191. Pepillo Salcedo, 5 km SE (19.7, −71.75, 15 m). **Nma** (9): KU 150713–150720, 152361.

Samaná

192. Cueva de Morón (19.3138, −69.4230, 7 m). **Nma**.
193. El Limón (19.2833, −69.4333, 45 m). **Nma** (5): PSM 11526–11530.
194. Cueva de la Laguna Juan García (19.25, −69.45, 237 m). **Nma** (2): AMNH (AT 186, 187).
195. Samaná (19.21667, −69.31667, 156 m). **Cmi** (6): PSM 11598–11599, 12356–12359. **Nma** (9): PSM 11525, 11531–11538.
196. Cueva Vicente. **Cmi** (4): AMNH 216125–216128.
197. Arroyo Chico (19.25, −69.48333, 232 m). **Cmi** (1): AMNH (AT 188, female).
198. Sánchez (Moja Farm), 2 Miles NW of (19.21667, −69.6). **Nma** (1): USNM, 1.

Sánchez Ramírez

199. Cueva Grande de Julián, Don Miguel, 4 km E Platanal (19.1166, −70.0833, 86 m). **Nma** (1): AMNH 275506.
200. Don Miguel, Don Miguel, 4 km E Platanal (19.1423, −70.0643, 28 m). **Nma** (1): AMNH 275513

San Juán

201. San Juan de la Maguana (18.8, −71.23333, 403 m). **Nma** (4): PSM 11558–11561.

Santiago

202. Savaneta (19.6666, −70.3666, 10 m). **Nma** (2): USNM 101395 (holotype), 101396 (paratype).
203. Monción (19.4166, −71.1666, 344 m). **Nma** (22): PSM 11041–11060, 11556, 11557.

Santo Domingo

204. Cave, Guayacanes (18.41667, −69.5, 13 m). **Nma** (K. Christenson, personal commun.).
205. Unknown locality. **Nma** (2): USNM 49362, 96496.

EL SALVADOR
La Libertad

206. Cueva hedionda. **Nme** (Mitchell, 1965).
207. Hacienda San Diego. **Nme** (Mitchell, 1965).

La Unión

208. Tabanco. **Nme** (3): MVZ 130969–130971.

Morazán

209. Monte Cristo Mine, 1.5 mi W Divisadero, (13.6, −88.05, 204 m). **Nme** (3): MVZ 130972–130974.
210. Encuentros Mine, 3 mi W Divisadero, (13.6, −88.05, 204 m). **Nme** (2): MVZ 130975; ROM 37227.
211. Hacienda Santa Rosa. **Nme** (Mitchell, 1965).

San Miguel

212. Potosí Mine, Comacarán (13.5333, −88.0666, 182 m). **Nme** (11): MVZ 130976–130986.

Santa Ana

213. Cueva de los Ombrinos, Metapan (14.3333, −89.45, 480 m). **Nme** (Mitchell, 1965)
214. El Marne, 8 Km S of Santa Ana (13.9941, −89.5597, 645 m). **Nme** (2): MZUSP 15251–15252; ROM 37226, 37228.

FRENCH GUIANA

215. Roura (4.7305, −52.3306, 17 m). **Ntu** (Charles-Dominique et al., 2001)
216. Patawa (4.552, −52.151, 279 m). **Ntu** (B. Keeley, personal commun.)

GUADELOUPE
Grande Terre

217. Le Moule (16.3333, −61.3333, 22 m). **Nst** (2): KU 150727; SCFF 2.

Marie Galante

218. Morne Ducos, 1.5 km NE jct. rt D203 Grand Bourg along rt N9 50 m (15.926, −61.263, 117 m). **Nst** (1): CM 112377.

GUATEMALA
Alta Verapaz

219. Lanquín, Cave of Lanquín (15.5666, −89.9666, 493 m). **Nme** (63): FMNH 64730; KU 64926–64987.

El Progreso

220. Rio Uyus, San Cristóbal Acasaguastlán (14.9166, −89.8833, 241 m). **Nme** (1): ROM 99652.
221. Guastatoya, El Progreso (14.85, −90.05, 1009 m). **Nme** (6): AMNH 68583–68588.

Izabal

222. Puerto Barrios, 22 km S S W (15.7166, −88.6, 8 m). **Nme** (3): FMNH 143423, 143424; USNM 546495.
223. Gruta Silvino, 2 km ENE Navajoa (15.5486, −88.9094, 42 m). **Nme** (14): FMNH 104883–104891; KU 83609–83612; MCZ 58477.
224. Near Livingston (15.82722, −88.74722). **Nme** (1): MCZ 56747.
225. Cueva, Cascada de Agua Caliente (15.5905, −89.2097, 15 m). **Nme** (A. Tejedor, field notes).
226. Quiriguá (15.2666, −89.0833, 94 m). **Nme** (1): USNM 174952.

Petén

227. Tikal National Park (17.25, −89.65, 279 m). **Nme** (1): FMNH 1212086.
228. 4 mi W Flores, Santa Elena Jobitzinal Cave (16.93694, −89.94639, 117 m). **Nme** (18): FMNH 64808–64822, 64648, 64649, 51076.
229. Cave, 2 mi S Flores, Flores (16.9167, −89.8833, 122 m). **Nme** (60): MVZ 106200, 106201; AMNH 144712–144715, 144762; USNM 245155–245208.

Zacapa

230. Sierra de Las Minas, Río Teculután, Santa Clara (14.9833, −89.7166, 219 m). **Nme** (83): FMNH 64489–64494, 64731–64807.

GUYANA

Upper Takutu-Upper Essequibo

231. Warimure, Quash Wau, Weri More, 12 mi NE of Dadanawa (2.9333, −59.4833, 112 m). **Ntu** (1): Rom 52161.
232. Ruawau River, Raa Wau, 35 mi W of Dadanawa (2.755, −59.991, 100 m). **Ntu** (2): Rom 53766, 53767.
233. Ruawau River, Takatu River Area, 40 mi SW of Dadanawa (2.347, −59.855, 126 m). **Ntu** (1): Rom 58840.

HAITI

Departement du L'Ouest

234. Port-au-Prince (18.5667, −72.2833, 46 m). **Nma** (Sanborn, 1941).

Departement du Sud

235. Camp Perrin, Les Cayes (18.3167, −73.8667, 202). **Nma** (1): KU 150721.

HONDURAS

Francisco Morazán

236. Parque Nacional La Tigra, 15 km NE Tegucigalpa (14.097, −87.011, 950 m). **Nme** (1): TTU 83664.

Santa Bárbara

237. 12 Km N Santa Bárbara (14.9166, −88.2333, 287 m). **Nme** (1): Ttu 13418.

JAMAICA

Clarendon Parish

238. North Kellits (18.15, −77.2333, 402 m).
239. Jackson's Bay (17.7333, −77.2333, 1m). **Cmi** (2): ROM 37166, 37165.

Hanover Parish

240. Lucea (18.45, −78.1667, 9 m). **Cmi** (1): AMNH 12393.

Saint Ann Parish

241. Moneague (18.2667, −77.1167, 340 m). **Cmi** (1): USNM 251605

St. Elizabeth Parish

242. Oxford Cave, Auchtembeddie (18.2333, −77.65, 342 m). **Cmi** (3): AMNH 45194–45196.
243. Wallingford Cave, Balaclava (18.18361, −77.64331, 293 m). **Nja***: AMNH 147208.

Trelawny parish

244. Mahogany Hall Cave (18.38333, −77.46667, 399 m). **Cmi** (Genoways et al., 2005).
245. Windsor Cave (18.3513, −77.6474, 104 m). **Cmi** (34): FMNH 44215–44217; USNM 256321–256342, 256414–256417; TTU 22065.

Clarendon Parish

246. Portland Cave, Portland Cottage (17.7667, −77.2333, 1 m). **Nja** (Fincham 1997; disputed observation, see Dávalos and Eriksson, 2003).

Portland Parish

247. Port Antonio (18.1833, −76.4667, 8 m). **Cmi** (5): USNM 113916–113920.
248. Paradise (in house) (18.1667, −76.65, 292 m). **Cmi** (1): UF 14060.

Saint Andrew

249. Kingston (18, −76.78333, 78 m). **Cmi** (1): BMNH (holotype).

St. Catherine Parish

250. St. Clair Cave, Linstead (18.1167, −77.0167, 97 m). **Cmi** (203): AMNH 214132, 246129, 2715577–2715579, 274630, 274631; CM 44570–44602; UF 13696–13701, 14060, 19076; LACM 15696–15697; MCZ 49306–49311; ROM 37030–37034, 37036–37064, 37153–37159, 89700, 89716–89719, 89961–89964; TTU 21977–22064, 47809. **Nja** (78): AMNH 181999, 182000 (holotype), 214131, 246123, 246126–246128, 271575, 271576; BMNH 65.4000a, 65.4000b; UF 13688–13692; FMNH 93784; JI No. 3, JI No. 4, (Goodwin, 1959); ROM 37029, 37065–37076; MCZ 49298–49304; MVZ 167948; TTU 29110–29127, 21946–21976.
251. Bog Walk (18.1, −77.0167, 348 m). **Cmi** (1): FMNH 46423.

James Parish

252. Montego Bay (18.4667, −77.9167,5 m). **Cmi** (1): USNM 172427.

Westmoreland Parish

253. Monarva Cave, Revival (18.2167, −78.2833). **Cmi** (observation) (McFarlane, 1997).
254. Unknown locality. **Cmi** (Genoways et al., 2005).

MARTINIQUE

Le Marin

255. Usine Petit Bourg (14.5333, −60.9667, 9 m). **Nst** (Genoways et al., 2001).

MEXICO

Baja California del Sur

256. Las Cruces (24.2031, −110.0908, 33 m). **Nme** (1): MSB 43837.
257. San Antonio, 2.5 Km N (23.8, −110.0167, 354 m). **Nme** (7): CNMA 4540, 9852; KU 94184, 94186–94189.
258. El Triunfo (includes Mina El Triunfito) (23.78, −110.12, 470 m). **Nme** (22): CNMA 27929, 14604–14612; TTU 47449; LACM 058425–058433, ROM 68179–68180.
259. El Carrizal, San Fernando (23.76, −110.31, 174 m). **Nme** (4): CNMA 25541–25544.
260. Las Cuevas (23.5333, −109.6833, 75 m). **Nme** (8): KU 27315–27320, 94190, 94191.
261. Cueva de los Mártires (23.5, −109.6, 113 m). **Nme** (1): CNMA 18016.

262. Santiago (23.46, −109.71, 144 m). **Nme** (5): CNMA 18008–18011; USNM 525291.
263. Tunel de Agua Caliente (23.4, −109.78, 256 m). **Nme** (3): CNMA 18012–18014.
264. La Mina camino a Miraflores (23.35, −109.75, 177 m). **Nme** (1): CNMA 18015.
265. 5 Km SE, Pescadero, ?, (23.3333, −110.15, 57 m). **Nme** (67): CNMA 25545, 25546; KU 94193–94256 (94210–94212, 94217, 94226, 94228, 94230, 94232, 94236, 94237, 94239, 94241, 94250–94252; 6 females, 9 males); USNM 528710.
266. Santa Anita (23.1333, −109.7167, 86 m). **Nme** (14): USNM 148460–148471, 96495, 96496 (holotype).
267. San José del Cabo (23.05, −109.6833). **Nme** (4): USNM 76508–76511.

Campeche

268. Champotón, 46 km S of (19.35, −90.71667, 4 m). **Nme** (3): KU 93531–93532.
269. 18 Km S of X-Kanha (19.1, −89.33, 142 m). **Nme** (1): ROM 97003.
271. 44 Km S of Constitución, 70 Km E of Escárcega (18.6, −90.74, 81 m). **Nme** (1): ROM 95708.
272. La Tuxpeña (18.4333, −90.0667, 183 m). **Nme** (3): USNM 170848–170850.
273. Zona Arqueologica Calakmul, Calakmul (18.1, −89.8, 258 m). **Nme** (1): CNMA 37301.

Chiapas

274. 7 Km S por Carretera, Rosendo Salazar, Cintalapa (16.41, −93.98, 855 m). **Nme** (1): CNMA 19264.
275. Ococingo (16.9, −92.03333, 868 m). **Nme** (1): USNM 554861.
276. Cueva de la Chepa, 2 km N Tuxtla Gutierrez (16.78333, −93.15, 809 m). **Nme** (Arita, 1997),
277. Cueva los Laguitos, Tuxtla Gutierrez (16.7833, −93.15, 809 m). **Nme** (Sorba et al., 2004),
278. 4 Km Nw, Tuxtla Gutierrez, Tuxtla Gutierrez (16.75, −93.15, 590 m). **Nme** (2): CNMA 5136–5137.
279. Tuxtla Gutierrez (16.75, −93.11, 544 m). **Nme** (40): UMMZ 109817; CNMA 5134, 20935–20937, 5135; KU 61121–61148, 66501; MCZ 47931, 47932, 48126; MMNH 4826, 4914.
280. Confluencia Arroyo Miranda Con Rio Lacantún, Ocosingo (16.14, −90.92, 155 m). **Nme** (3): CNMA 19265–19267.
281. Estación Chajul de Sedue, Ocosingo (16.12, −90.93, 166 m). **Nme** (3): CNMA 20934, 23735, 24466.
282. Tonalá, 15 mi ESE (16.0833, −93.75, 45 m). **Nme** (1): LACM 014083.

Chihuahua

283. Mojaráchic = Mafuaráchic (27.81667, −108.0167, 1179 m). **Nla** (1): USNM 265661.
284. Barranca del Cobre, 23 miles S, 1.5 miles E Creel (27.4429, −107.5909, 1500 m). **Nme** (2): KU 73521, 73522.
285. La Bufa (27.11667, −107.5667, 2028 m). **Nla** (1): KU 79448.
286. Mina Santo Domingo, Batopilas (27.01667, −107.7167, 1666 m). **Nme**: CRD 4603–4613, 4615.

Colima

287. Tunel Zamora near Mezcales, 5.5 Km from Comala (19.31667, −103.75, 637 m). **Nme** (11): ROM 62817–62827.
288. Rancho Tabarnillas, 6 Km N, Agua Zarca (19.26, −103.94, 777 m). **Nme** (3): CNMA 5628–5628.
289. Cardona, 1 Km SE, Colima (19.2, −103.6333, 512 m. **Nme** (6): CNMA 41786–41790, 41811.
290. Cueva de la Fábrica, Coquimatlán, 4 mi S (19.2, −103.8, 330 m). **Nme** (30): LACM 011246–011262, 012131–012141, 016702, 016703.
291. Tecoman, 12 km NW (18.9166, −103.8833, 42 m). **Nme** (3): LACM 012142, 012130.
292. Hacienda Los Ortices, 2km SE. **Nme** (2): UMMZ 79942, 79943.
293. Rancho Nuevo. **Nme** (Mitchell, 1965).

Distrito Federal

294. Cueva Ixtli, Tlálpan (19.28333, −99.16667, 2301 m). **Nme** (1): Lunaschi 2002.
295. 34 Km S Cd. Mexico, La Cima (19.12, −99.13, 3079 m). **Nme** (6): TTU 45076– 45080; CNMA 27781.
296. Cerro La Estrella (19.36, −99.1, 2239 m). **Nme**: Ceballos and Galindo, 1984

Durango

297. Ventana (25.01667, −106.7833, 573 m). **Nme** (Baker and Greer, 1962).
298. "Arroyo," 6 km E of San Juan de Camarones (24.9166, −106.35, 1886 m). **Nla** (1): CRD 2845.
299. "Agujero en ladera," 2.7 km S, 4 km E of San Juan de Camarones (24.90242, −106.3732, 1136 m). **Nla** (1): CRD 2830.
300. Chacala (24.8, −106.7333, 846 m). **Nme** (21): USNM 96876–96879; (= Chamala) USNM 96859–96875. **Nla** (1): USNM 96865.

Guerrero

301. Cacahuamilpa Cave (18.668, −99.509, 1175 m). **Nme** (1): FMNH 51077.
302. Los Sabinos, 12 Km E, Teloloapan, (18.36, −99.75, 1444 m). **Nme** (1): CNMA 35201.
303. Teloloapan (18.35, −99.85, 1600 m). **Nme** (1): CNMA 9981.
304. 10 mi E, 2 mi S, Teloloapan (18.33, −99.72, 1594 m). **Nme** (2): CNMA 1770, 1771.
305. El Ojo de Agua, Chapa (18.3166, −99.8166, 1453 m). **Nme** (1): CNMA 9027.
306. 4 Km W of Cocula (18.2333, −99.6667, 626 m). **Nme** (1): ROM 78777.
307. Zacatula, 12 Km N of (17.9833, −102.15, 9 m). **Nme** (1): ROM 78774.
308. Cueva del Huarache, 14 km S of Chilpancingo (17.55, −99.5, 1279 m). **Nme** (Arita, 1997).
309. Colotlipa, Colotlipa, Quechultenango (17.43, −99.16, 942 m). **Nme** (13): CNMA 22528, 25583–25585, 26887, 3711, 3715, 26884–26886; MCZ59203.
310. Colotlipa, 4 mi N; La Gruta de Juxtlahuaca (17.43, −99.16, 942 m). **Nme** (15): LACM 039415–039429.

311. Parque Natural Gruta de Juxtlahuaca, Quechultenango (17.43, −99.15, 874 m). **Nme** (33): CNMA 1584, 2688–2690, 5143–5147; KU 99711–99729; USNM 559716–559721.
312. Cueva del Salitre, 1 Km S, Palo Blanco 1 Km S, Chilpancingo de los Bravos (17.39, −99.46, 1065 m). **Nme** (5): CNMA 15563, 15567, 15568, 25586, 25587; USNM 559722.
313. Acahuizotla (17.3833, −99.45, 968 m). **Nme** (Lukens and Davis, 1957).
314. 2 mi Nw Acapulco (16.9122, −99.8959, 910 m). **Nla** (1): MSB 32665.
315. Unknown, **Nme** (13): UWBM 62653–62664, 63156.

Hidalgo

316. Tlanchinol, 4.6 Km Nne, Tlanchinol (20.98333, −98.65, 1354 m). **Nme**(1): CNMA 40947,00.

Jalisco

317. Cueva de Gines, Etzatlán (20.76, −104.08, 1418 m). **Nme** (10): CNMA 1748–1757; USNM 52114, 52116, 52117. (Itzatlán) USNM 50778.
318. Arroyo de los Camarones, 9 Km NW, Puerto Vallarta (20.66, −105.24, 3 m). **Nme** (6): CNMA 5458–5463.
319. Sierra de Cuale (20.6, −105.2333, 196 m). **Nme** (15): KU 92911–92917, 92920–92922, 92925, 92926, 92929, 92932, 92933, **Nla** (9): KU 92916, 92918, 92919, 92923, 92924, 92927, 92928, 92930, 92931.
320. Ameca (20.55, −104.0167, 1231 m). **Nme** (13): KU 33373–33391; USNM 87322, 87325, 87333. **Nla** (22), USNM 87323, 87326, 87328–87332, 87334–87339.
321. Mina de las Garrochas, 17 Km NNW, Soyatlán del Oro (20.44, −104.33, 1957 m). **Nme** (7): CNMA 2174–2179. **Nla** (1): 2180.
322. Zapotlán [=Ciudad Guzmán] (20.4333, −102.9167, 1536 m). **Nme** (1): USNM 52109.
323. Talpa de Allende, 12.5 mi SW, by road (20.367, −104.817, 1156 m). **Nme** (1): CM 79430. **Nla** (1): AMNH 254673.
324. Mina del Baladero, 3 km NW Talpa de Allende (20.367, −104.817, 1156 m). **Nme** (Mitchell, 1965).
325. Purificación (19.71667, −104.5833, 472 m). **Nme** (11): KU 92934–92944.
326. El Arado [= Lo Arado] (19.61667, −104.5667, 574 m). **Nme** (47): KU 31945–31984, 41341–41347.
327. Km 69 Carr. Barra de Navidad, Pto. Vallarta, Chamela (19.52, −105.07, 32 m). **Nme (**1): CNMA 4196. **Nla** (2): 16854, 16855.
328. La Huerta, 2 mi NE (19.467, −104.65, 320 m). **Nme** (5): CNMA 25581; KU 10555–105560.
329. Cave, Cuitzamala (19.3667, −104.9833, 46 m). **Nme** (Arita, 1997).
330. Pihuamo, 16 Rd. mi N, 900m (19.25, −103.3833, 738 m). **Nme** (1): UMMZ 113562.
331. Barra de Navidad (19.2, −104.6833, 7 m). **Nme** (1): KU 87412.
332. Mina Hedionda, 30 km W Rancho de los Ocotes. **Nme** (Mitchell, 1966).

México

333. Convento de Acolman, Municipio, Acolman (19.6333, −98.9167, 2257 m). **Nme** (Caballero, 1942a, 1942b).
334. Cueva Peña Blanca, Avandaro, Valle de Bravo (19.14, −100.1, 2185 m). **Nla** (2): CNMA 15565, 15566.
335. Cueva de la Estrella, Tonatico (18.74, −99.62, 1560 m). **Nme** (1): CNMA 2012.

Michoacán

336. Lagunita (19.7, −102.6167, 1738 m). **Nme** (Mitchell, 1965).
337. Rio Ostula, 12 Km SE, La Placita, Aquila (18.45, −103.53, 120 m). **Nme** (1): CNMA 17375,00.
338. Colola, 5 km N, Aquila (18.3, −103.4139, 12 m). **Nme** (Dávalos, 2005).
339. Los Hornos, 3 Km NNW, Caleta de Campos (18.08, −102.77). **Nme** (8): CNMA 17367–17374.

Morelos

340. Cueva del Salire, Tetecalita (18.7667, −99.1833, 1147 m). **Nme** (16): CNMA 25582, 5138–5142, 5148; MMNH 6206–6209, 6471, 6223, 6224, 6238, 6245; AMNH 180320, 180321, 180447–180450.
341. Tunel del Arco, 3 Km S, Chinameca, Tlaltizapan (18.61667, −99, 1074 m). **Nme** (5): CNMA 15564, 18809–18812.
342. Tequesquitengo, 2 Km W (18.6, −99.26667, 974 m). **Nme** (2): ROM 78773, 78778.
343. Cueva del Ídolo, Jojutla de Juárez (18.6, −99.25, 954 m). **Nme** (6): CNMA 18813–18818.
344. Lago de Tequesquitengo, 1 Km S, (18.59, −99.26, 959 m). **Nme** (1): CNMA 22563.
345. Chinameca, 6 Km S, 2 Km E, San Pablo Hidalgo, Tlaltizapan (18.58, −99.02, 1080 m). **Nme** (1): CNMA 18808.
346. Cueva del Cerro, Tequesquitengo (18.58, −99.27, 926 m). **Nme** (35): CNMA 9091–9108, 9868–9873, 10673–10679, 5149; TTU 41142–41144; LACM 39576–39578, MMNH 6210.
347. Unknown locality. **Nme** (6): UWBM 62665–62670.

Nayarit

348. Río del Bajar, Huajicori (22.6383, −105.3192, 71 m). **Nme** (3): LACM 019178–019180.
349. La Cuchara, Acaponeta, 40 mi E (22.4963, −105.3594, 30 m). **Nme** (17): LACM 017486–017502.
350. Rancho Palo Amarillo, Tepic near Amatlán (21.5, −104.9, 961 m). **Nme** (10): FMNH 20103; AMNH 25102–25105, 25107–25111. **Nla** (1): AMNH 25106.
351. Santa María Del Oro, 0.5 mi N, 0.7 mi E (21.33333, −104.5833, 1173 m). **Nme** (1): TTU 33710.
352. Platanares (= Puerta de Platanares [21.8667, −105.0333, 46 m]). **Nme** (10). KU 85719–85728.
353. San Blás (21.51667, −105.2667). **Nme** (10): KU 36607; (Paso de Soquilpa) USNM 50885, MSB 16853, 16854; LACM 013925–013930.

354. Jalcocotan, 2 miles SE (21.46667, −105.1167, 446 m). **Nme** (14): MSU MR.49; KU 36615–36626, 36654.
355. Aticama (21.46667, −105.2167). **Nme** (1): KU 36627.
356. Isla María Magdalena (21.41667, −106.4, 5 m). **Nme** (5): Islas Tres Marías. AMNH 180560, 180839, 180877, 180879, 180880.
357. Las Varas (21.0863, −105.1433, 350 m). **Nme** (81): KU 39622–39627, 39629–39682, 39684–39689, 39692–39699, 39701–39703, 39706–39708, 39710. **Nla** (10): AMNH 39620, 39621, 39628, 39683, 39690, 39691, 39700, 39704, 39705, 39709.
358. Barranca del Oro (20.9167, −104.4667, 789 m). **Nme** (1): USNM 523440.
359. Mineral del Tigre, 1340 feet. **Nme** (1): MSU MR.17130.

Nuevo León

360. Cueva La Boca, Santiago (25.4167, −100.15, 476 m). **Nme** (Davis and Carter, 1962).

Oaxaca

361. Las Minas (17.35917, −98.25194, 1938 m). **Nme** (2): TTU 82626, 82627.
362. Matías Romero, 12 mi N (16.8833, −95.0333, 212 m). **Nme** (1): LACM 019389.
363. Matías Romero, 17 mi. N and 2 mi. E of (16.8833, −95.033, 212 m). **Nme** (1): MSU MR.7917.
364. Río Guamol, 34 mi S by highway 190 La Ventosa Jct, El Guamol (16.49, −94.4730, 30 m). **Nme** (1): MSB 27600.
365. El Jícaro = General Pascual Fuentes, 3 mi N, Santo Domingo Zanatepec (16.47, −94.26, 178 m). **Nme** (12): CNMA 5344; AMNH 186395–186405.
366. Tapanatepec, 8 km NW; Rancho Sol-y-Luna (16.35, −94.2, 41 m). **Nme** (3): LACM 016841, 018115; AMNH 177420.
367. San Gabriel Mixtepec, 9 miles W (16.0833, −97.1, 736 m). **Nme** (1): CAS 14989.
368. El Salado (16.4167, −95.5167, 195 m). **Nme** (4): AMNH 178758–178761.
369. Mixtequilla (16.3911, −95.2608, 219 m). **Nme** (24): AMNH 185025, 185026, 185044–185065.
370. Tehuantepec (16.3183, −95.2183, 31 m). **Nme** (50): AMNH 178746; (Bisilana) AMNH 145148; (Dani Liesa) AMNH 171563–171590 (171567, 171568, 171570, 171573, 171575, 171576, 171577, 171578, 171579, 171584, 171586, 171588, 171589; 6 females,7 males); (Escurano) AMNH 208906; (Guiengola) AMNH 148386–148391, 185066–185072. (San Antonio) AMNH 165945–165950.
371. Río Grande, 7 mi W. **Nme** (1): MSU MR.14051.

Puebla

372. Cueva El Sapo, 2.75 Km S, 0.25 Km W, Tenampulco (20.14, −97.24, 280 m). **Nme** (1): CNMA 40432,00.
373. Cueva La Salamandra, Ayotoxco and Tenampulco (20.1333, −97.4, 209 m). **Nme** (Brunet and Medellín, 2001).
374. Cueva Virgen, Ayotoxco and Tenampulco (20.1333, −97.4, 209 m). **Nme** (Brunet and Medellín, 2001).
375. Cueva de las Vegas, Ejido el Zapote, 2.5 Km S, 0.5 Km W, El Zapote, Tenampulco (20.08, −97.4, 285 m). **Nme** (13): CNMA 16323–16330, 17030. **Nla** (4): CNMA 16356, 17027–17029.
376. Raboso (18.5667, −98.4167, 1291 m). **Nme** (77): KU 61104–61120, 62358–62364, 63150, 63151, 67414–67464.

Quintana Roo

377. Felipe Carrillo Puerto, 8 km SW (20.79, −86.93). **Nme** (1): CNMA 34920.
378. Felipe Carrillo Puerto, 4 Km NNE (18.63, −88.02). **Nme** (3): CNMA 25592; KU 91903, 91904.
379. San Miguel de Cozumel (20.50083, −86.94583, 7 m). **Nme** (37): USNM 318491–318519. (Includes "Santa Rita, 10 km E of San Miguel de Cozumel"; KU 150722–150725, 151194–151197).
380. Chumpón-La Glorieta, Sian K'an (19.8180, −87.5805, 11 m). **Nme** (Pozo de La Tijera and Escobedo-Cabrera, 1999).
381. Cenote, 2 km N of Felipe Carrillo Puerto (19.5833, −88.05, 15 m). **Nme** (Arita, 1997).
382. Laguna Noh-Bec, 2 Km W, Noh-Bec (19.12, −88.16, 22 m). **Nme** (10): ROM 97440–97445, 97518, 97519; CNMA 31756, 31757.
383. Bacalar, 4 Km S, 1 Km W, (18.64, −88.4, 2 m). **Nme** (1): CNMA 20163.

San Luis Potosí

384. Cueva A 10 Km S, Rancho El Estribo, El Naranajo, Ciudad Del Maiz (22.43, −99.3, 260 m). **Nme** (8): CNMA 21997–22001; CNMA 219–21996.
385. Cueva Chica, 11 mi Se Ciudad Valles (21.9833, −99.0167, 75 m). **Nme** (1): TTU 9242.
386. Cueva De Taninul #1, 8.8 mi S Ciudad Vallés (21.9833, −99.0167, 75 m). **Nme** (11): TTU 9226–9234, 8343; CNMA 2200.
387. Rancho nacimiento del Río Coy (21.8, −99.07, 216 m). **Nme** (Constantine, 1958).
388. Rancho el Estribillo, Ciudad Del Maiz. **Nme**: CNMA 30154,00.

Sinaloa

389. Rio Corsala, Ca 72 mi S by Hwy 15 Culiacán (24.06, −106.8, 101 m). **Nme** (1): MSB 32128.
390. Santa Lucía (23.4333, −105.8667, 1028 m). **Nme** (10): CNMA 4513, 9851; KU 94257, 95011–95017.
391. Pánuco (23.41667, −105.9167, 535 m). **Nme** (4): CNMA 25571, 25574–25576; KU 85704–85718, 85911–85914, 95839–95874, 145428.
392. Puerta de Canoa, 11 mi N, 2.5 mi E Mazatlán (23.3667, −106.3833, 109 m). **Nme** (10): LACM 088107, 012437–012445.
393. Copala (23.3667, −105.9333, 391 m). **Nme** (30). LACM 009322, 009327, 009453, 009482, 009511, 009514, 009539, 009607, 009626, 009686, 009782–009790; CNMA 25578; KU 94259, 105548–105555.
394. El Cajón, 1 mi S (23.35, −106.0167, 373 m). **Nme** (5): CNMA 25577; KU 100380–100383.
395. Cueva Playa Cerritos, 5 Km W, Mazatlán (23.31, −106.48, 9 m). **Nme** (1): CNMA 36394.
396. Río Arroyo De Mesilla, 0.5 mi S Concordia (23.28333, −106.0667, 114 m). **Nme** (1): MSB 37234.

397. Mazatlán (23.21667, −106.4167, 6 m). **Nme** (51): CAS 13250–13258; CNMA 25579; ROM 78775; LACM 014724–14737; KU 85678–85703, USNM 96995.
398. Mazatlán Cave, 5 mi N (23.2167, −106.4167, 6 m). **Nme** (15): LACM 015532–015544, 015568, 15575; ROM 77324.
399. Plomosas (23.0667, −105.4667, 891 m). **Nme** (32): KU 92894–92910; USNM 92394–92408.
400. Matatán, (23.0167, −105.7167, 140 m). **Nme** (7): CNMA 25572, 25573; KU 90726–90730.
401. Rosario (23, −105.8667, 34 m). **Nme** (96): TTU 40995, 40996; FMNH 44212–44214; CM 51886; AMNH 217558–217560, 243867, 243868; KU 39622–39676, 91334–91339, 92288–92291, 92293, 92341–92349, 92351–92355, 92363–92376. **Nla** (1): USNM 91333.
402. Hwy 15 at Sinaloa-Nayarit Border, Rio Cañas (22.5325, −105.4508, 16 m). **Nme** (15): MSB 27341–27355.

Sonora

403. Guano Cave [= Cueva del Tigre], Carbó, 14.9 MI ESE by road (29.7, −110.9667, 486 m). **Nme** (1): MSB 7851.
404. Mine, 13 mi SW of Ures (29.43333, −110.4, 380 m). **Nme** (Broadbooks, 1961).
405. Rancho Pressa, 20.7 mi E Mazatán (29, −110.1333, 545 m). **Nme** (9): TTU 10800–10803, 10809–10813.
406. Jct Rds to Soyopa and Novillo, 12.7 mi W Novillo (28.9333, −109.6333, 269 m). **Nme** (1): TTU 10524.
407. Rio Yaqui, 4 mi S El Novillo Dam (28.9333, −109.6333, 269 m). **Nme** (1): MSB 34157.
408. Mina Santa Clara, 7 Km W Tonichi (28.5833, −109.5667, 225 m). **Nme** (6): TTU 46843–46848.
409. San Carlos, 8 mi NNW, 28.20n 111.10w (28.3167, −111.3167, 12 m). **Nme** (2): MSB 60914, 61126.
410. Algodón Beach, 20 Km NW Guaymas (27.9333, −110.9, 18 m). **Nme** (1): MSB 42664.
411. San Carlos Bay (27.9333, −111.05). **Nme** (1): MSB 32129.
412. Quiriego, 11.9 mi N (27.5167, −109.2667, 211 m). **Nme** (1): TTU 33711.
413. Tesia (27.1667, −109.3667, 46 m). **Nme** (4): AMNH 172023–172026.
414. Alamos, 4 mi N (27.08, −108.93, 491 m). **Nme** (1): CNMA 2710.
415. Mina Armolillo, 5 mi NNW, Alamos (27.05, −109, 481 m). **Nme** (6): CNMA 9936–9941.
416. Mine, ca. 0.25 mi W La Aduana (27.05, −109, 481 m). **Nme** (7): MSB 31547–31553.
417. La Aduana (27.03, −109, 590 m). **Nme** (79): CAS 12035–12038; CNMA 25547–25562, 25563–25567, 27932; MSB 32159, 4554, 19084–19099, 19561–19569, 22580–22585, 24057–24059, 27432–27435; LACM 9976, 013248–013257; LSUMZ 20883; TTU 6316, 6365; ROM 91201.
418. La Aduana, 0.8 Km N (27.01667, −108.9333, 378 m). **Nme** (2): MSB 11050; ROM 78776.
419. 5 mi N Alamos (27.0167, −108.9333, 378 m). **Nme** (6): TTU 47005–47010.
420. Álamos (27.0167, −108.9333, 378 m). **Nme** (52): KU 24843–24848, 25074–25118. CNMA 25580.
421. Minas Nuevas, 4 mi NW Alamos (27.0167, −108.9333, 378 m). **Nme** (8): TTU 36621–36628.
422. Mina Santo Domingo, La Aduana (26.99, −109.04, 647 m). **Nme** (29): MSB 53761–53777, 48545, 48546, 55436–55440, 42664, 61990; CNMA 5049, 27930, 27931.
423. Unknown locality. **Nme** (3): USNM 314691–314693.

Tabasco

424. Cueva de Don Luis, 3.3 Km NE, Teapa (17.56, −92.92, 40 m). **Nme** (2): CNMA 7025, 7026.
425. Teapa, 3 Km E (17.55, −92.95, 50 m). **Nme** (2): CNMA 7445; KU 66502.
426. Cueva Cocona, 4 Km E Teapa (17.54, −92.91, 119 m). **Nme** (1): CNMA 7673.

Tamaulipas

427. Cueva del Rancho Río Escondido, 19 Km NNW, S. de Jiménez (24.37, −98.55, 240 m). **Nme** (3): CNMA 22491, 27933, 25568.
428. S. de Jiménez, 13 mi W, 6.5 mi N, S. de Jiménez (24.3, −98.68, 295 m). **Nme** (2): CNMA 25569, 25570.
429. Cueva el Rancho (Rancho el Tinieblo), Jiménez (24.21667, −98.46667, 108 m). **Nme** (174): KU 88377–88390. USNM 556328–556487.
430. Cueva la Esperanza (23.91667, −99.28333, 297 m). **Nme** (27): KU 57539–57565.
431. Ciudad Victoria, 8 Km SSW, Ciudad Victoria (23.66, −99.17, 1042 m). **Nme** (7): CNMA 7666–7672.
432. Piedra (23.5, −98.1, 74 m). **Nme**(8): KU 54992–55000 (54993, 54995, 54997–55000; 6 males).
433. Cueva el Resumidero, 0.85 Km NW of Gómez Farías (23.05, −99.16, 328 m). **Nla** (2): CNMA 34800, 34801.
434. Cueva el Ojo de Agua, 3.1 Km SE of Gómez Farías (23.02, −99.13, 162 m). **Nme** (1): CNMA 34802.
435. Cueva de los Cuarteles, Aldama (22.91, −98.07, 126 m). **Nme** (5): CNMA 1573–1577.
436. El Mante, 13 mi S (22.74, −98.97, 85 m). **Nme** (1): UMMZ 98847.
437. Ejido Ojo de Agua, 20 miles N of El Mante (22.7167, −98.9667, 78 m). **Nme** (20): KU 60276–60295.
438. Cueva de Quintero, Quintero, El Mante (22.66, −99.03, 111 m). **Nme** (1): CNMA 1236.
439. Cueva del Abra, 10 Km NNE, Antiguo Morelos (22.63, −99.04, 343 m). **Nme** (1): CNMA 4862.
440. Cueva de La Florida, 2 mi N El Pachón (22.6167, −99.0333, 289 m). **Nme** (22): TU 6591–6604, 6623, 6624, 63385–63392.
441. Cueva en El Pachón (22.6167, −99.0333, 289). **Nme** (153): AMNH 147903–147911, 148058–148194, 164436–164441; CM 83523; KU 17846.
442. Cueva del Nacimiento del Río Frío. **Nme** (1): TTU 47450.
443. Mina A 5 Km SW Cañon de La Boca, Hacienda La Boca, **Nme** (1): CNMA 1594.

Veracruz

444. Tuxpan, 9 Km Nw (21.0496, −97.5069, 36 m). **Nla** (17): CNMA 27934; KU 82893–82908.
445. Cerca de Jalapa (19.54, −96.92, 1448 m). **Nme** (4): CNMA 9229–9232.
446. Mirador (19.2833, −96.9, 957 m). **Nme** (3): USNM 8217, 8218, 102420;
447. Potrero (18.9452, −96.9059, 582 m). **Nla** (10). KU 29693–29702.
448. Fortín [= Fortín de las Flores] (18.9255, −97.0295, 975 m). **Nla** (1): KU 17845.
449. Orizaba (18.85, −97.0833, 1189 m). **Nla** (1): USNM 1840, 7838.
450. Ojo de Agua del Río Atoyac, Atoyac (18.71, −96.8, 382 m). **Nme** (1): CNMA 10680.
451. Reserva Ecológica Los Tuxtlas (18.58, −95.07, 204 m). **Nme** (Estrada and Coates-Estrada, 2001).
452. Cueva del Boquerón, 3 Km E San Andrés Tuxtla (18.4333, −95.2167, 254 m). **Nme** (5): CM 80234–80237; UMMZ 110439.
453. San Andrés Tuxtla (18.4333, −95.2167, 254 m). **Nme** (110): KU 23772–23814, 23815 (holotype of *Natalus mexicanus saturatus*), 23816–23838, 24725–24744; USNM 65473, 70438, 70439.

Yucatán

454. Hacienda San Antonio Teztiz, 6 Km S, 5 Km W Kinchi [= Kinchil (20.9167, −89.95, 7 m). **Nme** (1): TTU 29072.
455. Cueva de Hoctún, Hoctún (20.85, −89.2, 17 m). **Nme** (8): MMNH 12077, 12811; CNMA 32861–32864, 1578, 1579; USNM 260814.
456. Gruta de Las Ruinas de Mayapán, 2 Km S, Telchaquillo, Tecoh (20.62, −89.46, 17 m). **Nme** (2): CNMA 32865, 32866.
457. Cueva de Oxkintoc, 3 Km S, 1 Km W Calcehtoc, Opichen (20.56667, −89.91667, 15 m). **Nme** (3): TTU 18448; MMNH 12076; CNMA 18908.
458. Cueva de Loltún, 8 Km Sw Oxkutzcab (20.3, −89.41667, 44 m). **Nme** (3): MMNH 1282; TTU 25901, 29073.
459. Cueva de Los Murciélagos, 0.5 Km SW Ticum, Tekax (20.14, −89.22, 40 m). **Nme** (3): CNMA 32860, 32866, 32868.
460. Gruta de Balankanche, Xkalakob, 5 Km E Chichén Itzá. **Nme** (33): FMNH 49992–50018; CNMA 25588–25591; CM 92759, 92760; KU 91847–91902, 260809–260813, 260815.

Zacatecas

461. Santa Rosa, Río Juchipila (21.6, −102.95, 1558 m). **Nme** (1): LACM 034286

MONTSERRAT

Saint Anthony

462. BVR Tarrish Pits, Aymers Ghaut (16.7, −62.2, 205 m). **Nst** (S.C. Pedersen, personal commun.).
463. Danforth, unknown. **Nst** (1): FMNH 47702.

NETHERLANDS ANTILLES

Bonaire

465. Kralendijk, 8.5 Km N, 2 Km W (12.15, −68.2667, 4 m). **Ntu** (1): CM 52202.

Curaçao

466. Kueba Bossa 2 (12.3326, −69.084, 41 m). **Ntu** (Petit, 1995).
467. Hatto (12.2198, −69.0046). **Ntu** (1): USNM 102106.
468. Cueva di Raton (12.199, −68.987, 24 m). **Ntu** (4): NNM 16521, 16571, 14387, 16682.
469. Grot Van Hato (8 km N Willemstad (12.1807, −68.9597, 56 m). **Ntu** (1): MBUCV 2312.
470. Kueba Noordkant (12.1686, −68.89, 11 m). **Ntu** (Petit, 1995).
471. NW side of island. **Ntu** (1): USNM 102105.

Saba

472. Mary's Point Mountain (17.6381, −63.2422, 440 m). **Nst** (8): TTU 101951–101965.
473. unspecified locality. **Nst** (1): FMNH 47701.

St. Maarten

474. Billy Folly (18.0325, −63.0922). **Nst** (Genoways et al., 2007).

NEVIS

Saint James Windward

475. Lower Cave at Mount Pleasant Estate, Mt. Pleasant (17.175, −62.61417, 95 m). **Nst** (Pedersen et al., 2003).
476. Middle cave at Mt. Pleasant (17.175, −62.6141, 95 m). **Nst** (Pedersen et al., 2003).

St. Thomas Lowland Parish

477. Cades Estate (17.1922, −62.6141, 27 m). **Nst** (1): USNM 28159.

NICARAGUA

Granada

478. Nandaime, 6 Km S of (11.75, −86.05, 118 m). **Nme** (5): KU 97832–97836.

Rivas

479. 5 mi N, 1 mi W San Juan Del Sur (11.25, −85.8667, 112 m). **Nme** (1): TTU 17127.

Zelaya

480. El Recreo; S side of Río Mico (12.1667, −84.3167, 23 m). **Nme** (2): KU 106280, 111223.

PANAMA

Coclé provincia

481. Penonome (8.516667, −80.36667, 64 m). **Nme** (5): MCZ 28228, 28229, 33514–33516.

Colón

482. Sea Cave, Fort Sherman, Below FT. San Lorenzo (9.32278, −80.0028, 0 m). **Nme** (36): UMMZ 122343; USNM 314726, 319065–19083; MVZ 118799–118805, 118968–118974, USNM 305570.

Panamá

483. Camp Chagres, Madden Dam (9.20833, −79.6167, 67 m). **Nme** (1): USNM 396478.
484. Cave near mouth of Río Puente (9.1933, −79.5541, 97 m). **Nme** (1): USNM 396404.

485. Madden Dam (includes Chilibrillo Caves, Camp Chagres) (9.1833, −79.6167, 59 m). **Nme** (2): AMNH 80962, KU 45088.

Veraguas

486. Coiba Island (unspecified)(7.45, −81.76667, 310 m). **Nme** (1): AMNH 18729.

PARAGUAY

Concepción

487. Parque Nacional Serranía de San Luis (−22.6723, −57.3493, 183 m). **Nes** (1): TTU 75277.

SURINAME

488. Sipaliwini Airstrip, Sipaliwini (2.0333, −56.1333, 281 m). **Ntu** (1): CM 76809.

THE BAHAMAS

Abaco

489. Eight Mile Cave, 13 km N of Hole in the Wall (25.97417, −77.19639, 11 m). **Ctu** (11): UF 24850–24856, USNM 576614, 576619, 576619, 576620.
490. Hole in the Wall Cave, Hole in the Wall Point (25.84556, −77.2125). **Npr***: UF (fossil), (Morgan, 1994, 2001).
491. "Cave," Israel's point, NE of Island. **Ctu** (Allen, 1905)
492. Golden Cave. **Ctu** (1): UF 22398.
493. Unspecified loc. **Ctu** (58): AMNH 40026; FMNH 34069, 34070, 34182; MCZ 10868–10922.
494. Long Bay Cave. **Npr***: (G.S. Morgan, personal commun.).

Andros

495. King Cave, Morgan's Bluff (25.1667, −78.0333, 7 m). **Nyl***: UF 79108, 79109; **Ctu***: UF 79111–79171, 79244–79264, 79305–79321. **Npr***: UF 79110, (Morgan, 1989).
496. Coleby Bay Cave, Morgans Bluff (25.1667, −78.0333, 7 m). **Npr***: UF 79324
497. Morgan Bluff Cave, Morgan's Bluff (25.1667, −78.0333, 7 m). **Ctu** (4): CM 92459–92462.
498. Ashton cave. **Ctu***: UF 79408–79464.

Cat

499. Crown Cave, Dumfries (24.6333, −75.6667, 1 m). **Nyl** (1): AMNH 275535.
500. Crawling Cave, Industrious Hill (24.45, −75.55, 0 m). **Nyl** (1): AMNH 275537.
501. Sheep Hill Cave. **Nyl** (109): MCZ 32809–32870, 58500–58546.
502. Turtle Scratch Cave. **Ctu***: UF 79809–79811.

Eleuthera

503. Wemyss Bight, South Eleuthera (24.73583, −76.21709, 7 m). **Nyl** (39): MCZ 28558–28596.
504. Eleuthera. **Npr*** (G.S. Morgan, personal commun.).

Great Exuma

505. Anne's Creek Cave 3, near Stephenton (23.65703, −75.9594, 2 m). **Nyl** (K. Murray, personal commun.).
506. Max Bowes Cave, Forest (23.5833, −75.9167, 7 m). **Nyl*** (Koopman et al., 1957); **Ctu*** (Koopman, 1957).
507. Nursery Cave (Lower), near Moss Town (23.5740, −75.9058, 5 m). **Nyl** (Kevin Murray, in litt.).
508. Cabbage Hill Cave, near Moss Town (23.5558, −75.8820, 0 m). **Nyl** (Kevin Murray, in litt.).

Little Exuma

509. Pasture Cave, near Ferry (23.4555, −75.6396, 9 m). **Nyl** (Kevin Murray, in litt.).
510. Palm Beach Cistern, near Ferry (23.4542, −75.6352, 9 m). **Nyl** (Kevin Murray, in litt.).
511. Ferry, 6 mi E (23.4333, −75.5833, 5 m). **Nyl** (2): AMNH 167130, 167133.

Long

512. Miller's Cave (23.4, −75.1667, 7 m). **Nyl** (112): FMNH 44535–44626; KU 157503–157522.
513. Pinder's Settlement, 24 Miles NW Clarence Town (23.2833, −75.1, 21 m). **Nyl** (43): UF 12833–12837; KU 151173–151180, 157523–157541; UMMZ 99141–99151.
514. Mortimer's (South Point) (22.9, −74.8667, 6 m). **Nyl** (14): FMNH 46063–46066; KU 157499–157502; MCZ 33774–33779.

New Providence

515. Sir Harry Oakes Cave (25.0667, −77.45, 7 m). **Ctu***: UF 79799–79801.
516. East Cave (25.05, −77.2667, 18 m). **Ctu***: UF 27732–27779, 79852–79855.
517. Hunts Cave (25.0333, −77.3667, 7 m). **Ctu***: UF 79749, 79750, 79842; **Npr***: UF 27694, 79751–79759, 79761–79766, 79843–79848.
518. Banana Hole (25.0167, −77.55, 6 m). **Ctu***: UF 79994–79999; **Npr***: UF 79986–79990.

San Salvador

519. Bernies Cave, NE Side, NE point (24.12, −74.45472, 8 m). **Ctu** (2): CM 111960, 111961.
520. Lighthouse Cave (includes Crescent Top cave; Hall et al., 1998), NE Side, NE point (24.12, −74.45472, 8 m). **Ctu** (2): CM 111962, 111965.
521. Reckly Maze Cave (includes Reckly Water Cave; Hall et al., 1998), Reckley Hill, NE point (24.12, −74.45472, 8 m). **Ctu** (10): AMCC 121971–121979; CM 111966–111975.
522. North Victoria Hill (24.07667, −74.52667). **Ctu** (2): USNM 239657, 239658.
523. Altar Cave, Sandy point, south point of the island (23.94417, −74.56472, 15 m) **Ctu** (27): USNM 122024 (holotype), 540739–540770.
524. unspecified loc. **Ctu** (5): USNM 122021–122023, 122482, 122483.
525. unknown. **Ctu** (1): USNM 217270.

TRINIDAD AND TOBAGO

Saint Andrew

526. Platanal (10.73333, −61.15, 159 m). **Ntu** (2): AMNH 178684, 178685.
527. Tamana Cave (10.46667, −61.2, 302 m). **Ntu** (136): CM 45372–45379; AMNH 178686–178691, 176587–176598, 175856–175861, 275516, 275517; TTU 24087–24116, 26714–26742; MVZ 158290–158293, 167627, 167635, 167636, 173871–173875, 183511–183513; KU 76719–76727; ROM 31434,

31435, 31450–31452; MSU 32457–32460; USNM 347109–347132; LACM 015869–015871.

Saint Andrew

528. Guacharo Cave. **Ntu** (2): MCZ 16624, 16625.

Saint David

529. Montevideo (10.8167, −61.0333, 142 m). **Ntu** (1): LACM 15872.

St. George

530. Blanchisseuse (10.7833, −61.3, 113 m). **Ntu** (2): TTU 26743, 24117.
531. Las Cuevas (10.7833, −61.3833, 252 m). **Ntu** (6): TTU 24118, 24119, 5436, 5445, 24120, 24121.
532. Saut D'eau Cave near Maracas Bay (10.75, −61.4333, 275 m). **Ntu** (3): TTU 9822–9824.
533. "Cave," Heights of Guanapo, (10.6, −61.25, 30 m). **Ntu** (3): AMNH 178687; MVZ 167626, 167634.

Tobago

534. Effigy Cave, Amblypygid Cave, and Robinson Crusoe Cave, Crown Point (11.1474, −60.8392, 13 m). **Ntu*** (Eshelman and Morgan, 1985)
535. Tobago (11.23, −60.66). **Ntu** (6): TTU 48834–48839.

TURKS AND CAICOS
Middle Caicos

536. Conch Bar Cave (21.8295, −71.7754, 9 m). **Nma**(1): UF 246. (Morgan, 1989).

UNITED STATES
Florida

537. Thomas Farm, 12 km northeast of Bell (29.7553, −82.8628, 20 m). **Ppr***: UF 108641–108647, 121136–121145.

VENEZUELA
Apure

538. Caño La Guardia, afluente del Río Capanaparo (6.9333, −67.3000, 47 m). **Ntu** (1): MHNLS 7627.

Aragua

539. Ocumare de La Costa, Aponte (10.4845, −67.7700, 8 m). **Ntu** (1): EBRG 2243.
540. Quebrada Palmarito, Municipio Girardot, Maracay (10.3917, −67.2750, 1694 m). **Ntu** (1): EBRG 23463.
541. Rancho Grande, Pque Natl Henry Pitier(10.34900, −67.68400, 1116 m). **Ntu** (2): MBUCV 35, 34.
542. Facultad de Agronomía; Maracay (10.2750, −67.6097, 450 m). **Ntu** (1): MHNLS 9320.
543. Cueva Candelaria Cerca El Pao, La Victoria (10.2333, −67.3333, 574m). **Ntu** (8): EBRG 3046, 3047, 12002–12007.
544. Cuevas Cumbocito, Santa Lucía, El Pao de Zárate, 15 Km SE La Victoria (10.1500, −67.2167, 702 m). **Ntu** (5): MHNLS 8765–8767, 8782, 8783.
545. Fundo Paso del Medio, 10 Km ENE San Juan de Los Morros (9.9178, −67.2633, 385 m). **Ntu** (3): EBRG 23919, 23923, 23924.
546. Cuevas Pao Quebrada el Volcán. **Ntu** (4): EBRG 2493–2496.

Bolívar

547. Hato La Florida, 14 Km S 45 Km E Caicara (7.5000, −65.7833, 80 m). **Ntu** (11): EBRG 13661–13663; USNM: 405774–405782.
548. Pijiguaos (Serranía Pijiguaos) 140 Km SW Caicara (6.5834, −66.8416, 79 m). **Ntu** (2): EBRG 15928–15929.
549. Campamento Ucaima; Parque Nacional Canaima (6.2424, −62.8332, 422 m), **Ntu** (1): MHNLS 11002.
550. Parque Nacional Canaima, Laguna Canaima (6.2424, −62.8332, 422 m). **Ntu** (1): EBRG 22693.
551. Morichal, aproximadamente 3.7 Km S de La Laguna de Canaima, Parque Nacional Canaima (6.2096, −62.8528, 378 m). **Ntu** (1): MHNLS 11617.

Carabobo

552. San Esteban, Venezuela (10.4352, −68.0563, 25 m). **Ntu** (8): AMNH 31510–31516; BMNH 5.11.12.25 (holotype of *Phodotes tumidirostris continentis*).

Delta Amacuro

553. unspecified locality. **Ntu** (Ochoa et al., 1993).

Falcón

554. Cueva Piedra Honda Cerca de San José De Cocodite, Peninsula de Paraguaná (11.9341, −69.9817, 203 m). **Ntu** (56): EBRG 23554, 23555; MBUCV 2146–2180, 2225–2235, 2359–2362, ULA 429–432.
555. Cueva del Guano, 49 Km N 34 Km W Coro (11.8786, −69.9414, 96 m). **Ntu** (27): AMNH (P 1–3, AT 113–115, collection numbers); EBRG 13690–13693, 13046–13049; USNM 455968–455983, 494812–494818.
556. Cueva Ojo de Agua, Píritu (11.3739, −69.1372, 179 m). **Ntu** (7): AMNH (AT 118–124).
557. La Pastora, 11 km ENE Mirimiri (11.2000, −68.6333, 121 m). **Ntu** (2): USNM 441631, 494786.
558. Cueva el Zumbador 15.5 km al SSW de Yaracal (10.8572, −68.6113, 459 m). **Ntu** (3): AMNH (Z 1–3, field catalog number).
559. Cueva Copa de Oro (10.8408, −68.5937, 444 m). **Ntu** (1): AMNH (CO 1, field catalog number).
560. Cueva Pararille, La Chara (10.73722, −69.42056, 474 m). **Ntu** (10): AMNH (AT 101–110, field catalog number).

Lara

561. Caserío Boro, 10 KM N El Tocuyo (9.8833, −69.7833, 803 m). **Ntu** (1): USNM 456549.

Miranda

562. Cueva Cajigal, Birongo (10.5202, −66.2530, 258 m). **Ntu** (5): MHNLS 1498, 2008–2011; MBUCV 3070.
563. Cueva en el Río Salmerón (10.4833, −66.3667, 556 m). **Ntu** (3): MHNLS 1155, 1156, 1211.
564. Quebrada de Caurimare, Petare (10.4833, −66.8167, 845 m). **Ntu** (1): MBUCV 1110.
565. Cueva Walter Dupouy, 5 Km S 60 Km E Caracas, 4 km SW Birongo (10.4811, −66.2394,

59 m). **Ntu** (9): EBRG 13686–13689, 2610, 2611; ULA 3158–3160.

566. Cueva del Indio, cerca del Hatillo (10.4333, −66.8167, 1289 m). **Ntu** (3): MBUCV 1659–1661.

567. Cueva Ricardo Zuloaga, 15 KM SE, Caracas cerca del Encanto (10.4025, −66.7405, 545 m). **Ntu** (234): AMNH (AT 131–136, field numbers); EBRG 13651–13685, 13036–13045; MHNLS 950–966, 1613–1615, 2000, 2080, 2081, 10850; MBUCV 1945–1949, 2204–2211, 170, 849–875, 1347–1350, 2042–2057, 5512, 2437; ULA 326–328, 332, 340, 341, 346, 351, 737, 476, 475, 7368, 7384, 7387; USNM 373888–373900, 441641–441703, 494780–494796, 494800–494811, 496847.

568. Los Guayabitos; Caracas (10.3000, −66.5167, 616 m). **Ntu** (1): MHNLS 1188.

Nueva Esparta

569. Piedra de Rivero, Isla margarita (11.03700, −64.27500, 82 m). **Ntu***: AMNH (AT 213, collection number).

Sucre

570. Parque Nacional Península de Paria, Uquire (10.7000, −61.9667, 848 m). **Ntu** (6): EBRG 18674–18677, 20421, 20422.

571. Cueva de las Ánimas, Turimiquire (10.19722, −64.29111, 935 m). **Ntu** (13): AMNH (AT 85–97, collection numbers).

572. Represa Neverí (10.1744, −64.2972, 350 m). **Ntu** (2): EBRG 2644, 2645.

Yaracuy

573. Mina San Antonio, Aroa (10.4386, −68.8941, 257 m). **Ntu** (2): EBRG 23162, 23163.

574. Tunel detras de Mina Santa Barbara, Aroa (10.4386, −68.8941, 257 m). **Ntu** (1): EBRG 23394.

Zulia

575. Cueva de los Gavilanes, Perijá (10.93, −72.42, 328 m). **Ntu** (4): MBUCV 1577–1580.

576. Cueva de Toromo, Machiques (10.0556, −72.6667, 398 m). **Ntu** (12): AMNH (T 1–11, field numbers).

577. Kasmera, Perijá (9.9525, −72.7508, 369 m). **Ntu** (1): MBUCV 169.

Plate 1. *Top:* Inundated cockpit karst covered with evergreen forest; Los Haitises, Hato Mayor, Dominican Republic; habitat of *Natalus major*. *Bottom:* Tower karst covered with xerophytic and semideciduous forest on the ridges and evergreen forest in the valleys; Sierra de Viñales, Pinar del Río, Cuba; habitat of *Chilonatalus macer*.

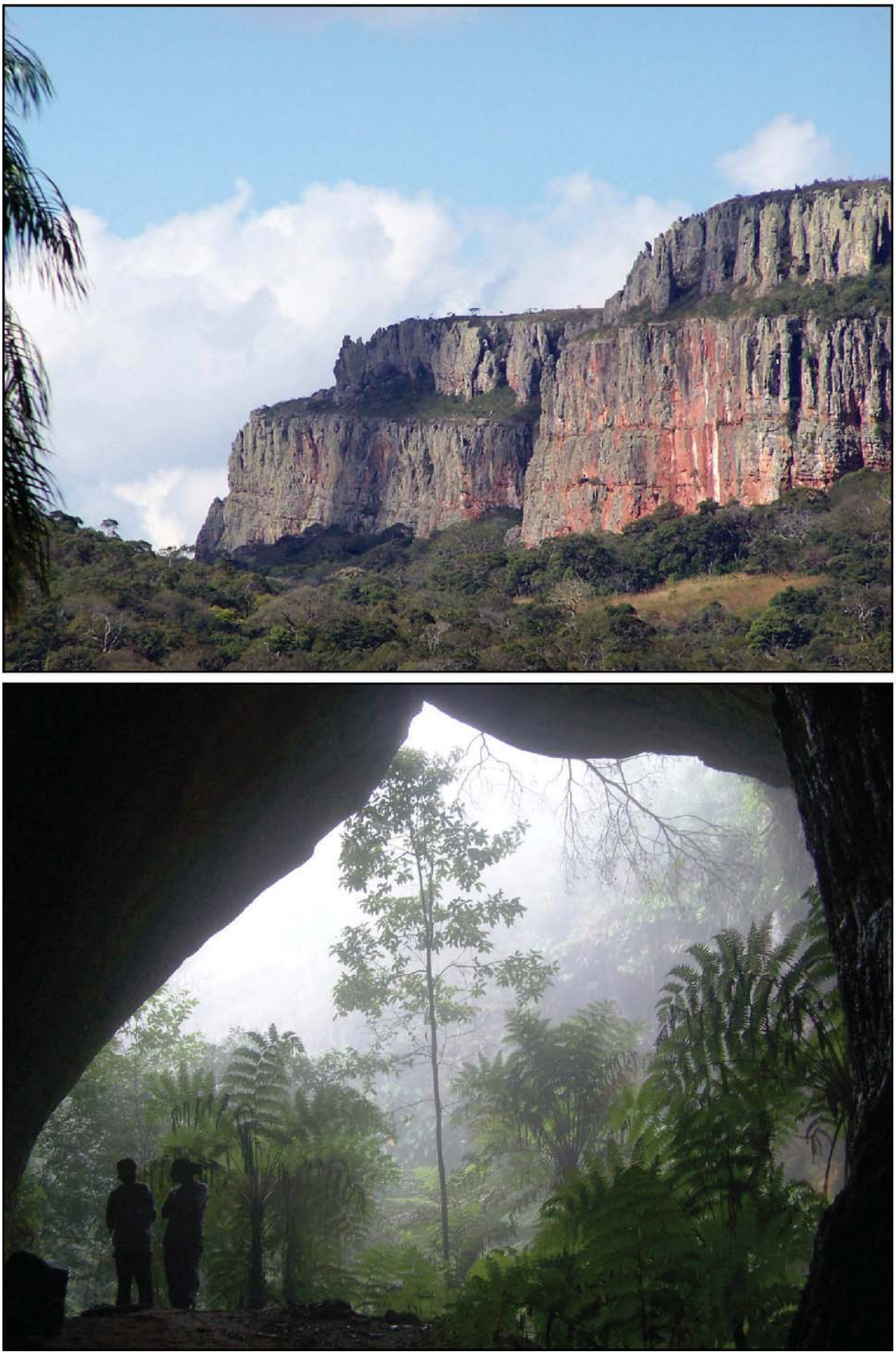


Plate 2. *Top:* Sandstone mesas with savanna (*cerrado*) on the tops and semideciduous forest at the base; Serranía de Santiago, Santa Cruz, Bolivia; habitat of *Natalus espiritosantensis*. *Bottom:* Gullies cut deep into these mesas support a more humid forest.

Plate 3. *Top:* Alluvial sediments covered with thorn scrub; Las Cuevas, Baja California Sur, Mexico; habitat of *Natalus mexicanus*. *Bottom:* Granite inselbergs covered in sparse xaxicolous vegetation with rainforest at the base; Les Nouragues, French Guiana. Rocks piled at the base of these inselbergs often form caves that may harbor *Natalus tumidirostris*.

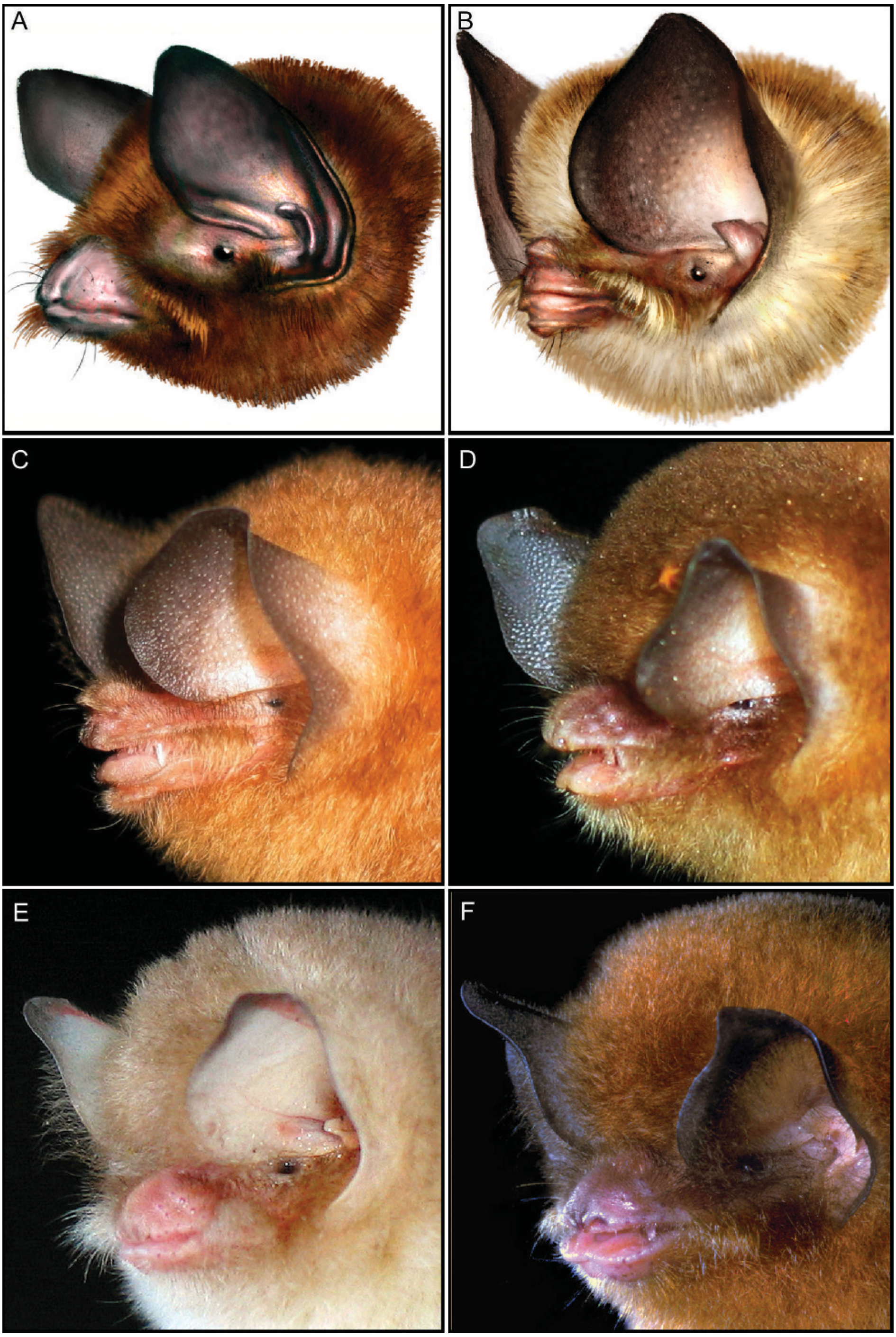


Plate 4. **A,** *Nyctiellus lepidus,* Cueva del Calabazar (locality 142), Pinar del Río, Cuba (illustration A. Tejedor); **B,** *Chilonatalus macer*, Cueva del Calabazar (locality 142), Pinar del Río, Cuba (illustration: A. Tejedor); **C,** *Chilonatalus micropus*, Arroyo Chico (locality 197), Samaná, Dominican Republic (photo: G. Nuñez/A. Tejedor); **D,** *Natalus major*, Cueva de la Laguna Juan García (locality 194), Samaná, Dominican Republic (photo: G. Nuñez/A. Tejedor); **E,** *Natalus mexicanus*, Cueva Chica, Las Cuevas (locality 260), Baja California Sur, Mexico (photo: G. Nuñez/A. Tejedor); **F,** *Natalus tumidirostris*, Patawa (locality 216), Kaw, French Guiana (photo: Brian W. Keeley).

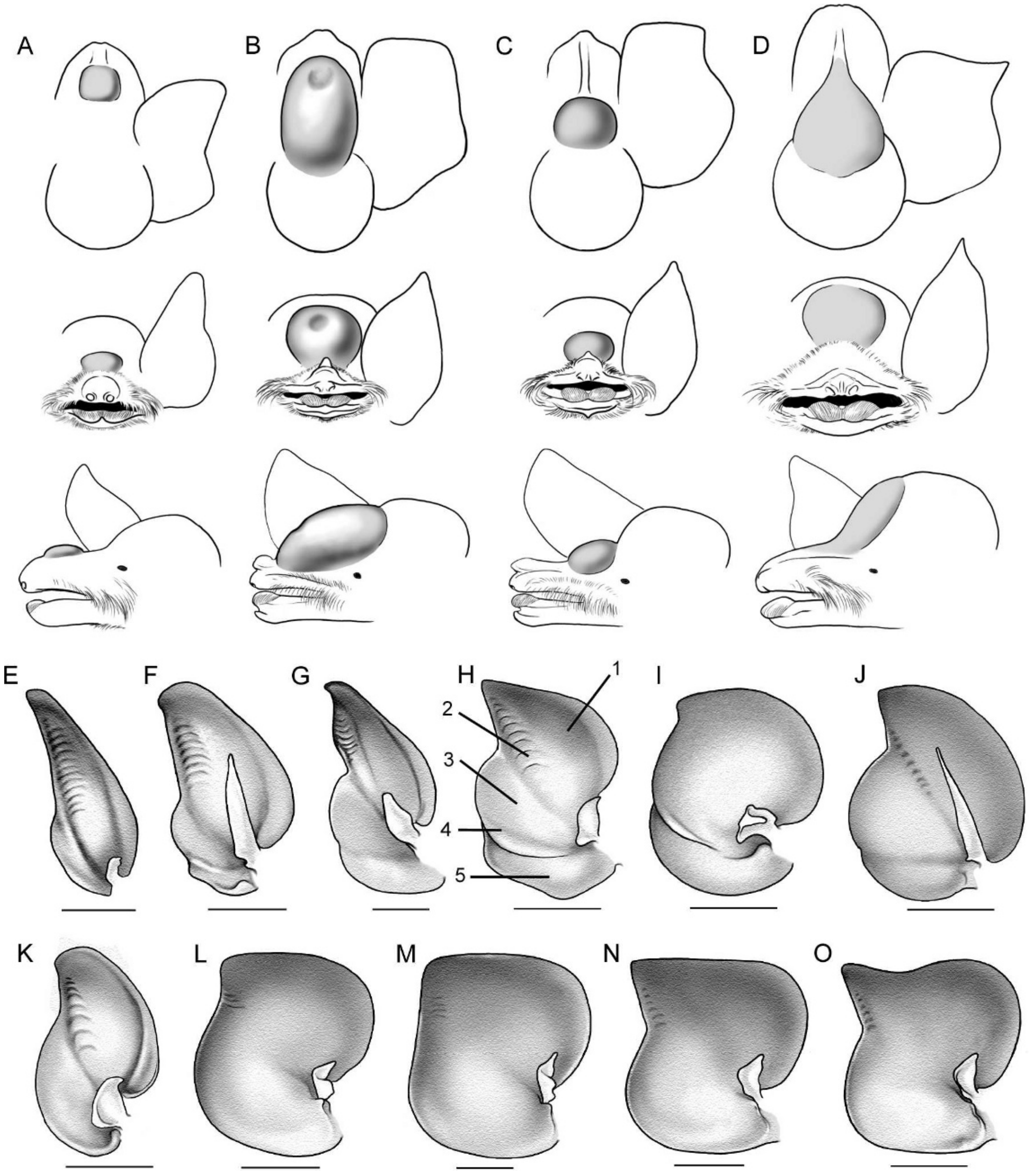


Plate 5. Dorsal, frontal, and lateral views (first, second, and third rows, respectively) of the natalid organ (in gray shading) in four species of Natalidae: **A,** *Nyctiellus lepidus*; **B,** *Chilonatalus macer*; **C,** *Chilonatalus micropus*; **D,** *Natalus tumidirostris*. Anteroventral view of the maximally extended ear pinna in six bat species with lanceolate ear pinna: **E,** *Saccopteryx bilineata*; **F,** *Myotis nigricans*; **G,** *Pteronotus pranelli*; **H,** *Thyroptera tricolor*; **I,** *Furipterus horrens*; **J,** *Kerivoula hardwickei*; and in five species of Natalidae: **K,** *Nyctiellus lepidus*; **L,** *Chilonatalus micropus*; **M,** *Natalus primus*; **N,** *Natalus major*; **O,** *Natalus tumidirostris*. Regions of the ear pinna: 1, distal pinna; 2, ear folds; 3, lateral extension of the pinna; 4, basal (ventral) extension of the pinna. Scale bars = 5 mm.

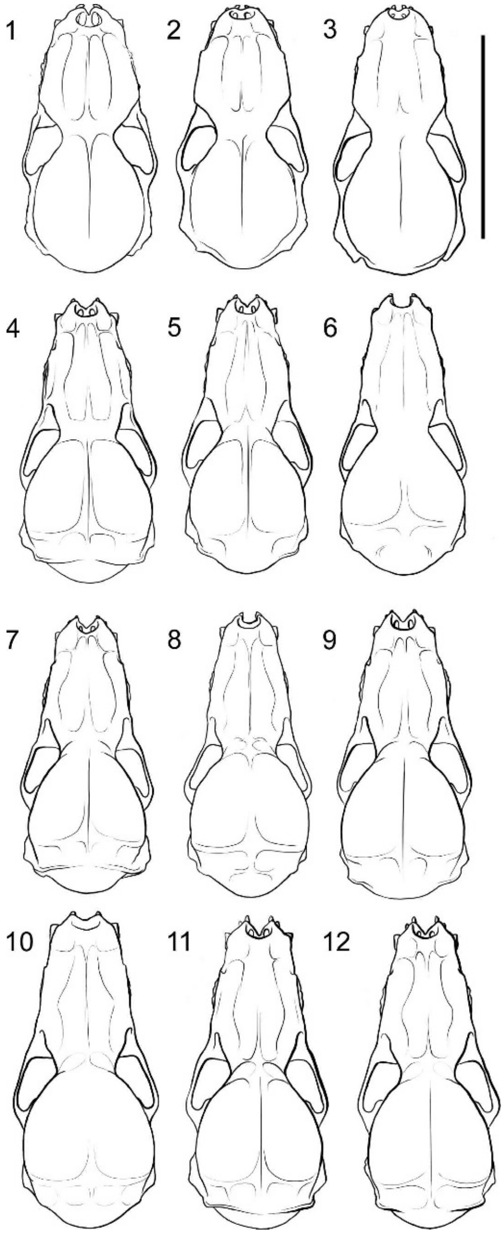


Plate 6. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: Dorsal view. Specimens: *Nyctiellus lepidus*: (1) AMNH 167133, male, Little Exuma, Bahamas; (2) AMNH 61169, male, Havana, Cuba; (3) UF 4454, Long, the Bahamas; *Chilonatalus micropus*: (4) AMNH 216125, male, Samaná, Dominican Republic; (5) USNM 15849, Providencia Isl., Colombia; (6) BMNH 80.12.14.1, holotype, Kingston, Jamaica; *Chilonatalus macer*: (7) AMNH 186980, male, Isle of Pines, Cuba; (8) USNM 113724, holotype, female, Baracoa, Cuba; (9) AMNH 126161, La Habana, Cuba; *Chilonatalus tumidifrons*: (10) USNM 122024, male, San Salvador Isl., the Bahamas; (11) USNM 576614, male, Abaco, the Bahamas; (12) UF 24853, male, Abaco, the Bahamas.

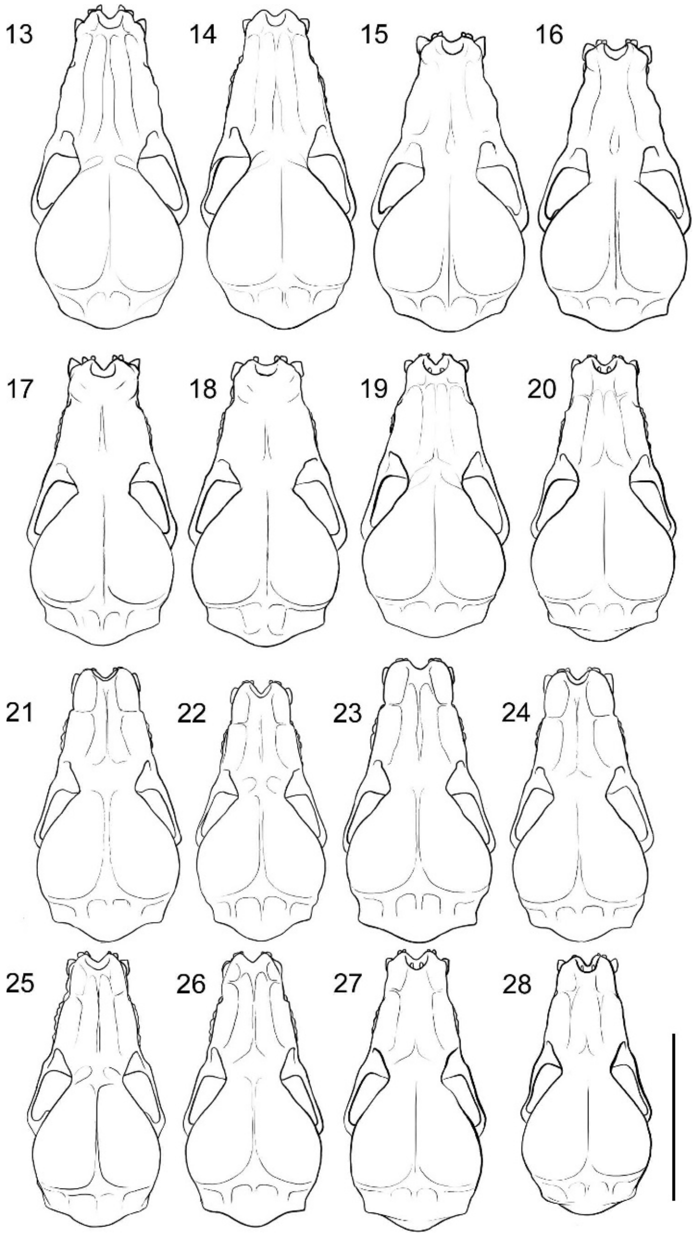


Plate 7. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: dorsal views, continued. Specimens: *Natalus primus*: (13) AMNH AT 1, field number, female, Pinar del Río, Cuba; (14) AMNH AT 2, collector number, female, Pinar del Río, Cuba; *Natalus jamaicensis*: (15) AMNH 182000, male, St. Catherine, Jamaica; (16) AMNH 246127, male, St. Catherine, Jamaica; *Natalus major*: (17) USNM 101395, holotype, male, Puerto Plata, Dominican Republic; (18) AMNH 275487, field number, male, Maria Trinidad Sánchez, Dominican republic; (19) AMNH 97589, female, Barahona, Dominican Republic; (20) KU 150721, male, Department du L'Ouest, Haiti; *Natalus stramineus*: (21) BMNH 70.2324, male; (22) FMNH 47702, female, Montserrat; (23) USNM 544834, male, Anguilla; (24) BMNH 18.4.1.4, Antigua; (25) USNM 113605, holotype of *Natalus dominicensis*, male, Dominica; (26) USNM 113601, male, Dominica; (27) 18215, Dominica; (28) KU 150727, female, Grande Terre, Guadeloupe.

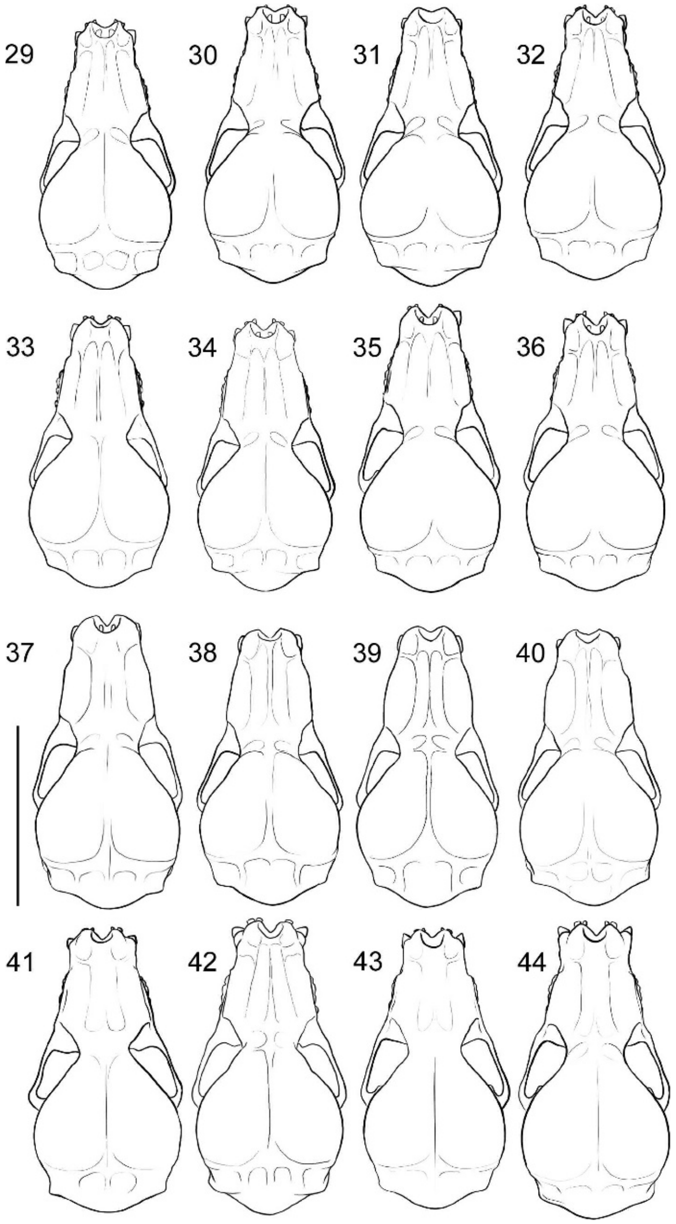


Plate 8. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: dorsal views, continued. Specimens: *Natalus lanatus*: (29) KU 39628, male, Nayarit, Mexico; 30) KU 39620, holotype, female, Nayarit, Mexico; (31) KU 82901, male, Veracruz, Mexico; (32) MSB; *Natalus mexicanus*: (33) USNM 96476, holotype, female, Baja California Sur, Mexico; (34) KU 39677, female, Nayarit, Mexico; (35) KU 23815, male, Veracruz, Mexico; (36) USNM 519080, male, Canal Zone, Panama; *Natalus espiritosantensis*: (37) USNM 549504, male, Pará, Brazil; (38) USNM 242830, holotype of *Natalus stramineus* natalensis, Rio Grande do Norte, Brazil; (39) MBML 1801, holotype, Espirito Santo, Brazil; (40) MNK 2072, male, Santa Cruz, Bolivia; *Natalus tumidirostris*: (41) ROM 45239, male, Sucre, Colombia; (42) AMNH T7, field number, male, Zulia, Venezuela; (43) USNM 102106, holotype, male, Curaçao; (44) female, Kaw, French Guiana.

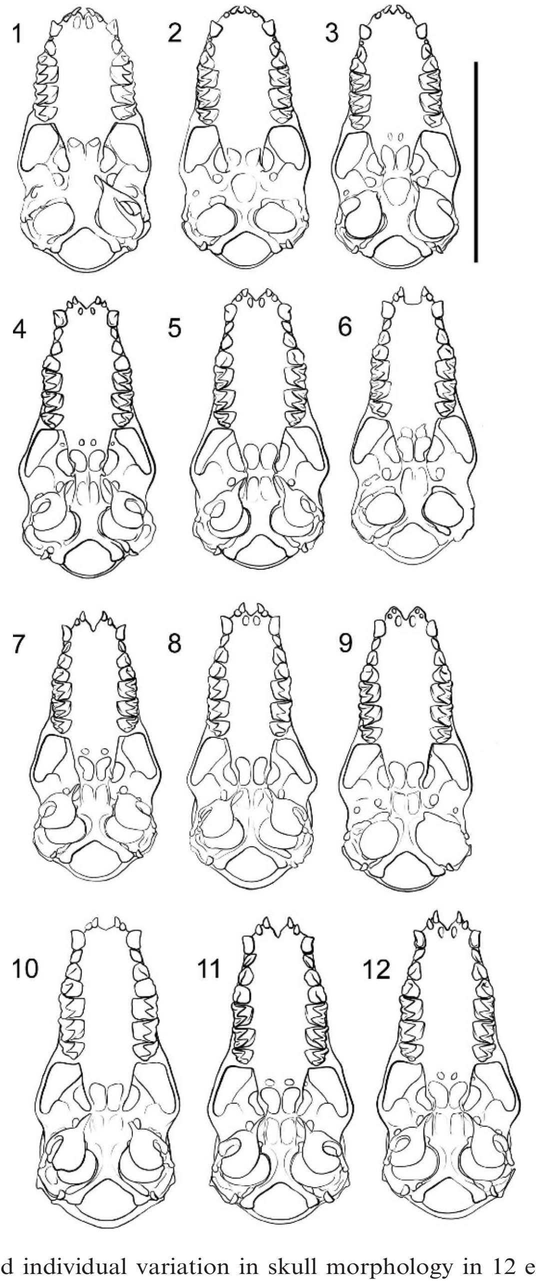


Plate 9. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: ventral views. For specimen numbers, see plate 6.

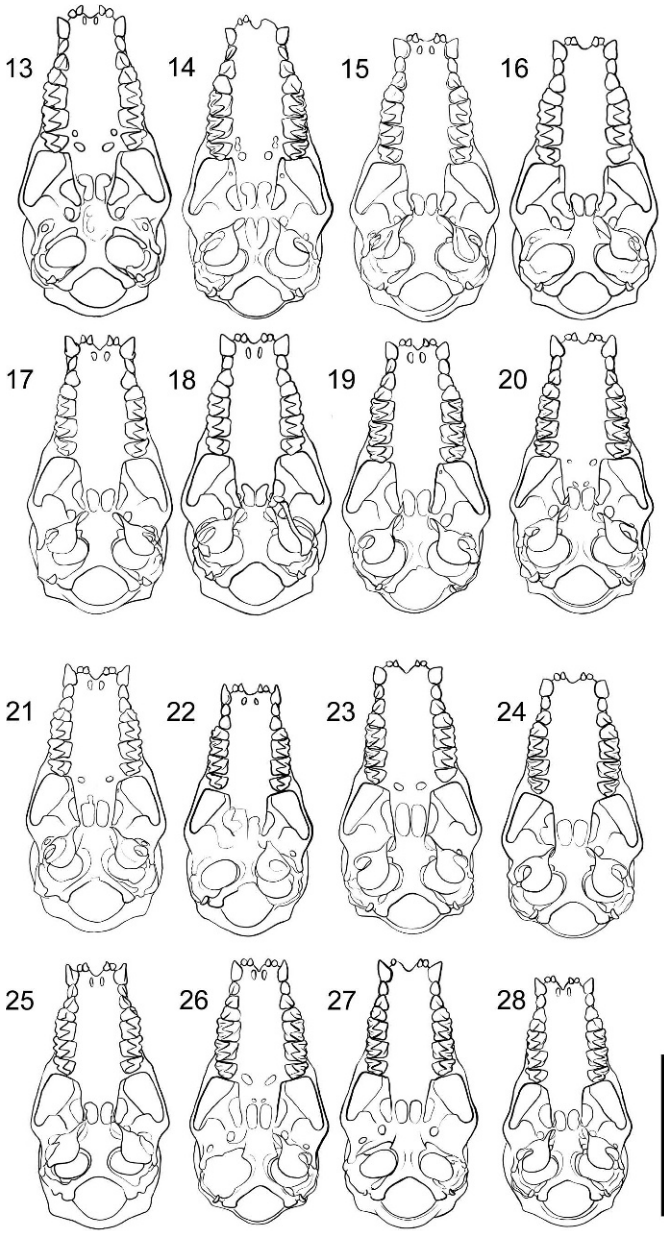


Plate 10. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: ventral views, continued. For specimen numbers, see plate 7.

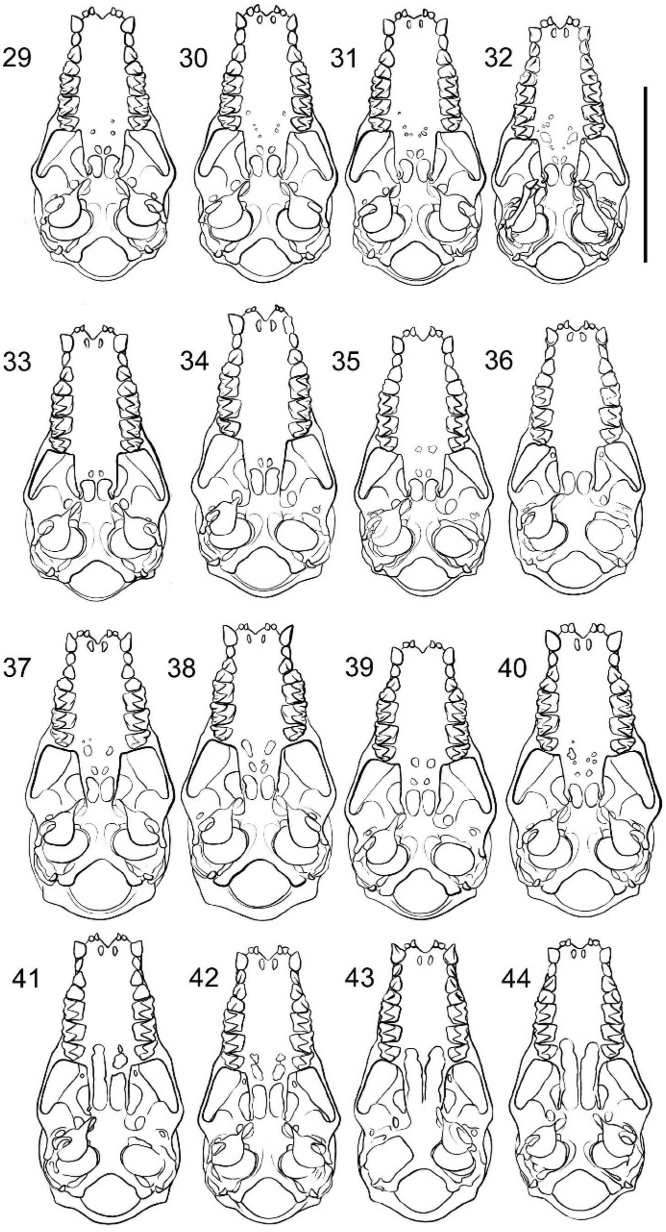


Plate 11. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: ventral views, continued. For specimen numbers, see plate 8.

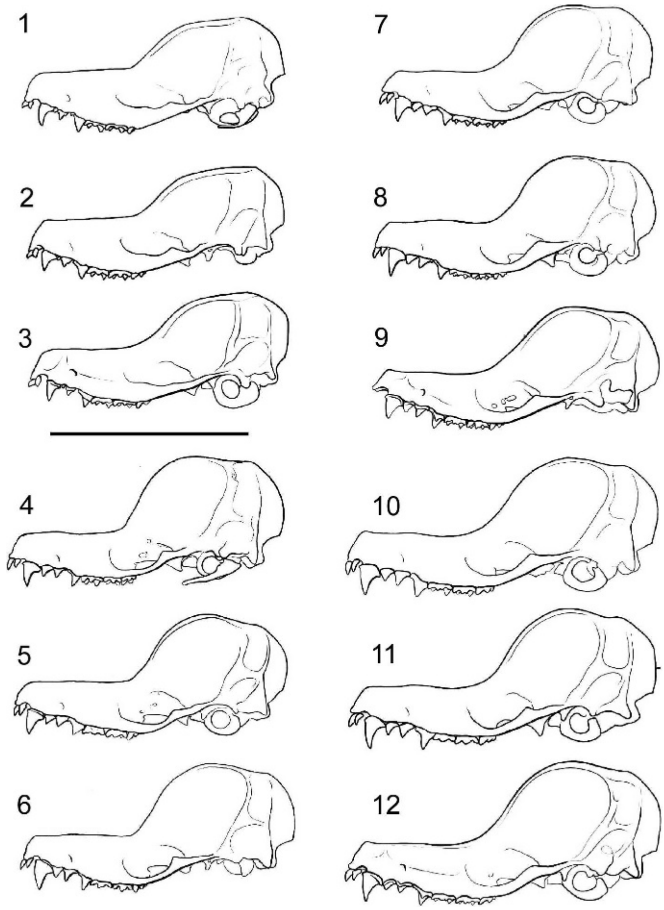


Plate 12. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: lateral views. For specimen numbers, see plate 6.

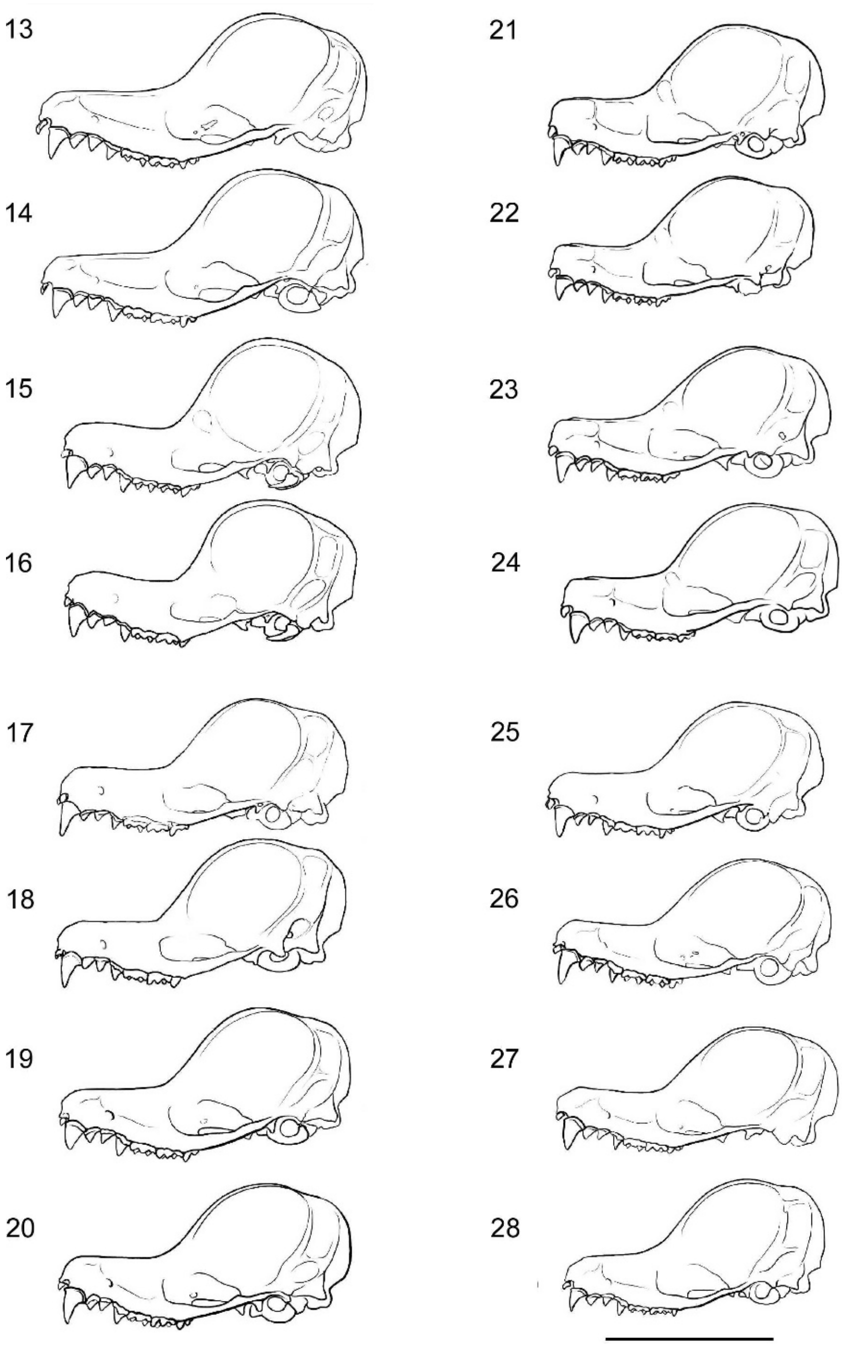


Plate 13. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: lateral views, continued. For specimen numbers, see plate 7.

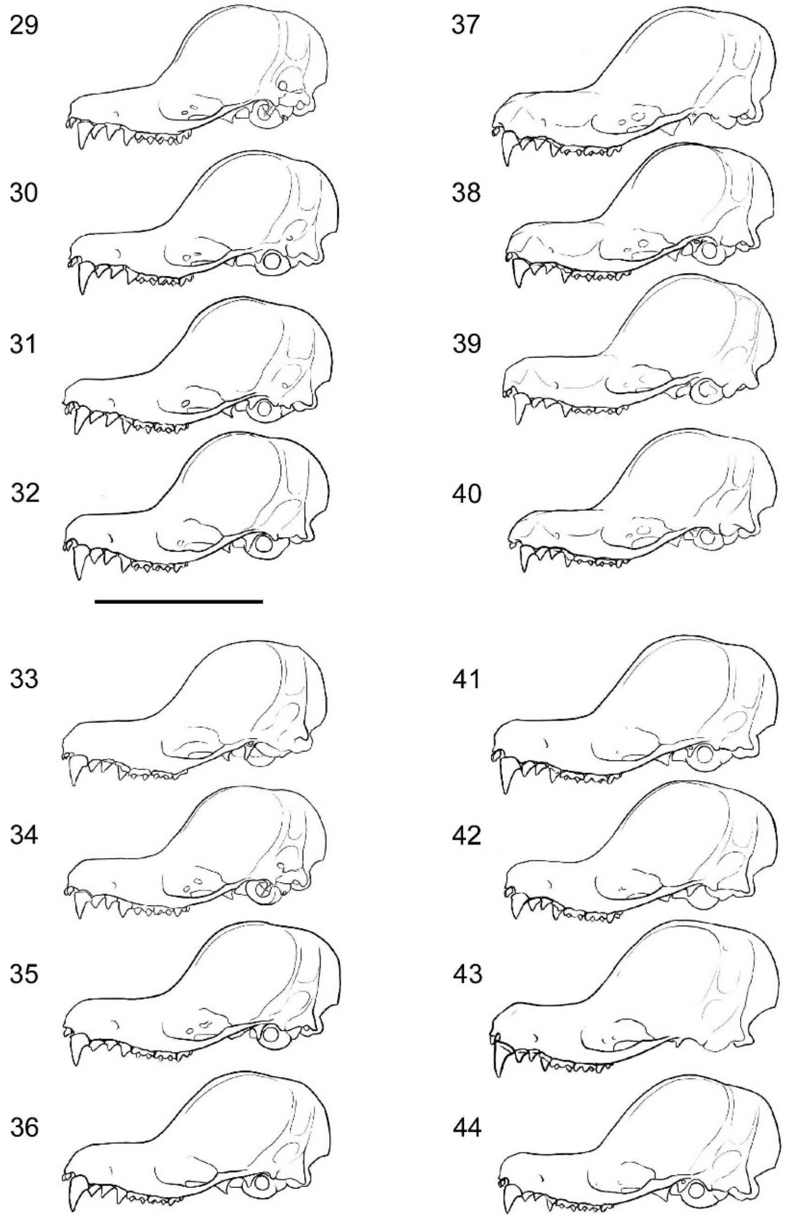


Plate 14. Geographic and individual variation in skull morphology in 12 extant species of Natalidae: lateral views, continued. For specimen numbers, see plate 8.

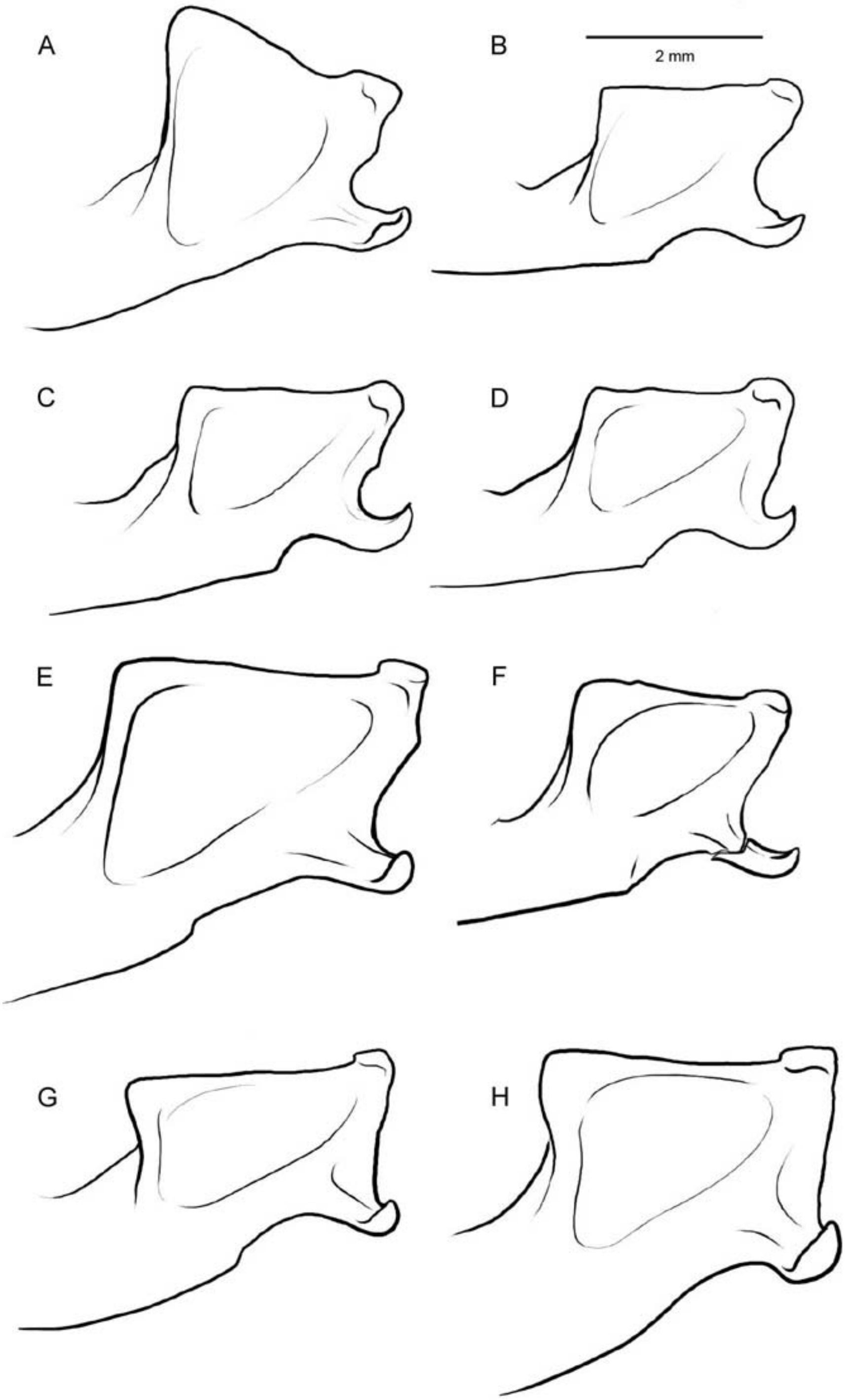


Plate 15. Lateral view of the ascendant ramus of the left dentary of *Myotis* (**A,** included for comparison) and seven species of Natalidae: **B,** *Nyctiellus lepidus*; **C,** *Chilonatalus micropus*; **D,** *Chilonatalus macer*; **E,** *Natalus primus*; **F,** *Primonatalus prattae*; **G,** *Natalus mexicanus*; **H,** *Natalus major*.

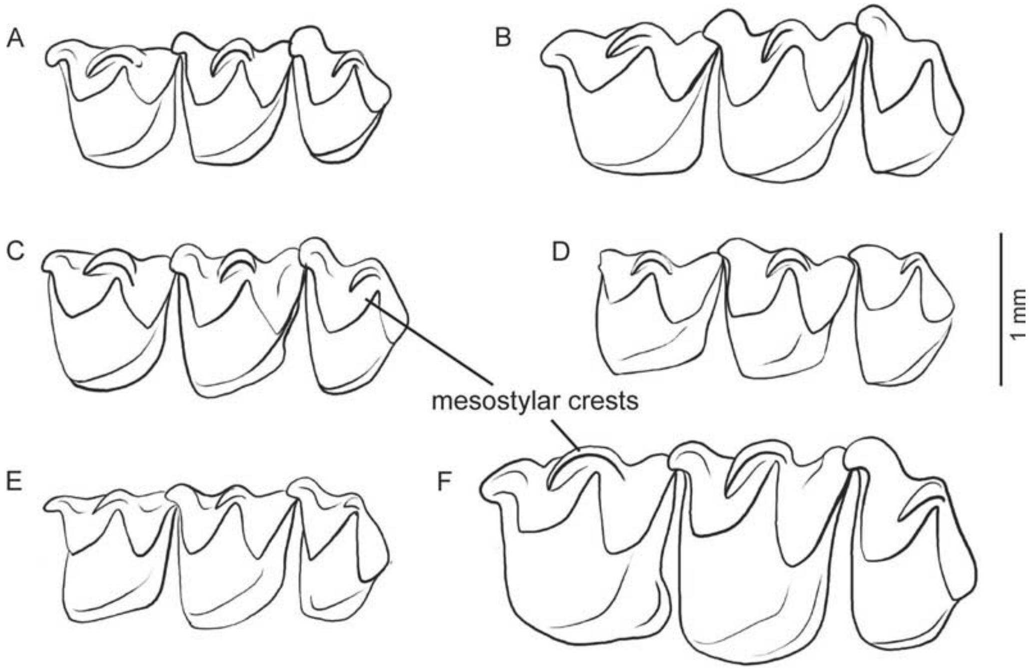


Plate 16. Left upper molar tooth row in 6 species of Natalidae: **A,** *Nyctiellus lepidus*; **B,** *Chilonatalus tumidifrons*; **C,** *C. micropus*; **D,** *Natalus primus*; **E,** *Primonatalus prattae*; **F,** *Natalus mexicanus*.

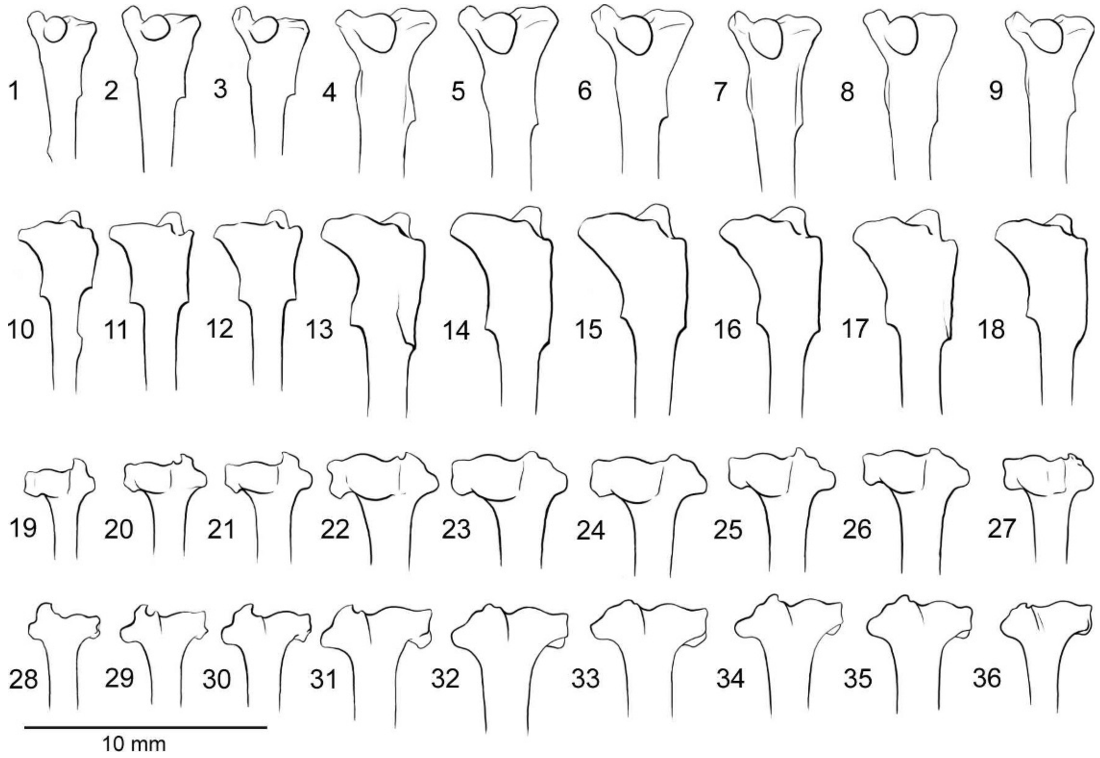


Plate 17. Proximal (two upper rows) and distal (two lower rows) epiphyses of the left humerus (ventral views: 1–9, 19–27; dorsal views: 10–18; 28–36) in 10 species of Natalidae:—1, 10, 19, 28, *Nyctiellus lepidus*;—2, 11, 20, 29, *Chilonatalus micropus*;—3, 12, 21, 30, *C. macer*;—4, 13, 22, 31, *Natalus primus*;—5, 14, 23, 32, *N. major*; —6, 15, 24, 33, *N. jamaicensis*;—7, 16, 25, 34, *N. tumidirostris*;—8, 17, 26, 35, *N. espiritosantensis*;—9, 18, *N. mexicanus* (proximal epiphysis only);—27, 36, *Primonatalus prattae* (distal epiphysis only).

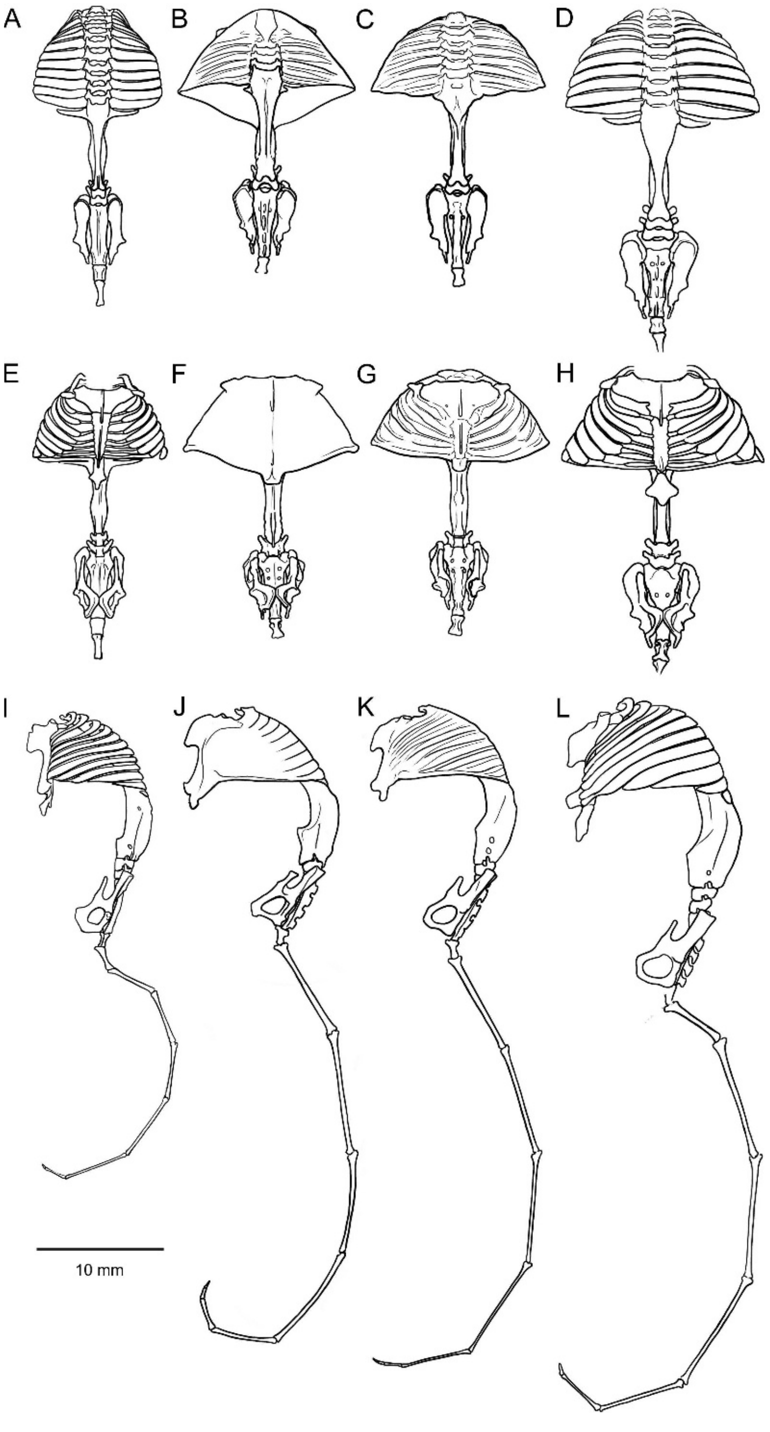


Plate 18. Dorsal (top), ventral (middle), and lateral (bottom) views of the axial skeleton of four species of Natalidae: **A, E, I,** *Nyctiellus lepidus*; **B, F, J,** *Chilonatalus macer*; **C, G, K,** *C. micropus*; **D, H, L,** *Natalus tumidirostris*.

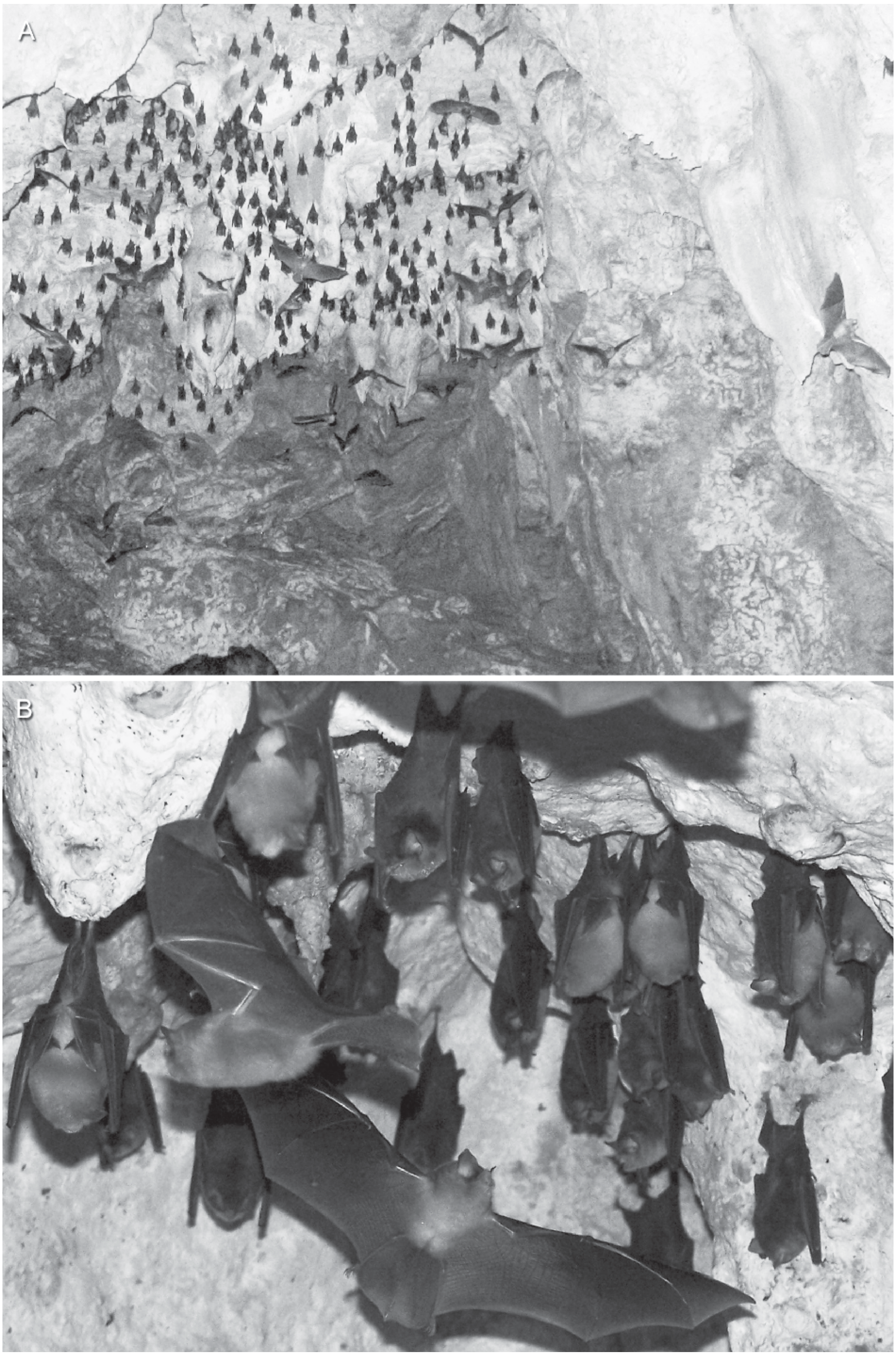


Plate 19. Roosting habits of *Natalus major*. **A,** Roosting group of females in Cueva de Cristian (locality 185), Hato Mayor, Dominican Republic. Natalids often roost in loose aggregations of uniformily spaced out individuals of a single sex. **B,** Group of adult females and young adults of both sexes in Cueva de Murciélagos (locality 190), María Trinidad Sanchéz, Dominican Republic. When disturbed, adult bats are the first to fly away to alternative roosting sites within caves.