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SYSTEMATICS AND PHYLOGENY OF THE NEW WORLD BAT FAMILY NATALIDAE

by

ADRIAN TEJEDOR

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

2007

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Abstract

SYSTEMATICS AND PHYLOGENY OF THE NEW WORLD BAT FAMILY NATALIDAE

by

Adrian Tejedor

Adviser: Dr. Nancy B. Simmons

The current Biodiversity Crisis has made the cataloging and understanding of the planet's biological diversity an urgent matter. Living groups with poorly-understood diversity may become extinct before their potential contribution to understanding the organizing principles of life, or their direct benefits to humanity, may be realized. By attempting to deepen our knowledge on even comparatively small sections of the world's biota, systematists counter the loss of biodiversity. Here, I present a systematic study of Natalidae, a little-known bat family that provides a clear example of underestimated biological diversity. The family was traditionally assumed to comprise a small assemblage of uniform species, and therefore interesting patterns of morphological diversification and biogeography contained in the family had been overlooked. In this work, I revise the recognized diversity of Natalidae by compiling recent changes in the taxonomy of the family and by redefining its distributional and species limits. In addition, I provide hypotheses of the phylogeny of the family that lay the groundwork for comparative analyses of the functional morphology, reproductive biology, and biogeographic history of these bats. As a result, Natalidae is shown here to be much more diverse in terms of number of species and morphological adaptations than what was previously supposed. Moreover, the unique biogeographic history of the family interpreted from estimations of its phylogeny provides a potentially crucial datum for understanding the process of faunal formation among Neotropical bats.

ACKNOWLEDGEMENTS

I express my greatest gratitude to my dissertation committee members, Nancy B. Simmons, John H. Wahlert, Robert. S. Voss, Christopher Raxworthy, Robert. F. Rockwell, who for the last seven to five years have selflessly provided continued support, have demonstrated immense patience with the planning of committee meetings, have read manuscripts, dissertation and grant proposals, and have gone out if their way to keep me on the right way.

Among them I would like to highlight the role of my primary advisor Nancy B. Simmons and of my officemate and professor of Mammalogy John H. Wahlert. The first gave me a true home in the Department of Mammalogy of the American Museum of Natural History (AMNH), allowing me to benefit from the material and intellectual resources of this institution, cheerfully supported and shaped my often incongruous ideas about how to do a PhD dissertation, and showed inexhaustible tolerance for my various excursions from the dissertation. The second was a kind of guardian angel, reminding me of deadlines, providing enormous help with illustration software, hardware, and advice, and creating a friendly and stimulating working environment.

The completion of this thesis was possible thanks to the accumulated help from a long list of people and institutions. I acknowledge them below and apologize for those that I may have inadvertently missed.

I am very thankful to the staff of the AMNH, and of the PhD program in Biology at CUNY. At the AMNH Department of Mammalogy, Patricia Brunauer, Eileen Westwig, Ruth O’Leary, Erica Pannen, Darrin Lunde, Neil Duncan, Chris Norris, Ross MacPhee, Patricia Wynne, and Richard Monk helped with everything from paperwork to

specimen preparation. The staff of the AMNH library, most specially Mary DeJong, kindly searched for and made available rare and crucial publications. At CUNY, Joan Reid, Jane Gallagher, Rocky Rockwell and John Wahlert helped me navigate the bureaucratic maze of the PhD program.

This thesis received generous support from several funding programs. My life and work in New York was possible thanks to a Graduate Student fellowship from the Office of Grants and Fellowships, AMNH, and to a Magnet Dissertation fellowship from the Graduate Center at CUNY. Laboratory expenses and trips abroad were funded by the National Science Foundation Dissertation Improvement Grant (DEB−0407950), The Theodore Roosevelt Memorial Grant (AMNH), The American Society of Mammalogists Grants-in-aid Program, the Sue Rosenberg Zalk Student Grant (Graduate Center, CUNY), an Ernst Mayr Travel Award (Museum of Comparative Zoology, Harvard University), and an Exploration Grant from the Explorer's Club. The staff of the AMNH Grants and Fellowships office, Diane Bynum, Maria Dickson-Ríos, and Barbara Green, was especially helpful in delivering these funds.

My work at the Genomics Laboratory of the AMNH would not have progressed without the support and guidance of Eric Stiner, Jose G. Tello, Matthew Leslie, Cathi Lehn and Rob DeSalle. Lots of additional help was offered by lab-mates and lab staff: Chanda Benett, Francisca Almeida, Diana Warren, Martín Méndez, Mike Friedman, Angelica Cibrián. Fabricio Santos and Rodrigo Redondo kindly supplied a gene sequence obtained at their laboratory of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil.

My visits to museums abroad (acronyms listed in Chapter 2: Appendix I) were graciously hosted and arranged by Richard Harbord, Paula Jenkins (BMNH), Renato Gregorin (DZSJRP), Javier Sánchez (EBRG), Candace McCaffery (FLMNH), Belkis Rivas (FLS), William Stanley and Michi Schulenberg (FMNH), Thor Holmes (KU), Marlene Hoffman and Helio de Q. B. Fernandes (MBML), Mercedes Salazar and Carmen Ferreira (MBUCV), Judith Chupasko and Mark Omura (MCZ), Robert Asher and Irene Thomas (MFN), Norka Rocha (MNK), Gilberto Silva-Taboada (MNHN), Cindy Ramotnik (MSB), Mario de Vivo (MZUSP), Gary Morgan (NMMNH), Pascual Soriano (ULA), Linda Gordon, Helen Kafka, Jeremy Jacobs (USNM). In addition, Jim Dines (LACM), Judith Eger (ROM), Robert Baker, Heath Garner, and Peter Larsen (TTU), and Annie Tibbels kindly loaned tissue and/or specimens in their care.

Many people helped with field work with their direct participation and/or arranging collecting permits and logistics. They include Brian Keeley, Scott Mori, and Vanessa Hequet (French Guiana), Aidee Vargas (Bolivia), Johanset Orihuela, Kevin Murray, Gabriela Nuñez, Isaias Olmo, Miqueas, Nelson García Marcano, and Renato Rimoli (Dominican Republic), Carlos Mancina, and Valeria Tavares (Cuba), Flavio, Ricardo, Rodrigo Redondo, and Maria Olimpia Lopes (Brazil), Ascanio Rincón, Jafet Nassar, and Jose Reyes (Venezuela), Celia López González, Gabriel Villegas, and Gabriela Nuñez (Mexico).

During my thesis years, colleagues and friends at the AMNH and abroad made life more productive and pleasurable by stimulating discussion, sharing information, and providing companionship and hospitality. They are Marcela Gómez-Laverde, Lara Lopardo, Neusa, Francisco and Rachel Rocha, Bernal Rodriguez, Richard Kraft, Alexandra Bezerra, Marcelo Weksler, Ana Luz Porcekanzki, Ilya Temkin, Luis Orioni, Louise Crawley, Patricia Brito, Roberto Keller, Liliana Dávalos, Suzanne McLaren, Megan Cevasco, Milena Rodríguez, Elisa Bonaccorso, Fernando A. Cervantes, Luis Aguirre, J. M. Guayasamín, Janet Castro, Anikka Keeley, Jose Belliard, and Johanset Orihuela. Among them, Robert P. Anderson, Norberto P. Giannini, and Jose G. Tello, have blurred the distinction between friend and mentor, whereas Gabriela Nuñez, Pere Bover, Sara Bertelli, Enrique Peñalver, and David Flores (el Turco) have blurred the distinction between friend and family. To them, I am inmensely greatful.

The topic of this dissertation owes much to the late Justine Salton and most especially to Valeria Tavares, who exhorted me to pursue the questions that intrigued me the most. The fact that I chose bats, owes much to the guidance and inspiration I got from two world-class scholars in the field, Gilberto Silva Taboada, and Theodore H. Fleming.

I am most deeply indebted to my biological family: Sylvia Gutierrez, Oscar Tejedor Jr., Denis Tejedor, Oscar Tejedor Sr., Adela Alvarez, Sylvia Valliciergo, Rafael Gutierrez, and Clara Albear (honorary ancestor). Throughout my life, they have given unconditional love and support and have taught me to look at nature with awe and skepticism.

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Chapter 4: Ecomorphological evolution and biogeography of Natalidae

Introduction

In recent decades, the study of the Earth's biological diversity has gained new momentum (Wilson, 2004). This increase has stemmed from the urgent challenges of the current Biodiversity Crisis (Savage, 1995) and from the incorporation of new methods into comparative biology including phylogenetic analyses, molecular technologies, and geographic informatics (Becerra, 1997; Bisby, 2000; Huelsenbeck and Rannala, 1997). As a consequence, our knowledge of the planet's biological diversity is rapidly increasing(Patterson, 2001; Wilson, 2002), and estimates of the maximum global number of species have risen from 3–5 million to 10 million (May, 1988; Wilson, 2004) or even 100+ million (Curtis et al., 2003). The increasing knowledge of the diversity and history of life has had a profound impact in understanding principles of morphological evolution, the ecological organization of life, and the preservation of life itself, allowing biologists to see under finer focus the critical species and groups in need of conservation measures (Pratt and Pratt, 2001). The global increase in biodiversity awareness is the sum of the work of many taxonomists (*ca.* 6000?; Wilson, 2004) currently working separately on comparatively minute samples of the living world, sometimes focusing on a single family (e.g. Hylidae; Faivovich et al., 2005) a single genus (e.g. *Platyrhinus*; Velazco, 2005) or even a single species complex (e.g. *Astraptes fulgerator*; Herbert et al., 2004).

This dissertation aimed at improving our understanding of the diversity and evolutionary history of the bat family Natalidae. Natalidae comprises bats widespread throughout the tropics of the New World and which are among the most frequently encountered and distinctive members of many Neotropical bat faunas (Emmons, 1990;

Reid, 1997). Natalids are characterized by a small size, a slender and apparently delicate anatomy, and very long legs and tails (Koopman, 1994). These features, together with their very small eyes, pale coloration, and large-funnel shaped ears make them immediately recognizable to mammalogists. As a rule of thumb they are known to roost in caves and to feed on insects but the details of their ecology are largely unknown (Nowak, 1994).

The morphological uniqueness of Natalidae has led to myopic interpretations of their diversity. Their highly-recognizable features allow for easy identification and categorization, so that the subtle but intricate variation present in the family has been overlooked. As many other living groups, Natalidae has gone through waves of proliferation of names and waves of simplification by merging of taxa. The highest diversity recognized within the family was four genera (Miller, 1907) and 11 species (Dalquest, 1950). By contrast, the most conservative treatments of the family have listed only one genus and five species (Varona, 1974; Hall, 1981). The conservative view dominated the last third of the 20th century and obscured interesting patterns of the morphological evolution and biogeography of the group.

In this dissertation, I propose a new systematic revision of Natalidae that strives to represent the diversity of the family in detail. In addition, I provide hypotheses of the phylogeny of the family and use them to understand their biogeographic history and aspects of their morphological variation. Chapter 2 provides a history of the taxonomy of the group, followed by a systematic account of its genera and species, including morphological descriptions, comparisons, summaries of natural history, and discussions of the conservation status for each species. Chapter 3 presents comprehensive estimates of phylogeny for the family, including all recognized extant and fossil natalid taxa. These phylogenies are based on morphological and molecular characters, including new genetic sequences generated for this study. Chapter 4 examines the morphological diversity and pattern of distribution of the family in light of their evolutionary history, and discusses possible ecological and historical mechanisms for the assembly of natalid faunas.

Systematics of funnel-eared bats (Chiroptera: Natalidae)

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 and four or five species. In the past decade, the taxonomy of Natalidae has been revolutionized 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 species and genus rank on the basis of new morphological and molecular evidence. This taxonomic backswing has resulted in a greater than two-fold increase of the recognized species diversity of Natalidae, with profound implications for our understanding of the pattern of diversification of the family, and for the conservation of natalid taxa now recognized as relictual endemics. In spite of these changes, the family has not received a formal taxonomic revision at both the genus and species level for 100 years. Therefore, a comprehensive review of the family Natalidae is needed in order to evaluate the recent changes in the taxonomy of the family and compile and systematize the current understanding of its diversity. Here, I provide a complete taxonomic revision of Natalidae based on the examination of all taxa described thus far within the family. A total of 13 taxa are recognized here as distinct species, including an extinct form. New diagnoses, descriptions, and illustrations are provided for each species, as well as summaries of published information on their natural history and discussions of their conservation

status. As this revision is aimed at aiding proper identification of natalid species both in the field and museum collections, detailed comparisons among species are presented and an illustrated identification key is provided.

INTRODUCTION

The systematic history of Natalidae has gone through three distinct stages: 1) the stage of alpha taxonomy or the description of species and genera; 2) the stage of revision and synonymization; and 3) the evaluation of interrelationships among taxonomic units (beta taxonomy), including numerous revalidations of old synonyms. This succession of taxonomic stages has been common to most living groups (Patterson 2001). As many as three extant genera, one subgenus, 12 species, and 6 subspecies were described in the family Natalidae between 1837 and 1971 (table 1). During the last third of the 20th Century, however, the recognized diversity of Natalidae was in sharp decline, reaching an absolute minimum of one genus and 4 species (table 2). At present, the recognized diversity of the family is greater than ever 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) created the new genus and species *Natalus stramineus* on the basis of a single specimen (Goodwin, 1959; Handley and Gardner, 1990), giving neither information of the geographic origin of that specimens nor his reasons for choosing the generic name. In 1840, the taxon that served as basis for the description of *V. lepidus* was independently renamed as *Vespertilio barbatus* by Gundlach (1840) and latter assigned to the genus *Nyctiellus* by Gervais (1855). Two enigmatic taxa that have been considered synonyms of *Natalus* were also described during this time. One was *Spectrellum macrurum* described by Gervais (1856) from Bahia, Brazil, and of which no holotype, other specimens, or illustrations remain. The second was *Vespertilio splendidus*, a taxon that appears to be referable to *Myotis*, which was described by Wagner (1845) from the island of St. Thomas. The true identity of *S. macrurum* 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* for the first time. In addition, Dobson (1878; page 342) included *Natalus* within Vespertilionidae, noting that the genus was "evidently the representative of [the old world genus] *Kerivoula* in the New World", but stating that characters of the upper incisors allied them 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 taxonomist of this period was Gerrit S. Miller who established Natalidae as a distinct bat family (originally including the genera

Natalus, *Thyroptera*, *Furipterus*, and *Amorphochilus*; 1899), and described 8 taxa. These included one subgenus (*Chilonatalus*, 1898, to include Dobson's *N. micropus*), one genus (*Phodotes*, 1906), and 6 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 4 genera and 8 species within Natalidae and giving it its essential modern form (table 2). Additional taxa described by other 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 to 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 reduced all natalid genera (except *Phodotes* which he deemed indistinguishable from *Natalus*) to subgenera of *Natalus* (Dalquest, 1950). 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 that was 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 trough 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) arrangement, 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 last three decades of natalid taxonomy has been dominated by a backswing toward the revalidation of synonyms as distinct species. In 1982, Ottenwalder and Genoways argued for the separation of *Natalus tumidifrons* from *Natalus 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, USA, 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 3 genera and 8 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 (in press) revalidated *N. espiritosantensis* and *N. mexicanus* as species distinct from *N. stramineus*, but synonymized *N. saturatus* with *N. mexicanus*. 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 (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 25 museums, all of which are listed in Appendix I. Museum abbreviations are also listed in Appendix I.

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 8 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 anterior-most point of the skull, including the incisors, and the posterior-most 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 toothrow, measured from the anterior-most edge of the canine to the posterior-most edge of M3.

Mandibular toothrow length: Greatest crown length of the mandibular toothrow, measured from the anterior-most edge of the canine to the posterior-most edge of m3.

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

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

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

In addition, to graphically represent interspecific variation in cranial shape, several indexes 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. In figures, tables and Appendix II, 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: Two-way ANOVAs were used to detect overall differences among species, populations (geographic subsets within a given species), between sexes, and interaction effects between populations/species and sex. Where interaction effects were found to be absent, one-way MANOVAs (performed over all variables simultaneously) were used to detect sexual differences within species. One-way MANOVAs (performed over all variables simultaneously) were used to detect differences between populations in the best represented sex only in species for which the sample size of one of the sexes was very small, for which sexual differences had been detected with previous ANOVAs, and for which only two populations were being compared. In species where simultaneous one-way MANOVAs were impractical due to unequal distribution of missing values among variables, one-way ANOVAs were performed separately for each variable. Tukey tests (for unequal sample sizes) were performed as post-hoc comparisons over the results generated by the two-way ANOVAs and the one-way MANOVAs to detect pair-wise 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.

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), northern South America (N 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 semi-arid to wet), below 2500 m (fig. 1).

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; very 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 ectocyngulum; manubrium of sternum expanded laterally into plate-like structure; very 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 middle 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. Wing membranes are very thin and translucent. The plagiopatagium inserts variously 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. Their body pelage is long, usually lax, and variously woolly, ranging widely in coloration from pale buff to rich chestnut brown (Appendix II: Plate 1). Usually, ventral hairs are monocolored and dorsal hairs are bicolored with darker tips and lighter bases, with the exception of one species (*N. lanatus*) in which both ventral and dorsal hairs have darker bases and lighter tips. Their faces are long, slender, and dorsoventrally flattened. Natalids have a relatively simple facial anatomy, lacking, with the exception of the genus *Chilonatalus*, dermal folds and excrescences that are typical of other tropical bat families. Their relatively smooth faces show areas of dense pelage along the lateral margins of the upper lips and usually on the dorsum of the rostrum, giving these bats the appearance of having thick mustaches. The mustache hairs are curved ventrally and may direct airflow toward their mouths and or ears, as has been suggested for the bat family Mormoopidae (Smith, 1972). Their nostrils in general are oval-shaped, ventrolaterally oriented and open at the end of a dorsally prominent longitudinal nasal ridge and virtually on the edge of the upper lip. Their lower lips are thickened and show a paired central pad incised by dozens of diagonal grooves with the appearance of primate dermatoglyphs.

In the dorsum of the rostrum, in males, there is a unique organ called the natalid organ. This organ is generally visible externally as a swollen mass, which can reach relatively large proportions in the genus *Chilonatalus*. The natalid organ secretes a translucent, greenish, and viscous liquid, with possible communication functions.

The ear size is medium to large, 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 are relatively smooth, having the typical bat ear ridges extremely reduced in size and restricted to a narrow area near the lateral margin of the distal pinna. The hair follicles of the ventral surface of the ear, on the other hand, are relatively conspicuous. A cartilaginous ridge (between the lateral and ventral regions of the ear pinna) is absent. The tragus is small, with a lanceolate, pointed tip, and contorted into a funnel-shaped structure. The eyes are very small, seem to be surrounded by the ears, and are partially hidden by the profuse facial pelage.

The skull of funnel-eared bats is long and delicate, with a long, narrow, and dorsoventrally flattened rostrum (Appendix II: Plates 2–10). 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. Palatal branches of premaxilla fused along median line leaving two small foramina and a slight rostral emargination. The infraorbital canal is very long, extending from P2 to M2. Caudally, the infraorbital canal opens in a depression termed the lachrymal fossa (Morgan and Czaplewski, 2003). The ectotympanic is expanded rostrally into a styliform process. The dental formula is 2/3, 1/1, 3/3, 3/3 = 38. There is a small diastema 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).

The axial skeleton has various degrees of fusion between its constituting bones. The vertebrates C7 to T1 up to C7 to T6 are fused among them and with the ribs. The vertebrae from last dorsal to antepenultimate or penultimate lumbar are fused into a continuous, laterally compressed column with no evidence of sutures between the constituting elements. The sternum is expanded laterally into a plate-like structure. The ribs are greatly expanded craniocaudally or fused entirely among them and with sternum into a continuous thoracic bell-shaped structure. The tail vertebrae are greatly elongated.

IDENTIFICATION KEY FOR 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

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. 5A); in males, penis long (3.6–6.5 mm) and natalid organ small and hemispheric (fig. 5A)..... *Chilonatalus micropus*

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

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*

SPECIES ACCOUNT

Genus *Nyctiellus* Gervais, 1855

Natalus Dobson, 1878: 344.

Natalus (*Nyctiellus*) Dalquest, 1950: 443.

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 7 or more ear ridges; ear tip rounded; funnel-like form restricted to lateral and basal portions of ear pinna; broad, deep rostrum; swollen maxilla; low braincase; slight cranial flexion, anterior portion of zygomatic arches wider (deeper) than twice the height of last molars; 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; basisphenoid pit deep and lacking longitudinal septum; slight palatal emargination; free edge of uropatagium lacking fringe of hairs; natalid organ low, rather square-shaped (with nearly parallel lateral margins) never reaching forehead. A comparison of diagnostic characters between *Nyctiellus*, and other natalid genera is summarized in table 3.

ETYMOLOGY: Latinized diminutive from “Nychta”, Greek for “Night”. Little nocturnal being.

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 (1855) transferred *V. lepidus* to the genus *Nyctiellus*.

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

Nyctiellus lepidus: Gervais, 1855: 84. New name combination.

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

Vespertilio (*Natalus*) *lepidus*: Gundlach, 1867: 52. New name combination.

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

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

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

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 funnel like; medial ear margin rigid, with longitudinal fold along ventral face; tragus short, wedge-shaped, and contorted into funnel-like 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 mustache-like 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 and steep sided; 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 among themselves and 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 (notoriously 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 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 smaller sagittal crest that is more prominent in its rostral half. In *N. lepidus*, the maxillary 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 caudal 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 very small so that the inner incisors (I1) almost touch each other along the midline, whereas in all other natalids the emargination is wider so that the tips of 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 that is always bisected by a longitudinal ridge in all 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 so that a large portion of the periotic can be observed in ventral view.

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

Male specimens of *Nyctiellus lepidus* from the Bahamas averaged smaller than those from Cuba in forearm length ($P < 0.05$; fig. 12) but had broader and deeper skulls (larger means of braincase breadth, postorbital breadth, and braincase depth; $P < 0.05$; fig. 12) and longer maxillary toothrow ($P < 0.05$; fig. 12). *Nyctiellus 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 (in 36 of which it has been found at 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 lit.). Caves occupied by *N. lepidus* vary widely in size (e.g. large, Cueva del Jagüey, with 1700 m of linear extension, Silva-Taboada, 1974; small, Cueva del Calabazar, less than 10 m, Tejedor et al., 2005a). *Nyctiellus lepidus* selects caves or cave chambers with 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 commonly roosts in caves with temperatures toward the low end of that range (Silva-Taboada, 1979). It can be found coexisting with 15 other bat species in the same cave (*Artibeus jamaicensis*, *Brachyphylla nana*, *Chilonatalus macer*, *Eptesicus fuscus*, *Erophylla sezekorni*, *Macrotus waterhousii*, *Mormoops blainvillii*, *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 a very close proximity of human observers (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 up 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 study of food volume consumption by this species in Cueva Caguanes, Cuba, in 1969 it was found that females of this species can carry up to near 30% of their body weight in terms of stomach contents, versus up to 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 less food (about 15 % of body weight) than full adults (about 21%, Silva-Taboada, 1979).

Nyctiellus lepidus has a single annual estrous, and bears one pup per litter. In Cuba, copula 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. Non-reproducing adult females are found throughout the year and pre-adults 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 set 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. Non-reproductive females may be occasionally 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 on average weight 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 113). 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 anguliscuta*, *Eutrombicula lipovskyana*), and streblids (*Trichobius wenzeli*; Milán and Stekolnikov, 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 seasonally 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). It is susceptible to rapid dehydration outside their roost, being the species with 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 near-threatened by the IUCN under (IUCN, 2006). Its ability to form large colonies in very small caves or cave like 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 roosts sites are left undisturbed.

Genus *Primonatalus* Morgan and Czaplewski, 2003

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 arc thin, nearly as deep as crown height of M2; p3 with labial cingulum distinctly indented between roots; oclusal 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: FLMNH 108641, partial right dentary with m1–3, collected by A. E. Pratt in Thomas Farm, 12 km northeast of Bell, Gilchrist County, Florida (fig. 14). Age of fossil deposit: early Miocene, early Hemingfordian.

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 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 diastema; oclusal 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; oclusal 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 three-lobed, 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 can not 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 mot 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, lower and upper dentition are mot similar to those of *Chilonatalus*, and the distal humerus is mot 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 of 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 the fossils assigned to *Primonatalus* belong to a single taxon.

Genus *Chilonatalus* Miller, 1903

Natalus Dobson, 1880: 443.

Natalus (*Chilonatalus*) Miller, 1898: 326.

DIAGNOSIS: Ribs fused into a rigid thoracic bell; dermal outgrowths on dorsum of rostrum and on chin, producing in profile a double-lipped aspect; ears large, without ear ridges; 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; plagiopatagium attaching at mid tibia; mustached formed by parallel hairs forming a compact row. 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 15

Chilonatalus micropus: Miller, 1904: 340. Miller recorded as *C. micropus* a specimen (USNM 113724) collected in Baracoa, Guantánamo, Cuba, which he later renamed as *C. macer* (Miller, 1914).

Chilonatalus macer Miller, 1914: 225. Original description based on material (holotype USNM 113724) collected in Guantánamo, Cuba.

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

Natalus micropus macer: Viña and Deas, 1970: 7. New name 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 16.

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 ½ 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 tube like 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 one half 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 helix-like structure; tibia (18.2–20.3 mm) longer than half the length of the forearm; calcar very long and thin, occupying about two thirds 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 (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 mustache-like 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 convex 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; oclusal 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 to 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 3 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 ½ 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 degrees 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 nor between Cuba and the Isle of Pines.

NATURAL HISTORY AND CONSERVATION: *Chilonatalus macer* is know 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 sleeping tent, and 3) on a sugar-cane plant. 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. It has been found coexisting in the same caves with 13 other bat species (*Artibeus jamaicensis*, *Brachyphylla nana*, *Eptesicus fuscus*, *Erophylla sezekorni*, *Macrotus waterhousii*, *Mormoops blainvillii*, *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 up to 2521 mm of annual precipitation (Baracoa, Cuba; locality 152) but is occasionally found in xeric environments (e.g. Maize, locality 154; 834 mm, annual precipitation). 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 up to 28.6 % of its body weight in terms of stomach contents (Silva-Taboada, 1979).

The reproductive pattern of *C. macer* is largely unknown. Two pregnant females found in May carried embryos of 10 mm in crown-rump length. Of two females taken in August, one was lactating and another post-lactating. 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, 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 hours) 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 outside their caves during day time.

It is not listed as endangered in IUCN's Red List of Threatened Species (IUCN, 2006) under any taxonomic synonym. Given its habit of aggregating in relatively small numbers the study of its population status merits attention to accurately evaluate its conservation needs.

Chilonatalus micropus (Dobson, 1880)

Figure 17

Natalus micropus Dobson, 1880: 443. Original description based on an unidentified BMNH specimen collected near Kingston, Jamaica. The holotype was subsequently identified and labeled as such by BMNH staff.

Natalus (*Chilonatalus*) *brevimanus* (part): Miller, 1898: 328. Subjective synonym. Original description based on material (holotype USNM 15835) from Providencia Isl. (= Old Providence), Colombia.

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

Chilonatalus brevimanus (part): Miller, 1907: 185. New name combination.

Natalus micropus brevimanus (part): Varona, 1974: 31. New name combination.

Natalus micropus micropus (part): Varona, 1974: 32. New 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. 18.

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 ½ 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 70º 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 tube like 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 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 helix-like structure; tibia (14.7–17.9 mm) slightly shorter than half the length of the forearm; calcar very long and thin, occupying about two thirds 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 two thirds 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 mustache-like 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; oclusal 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 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*, *C. micropus* can be distinguished on the basis of generic characters (see comparisons under account of *Chilonatalus macer*). From other species of *Chilonatalus* (i.e. *Chilonatalus tumidifrons* and *Chilonatalus 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 at 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 Jamaica).

The inflation of the braincase decreases westward, with animals from Hispaniola having the most globular braincase within both the species and the entire family Natalidae (means of braincase breadth also follow this trend yet the differences were not statistically significant; $P > 0.01$; fig. 18). 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. 18). 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 toothrow (males only).

NATURAL HISTORY AND CONSERVATION: Species known from 21 localities of which 8 have been day roosts, all of them caves. All caves known to harbor *C. micropus* are warm and humid, and at least 5 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 9 other bats species (*Artibeus jamaicensis*, *Erophylla sezekorni*, *Monophyllus redmani*, *Mormoops blainvillii*, *Natalus jamaicensis*, *Phyllonycteris aphylla*, *Pteronotus macleayi*, *Pteronotus parnellii*, and *Pteronotus quadridens*. Osburn (1865; in Genoways et al., 2005) observed it 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 the walls at about 1m above the floor (Kerridge and Baker, 1978).

Chilonatalus micropus occurs most commonly in mesic environments up to 2899 mm in annual precipitation (Port Antonio, Jamaica; locality 247) and from sea level to 400 m in elevation (Mahogany Hall Cave, Jamaica; locality 244).

Its food habits are unknown, but as other representatives of Natalidae, *C. micropus* is most certainly insectivorous.

The reproductive pattern is also little known. Female samples taken in mid July have contained 2.6 % (Genoways et al., 2005) to 90 % (Kerridge and Baker, 1978) lactating females. Fourteen females taken in 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, in Cueva los Patos, Dominican Republic, and in 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 apparently coming out the upper entrance of Cueva los Patos, Barahona, 1.5 hours after the end of the exodus of 6 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 not listed in IUCN’s Red List of Endangered Species (IUCN, 2006). 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 a vulnerable species. The geographic range of this species is fragmented between 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 asses its conservation needs.

Chilonatalus tumidifrons Miller, 1903

Figure 20

Chilonatalus tumidifrons Miller, 1903. Original description based on material (holotype USNM 122024) from San Salvador, Bahamas.

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

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

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

HOLOTYPE: USNM 122024, adult male, skin in alcohol with skull removed, collected by J. H. Riley on 12 July 1903 at Sandy Point (locality 524 in Appendix I), 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. 21.

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 ½ 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 tube like 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 half 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 helix-like structure; tibia (17.8–20.1 mm) longer than half the length of the forearm; calcar very long and thin, occupying about two thirds 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 (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 mustache-like 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 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; oclusal 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 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 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 ½ of the tibia, a short penis (1.1–2.25 mm), a long tibia (17.8–20.05 mm), and a large, elliptic natalid organ (length of natalid organ 3.6–8.5). *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 *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°C degrees 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. 22).

NATURAL HISTORY AND CONSERVATION: *Chilonatalus tumidifrons* known from 20 localities (including 8 represented by bone remains only) of which 8 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 coexists in caves with 2 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 forming 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, un-surveyed 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 4 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 is reported to be 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 to18:10 (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, 2006). The extremely reduced range of this species, fragmented between 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

Phodotes Miller, 1906: 85.

DIAGNOSIS: 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; 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; 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 mid point; sagittal crest moderately high and most pronounced in its anterior half. 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*. Goodwin (1959) speculated that the name (relative to "birth") was related to the unknown origin or "birth-place" of the taxon. Other authors have suggested that the name derives from the neotenic aspect of the bat, as in new-born (e.g., Gómez-Laverde, 1986).

CONTENTS: *N. 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 23

Natalus stramineus: Winge, 1893: 36. Based on the first specimen (a subfossil skull) of *Natalus* recorded for South America (Lagoa Santa, Minas Gerais, Brazil). The characters observed in the specimen's illustration indicates that it belongs to *N. espiritosantensis*.

Myotis espiritosantensis Ruschi, 1951: 7. Original description based on material (holotype MBML 1801) from Itauna, Espirito Santo, Brazil.

Natalus espiritosantensis Ruschi, 1970: 7. Secondary description based on the same MBML specimen named by Ruschi (1951).

Natalus stramineus natalensis (part): Goodwin, 1959: 5. Subjective synonym. Original description based on material (holotype USNM 242830) from Natal, Rio Grande do Norte, Brazil.

Natalus stramineus espiritosantensis (part): Pine and Ruschi, 1976: 184. New name combination.

HOLOTYPE: MBML 1801 male, skin in alcohol with skull extracted, collected by A. Ruschi in April 1953, Gruta Itaúnas (locality 37 in Appendix I), Conceicão da Barra, Espirito Santo, Brazil. The skull is missing the right petrosal, and the right pterygoid process (along with parts of the posterior palate), but is otherwise complete. The skin is in fairly good condition but has the 3 right metacarpals broken, 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. 24).

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 size (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 transversal grooves; small, smooth central pad on dorsal margin of lower lip; natalid organ medium size 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 helix-like 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 (34.7–39.1mm); 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 (Plate 1); dorsal hairs bicolored, with tips darker than bases; ventral hairs usually monocolored; dense mustache-like 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 peg-like; I2 obscuring I1 in lateral view; oclusal 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 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 *N. 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 which 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 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 toothrow in, 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 toothrows.

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. 25A) of individuals from northeast Brazil (Ceará, Rio Grande do Norte), no morphometric differences were apparent in the sample available for this species (fig. 25B.

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 lit.).

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).

Natalus espiritosantensis is not listed in IUCN's Red List of Threatened Species (IUCN, 2006). 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 26

Natalus major jamaicensis Goodwin, 1959: 9. Original description based on material (holotype AMNH 182000) from St. Catherine, Jamaica.

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

Natalus major: Morgan and Czaplewski, 1989: 744. New name combination. Morgan and Czaplewski ascribed all greater Antillean Natalus to N. major but listed only specimens from Jamaica.

Natalus jamaicensis: Dávalos, 2005: 95. New name combination. Dávalos restricted the epithet *jamaicensis* to the Jamaican taxon.

HOLOTYPE: AMNH 182000, adult male, skull and skin in fluid, collected by C. B. Lewis in St. Clair Cave (locality 250 in Appendix I), 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. 27).

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 and; 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 helix-like 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; Plate 1); ventral hair bases are buff with tips pinkish-buff; dense mustache-like 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 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 peg-like; I2 obscuring I1 in lateral view; upper premolars of 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*, (*Natalus primus* and *Natalus 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 inflated and almost as wide as long, hence showing 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 toothrow (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 9 other bat species are found in St. Clair, including *Artibeus jamaicensis Chilonatalus micropus*, *Erophylla sezekorni*, *Monophyllus redmani*, *Mormoops blainvillii*, *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 moth-like (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 is not listed in IUCN's Red List of Threatened Species (IUCN, 2006). 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 28

Natalus stramineus saturatus: Hall and Dalquest, 1963: 242. A specimen of *N. lanatus* from Fortín, Veracruz, Mexico, was ascribed to *N. stramineus saturatus*.

Natalus stramineus mexicanus: Anderson, 1972: 241. Two specimens of *N. lanatus* from Chihuahua, Mexico, were ascribed to *N. stramineus mexicanus.*

Natalus stramineus: Rodríguez-Herrera, 2004: 56. A specimen of *N. lanatus* mistnetted in the Río Savegre basin, Costa Rica, was ascribed to *N. stramineus*.

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 I), 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; fig. 29).

DIAGNOSIS: A small species of funnel-eared bat (forearm length 16.0–19.2 mm); legs considerably shorter than forearm; with 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 at 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 helix-like 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) (Plate 1); dorsal hairs bicolored or tricolored, with tips dark bases, light middle part and medium dark tips; ventral pelage from gray to ochraceous but hairs markedly bicolored, with bases darker than tips; dense mustache-like 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; oclusal 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 being 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 tufts of relatively long hair projecting from the base of each claw (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 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 laxer, 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 toothrow 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. 30). 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 *N. lanatus* from Mexico (B. Rodríguez, pers. comm.).

NATURAL HISTORY AND CONSERVATION: *Natalus lanatus* is known from 16 localities in Mexico and from two localities in Costa Rica (B. Rodríguez and R.K. LaVal, pers. comm.; fig. 29). 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 roots.

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 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 above sea level. The record from Río Macho, Costa Rica, a wet mountain forest habitat (1300 m above sea level, 2700 mm annual precipitation) without known caves, most likely correspond 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 I; and in Ameca, Jalisco, locality 320), over half of the collection localities of this species are represented by a single museum specimen each (Appendix I). 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 Chapter 3), however, may reflect some ecological divergence between these 2 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 not listed in the IUCN's Red List of Threatened Species (IUCN, 2006). More data is needed from this poorly-known species before accurate conservation assessments can be undertaken.

Natalus major Miller, 1902

Figure 31

Natalus major Miller, 1902: 398. Original description based on material (holotype USNM 101395) from Savaneta, Santiago, Dominican Republic.

Natalus major major: Goodwin, 1959: 8. New name combination.

Natalus stramineus major: Linares, 1971: 83. New name 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 I), Dominican Republic”. The skull is complete (fig. 31) and the skin is in good condition.

DISTRIBUTION: Hispaniola, including the Dominican Republic and Haiti (fig. 32)

DIAGNOSIS: Forearm long (41.1–45.0), skull long relative to forearm, breadth across canines large (3.9–4.5), maxillary toothrow (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 at 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 helix-like 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 (Plate 1); ventral hairs cream-buff; dense mustache-like 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 short and broad, with moderate sulcus between nasals; moderate rostral palatal emargination; maxilla convex dorsal 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 peg-like; I2 obscuring I1 in lateral view; upper premolars of 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 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 smaller than 40.0 mm. Only very large individuals of *Natalus stramineus*, *Natalus tumidirostris*, and *Natalus 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 length is smaller 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 smaller 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 diastema between I2 and the upper canine and a rostrally projecting I1; in *N. major* neither the diastema 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 from it on the basis of cranial characters. Relative to *Natalus jamaicensis*, *N. major* has a wide postorbital region with sides widely diverging anteriorly, whereas the postorbital region in *N. jamaicensis* is narrow and with sides nearly parallel. Also, the maxilla of *N. major* is convex dorsal to the molars, whereas that of *N. jamaicensis* is concave. Finally, 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 in 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, 9 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 in their interior. Most of these caves have a phreatic origin, with wide chambers and constricted entrances but some are also fluvial caves characterized by linear passages. One of these caves 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. 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 blainvillii*, *Phyllonycteris poeyi*, *Pteronotus quadridens*, and *Pteronotus parnellii*) but it has never been found forming multispecies groups. It usually tolerates disturbance for long periods and can occasionally be caught by hand while roosting, but this only happens 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 light of a flashlight). When retreating from disturbance, the bats fly close to the floor and walls of the caves.

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 Hispaniola. 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 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 the daytime.

Natalus major is not listed in IUCN’s Red list of Threatened Species (IUCN, 2006). 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 on 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 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 33

Natalus mexicanus Miller, 1902: 399. Original description based on material (holotype USNM 96476) from Santa Anita, Baja California Sur, Mexico.

Natalus mexicanus saturatus (part): Dalquest and Hall, 1950: 153. Subjective synonym. Original description based on material (holotype KU 23815) from San Andrés Tuxtla, Veracruz, Mexico.

Natalus mexicanus mexicanus (part): Villa-R, 1966: 346. New name combination.

Natalus stramineus mexicanus (part): Goodwin, 1959: 6. New name combination.

Natalus stramineus saturatus (part): Goodwin, 1959: 7. New name combination.

Natalus saturatus: Dávalos, 2005: 5. New name combination.

HOLOTYPE: USNM 96496, adult female, skin in alcohol with skull extracted, collected by J. F. Abbot in August 1897, at Santa Anita (locality 266 in Appendix I), Baja California Sur, Mexico. Both the skull and skin are 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); figs. 34–37.

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 at 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, sometime at the end of tube like 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; pinna with markedly pointed tip; medial margin of pinna slightly concave; 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 helix-like 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 (Plate 1); dorsal hairs bicolored, with tips darker than bases; ventral hairs usually monocolored; dense mustache-like 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 peg-like; I1 visible in lateral view, not being obscured by I2; oclusal 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 *Natalus lanatus*. Its forearm is smaller than that of all insular (*N. primus*, *N. major*, *N. jamaicensis*, *N. stramineus*, and *N.* dominicensis) 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*, *N. dominicensis* and *N. stramineus*. In addition, in most cases, it 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 toothrow, yet there are overlaps in measurements therefore, as with *N.* dominicensis, 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 8 external and cranial measurements (table 15).

Size variation in *N. mexicanus* is mostly due to variation within populations rather than to variation among populations. Nonetheless, as a general trend, individuals from eastern Mexico (Tamaulipas to Chiapas) and Central America (Guatemala, Colombia [San Andrés y Providencia], and Panama) average larger in forearm length (fig. 38A) than individuals from western Mexico (Jalisco to Sonora and Baja California). This trend, however, is not uniform, with individuals from Yucatan attaining the smallest means and those of the Isthmus of Tehuantepec the largest means in most measurements. Differences in body proportions are slight, but specimens from Panama are notable in their relatively shorter and wider rostra (fig. 38).

Natalus mexicanus exhibits the widest color variation of any natalid but most of it 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, can exhibit color variants ranging from buff to bright orange brown and yellow, and it seems that the apparent lack of variants within a population is mostly due to sampling error.

NATURAL HISTORY AND CONSERVATION: *N. mexicanus* is known from 253 localities, in 85 of which it has been taken at roost sites (63 are reported as caves, 21 as mines, 2 were hollow trees, and 1 was drainage pipe under a road [Moreno, 1996]) but the number of known roost sites is probably much higher given that museum specimen-tags (especially older ones), the main source of this information, often omit references to the circumstances under which the specimens were captured. Some reported localities for this species are represented by specimens not examined in this work, and 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; Mitchel, 1965; AT personal observation). The relative humidity of roost sites have been reported to range from 74 to 99% (Ávila-Flores and Medellín, 2004; Mitchel, 1965, McNab, 1969). In one occasion, the relative humidity of a roost was been as low as 54% (deep end of Cueva Chica, Baja California; AT personal observation), 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 communication in Mitchell, 1965) mentioned that 2 groups of 3–5 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 (Goodwin, 1969).

Natalus mexicanus has been found coexisting in caves with 32 other bat species (*Artibeus hirsutus*, *Artibeus jamaicensis*, *Artibeus 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 (Mitchel, 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* seem to move between alternative roosting 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 2 bats on 2 January 1948, and a high of about 300 on 10 January 1948. Also, the population of Mina Armolillo, Sonora, decreased from about 1000 bats present in the mine during November-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 (< 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 the populations of *Leptonycteris* sp. And *Glossophaga* sp. (identified as *L. nivalis* and *G. soricina* in the original account) in that mine (Mitchell, 1965).

Based on correspondence analysis between collection localities for the state of Michoacán and environmental factors, 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 desertic scrub (Pescadero, Baja California, Mexico, 156 mm annual precipitation; locality 265) to degraded rain forest (Teapa, Mexico, more than 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 altitude localities of *N. mexicanus* may actually represent *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. This study showed that *N. mexicanus* is monoestrous and bears a single pup per litter. 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 performing dissection. Beginning in October, the testes increased in size from about 1.5 mm long to slightly over 2.0 mm long 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 in the case of the weight and 40 days after birth in the case of forearm length. At birth, which took place between 12–20 July, the newborn weighted 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 weight at birth) and forearm lengths at 34–35 mm (about a 185% increase from forearm length at birth). The end of the growing spur 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 it had reached 5.7–6.2 g, nearly the same as the weight of the adults (5.7–6.6 g). During this period, forearm length increased even more slowly than the weight, also reaching a range (35–38 mm) near that of full 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. Finally, 2 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 of the mine, about 1 m from the floor and much closer to the entrance of the mine (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 of both sexes of *N. mexicanus* seems to be sexually mature in their first year.

N. mexicanus is the natalid species 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. tumidirostris* 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 it is 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 remained entering and leaving the cave for the remainder of the night. Before the beginning of emergence, most individuals were at 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 with 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 calls consist of short (about 2 ms) FM sweeps with most energy in the second harmonic at 100–130 kHz, but with occasional emphasis in 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.

N. 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). Saldach (in Nowak 1994) reported torpid *N. mexicanus* in a cave in Tamaulipas, in an oak forest area, with an outside temperature of 12°C.

Natalus mexicanus is not listed in the IUCN Red List of Threatened Species (IUCN, 2006). 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 it should receive a status of lower concern.

Natalus primus Anthony, 1919

Figures 39, 40

Natalus primus Anthony, 1919: 642. Original description based on fossil material (holotype AMNH 41009) from Daiquirí, Santiago de Cuba, Cuba.

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

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

Natalus major Tejedor et al., 2004: 153. Extant specimens of *N. primus* from Pinar del Río, Cuba were ascribed to *N. major.*

HOLOTYPE: AMNH 41009, a fossil right dentary (fig. 39), 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 known extant locality (Cueva La Barca, Cuba; Tejedor et al., 2004) and 14 fossil localities (fig. 41).

DIAGNOSIS: Largest extant 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 ear margin straight; lateral ear margin straight, not notched; 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; palate ending caudally at 1/2 of the distance between M3 and tip of pterygoid; caudal margin of palatine wing of maxilla almost perpendicular to longitudinal axis of skull; basisphenoid pits deep and steep sided; caudal margin of dentary forming a 70 deg. Angle with alveolar margin of lower molars; I1 visible in lateral view, not obscured by I2; mesostylar crest present on M3. A comparison of diagnostic characters between *N. primus*, and other species of *Natalus* is 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 tube like projections on shallow depression on margin of upper lip; upper and lower lips markedly thickened; lower lip markedly constricted along dorsal and ventral margin, 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; pinna 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 helix-like 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 mustache-like 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 oclusal profile of; 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 only overlaps in range of forearm length with *Natalus jamaicensis*. *Natalus 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 representatives of the genus *Natalus*, the lateral ear margin is concave or notched and the ear tip is much more pointed. Similarly, *N. primus* lacks the band of dark hairs that in all other species of *Natalus* connects the labial mustache-like hair tufts characteristic of the family.

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 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 if 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 between the three island groups (table 17, fig. 42). The sample from the Bahamas is the largest and overlaps either slightly in range of mental length with the fossil sample from Cuba, and does not 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, *Natalus 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.

A total of 10 other bats (*Phyllonycteris poeyi*, *Pteronotus quadridens*, *Pteronotus macleayi*, *Pteronotus parnellii*, *Mormoops blainvillii*, *Brachyphylla nana*, *Erophylla sezekorni*, *Monophyllus redmani*, *Artibeus jamaicensis*, and *Chilonatalus macer*) roost together with *Natalus primus* in Cueva La Barca, yet none of the species were ever observed in mixed groups. Groups of *N. primus* sometimes roost adjacent to groups of *M. blainvillii* (which also appear to favor the cave's walls as roosting areas). Captive individuals of *Natalus primus* are aggressive and frequently attack bats of other species, even of larger size, if confined together in a small enclosure.

In general, individuals of *Natalus primus* remain active while roosting during the day, taking flight at the slightest sign of disturbance (human steps, distant glare from a flash light), 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 little disturbed semideciduous forest of moderate precipitation (1402), 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 *Natalus primus* is largely unknown. Three females of *N. primus* collected on 1 May 1992 were pregnant, each holding a single large embryo. At midday, on 17 April 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 seemingly 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 pers. comm.). 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 hours 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 *Natalus primus* are unknown but it produces weak and high-pitched audible sounds when held in the hand.

Natalus primus is a critically endangered bat (Tejedor et al., 2005). Treated as *Natalus stramineus*, it was not listed in the 2006 IUCN Red List of Threatened Species (IUCN 2006). The only known extant population of *N. primus* (e.g. 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 status is unknown and should be evaluated to adequately formulate conservation plans for this species.

Natalus tumidirostris Miller, 1900

Figure 43

Natalus tumidirostris Miller, 1900: 160. Original description based on holotype (USNM 102106).

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

Phodotes tumidirostris continentis (part) Thomas, 1911: 513. Subjective synonym. Original description based on material (holotype BMNH 5.11/12.25) from San Esteban, Carabobo, Venezuela.

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

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

Natalus tumidirostris haymani (part): Goodwin, 1959: 12. Subjective synonym. Original description based on material (holotype AMNH 176590) from Mt. Tamana, Trinidad, Trinidad and Tobago.

Natalus stramineus tronchonii: (part): Linares, 1971: 81. Subjective synonym. Original description based on material (holotype MBUCV 1578) from Rio Guasare, Zulia, Venezuela.

Natalus stramineus: Linares, 1998: 515. Linares ascribed all Venezuelan *Natalus* to *N. stramineus.*

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 I), 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: South America north of the Amazon River in the countries of Colombia, Venezuela, Guyana, Suriname, and French Guiana. 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. 44).

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 helix-like 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, 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 (Plate 1); dorsal hairs bicolored, with tips darker than bases;

ventral hairs usually monocolored; dense mustache-like 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, 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 peg-like; I2 obscuring I1 in lateral view; oclusal 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 *N. tumidirostris*, the maxillae are conspicuously inflated (although less so in individuals from Colombia and W 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 giving 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, *N. 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 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*.

N. tumidirostris has a larger 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 three other species of the genus: *N. espiritosantensis*, *N.* dominicensis, and *N. stramineus*. Nonetheless, its canine width is larger than that of *N.* dominicensis and 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.

Individual variation in pelage color is very wide in *N. tumidirostris*. Some specimens from Miranda (Cueva Ricardo Zuloaga) are bright orange brown, whereas most individuals from Paraguaná are extremely pale, being pale buff dorsally and pale cream-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 mostly due to sampling error.

Males of *N. tumidirostris* are larger than females in 10 of the 14 measurements taken in both sexes ($P < 0.05$; table 20). Females from Colombia, however, had a larger 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 analysis based on one external (forearm length) and 7 skull measurements. Specimens from Colombia, the coastal ranges in Venezuela, the 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 small forearm but a relatively large skull ($P < 0.05$, fig. 45).

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 (Plate 7).

NOTE: The population from Perijá was originally described as a subspecies of *Natalus stramineus* (*N. s. tronchonii*) by Linares (1971) mainly on the basis of a supposedly unique pattern of palatal fenestration. A subsequent examination of the holotype skull of *N.* s. *tronchonii* revealed that it had been incompletely cleaned and that the remaining soft tissue obscured a pattern of palatal fenestration similar to that of specimens from Colombia (AT pers. observ.).

NATURAL HISTORY AND CONSERVATION: *N. 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 disturbed (Genoud et al., 1990). Some of the caves inhabited by *N. tumidirostris* may contain high levels of ammonia (e.g. Ricardo Zuloaga). Most caves known to harbor *N. tumidirostris* are formed in limestone. Linares and Löbig-A (1973) mentioned that *N. tumidirostris* migrates to alternative 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 eroding Precambrian granite inselbergs, which dominate the Guianan landscape. It is therefore likely that in the Guianan shield *Natalus tumidirostris* roosts in such types of caves too.

Natalus tumidirostris has been found coexisting 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 often forms mixed groups (as in Macaregua, Gómez-Laverde, 1986; and Cueva las Animas, AT). Within roosting groups individuals hang widely spaced and are generally quiet, sometimes allowing themselves to be caught by hand. Occasionally, when large multi-species groups of bats abandon certain areas of a given cave due to the presence of visitors, individuals of *N. 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 litter. 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 of 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, the latter of which flew away after being disturbed. By mid April, this group had consolidated into a large mass of many juveniles that occupied a 1 by 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 instance in Macaregua, where a piece of cave ceiling fell to the floor with about 10 non-flying pups still clung to it, the pups continued to be fed in spite of the accidental change in location, because 15 days after the initial observation they were still on the piece of fallen ceiling and had appreciably grown. A photograph taken in Cueva Ricardo Zuloaga, Venezuela, in an unspecified date, documents a similar cluster-forming behavior of newborn *N. tumidirostris* (Carreño, 1998). Sexual 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 3 localities: Cueva Macaregua, Colombia; Cueva Ricardo Zuloaga, Venezuela; and Tamana Caves, Trinidad. It appears most densely distributed along the north of Venezuela. 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 which 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 the observations were stopped.

Occasionally there was a peak in the number bats leaving the cave about half an hour after sunset.

The flight of *N. 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, *N. tumidirostris* dies quickly (in less than 20 hours) of starvation and/or dehydration when kept in captivity. Its basal metabolic rate (1.54 mlO_2/ghr) is very low (30% below expected value) relative to that of other Neotropical insectivorous bats of similar body mass. This low basal metabolic rate may help this bat reduce the 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 $mlO_2/ghr°C$), 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 beyond 20°C. It seems, however, unable to survive ambient temperatures below 10°C for longer than 2 hours (Genoud et al., 1990).

Natalus tumidirostris was treated as less concern in IUCN's Red List of Threatened Species (IUCN, 2006). In northern Venezuela it seems a ubiquitous and locally abundant bat and therefore not threatened. Petit (1995) considered it a threatened bat in Curaçao, with an island-wide 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.

Natalus stramineus Gray, 1838

Figure 46

Natalus stramineus Gray, 1838: 496. Original description based on unidentified 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.

Natalus stramineus stramineus: Goodwin, 1959: 2. New name combination.

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).

NOTE: The name *Natalus stramineus* has been historically applied to populations of the genus *Natalus* from virtually the entire 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 had been made 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 (in press.), 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 toothrow (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 acute 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 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 (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 helix-like 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 (Plate 1); ventral hairs pale smoke gray or pinkish buff to light amber-chestnut or orange brown; dense mustache-like 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 peg-like; I2 obscuring I1 in lateral view; oclusal 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 anterior-most margin of the premaxilla (fig. 3, 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, *N. stramineus* can be distinguished from the large Greater Antillean species *Natalus primus*, *Natalus major*, and *Natalus 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 better 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* the medial margin of the ear 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 toothrow, $P < 0.01$; 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 18). Canonical variates 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, having, in particular, longer 3rd metacarpals (fig. 49A) and narrower breadths across canines (fig. 49B). 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 brown (amber brown) to light brown (tawny olive) 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 one female from Montserrat. Two adult females and one adult male from Saba, whoever, lacked this trait, being indistinguishable, at least cranially, from specimens from Guadeloupe and Dominica.

NATURAL HISTORY AND CONSERVATION: *Natalus stramineus* is known from 35 localities (including three represented by bone remains only), 15 of which have been caves. 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; Pedersen et al., 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, non-pregnant and pregnant individuals, yet a sample from July was composed entirely of non-reproductive females (Genoways et al., 2001). *N. stramineus* is parasitized by the streblid *Trichobius caecus* (Genoways et al., 2001).

In an ecomorphological study, Jennings et al. (2004) stated that *Natalus stramineus stramineus* can fly very slowly in clutter and that it hunts by slow hawking and/or by gleaning. They found that *Natalus 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).

Under the widespread-species definition, *N. stramineus* is not listed in the current global red list of threatened species (IUCN, 2006), yet its small, naturally fragmented geographic range and its apparent requirement of humid caves, point to a limited availability of suitable habitat and therefore to a vulnerable conservation status. The species seems, nonetheless, locally common in at least 4 islands (Antigua, Barbuda, Dominica and Saba; Genoways et al., 2001, Pedersen et al., in press), 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 (S. Pedersen*,* in litt). 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. 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.

APPENDIX I: GAZETTER 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 World Wide Web based geographic databases (Fallingrain, Geonames, GoogleEarth). 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, Chilo*natalus macer*; Cmi, Chilo*natalus micropus*, Ctu, Chilo*natalus 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*; and Ppr. Localities represented by bones remains only list species abbreviations followed by a † symbol. A count of specimens follows the species abbreviation if the species are represented at that locality by voucher specimens. 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, except for those marked with an asterix [*] for which only a sample of their Natalidae collection was examined 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, Pittsburg, USA; CNMA—Colección Nacional de Mamíferos, Universidad Autónoma de México, Mexico, Mexico; **CRD** — Colección Regional Durango, Instituto Politécnico Nacional Unidad Durango, Durango, Mexico; **DZSJRP** — Department of Zoology, Universidade Estadual Paulista, São José do Rio Preto, Brazil; **EBRG** — Estación Biológica Rancho Grande, Maracay, Venezuela; **FLMNH (UF)** — Florida Museum of Natural History, Gainesville, Florida, USA; **LACM*** — Los Angeles County Museum, Los Angeles, USA; **MHNLS** — Museo de Historia Natural La Salle, Fundación La Salle, Caracas, Venezuela. **FMNH** — Field Museum of Natural History, Chicago, USA; **KU**, University of Kansas Natural History Museum , Lawrence, Kansas, USA. **MBML** — Museu de Biologia Professor Mello-Leitao; Santa Teresa, Brazil; **MFN** — Museum für Naturkunde der Humboldt Universität, Berlin, Germany; **MBUCV** — Museo de Biología, Universidad Central de Venezuela, Caracas, Venezuela; **MCZ** —Museum of Comparative Zoology, Harvard University, Cambridge, USA. **MNK** — Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia; **MNHN**—Museum National d'Histoire Naturelle, Paris, France; **MNHNc** — Museo Nacional de Historia Natural, Havana, Cuba; **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; SDNHM—San Diego Natural History Museum, San Diego, USA; **TTU (TK)***—Museum of Texas Tech University, Lubbock, USA; **UFMG**—Chiroptera Collection, Faculdade de Biologia, Universidade Federal de Minas

Gerais, Belo Horizonte, Brazil; UMMZ—University of Michigan Museum of Zoology, Ann Harbor, 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 (18.21667, -63.05, 27 m). **Nst** (2): AMNH 72368 72369.
2. Cave at head of Katouche Bay North Hill Village (18.2, -63.06667, 8 m) **Nst** (1): USNM 544834.

ANTIGUA AND BARBUDA

Antigua

3. Bat Cave at UHSA St. John's, St. John (17.11667 -61.85, 6 m). **Nst** (S. C. Pedersen, pers. comm.).
4. Montpelier Cave, 1.2 Km E, 0.2 Km S, St. Philips (17.04333 -61.71444, 67 m). **Nst** (3): TTU 101719-101721.
5. Christian Valley, St. Paul (17.03333, -61.75, 21 m). **Nst** (S.C. Pedersen, pers. comm.)
6. English Harbor, St. Paul (17.01667, -61.76667). **Nst** (4): BMNH; MCZ 17469-17472.

Barbuda

7. Dark Cave (17.62389, -61.75333, 27 m). **Nst** (12): TTU 101723--101729, 101738-101742.
8. Bryants Cave. **Nst** (S.C. Pedersen, pers. comm.).
9. Cave 1 **Nst**: FLMNH 3366, 24019-24023.
10. Cave 2 **Nst**: FLMNH 2812.
11. Indian Cave. **Nst** (Pedersen, pers. comm.).
12. New Cave. **Nst** (Pedersen, pers. comm.).

BELIZE

Cayo District

13. Sibun Camp, Military Bldg along Sibun R (17.083, -88.65, 302m). **Nme** FMNH 58480 1.
14. 0.75 Km W Augustine (16.96667, -88.9833333, 483 M). **Nme** Cm 91907–9190711 5.
15. 1.5 Km N Augustine (16.96667, -88.9833333, 483 m). **Nme** (5): CM 91912–91916.
16. Las Cuevas Research Station Belmopan (16.73333, -88.98333, 592 m). **Nme** (1): BMNH 2003.201.

Orange Walk District

17. Richmond Hill, 8.9 Km Ssw Orange Walk Town (18.06667, -88.55, 8 m) **Nme**: CM 91917, 1.

Stann Creek

18. Kendal at Sittee R, Dunker Ranch (16.8, -88.367, 30 m) **Nme** FMNH 58479, 1.
19. Cockscomb Basin (16.76667, -88.61667, 305 m) **Nme**: USNM 583063, 583064, 2.

Toledo District

20. 1.2 Km E Aguacate Village (16.16222, -89.0938889, 53 m). **Nme**: CM 90567-90569, 4.
21. Blue Creek Village, 1 Km Upstream From Village (16.19778, -89.04222, 40 m). **Nme**: MSB 53573, 1.
22. Carib Reserve Rd, Vista Hermosa Ranch, S Cerro Hill, Cave, Carib (16.11667, -88.78333). **Nme**: FMNH 121072-12085, 14.
21. Blue Creek Village, 1 Km Upstream From Village, In (16.19778, -89.04222, 40 m) **Nme** MSB 53573, 1.
22. Carib Reserve Rd, Vista Hermosa Ranch, S Cerro Hill, Cave Carib (16.11667, -88.78333) **Nme** FMNH 121072–12085, 14.

BOLIVIA

Santa Cruz

23. Flor de Oro, (-13.55083, -61.06, 179 m) **Nes** MNK 1927 (male), 1.
24. Los Fierros, (-14.58611, -60.92, 199 m) **Nes** MNK 3199 (male), 1.

25. Cueva Concesión Minera Don Mario, San Juán de Chiquitos (-17.33861 -59.7, 337m). **Nes**: MNK 2070–2074 (2 males, 3 females), 5.
26. “Cave at creek source”, Santiago de Chiquitos (-18.34417 -59.55, 847 m). **Nes**: AV *Natalus* 1-2, 2.
27. Cueva Concepcioncita), Motacucito, Puerto Suarez . (-19.01716 -57.87, 199 m) **Nes**: SJRP 14507, 1.

BRAZIL

Bahia

28. Toca da Boa Vista), Laje Dos Negros, Campo Formoso (-10.1625 -40.86, 554 m) **Nes**: MCL 10201, 10237 (fossils)(Czaplewski and Cartelle, 1998).
29. Poço Encantado, Itaetê. MZUSP (-12.94472 -41.11, 385 m) **Nes**: MZUSP 29054-066, MZUSP 29499, 14.
30. Gruta Toca dos Morcegos, (-15.45 -39.65, 209 m) **Nes**: MBML 1965 male; 1.
31. Gruta California Pau Brasil (-15.45 -39.65, 209 m) **Nes** (R. Lopes Ferreira, pers. comm.).

Ceará

32. 9 Km S Crato, Floresta Nacional Araripe (-7.228889 -39.38, 419 m) **Nes**: CM 100753, 1.
33. Chapada do Araripe, Crato (-7.228889 -39.38, 419 m) **Nes** (Willig, 1983).
34. Floresta nacional Araripe Crato (-7.228889 -39.38, 419 m) **Nes**: USNM 555711, 1.
35. Barbalha Serra do Araripe Arajara (-7.316667 -39.28, 456 m) **Nes** (1): USNM 536442,

Distrito Federal

36. Gruta da Saúva, Sobradinho (-15.63333 -47.83, 1079 m) **Nes** (Tadei and Uieda, 2001)

Espirito Santo

37. “Gruta do rio Itaúnas”, Itaúnas, Conceição da Barra (-18.42222 -39.71, 3 m) **Nes** 3: MBML 1801 (holotype) 1802, 1803.

Goias

38. Faz. São Domingos. **Nes**: UNB1022 1

39. Fazenda Pé da Serra. **Nes**: UNB 921 1
40. Serra da Mesa. **Nes†** (Fracasso and Salles, 2005).
41. Colinas do Sul (-14.14944 -48.08, 526 m) **Nes** (Tadei and Uieda, 2001).
42. Gruta de Porcos, Mambaí (-14.49306 -46.11, 727 m) **Nes**: CZUFMG male, i1.
43. Lapa do Fuzil, Goianésia (-15.32694 -49.12, 647)m **Nes** (Tadei and Uieda, 2001).
44. Padre Bernardo (-15.33333 -48.5 677 **Nes** (Tadei and Uieda, 2001)

Minas Gerais

45. Caverna Olhos D'Agua, Itacarambi (-15.11278, -44.16917, 515 m). **Nes** (Trajano, 1998).
46. Furna Misteriosa, Sete Lagoas (-19.0925, -44.34972, 859 m). **Nes** (E.C. Moreira, pers. comm.)
47. Lagoa Santa (-19.63333, -43.88333, 801 m). **Nes†** (Winge, 1893)

Matto Grosso do Sul

48. Rio Verde de Mato Grosso (-18.91667, -54.83333, 327 m). **Nes**: SJR*P* 16748-16752, 5.
49. Paranaíba (=Paraíso)(-19.05, -52.96667, 612 m). **Nes**: SJR*P* 12116-12118, 12120, 12122, 12124, 12125, 12127-12129, 12249, 12251, 12252, 12254-12257, 12261, 12263-12266, 12268, 12269 , 24.

Mato Grosso

50. Aripuanã (-9.183333, -60.63333, 143 m). **Nes** (Mok et al., 1982).

Pará

51. Altamira (Medicilândia (-3.2, -52.2, 105 m). **Nes** (Tadei and Uieda, 2001).
52. Caverna do Tatajuba, Altamira, 17 km S by road (-3.334444, -52.28028, 158 m). **Nes**: USNM 549504, 1.
53. Caverna planaltina (-3.375, -52.5717, 230 m).
54. Caverna do limoeiro (-3.538889, -52.7853, 224 m).
55. Cachoeira Espelho, Rio Xingú (-3.65, -52.38333, 108 m). **Nes**: MZUS*P* 21360, 1.

Piauí

56. São João do Piauí (-8.333333, -45.25, 508 m). **Nes** (Tadei and Uieda, 2001).

Rio Grande do Norte

57. Natal (-5.783333, -35.21667, 5 m). **Nes**: USNM 245517. 242828-242830, 4.

São Paulo

58. Caverna Gurutuva, Iporanga (-24.53333, -48.65, 546 m). **Nes**: MZUSP 12073, 1.

59. Caverna Santana, Iporanga (-24.53333, -48.7, 472 m). **Nes**: MZUSP 13228, 1.

CAYMAN ISLANDS

Grand Cayman

60. Dolphin cave (19.35167, -81.12639, 7 m). **Npr**: FLMNH (fossil), Morgan (1994).

61. Bodden Cave, Bodden Town (19.26667, -81.25). **Npr**: FLMNH (fossil), Morgan (1994).

COLOMBIA

Bolívar

62. Cartagena (10.39972, -75.51444, 34 m). **Ntu**: USNM, 1.

Santander

63. S.A.: Cueva del Nitro", N.San Gil, (9.453611, -75.44278, 55 m). **Ntu**: AMNH 183854, 183855, 2.

Isla Providencia

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

Isla San Andres

65. Cave near South End (12.4824, -81.7303). **Cmi**: LACM 38872-38877, 6; **Nme**: LACM 038850-038871 (22), 22.

66. Room and Hall Cave, May's Cliff. **Nme**: LACM 028872-028878 (7), 7.

Santander

67. Macaregua Cave, 14 Km N Of Sangil (6.674167, -73.17778, 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**: ROM 45532, 45104-45108, 45231-45237; FMNH 65637, 65638, 15.

Sucre

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

COSTA RICA

Alajuela

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

Cartago

71. Río Macho (9.766667, -83.85, 1306 m). **Nla** (Riba-Hernández, 1996).

Guanacaste

72. St. Rosa Ntl. Park (10.78639, -85.60472, 205 m). **Nme**: USNM 563306, UCR 1851, 2.
73. Palo Verde =2 Km S, 12 Km E Bolson, 6 M (10.34444, -85.33833, 7 M). **Nme**: KU 158310; USNM 506598, 563306; MMNH 14103, UCR 1961, 1995; MNCR 186, 736-739, 11.
74. Mina Tres Hermanos, Cueva Calcarea, Abangares, (10.3, -84.96, 317 m). **Nme**: CNMA 5124,00, 1.
75. Hacienda Solimar, ABANGARES, (10.275, -85.13333, 12 m). **Nme**: UCR 1989 , 1.
76. Curiol de Santa Rosa = Curiol (10.23333, -85.5, 340 m). **Nme**: LACM 024742, 024759, 024760, 3.

Guanacaste

77. Cueva La Trampa, Parque Nacional Barra Honda (10.15, -85.36667, 103 m). **Nme**: USNM 543423, 1.
78. Cueva Nicoa, Parque Nacional Barra Honda (10.15, -85.36667, 103 m). **Nme**: USNM 543420-543422, UCR 885, 5.

Puntarenas

79. Cuenca Rio Savegre (unspecified), Rio Savegre (9.366667, -84.01667, 17 m). **Nla** (Rodríguez-Herrera, 2004).

CUBA

Camagüey

80. Cueva de los Portales de Pinto, Jaronú, (21.8, -77.95, 23 m). **Npr**: MCZ (Koopman and Ruibal, 1955).

81. Cueva del Jaguey, Cerro Limones (21.61306, -77.82694, 212 m). **Nyl** (Silva Taboada, 1979).
82. Cueva Bonita, Cairije, (21.6, -77.66667, 35 m). **Nyl**: IES 1.3303-1.3332 , 30.
83. Cueva de la Tripa, Cairije (21.6, -77.66667, 35 m). **Nyl**: IES 1.3359-1.3273 , 15.
84. Cueva del Círculo,, Cairije, (21.6, -77.66667, 35 m). **Npr** (Silva-Taboada, 1979).
85. Cueva Pichardo, cerro tuabaquey, Cerro Tuabaquey, (21.59889, -77.79833, 135 m). **Cma** (Silva-Taboada, 1979).
86. Cueva Bonita, Sierra de Cubitas, **Nyl**: ROM (6) 63176-63181, 6.

Cienfuegos

87. Cueva de la Macha, Soledad (22.11667, -80.31667, 59 m). **Npr**: AMNH (Goodwin, 1959).,
88. Cueva de la Luz, Juragua (22.09889, -80.55639, 14 m). **Nyl** (Silva Taboada, 1979).
89. Punta de San Juan, San Juan, (21.92028, -80.26833, 21 m). **Nyl** (Silva Taboada, 1979).

Ciudad de La Habana

90. Cueva de Doña Juana (no longer existing), Almendares (23.09, -82.48278, 5 m). **Nyl** (28): AMNH 61169-61190; MCZ 17493-17498.

Isla de la Juventud

91. Nueva Gerona (21.88333, -82.8, 14 m). **Nyl**: USNM 103898, 1.
92. Cueva de la Cantera, Sierra de Colombo, Sierra de Caballos (21.87278, -82.77667, 39 m). **Nyl**: IES 1.3369-1.3374, 5.
93. Cueva de los Lagos, Sierra de Caballos (21.87278, -82.77667, 39 m). **Nyl**: AMNH 186982, 186983; FMNH 93686, 93687; IES 1.3376-1.3385, 1.3244-1.3263, 34.
94. Cueva del Abuelo, Sierra de Caballos (21.86667, -82.76667, 17 m). **Npr** (Silva-Taboada, 1979).
95. Cueva del Agua, Sierra de Casas (21.85806, -82.82111, 96 m). **Nyl** (Silva Taboada, 1979).
96. Eastern base of Sierra de Casas, Sierra de Casas (21.85806, -82.82111, 96 m). **Nyl**: KU 150708-150711, 151181-151184, 8.

97. Gruta Grande de Santa Isabel, Santa Fe. (21.74222, -82.755, 27 m). **Nyl** (Silva Taboada, 1979), (Silva-Taboada, 1974).
98. Cueva de la Casimba, Punta del Este (21.5625, -82.55861, 16 m). **Nyl**: IES 1.3375, 1; **Cma**: IES 1.3182- 1.3186, 5.
99. Cueva del Promontorio = Cueva de Cayamas, Punta del Este (21.5625, -82.55861, 16 m). **Cma**: ROM 38800-38805; IES 1.3187-1.3203, 1.3205, 1.3206, 25.
100. Cueva No. 2 de Punta del Este, Punta del Este, (21.5625, -82.55861, 16 m). **Cma**: IES 1.3129-1.3155, 27 (Silva-Taboada, 1979).
101. Furnia de Punta del Este, Punta del Este (21.5625, -82.55861, 16 m). **Nyl** (Silva Taboada, 1979).
102. Cueva de Los Murcielagos, Punta Pedernales (21.55694, -83.15472). **Cma**: IES1.3208- 1.3215, 8.
103. Cueva de Punta Brava, Punta Brava, (21.52583, -82.60444, 12 m). **Cma**: AMNH 186978-186981; FMNH 93682--93685, 8.

La Habana

104. Cueva del Jaguey, Boca de Jaruco (23.17528, -82.01111, 8 m). **Nyl** (Silva-Taboada, 1979).
105. Cueva del Maja, Santa Cruz del Norte (23.17528, -82.01111, 8 m). **Cma** (Silva-Taboada, 1979).
106. Cueva del Indio, La Jaula (23.01667, -82.08333, 233 m). **Nyl**: IES 1.3416, 1.3417, 2; **Cma**: IES 1.3161, 1, (Silva-Taboada, 1979).
107. Camoa, Jamaica (22.97917, -82.17028, 134 m). **Cma** (Silva-Taboada 1979).
108. Cueva de Cotilla, Cotilla, San José de las Lajas (22.96139, -82.15111, 138 m). **Nyl**: IES 1.3350-1.3357, 8, (Silva-Taboada, 1979).
109. Cueva de William Palmer, San José, Guanajay (22.95, -82.68333, 124 m). **Nyl**: KU 151185-151193, 152351-152356; ROM (8) 38806-38811, 78779, 78780; IES 1.3387, 1.3388, 1.3274, 1.3275--1.3302 , 54; **Cma**: IES 1.3160, 1.3204, 1.3178, 3.
110. Cueva del Mudo, Cuarto, Catalina de Güines (22.92694, -81.97722, 89 m). **Nyl** (Silva-Taboada, 1979).

111. Cuevas Blancas, Quivican (loc. Modf. Aguacate) (22.885, -82.32111, 126 m). **Npr** (Jiménez et al., 2006).
112. Ceiba del agua ( ). (22.87722, -82.64139, 89 m). **Cma**: AMNH 176161, 1; (Silva-Taboada, 1979).
113. Cueva del Túnel, Yarey, Pueblo, La Salud (22.87139, -82.42389, 62 m). **Nyl** (Silva-Taboada, 1979).
114. Finca Aston, Cañas (22.80694, -82.70944, 36 m). **Cma**: IES 1.3207, 1; (Silva-Taboada 1979).
115. Cueva de Paredones. **Cma** (Silva-Taboada, 1979).
116. Cueva de Sandoval. **Cma**: IES 1.781, 1.

Matanzas

117. Varadero (23.15361, -81.25139, 2 m). **Nyl** (Silva-Taboada 1979).
118. Camarioca (23.06083, -81.35694, 38 m). **Nyl** (Silva-Taboada, 1979).
119. Cueva de Pluma, Seboruco, Corral Nuevo (23.05889, -81.67389, 63 m). **Nyl** (Silva-Taboada, 1979).
120. Cueva del Palenque (23.01889, -81.71639, 113 m). **Nyl** (Silva-Taboada, 1979); **Npr** (J. Orihuela, pers. comm.).
121. Cueva de la Eloísa, Bellamar (23.01667, -81.55, 55 m). **Npr** (Silva-Taboada,1979).
122. Cueva del Gato, Bellamar (23.01667, -81.55, 55 m). (J. Orihuela, pers. comm).
123. Cueva de Santa Catalina, Camarioca. **Nyl**: IES 1.3386, 1; **Cma**: CNMA 39848,00, 1.

Pinar del Río

124. Cueva de Los Majáes, Galalón (22.69222, -83.47, 153 m). **Cma** (Tejedor et al. , 2006).
125. Cueva del Indio, Viñales (22.66944, -83.7075, 153 m). **Cma**: AMNH 176160; KU 152357-152360 , 5.
126. Valle de Pica Pica, Sumidero (22.41583, -83.92667, 116 m). **Cma** (Silva-Taboada, 1979).
127. Cueva del Calabazar, Vallecito (21.94528, -84.33194, 8 m). **Nyl** (Tejedor et al., 2005a). **Cma** (Tejedor et al., 2005a).

128. El Veral (40 Km W of El Cayuco), Guanahacabibes (21.94194, -84.55833, 23 m). **Nyl**: KU 150712; IES 1.793, 2; **Cma**: IES 1.4877, 1.
129. Cueva del Chelao, Leña, Consolación. **Nyl** (Silva Taboada, 1979).
130. Cueva La Barca, Guanahacabibes (21.86944, -84.76222, 16 m). **Cma** (Tejedor et al., 2005a); **Npr** (58): MNHN 1–26 G. Silva-Taboada field numbers (male), 27–51 G. Silva-Taboada field numbers (female), FLMNH 26810 (female); IES 1.5557-1.5559, 1.5582-1.5584.

Sancti Spíritus

131. Cueva de Colón, Cayo Caguanes (22.39028, -79.12306, 5 m). **Nyl**: IES 1.3389, 1.3418, 2.
132. Cueva de Humboldt, Cayo Caguanes (22.39028, -79.12306, 5 m). **Nyl** (Silva-Taboada, 1979).
133. Cueva de las tres dolinas, Cayo Caguanes (22.39028, -79.12306, 5 m). **Nyl**: IES 1.3390-1.3415, 1.3421- 1.3487, 1.3216-1.3234, 112.
134. Cueva de Ramos, Cayo Caguanes (22.39028, -79.12306, 5 m). **Nyl** (Silva-Taboada, 1979).
135. Cueva Grande de Caguanes, Cayo Caguanes (22.39028, -79.12306, 5 m). **Nyl**: IES 1.3358, 1.
136. Cueva Sandalio Noda, Cayo Caguanes (22.39028, -79.12306, 5 m). **Nyl** (Silva-Taboada, 1979).
137. Lomas de Judas, Yaguajay (22.1, -78.45, 211 m). **Npr** (Silva Taboada, 1979).
138. Cueva de los Masones, Trinidad (21.8, -79.98333, 51 m). **Nyl**: IES 1.3236-1.3243, 1.3333-1.3349, 25; **Cma** (Silva-Taboada, 1979); **Npr**: ROM 59133–59135; (Silva-Taboada 1974).
139. Cueva del Jagüey, Trinidad (21.8, -79.98333, 51 m). **Nyl** (Silva-Taboada, 1979); **Npr** (Silva-Taboada, 1979).
140. Sierra de Jatibonico. **Nyl**: AMNH 32685, 1.

Santiago de Cuba

141. Santiago de Cuba (21.02472, -75.82194, 227 m). **Cma**: IES 1.3159, 1.3162--1.3177, 1.3179, 1.3180, 19.
142. Cueva del Tesoro, Mar Verde (19.9675, -75.93639, 18 m). **Cma**: IES 1.3181, 1.

143. Cueva de la Cantera, Siboney (19.95, -75.7). **Cma** (Silva-Taboada, 1979); **Npr** (Silva Taboada, 1979).

144. Cueva de Los Majáes, Siboney (19.95, -75.7). **Cma** (Silva-Taboada, 1979).

145. Cueva de Los Indios, Daiquirí (19.91667, -75.65). **Npr**: AMNH 41009 (holotype); (Anthony, 1919).

Villa Clara

146. Gavilan, Santa Clara (22.4, -79.96667, 133 m). **Nyl**: UMMZ (2) 105766, 105767, 2.

Ciego de Ávila

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

Cienfuegos

148. Gruta de Yaguanabo, Yaguanabo (21.89194, -80.195, 92 m). **Nyl**: IES 1.3419, 1.3420, 1.3235, 3; (Silva-Taboada, 1979).

Ciudad de La Habana

149. La Habana (23.11444, -82.41167, 35 m). **Nyl**: FMNH 34057; MCZ 17127, 17129--17134; USNM 300528, 9; (Barbour, 1945).

Granma

150. Entre rocas Grandes, Cabo Cruz (19.85, -77.73333, 4 m). **Nyl** (observation); (Gundlach, 1866).

151. Faro de Cabo Cruz, Cabo Cruz (19.85, -77.73333, 4 m). **Nyl**: MCZ 12544, 1; (Barbour, 1945).

Guantanamo

152. Baracoa, Baracoa (20.35, -74.5, 14 m). **Cma**: AMNH 61191; MCZ 11667, 16662, 3.

153. Cueva de La Majana, Guiniao (20.31667, -74.43333, 53 m). **Cma**: AMNH 42710; USNM 113724 (holotype), 2.

154. Cueva de La Patana, Maisi (20.24944, -74.15, 12 m). **Cma**: IES 1.3156-1.3158 , 3.

155. Cave above power plant at Guaso, Guaso (20.23167, -75.16833, 117 m). **Cma**: USNM 300522-300527, 6; (Silva-Taboada, 1979).

156. El Yarey, Rio Seco. Yateras (20.16528, -75.10806, 59 m). **Cma**: USNM 300521 female, 1; (Miller, 1914).

157. Guantanamo (20.14528, -75.20611, 51 m). **Cma** (Silva-Taboada, 1979).

Holguín

158. Gibara, Gibara (21.10972, -76.13167, 7 m). **Nyl** (Silva-Taboada, 1979).

159. Cueva del Hoyito, Cuatrocientas Rosas, Mulas, Banes (20.91667, -75.8, 28 m). **Nyl** (Silva Taboada, 1979).

La Habana

160. Güines (22.83611, -82.02805, 66 m). **Nyl** (Silva Taboada, 1979).

161. Cueva San Javier, unknown. **Nyl**: USNM 300529, 300530, 2.

Pinar del Rio

162. Unspecified loc. **Cma**: MCZ 11646, 1.

Villa Clara

163. Cueva de Guanayara, Guanayara (21.96667, -80.03333, 422 m). **Nyl** (Silva Taboada, 1979); (Silva-Taboada, 1977).

DOMINICA

St. George

164. Trafalgar Falls (in mistnet) (15.31667, -61.35, 225 m). **Nst**: KU 104920-104930, 11.

165. 6 Miles NE Roseau (15.3, -61.38333, 73 m). **Nst** : KU 150726, 1.

166. Roseau (15.3, -61.4). **Nst**: USNM 62850, 113185, 113596-113614 (113605 holotype, male), 21.

St. John

167. 0.5 mi N Toucari (15.61667, -61.46667, 2 m). **Nst** : TTU 31457--31481, 25.

168. Tanetane (Cave above Douglas Bay, and brick tunnel (15.6, -61.46667). **Nst**: USNM 361906-361910, 362100-362104, 10.

St. Patrick

169. Berekua (15.23333, -61.31667, 164 m). **Nst**, ROM 69411, 1.

170. Corona = Mourne Couronne (15.39667, -61.36944, 465 m). **Nst**, AMNH 237393, 1.

St. Paul

171. Sylvania (15.36667, -61.36667, 473 m). **Nst**: AMNH 237394, 1.
172. Springfield (15.35, -61.36667, 400 m). **Nst**: TTU 31486, 1.
173. Massacre sea cave (15.33333, -61.4, 7 m). **Nst**: CM 111878--111880, 3.

St. Peter

174. Cave below highway, 1.1 km S Calihaut (15.48333, -61.48333). **Nst**: CM 112376, 1.
175. unspecified loc. **Nst**: MCZ 17781, 1.

DOMINICAN REPUBLIC

Barahona

176. Cabral, 3 mi S of (18.20972, -71.2425, 172 m). **Cmi**: PSM 11566, 1.
177. Cueva Los Patos No. 1 and No. 2, Los patos (17.96667, -71.16667). **Cmi**: AMNH (AT 158, male); PSM 25873, 11063, 11562-11565, 11567-11597, 14736, 39; **Nma**: AMNH 97590 (male), (AT 149, female); PSM 11045, 11551-11555, 8.
178. Maniel Viejo (17.96667, -71.31667, 278 m). **Nma**: AMNH 97589 (female)., 1.
179. Oviedo (17.80111, -71.40167, 37 m). **Nma**: MCZ-50055, 1.

Elias Piña

180. Net, Nalga de Maco (19.20556, -71.44444, 820 m). **Nma** (K. Christenson, pers. Com).
181. Cerro de San Francisco, Bánica (19.06667, -71.7, 282 m). **Nma**: FLMNH (without number); (Morgan, 2001).
182. Rancho La Guardia, Hondo Valle (18.71667, -71.66667, 1020 m). **Nma**: MCZ 52462-52465, 4.

Hato Mayor

183. Cueva Vangel ( ) (19.08515, -69.57667). **Nma**: AMNH (AT 172, 173, 176). 3.
184. Cueva de Cristian ( ) (19.03333, -69.4481, 92 m). **Nma**: AMNH (AT 181, 182). 2.

Independencia

185. Puerto Escondido, 9.9 km S (North slope Sierra de Bahoruco) (18.31667, -71.56667, 414 m). **Nma**: USNM 542274 (female, mummy), 1.

María Trinidad Sánchez

186. Cueva de Murciélagos, La Entrada (19.55, -69.9 m). **Nma**: AMNH 238148, 238149; (AT 44, 45, 49, 51, 52; 4 males, 1 female) AT 200–202. PSM 11061, 11062, 11542-11550, 18.

Montecristi

187. Pepillo Salcedo, 5 km SE (19.7, -71.75, 15 m). **Nma**: KU 150713-20, 152361 (7 males, 2 females); (Timm and Genoways, 2003), 9.

Samaná

188. Cueva de Morón (19.31389, -69.42306, 7 m). **Nma**: (AT pers. observ.).

189. El Limón (19.28333, -69.43333, 45 m). **Nma**: PSM 11526-11530, 5.

190. Cueva de la Laguna Juan García ( ) (19.25, -69.45, 237 m). **Nma**: AMNH (AT 186, 187)., 2.

191. Samaná (19.21667, -69.31667, 156 m). **Cmi**: PSM 11598-11599, 12356-12359, 6; **Nma**: PSM 11525, 11531--11538, 9.

192. Cueva Vicente (unknown), unknown. **Cmi**: AMNH 216125--216128, 4.

Sánchez Ramírez

193. Cueva Grande de Julián, Don Miguel, 4 km E Platanal (19.11667, -70.08333, 86 m). **Nma**: AMNH (female), (male), 1.

194. Don Miguel, Don Miguel, 4 km E Platanal (19.1423, -70.0643, 28 m). **Nma**: AMNH (AT 177); 1.

Santiago

195. Savaneta (19.66667, -70.36667, 10 m). **Nma(**2): USNM 101395a (holotype), 101395b (paratype).

Distrito Nacional

196. Santo Domingo (Ciudad Trujillo) (18.46667, -69.9, 16 m). **Nma**: FLMNH 5517 (male); MCZ 20659, 50055, 3.

Hato Mayor

197. Cueva de Johnny (19.0881, -69.5, -4 m). **Nma**: AMNH (AT 177), 1.

La Altagracia

198. Las Lagunas de Nisibon (18.85, -68.66667, 38 m). **Nma**: PSM 11539-11541, 12624, 4.

199. Boca de Yuma (18.38333, -68.6, 3 m). **Nma** (Garcia Marcano, pers. com).

Samaná

200. Arroyo Chico (19.25, -69.48333, 232 m).**Cmi**: AMNH (AT 188, female), 1.

201. Sánchez (Moja Farm), 2 Miles NW of (19.21667, -69.6). **Nma**: USNM, 1.

San Juan

202. San Juan de la Maguana (18.8, -71.23333, 403 m). **Nma**: PSM 11558--11561, 4.

Santiago

203. Monción (19.41667, -71.16667, 344 m). **Nma**: PSM 11041-11060, 11556, 11557, 22.

Santo Domingo

204. Cave, Guayacanes (18.41667, -69.5, 13 m).**Nma** (K. Christenson, pers. com).

205. Unknown locality. **Nma**: USNM 49362, 96496, 2.

EL SALVADOR

La Libertad

206. Cueva hedionda. **Nme** (Mitchell 1965).

207. Hacienda San Diego. **Nme** (Mitchell 1965).

La Unión

208. Tabanco. **Nme**: MVZ 130969--130971, 3.

Morazan

209. 1.5 mi W Divisadero, [Monte Cristo Mine] (13.6, -88.05, 204 m). **Nme**: MVZ 130972-130974, 3.

210. 3 mi W Divisadero, [Encuentros Mine] (13.6, -88.05, 204 m). **Nme**: MVZ 130975; ROM 37227, 2.

211. Hacienda Santa Rosa. **Nme** (Mitchell 1965).

San Miguel

212. Comacarán, [Potosi Mine] (13.53333, -88.06667, 182 m). **Nme**: MVZ 130976-130986, 11.

Santa Ana

213. Cueva de los Ombrinos, Metapan (14.33333, -89.45, 480 m). **Nme** (Mitchell, 1965)

214. El Marne, 8 Km S of Santa Ana (13.99417, -89.55972, 645 m). **Nme**: MZUS*P* 15251-252; ROM 37226, 37228, 2.

FRENCH GUIANA

215. Roura (4.7305, -52.3306, 17 m). (Charles-Dominique et al., 2001)

216. Patawa (4.552, -52.151, 279 m). (Keeley, B. Pers. Com.)

GUADELOUPE

Grande Terre

217. Le Moule (16.33333, -61.33333, 22 m). **Nst** : KU 150727; SCFF 2, 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**: CM 112377, 1.

GUATEMALA

Alta Verapaz

219. Lanquin, Cave of Lanquin (15.56667, -89.96667, 493 m). **Nme**: FMNH 64730; KU 64926–64987; (64926−64930, 64933, 64964−64967; 5 females, 5 males). 63.

El Progreso

220. Rio Uyus, San Cristobal Acasaguastlan (14.91667, -89.88333, 241 m). **Nme**: ROM 99652, 1.

221. Guastatoya, El Progreso (14.85, -90.05, 1009 m).**Nme**: AMNH 68583–68588. 6.

Izabal

222. Puerto Barrios, 22 km S S W (15.71667, -88.6, 8 m). **Nme**: FMNH 143423, 143424; USNM 546495. 3.

223. Gruta Silvino, 2 km ENE Navajoa (15.54861, -88.90944, 42 m). **Nme**: FMNH 104883-104891; KU 83609--83612; MCZ-58477, 14.

224. Near Livingston (15.82722, -88.74722). **Nme**: MCZ-56747, 1.

225. Cueva, Cascada de Agua Caliente (15.59056, -89.20972, 15 m). **Nme** (AT, personal observation).

226. Quiriguá (15.26667, -89.0833, 94 m). **Nme**: USNM 174952. 1.

Petén

227. Tikal National Park (17.25, -89.65, 279 m). **Nme**: FMNH 1212086, 1.

228. 4 mi W Flores, Santa Elena Jobitzinal Cave (16.93694, -89.94639, 117 m). **Nme**: FMNH 64808-64822, 64648, 64649, 51076; 18.

229. Cave, 2 mi S Flores, Flores (16.91667, -89.88333, 122 m). **Nme**: MVZ 106200, 106201; AMNH 144712–144715, 144762; USNM 245155–245208 (245155, 245161, 245168, 245174, 245180−245181; 4 females, 3 males). 60.

Zacapa

230. Sierra de Las Minas, R Teculutan, Santa Clara (14.98333, -89.71667, 219 m). **Nme**: FMNH 64489-64494, 64731-64807, 83.

GUYANA

Upper Takutu-Upper Essequibo; Rupununi

231. Warimure, Quash Wau, Weri More, 12 Mi Ne Of Dadanawa, Upper Takutu-Upper Essequibo (2.933333, -59.48333, 112 m). **Ntu**: Rom 52161, 1.

232. Ruawau River, Raa Wau, 35 Mi W Of Dadanawa (2.755, -59.991, 100 m). **Ntu**: Rom 53766, 53767, 2.

233. Ruawau River, Takatu River Area, 40 Mi Sw Of Dadanawa (2.347, -59.855, 126 m). **Ntu**: Rom 58840, 1.

HAITI

Departement du L'Ouest

234. Port-au-Prince (18.56667, -72.28333, 46 m). **Nma**: BM (1 specimen, unspecified); (Sanborn, 1941).

Departement du Sud

235. Camp Perrin, Les Cayes (18.31667, -73.86667, 202). **Nma** , KU 150721 (male), 1; (Timm and Genoways, 2003).

HONDURAS

Francisco Morazán

236. La Tigra Parque Nacional. **Nme**: Ttu 83664, 1.

Santa Barbara

237. 12 Km N Santa Barbara (14.91667, -88.23333, 287 m). **Nme**: Ttu 13418, 1.

JAMAICA

Clarendon Parish

238. North Kellits (18.15,-77.23333, 402 m).

239. Near End Jackson's Bay (17.73333,-77.23333). **Cmi**: ROM 37166, 37165,2.

Hanover Parish

240. Lucea (18.45,-78.16667, 9 m). **Cmi**: AMNH 12393, 1.

Saint Ann

241. Moneague (18.26667,-77.11667, 340 m). **Cmi** (Genoways et al., 2005)

St. Elizabeth Parish

242. Oxford Cave, Auchtembeddie (18.23333, -77.65, 342 m).**Cmi**: AMNH 45194--45196, 3.

243. Wallingford Cave, Balaclava (18.18361, -77.64331, 293 m). **Nja**: AMNH 147208 (fossil), (Koopman and Williams, 1951).

Trelawny parish

244. Mahogany Hall Cave (18.38333, -77.46667,399 m). **Cmi**: BMNH

245. Windsor Cave (18.35139,-77.64747,104 m). **Cmi**: FMNH 44215—44217; USNM (unspecified); TTU 22065; 4.

Clarendon Parish

246. Portland Cave Portland Cottage (17.76667, -77.23333,0 m). **Nja** (observation) (Fincham 1997).

Portland Parish

247. Port Antonio (18.18333,-76.46667, 8 m). **Cmi**: USNM 113916-113920, 5.

248 Paradise, in house (18.16667, -76.65, 292 m). **Cmi**: FLMNH 14060, 1.

Saint Andrew

249. Kingston (18, -76.78333, 78 m). **Cmi**: BMNH holotype, 1.

St. Catherine Parish

250. St. Clair Cave, Linstead (18.11667, -77.01667, 97 m). **Cmi**: AMNH 214132, 246129, 2715577-2715579, 274630, 274631, CM 44570-44602; LACM (2) 15696-15697; ROM ( )37030-37034, 37036-37064, 37153-37159, 89700, 89716--89719, 89961-89964 ; TTU () 21977-22064, 47809; FLMNH 13696-13701, 14060, 19076. MCZ 49306-49311, 203; **Nja**: AMNH 181999, 182000 (holotype), 214131, 246123, 246126–246128, 271575, 271576 (8 males, 1 female); FLMNH 13688–13692 (3 males, 2 females); FMNH 93784 (female); BMNH 65.4000a, 65.4000b; JI No. 3, JI No. 4, (Goodwin, 1959); ROM 37029, 37065–37076 (4 females); MCZ 49298-49304; MVZ 167948; TTU 29110-29127, 21946-21976, 78.

251. Bog Walk (18.1, -77.01667, 348 m). **Cmi**: FMNH 46423, 1.

James Parish

252. Montego Bay (18.46667, -77.91667,5 m). **Cmi**: USNM 172427, 1.

Westmoreland Parish

253. Monarva Cave, Revival (18.21667,-78.28333). **Cmi** (observation) (McFarlane, 1997).

254. Unknown locality. **Cmi**: USNM (unspecified)

MARTINIQUE

Le Marin

255. Usine Petit Bourg (14.53333, -60.96667, 9 m). **Nst** : SCFF 1, 1.

MEXICO

Baja California del Sur

256. Las Cruces (24.20306, -110.0908, 33 m). **Nme**(1): MSB 43837.

257. 2.5 Km N, San Antonio, ? (23.8, -110.0167, 354 m). **Nme**(7): CNMA 4540, 9852; KU 94184, 94186–94189 (5 males).

258. El Triunfo (includes Mina El Triunfito), El Triunfo (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 (23.53333, -109.6833, 75 m). **Nme** (8): (KU 27315–27320; 6 females), 94190, 94191.

261. Cueva De Los Martires, ? (23.5, -109.6, 113 m). **Nme**(1): CNMA 18016,00.

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 18015,00.

265. 5 Km Se, Pescadero, ?, (23.33333, -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 (23.13333, -109.7167, 86 m). **Nme**(14): USNM 148460–148471, 96495, 96496 (holotype of *Natalus mexicanus*)..

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 Constitucion, 44 Km S, 70 Km E of Escarcega (18.6, -90.74, 81 m). **Nme**(1): ROM 95708.

272. La Tuxpeña (18.43333, -90.06667, 183 m). **Nme**(3): USNM 170848–170850.

273. Zona Arqueologica Calakmul, Calakmul (18.1, -89.8, 258 m). **Nme** (1): CNMA 37301,00.

Chihuahua

274. Mojaráchic [= Mafuaráchic (27.81667, -108.0167, 1179 m). **Nla**(1): (USNM 265661*).

275. Barranca del Cobre,, 23 miles S, 1.5 miles E of Creel (27.75, -107.6167, 2385 m). **Nme** (2): (KU 73521, 73522; 2 males).

276. La Bufa (27.11667, -107.5667, 2028 m). **Nla**(1): (KU 79448*; male).

277. Mina Santo Domingo, Batopilas (27.01667, -107.7167, 1666 m). **Nme**: CRD 136362–136364, 136358 (AMNH frozen tissue collection numbers).

Chiapas

278. Ococingo (16.9, -92.03333, 868 m). **Nme**(1): USNM 554861.

279. Cueva de la Chepa, 2 km N Tuxtla G. (16.78333, -93.15, 809 m). **Nme** (Arita, 1997),

280. Cueva los Laguitos, Tuxtla Gutierrez (16.78333, -93.15, 809 m). **Nme** (Sorba et al., 2004),

281. 4 Km Nw, Tuxtla Gutierrez, Tuxtla Gutierrez (16.75, -93.15, 590 m). **Nme**(2): CNMA 5136-5137.

282. Tuxtla Gutierrez (16.75, -93.11, 544 m). **Nme**(40): UMMZ 109817; CNMA 5134, 20935-20937, 5135; MMNH 4826, 4914; MCZ-47931, 47932, 48126; KU 61121–61148, 66501(61136−61138, 61140−61143; 1 female, 6 males).

283. 7 Km S Por Carretera, Rosendo Salazar, Cintalapa (16.41, -93.98, 855 m). **Nme**(1): CNMA 19264,00.

284. Confluencia Arroyo Miranda Con Rio Lacantun, Ocosingo (16.14, -90.92, 155 m). **Nme** (3): CNMA 19265-19267,.

285. Estacion Chajul De Sedue, Ocosingo (16.12, -90.93, 166 m). **Nme**(3): CNMA 20934, 23735, 24466.

286. Tonala, 15 mi ESE (16.08333, -93.75, 45 m). **Nme**(1): LACM 014083.

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 Fabrica, Coquimatlan, 4 mi S (19.2, -103.8, 330). **Nme**(30): LACM 011246-011262, 012131-012141, 016702, 016703.

291. Tecoman, 12 km NW (18.91667, -103.8833, 42 m). **Nme**(3): LACM 012142, 012142, 012130.

292. Hacienda Los Ortices, 2km Se. **Nme**(2): UMMZ 79942, 79943.

293. Rancho Nuevo. **Nme** (Mitchell, 1965).

Distrito Federal

294. Cueva Ixtli, Tlalpan (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 (24.91667, -106.35, 1886 m). **Nla** (1): (CRD 2845*, male).

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*, female).

300. Chacala (24.8, -106.7333, 846 m). **Nme** (21): USNM 96876–96879 (96876, 96877; 2 females); (= Chamala) USNM 96859–96875 (96862, 96864, 96869, 96874; 2 females, 3 males). **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 35201,00.

303. Teloloapan, Teloloapan, Teloloapan (18.35, -99.85, 1600 m). **Nme**(1): CNMA 9981,0.

304. Teloloapan, 10 Mi E, 2 Mi S, Teloloapan (18.33, -99.72, 1594 m). **Nme**(2): CNMA 1770, 1771.

305. El Ojo De Agua, Chapa, Teloloapan (18.31667, -99.81667, 1453 m). **Nme**(1): CNMA 9027,0.

306. 4 Km W of Cocula (18.23333, -99.66667, 626 m). **Nme**(1): ROM 78777.

307. Zacatula, 12 Km N of (17.98333, -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) Murcielagos Cavernicolas de Mexico.

309. Colotlipa, Colotlipa, Quechultenango (17.43, -99.16, 942 m). **Nme**(13): CNMA 22528, 25583-25585, 26887, 3711, 3715, 26884-26886, MCZ-59203.

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 (99723, 99724, 99728, 99729.1 male, 3 females); 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 (17.38333, -99.45, 968 m). **Nme** (Lukens and Davis, 1957).

314. 2 Mi Nw Acapulco (16.85, -99.91667). **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, Etzatlan (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**(5): CNMA 7336--7340.

319. Sierra de Cuale (20.6, -105.2333, 196 m). **Nme**(9): KU 92911- 92917, 92920-92922, 92925, 92926, 92929, 92932, 92933 .15, **Nla**, KU 92916*, 92918*, 92919*, 92923*, 92924*, 92927*, 92928*, 92930*, 92931*.

320. Ameca (20.55, -104.0167, 1231 m). **Nme** (13): KU 33373–33391(33374, 33375, 33383, 33384, 33388, 33391; 3 females, 3 males); USNM 87322, 87325, 87333; 5 females, males). 22, **Nla**, USNM 87323* 87326*, 87328−87332*, 87334−87339*.

321. Mina De Las Garrochas, 17 Km Nnw, Soyatlan Del Oro (20.44, -104.33, 1957 m). **Nme** (8): CNMA 2174-2180.

322. Zapotlán [= Ciudad Guzmán (20.43333, -102.9167, 1536 m). **Nme**(1) (Watkins et al., 1972) p. 39]. USNM 52109.

323. Talpa De Allende, 12.5 Mi Sw, By Road (20.367, -104.817, 1156 m). **Nme**(1): CM 79430; (1, **Nla**, AMNH 254673*; female).

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,(33392–33394; 1 female, 2 males), 41341–41347.

327. Km 69 Carr. Barra De Navidad-Pto. Vallarta, Chamela (19.52, -105.07, 32 m). **Nme**: CNMA 4196, 16854, 16855, 3.

328. La Huerta, 2 Mi Ne (19.467, -104.65, 320 m). **Nme**(5): CNMA 25581; KU 10555–105560.

329. Cuitzamala (in a cave), Cuitzamala (19.36667, -104.9833, 46 m). **Nme** (Arita, 1997) Murcielagos Cavernicolas de Mexico.

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 (female).

332. Mina Hedionda, 30 km W Rancho de los Ocoles. **Nme** (Mitchell, 1966).

Mexico

333. Convento de Acolman, Municipio, Acolman (19.63333, -98.91667, 2257 m). **Nme** (Caballero, 1942a, 1942b).

334. Cueva Peña Blanca, Avandaro, Valle De Bravo (19.14, -100.1, 2185 m). **Nme**(2): CNMA 15565, 15566.

335. Cueva De La Estrella, Tonatico, Tonatico (18.74, -99.62, 1560 m). **Nme**(1): CNMA 2012,00.

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** (Davalos, 2005).

339. Los Hornos, 3 Km Nnw, Caleta De Campos (18.08, -102.77). **Nme** (8): CNMA 17367-17374.

Morelos

340. Cueva Del Salire, Cerca De, Tetecalita, (18.76667, -99.18333, 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 Idolo, Jojutla De Juarez (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 22563,00.

345. Chinameca, 6 Km S , 2 Km E, San Pablo Hidalgo, Tlaltizapan (18.58, -99.02, 1080 m). **Nme**(1): CNMA 18808,00.

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. **Nme**(6): UWBM 62665--62670.

Nayarit

348. Rio del Bajar; Huajicori, Huajicori (22.63833, -105.3192, 71 m). **Nme**(3): LACM 019178-019180.

349. La Cuchara, Acaponeta, 40 mi E (approx); (22.49639, -105.3594, 30 m). **Nme**(17): LACM 017486-017502.

350. Rancho Palo Amarillo, Tepic near Amatlan (21.5, -104.9, 961 m). **Nme**(1): FMNH 20103; AMNH 25102-25105, 25107-25111, 10, **Nla**, AMNH 25106*.

351. Santa Maria 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 (21.86667, -105.0333, 46 m). **Nme**(10). KU 85719–85728, (85719, 85722, 85724, 85725, 85728; 4 females, 1 male).

353. San Blas 21.51667, -105.2667. **Nme**(10): KU 36607; (Paso de Soquilpa) USNM 508851. MSB 16853, 16854; LACM 013925-013930.

354. Jalcocotan, 2 mi. SE (21.46667, -105.1167, 446 m). **Nme**(14): MSU MR.49; KU 36615–36626, 36654 (36625; male).

355. Aticama (21.46667, -105.2167). **Nme**(1): KU 36627.

356. Isla Maria Magdalena (21.41667, -106.4, 5 m). **Nme**(5), Islas Tres Marías. AMNH 180560,180839, 180877, 180879, 180880.

357. Las Varas (21.16667, -105.1667, 28 m). **Nme**(10): KU 39622–39627, 39629-39682, 39684-39689, 39692-39699, 39701-39703, 39706-39708, 39710 (39620*, 39621*, 39628*,39682, 39683*, 39685, 39690*, 39691*, 39694, 39695, 39700*,

39701, 39702, 39704*, 39705*, 39708, 39709*, 39710; 14 females, 4 males)., 81, **Nla**, AMNH 39620*, 39621*, 39628*,39683*, 39690*, 39691*, 39700*, 39704*, 39705*, 39709*.

358. Barranca del Oro (0.91667, -104.4667, 789 m). **Nme**(1): USNM 523440.
359. Mineral del Tigre, 1340 feet. **Nme**(1): MSU MR.17130.
360. Cueva La Boca, Santiago (25.41667, -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. Matias Romero, 12 mi N (16.88333, -95.03333, 212 m). **Nme**(1): LACM 019389.
363. Río Guamol, 34 Mi S by highway 190 La Ventosa Jct, El Guamol (16.49, -94.47306, 30 m). **Nme**(1): MSB 27600.
364. El Jícaro=General Pascual Fuentes, 3 Mi N, Santo Domingo Zanatepec (16.47, -94.26, 178 m). **Nme**(12): CNMA 5344,00; AMNH 186395–186405.
365. Tapanatepec, 8 km NW; Rancho Sol-y-Luna (16.35, -94.2, 41 m). **Nme**(3): LACM 016841, 018115; AMNH 177420.
366. San Gabriel Mixtepec, 9 miles west (16.08333, -97.1, 736 m). **Nme**(1): CAS 14989.
367. Matias Romero, 17 mi. N and 2 mi. E of (16.8833, -95.033, 212 m). **Nme** (1): MSU MR.7917.
368. El Salado (16.41667, -95.51667, 195 m). **Nme**(4): AMNH 178758–178761.
369. Mixtequilla (16.39111, -95.26083, 219 m). **Nme** (24): AMNH 185025, 185026, 185044-185065.
370. Tehuantepec (16.31833, -95.21833, 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, Tenampulco (20.14, -97.24, 280 m). **Nme** (1): CNMA 40432,00.

373. Cueva La Salamandra, Ayotoxco and Tenampulco (20.13333, -97.4, 209 m). **Nme** (Brunet and Medellin, 2001).

374. Cueva Virgen, Ayotoxco and Tenampulco (20.13333, -97.4, 209 m). **Nme** (Brunet and Medellin, 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, 16356, 17027-17030.

376. Raboso (18.56667, -98.41667, 1291 m). **Nme** (77). KU 61104–61120, 62358–62364,63150, 63151, 67414–67464 (61106, 61108, 62358−62362; 1 female; 6 males).

Querétaro

377. Felipe Carrillo Puerto, 8 Km Sw, Felipe Carrillo Puerto, Benito Juarez (20.79, -86.93). **Nme**(1): CNMA 34920,00.

378. San Miguel de Cozumel (20.50083, -86.94583, 7 m).**Nme**: USNM 318491–319245. (Includes “Santa Rita, 10 km E of San Miguel de Cozumel”; KU (8) 150722–150725, 151194–151197).

379. Chumpón-La Glorieta, Sian K'an (19.81806, -87.58056, 11 m). **Nme** (Pozo De LaTijera and Escobedo-Cabrera, 1999),

380. Cenote, 2 km N Of Felipe Carrillo Puerto, Felipe Carrillo Puerto, Felipe Carrillo Puerto (19.58333, -88.05, 15 m). **Nme** (Arita, 1997).

381. Laguna Noh-Bec, 2 Km W, Noh-Bec, Othon P. Blanco (19.12, -88.16, 22 m). **Nme**(10): ROM 97440-97445, 97518, 97519; CNMA 31756, 31757.

382. Bacalar, 4 Km S, 1 Km W, Bacalar, Othon P. Blanco (18.64, -88.4, 2 m). **Nme** (1): CNMA 20163,00.

383. Felipe Carrillo Puerto, 4 Km NNE (18.63, -88.02). **Nme**(1): CNMA 25592,00; KU 91903, 91904.

Sinaloa

384. Rio Corsala, Ca 72 Mi S By Hwy 15 Culiacan (24.06, -106.8, 101 m). **Nme**(1): MSB 32128.

385. Santa Lucia (23.43333, -105.8667, 1028 m). **Nme**(10): CNMA 4513, 9851; KU 94257, 95011–95017 (95013, 95014; 1 female; 1 male).

386. Pánuco (23.41667, -105.9167, 535 m). **Nme**(4): CNMA 25571, 25574-25576; KU 85704–85718, 85911–85914, 95839–95874, 145428 (95869−95873; 3 females, 2 males).

387. Puerta de Canoa, 11 mi N, 2.5 mi E Mazatlan (23.36667, -106.3833, 109 m). **Nme** (10): LACM 088107, 012437-012445.

388. Copala (23.36667, -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.

389. El Cajón, 1 Mi S, El Cajon (23.35, -106.0167, 373 m). **Nme**(5): CNMA 25577,00; KU 100380–100383.

390. Cueva Playa Cerritos, 5 Km W, Mazatlan (23.31, -106.48, 9 m). **Nme**(1): CNMA 36394,00.

391. Rio Arroyo De Mesilla, 0.5 Mi S Concordia (23.28333, -106.0667, 114 m). **Nme**(1): MSB 37234.

392. Mazatlán (23.21667, -106.4167, 6 m). **Nme** (51): CAS 13250-13258; CNMA 25579; ROM 78775; LACM 014724-14737; KU 85678–85703, USNM 96995.

393. Mazatlán Cave, 5 mi N (23.21667, -106.4167, 6 m). **Nme**(15): LACM 015532-015544, 015568, 15575; ROM 77324.

394. Plomosas (23.06667, -105.4667, 891 m). **Nme**(32): KU 92894–92910, USNM 92394–92408.

395. Matatan, (23.01667, -105.7167, 140 m). **Nme**(7): CNMA 25572, 25573; KU 90726–90730.

396. 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*; male.

397. Hwy 15 of Sinaloa-Nay Border, Rio Canas (22.5325, -105.4508, 16 m). **Nme**(15): MSB 27341-27355.

San Luis Potosí

398. 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.

399. Cueva Chica, 11 Mi Se Ciudad Valles (21.98333, -99.01667, 75 m). **Nme**(1): TTU 9242.

400. Cueva De Taninul #1, 8.8 Mi S Ciudad Valles (21.98333, -99.01667, 75 m). **Nme**(11): TTU 9226-9234, 8343; CNMA 2200.

401. Rancho nacimiento del rio Coy (21.8, -99.07, 216 m). **Nme**(1) (Constantine, 1958).

402. Rancho El Estribillo, Ciudad Del Maiz. **Nme**: CNMA 30154,00.

Sonora

403. Guano Cave (=Cueva del Tigre), 14.9 MI ESE (BY ROAD) CARBO, Carbo (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 Mazatan (29, -110.1333, 545 m). **Nme**(9): TTU 10800-10803, 10809-10813.

406. Jct Rds To Soyopa and Novillo, 12.7 Mi W Novillo (28.93333, -109.6333, 269 m). **Nme** (1): TTU 10524.

407. Rio Yaqui, 4 Mi S El Novillo Dam (28.93333, -109.6333, 269 m). **Nme**(1): MSB 34157.

408. Mina Santa Clara, 7 Km W Tonichi (28.58333, -109.5667, 225 m). **Nme**(6): TTU 46843–46848.

409. San Carlos, 8 Mi NNW, 28.20n 111.10w (28.31667, -111.3167, 12 m). **Nme**(2): MSB 60914, 61126.

410. Algodon Beach, 20 Km Nw Guymas (27.93333, -110.9, 18 m). **Nme**(1): MSB 42664.

411. San Carlos Bay, Ca 5 Mi (27.93333, -111.05). **Nme**(1): MSB 32129.

412. Quiriego, 11.9 Mi N (27.51667, -109.2667, 211 m). **Nme** (1): TTU 33711.

413. Tesia (27.16667, -109.3667, 46 m). **Nme**(4): AMNH 172023–172026.

414. Alamos, 4 Mi N, Alamos, ? (27.08, -108.93, 491 m). **Nme**(1): CNMA 2710,00.

415. Mina Armolillo, 5 Mi NNW, Alamos, Hermosillo (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 Of, 5 Km W Of Alamos (27.01667, -108.9333, 378 m). **Nme**(2): MSB 11050; ROM 78776.

419. Alamos, 5 Mi N, 1 Mi (27.01667, -108.9333, 378 m). **Nme**(6): TTU 47005-47010.

420. Álamos (27.01667, -108.9333, 378 m). **Nme** (52): (KU 24843–24848; 3 females, 3males), 25074–25118. CNMA 25580,00.

421. Minas Nuevas, 4 Mi Nw Alamos (27.01667, -108.9333, 378 m). **Nme**(8): TTU 36621-36628.

422. Mina Santo Domingo, 2.7 S 2.9 W, 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; 3 females).

Tabasco

424. Cueva De Don Luis, 3.3 Km Ne, Teapa, Teapa (17.56, -92.92, 40 m). **Nme**(2): CNMA 7025, 7026.

425. Teapa, 3 Km E, Teapa, Teapa (17.55, -92.95, 50 m). **Nme**(2): CNMA 7445,00; KU 66502.

426. Cueva Cocona, 4 Km E, Teapa, Teapa (17.54, -92.91, 119 m). **Nme**(1): CNMA 7673,00.

Tamaulipas

427. Cueva Del Rancho Rio Escondido, 19 Km Nnw, S. De Jimenez, S. De Jimenez (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 Jimenez (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, Gomez Farias (23.05, -99.16, 328 m). **Nme**(2): CNMA 34800, 34801.

434. Cueva El Ojo De Agua, 3.1 Km Se, Gomez Farias (23.02, -99.13, 162 m). **Nme**(1): CNMA 34802,00.

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 (22.71667, -98.96667, 78 m). **Nme**(20): KU 60276–60295.

438. Cueva De Quintero, Quintero, El Mante (22.66, -99.03, 111 m). **Nme**(1): CNMA 1236,00.

439. Cueva Del Abra, 10 Km Nne, Antiguo Mor (22.63, -99.04, 343 m). **Nme**(1): CNMA 4862,00.

440. Cueva De La Florida, 2 Mi N El Pachon (22.61667, -99.03333, 289 m). **Nme**(22): TU 6591-6604, 6623, 6624, 63385-63392.

441. Cueva en El Pachón (22.61667, -99.03333, 289). **Nme**(153): AMNH 147903–147911, 148058–148194,164436–164441. CM 83523, includes Antiguo Morelos KU 17846.).

442. Cueva Del Nacimiento Del Rio Frio. **Nme**(1): TTU 47450.

443. Mina A 5 Km Sw Cañon De La Boca, Hacienda La Boca, ?, ?, . **Nme**(1): CNMA 1594,00.

Veracruz

444. Tuxpan, 9 Km Nw (21.01, -97.46, 36 m). **Nme** (1): CNMA 27934,00.

445. Tuxpan (20.93333, -97.4, 10 m). **Nla** (16): KU 82893–82908.

446. Cerca de Jalapa (19.54, -96.92, 1448 m). **Nme** (4): CNMA 9229-9232.

447. Mirador (19.28333, -96.9, 957 m). **Nme**(3): USNM 8217, 8218, 102420;

448. Potrero (18.88333, -96.78333, 495). **Nla** (10). KU 29693–29702.

449. Fortín (= Fortín de las Flores)(18.88333, -97, 947 m). **Nla** (1): KU 17845.

450. Orizaba (18.85, -97.08333, 1189 m).**Nla**(1): USNM 1840, 7838.

451. Ojo De Agua Del Rio Atoyac, Atoyac (18.71, -96.8, 382 m). **Nme**(1): CNMA 10680,00.

452. reserva ecologica los tuxtlas (18.58, -95.07, 204 m). **Nme** (Estrada and Coates-Estrada, 2001).

453. Cueva del Boquerón, 3 KM E SAN ANDRES TUXTLA (18.43333, -95.21667, 254 m). **Nme**(5): CM 80234—80237; UMMZ 110439.

454. San Andrés Tuxtla (18.43333, -95.21667, 254 m). **Nme**(110): KU 23772–23814, 23815(holotype of *Natalus mexicanus saturatus*), 23816−23838, 24725–24744; USNM 65473, 70438, 70439 (23809, 23810, 23812, 23820, 23821, 23833, 23834, 23836−23838; 5 females, 5 males).

Yucatán

455. Hacienda San Antonio Teztiz, 6 Km S, 5 Km W Kinchi (= Kinchil)(20.91667, -89.95, 7 m). **Nme**(1): TTU 29072.

456. Cueva De Hoctún, Hoctún (20.85, -89.2, 17 m). **Nme** (8): MMNH 12077, 12811; CNMA 32861-32864, 1578, 1579; USNM 260814.

457. Gruta de Las Ruinas de Mayapán, 2 Km S, Telchaquillo, Tecoh (20.62, -89.46, 17 m). **Nme** (2): CNMA 32865, 32866.

458. 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.

459. Cueva De Loltún, 8 Km Sw Oxkutzcab (20.3, -89.41667, 44 m). **Nme** (3): MMNH 1282; TTU 25901, 29073.

460. Cueva De Los Murciélagos, 0.5 Km Sw, Ticum, Tekax (20.14, -89.22, 40 m). **Nme** (3): CNMA 32860, 32866, 32868.

461. 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

462. Santa Rosa, Rio Juchipila (21.6, -102.95, 1558 m). **Nme** (1): LACM 034286

MONTSERRAT

Saint Anthony

463. BVR Tarrish Pits, Aymers Ghaut (16.7, -62.2, 205 m). **Nst** (S.C. Pedersen, pers. comm.).

464. Danforth, unknown. **Nst**(1): FMNH 47702.

NETHERLANDS ANTILLES

Bonaire

465. Kralendijk, 8.5 Km N, 2 Km W (12.15, -68.26667, 4 m). **Ntu** (1): CM 52202.

Curaçao

466. Kueba Bossa 2 (12.3326, -69.084, 41 m). **Ntu** (Petit, 1995).

467. Hatto (= Hatto)(12.2198, -69.0046). **Ntu** (1): USNM 102106.

468. Cueva di Raton (12.199, -68.987, 24 m). **Ntu** (4): LM 16521, 16571, 14387, 16682.

469. Grot Van Hato (8 km N Willemstad (12.1807, -68.9597, 56 m). **Ntu**: MBUCV 2312, 1.

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 (17.63806, -63.24222, 440 m). **Nst** (8): TTU 101951-101965.

473. unspecified locality. **Nst** (1): FMNH 47701.

St. Maarten

474. Billy Folly (18.0325, -63.09222). **Nst** (S.C. Pedersen, pers. comm).

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, -62.61417, 95 m). **Nst** (Pedersen et al., 2003).

St. Thomas Lowland Parish

477. Cades Estate (17.19222, -62.61417, 27 m). **Nst** (1): UNSM 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, -85.86667, 112 m). **Nme**(1): TTU 17127.

Zelaya

480. El Recreo; S Side of Rio Mico (12.16667, -84.31667, 23 m). **Nme**(2): KU 106280, 111223.

PANAMA

Coclé provincia

481. Penonome (8.516667, -80.36667, 64 m). **Nme**: MCZ 28228, 28229, 33514-33516, 5.

Colón

482. Sea Cave, Fort Sherman, Below FT. San Lorenzo (9.322778, -80.00278, 0 m). **Nme** (36): UMMZ 122343; USNM 314726, 319065-19083; MVZ 118799-118805, 118968-118974, USNM 305570.

Panamá

483. Camp Chagres, Madden Dam (9.208333, -79.61667, 67 m). **Nme**(1): USNM 396478.

484. Cave near mouth of Río Puente (9.193333, -79.55417, 97 m). **Nme**(1): USNM 396404.

485. Madden Dam (includes Chilibrillo Caves, Camp Chagres) (9.183333, -79.61667, 59 m). **Nme** (2): AMNH 80962, KU 45088.

Veraguas

486. Coiba Island (unspecified)(7.45, -81.76667, 310 m). **Nme**: AMNH 18729, 1.

PARAGUAY

Concepción

487. Parque Nacional Serranía de San Luis (-22.67233, -57.34933, 183 m). **Nes** (1): TTU 75277.

SURINAME

488. Sipaliwini Airstrip, Sipaliwini (2.033333, -56.13333, 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): FLMNH 24850-24856, USNM 576614, 576619, 576619, 576620.

490. Hole in the Wall Cave, Hole in the Wall Point (25.84556, -77.2125). **Npr**: FLMNH (fossil), (Morgan, 1994), (Morgan, 2001).

491. "Cave", Israel's point, NE of Island. **Ctu** (Allen, 1905)

492. Golden Cave. **Ctu** (1): FLMNH 22398.

493. Unspecified loc. **Ctu** (58): AMNH 40026; FMNH 34069, 34070, 34182; MCZ 10868-10922.

494. Long Bay Cave. **Npr**: (G.S. Morgan pers. comm.).

Andros

495. King Cave, Morgans Bluff (25.16667, -78.03333, 7m). **Nyl**: FLMNH 79108, 79109;

Ctu: FLMNH 79111–79171, 79244–79264, 79305–79321. **Npr**: FLMNH 79110, (Morgan, 1989).

496. Coleby Bay Cave, Morgans Bluff (25.16667, -78.03333, 7 m). **Npr**: FLMNH 79324

497. Morgan Bluff Cave, Morgans Bluff (25.16667, -78.03333, 7 m). **Ctu**: CM 92459–92462, 4. **Ctu** (Andersen, 1990).

498. Ashton cave. **Ctu**: FLMNH 79408–79464.

Cat

499. Crown Cave, Dumfries (24.63333, -75.66667, 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**: FLMNH 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, pers. comm.).

Great Exuma

505. Anne's Creek Cave 3, near Stephenton (23.65703, -75.9594, 2 m). **Nyl** (K. Murray, pers. comm.).

506. Max Bowes Cave, Forest (23.58333, -75.91667, 7 m). **Nyl** (Koopman et al., 1957); **Ctu** (Koopman, 1957).

507. Nursery Cave (Lower), near Moss Town (23.57405, -75.90583, 5 m). **Nyl** (Kevin Murray, in litt.).

508. Cabbage Hill Cave, near Moss Town (23.55582, -75.88207, 0 m). **Nyl** (Kevin Murray, in litt.).

Little Exuma

509. Pasture Cave, near Ferry (23.4555, -75.63968, 9 m). **Nyl** (Kevin Murray, in litt.).

510. Palm Beach Cistern, near Ferry (23.45425, -75.6352, 9 m). **Nyl** (Kevin Murray, in litt.).

511. Ferry, 6 mi E (23.43333, -75.58333, 5 m). **Nyl** (2): AMNH 167130, 167133,.

Long

512. Miller's Cave (23.4, -75.16667, 7 m). **Nyl** (112): FMNH 44535-44626; KU 157503-157522.

513. Pinder's Settlement, 24 Miles NW Clarence Town (23.28333, -75.1, 21 m). **Nyl** (43): FLMNH 12833-12837; KU 151173-151180, 157523-157541; UMMZ (11) 99141-99151.

514. Mortimer's (South Point) (22.9, -74.86667, 6 m). **Nyl** (14): FMNH 46063-46066; KU 157499-157502; MCZ 33774-33779.

New Providence

515. Sir Harry Oakes Cave (25.06667, -77.45, 7 m). **Ctu**: FLMNH 79799–79801.

516. East Cave (25.05, -77.26667, 18 m). **Ctu**: FLMNH 27732–27779, 79852–79855.

517. Hunts Cave (25.03333, -77.36667, 7 m). **Ctu**: FLMNH 79749, 79750, 79842; **Npr**: FLMNH 27694, 79751–79759, 79761–79766, 79843–79848.

518. Banana Hole (25.01667, -77.55, 6 m). **Ctu**: FLMNH 79994–79999; **Npr**: FLMNH 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) Ct (27): USNM (27) 122024 (holotype), 540739-540770.

524. unspecified loc. **Ctu** (5): USNM 122021-122023, 122482, 122483.

525. unknown, **Ctu** (1): USNM 217270.

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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 (10.81667, -61.03333, 142 m). **Ntu** (1): LACM 15872.

St. George

530. Blanchisseuse (10.78333, -61.3, 113 m). **Ntu** (2): TTU 26743, 24117.

531. Las Cuevas (10.78333, -61.38333, 252 m). **Ntu** (6): TTU 24118, 24119, 5436, 5445, 24120, 24121.

532. Saut D'eau Cave near Maracas Bay (10.75, -61.43333, 275 m). **Ntu** (3): TTU 9822-9824.

533. Heights of Guanapo, cave, Trinidad, Guanapo (10.6, -61.25, 30 m). **Ntu** (3): AMNH 178687; MVZ 167626, 167634.

Tobago

534. Effigy Cave, Amblypygid Cave, and Robinson Crusoe Cave. **Ntu** (fossil; Eshelman and Morgan, 1985)

535. Specific Locality Unknown. **Ntu** (6): TTU 48834--48839,.

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Middle Caicos

536. Conch Bar Cave (21.8295, -71.7754, 9 m). **Nma**: FLMNH 246. (Morgan, 1989).

VENEZUELA

Apure

537. Caño La Guardia; afluente del Río Capanaparo (6.93333, -67.30000, 47 m). **Ntu** (1): MHNLS 7627.

Aragua

538. Ocumare De La Costa, Aponte (10.48450, -67.77000, 8 m). **Ntu** (1): EBRG 2243.

539. Quebrada Palmarito Palmarito Municipio Girardot, Maracay (10.39167, -67.27500, 1694 m). **Ntu**(1): EBRG 23463.

540. Rancho Grande, Pque Natl Henry Pitier(10.34900, -67.68400, 1116 m). **Ntu** (2): MBUCV 35, 34.

541. Facultad De Agronomia; Maracay (10.27500, -67.60972, 450 m). **Ntu**(1): MHNLS 9320.

542. Cueva Candelaria Cerca El Pao, La Victoria (10.23333, -67.33333, 574m). **Ntu** (8): EBRG 3046, 3047, 12002-12007.

543. Cuevas Cumbocito; Santa Lucia; El Pao De Zarate. 15 Km S.E. De La Victoria (10.15000, -67.21667, 702 m). **Ntu** (5): MHNLS 8765--8767, 8782, 8783.

544. Fundo Paso Del Medio 10 Km Ene San Juan De Los Morros (9.91778, -67.26333, 385 m). **Ntu** (3): EBRG 23919, 23923, 23924.

545. Cuevas Pao Quebrada el Volcán. **Ntu** (4): EBRG 2493-2496.

Bolívar

546. Hato La Florida, 14 Km S 45 Km E, Caicara (7.50000, -65.78333, 80 m).**Ntu** (11): EBRG 13661-13663; USNM: 405774-405782.

547. Pijiguaos (Serrania Pijiguaos) 140 Km So, Caicara (6.58340, -66.84160, 79 m). **Ntu** (2):EBRG 15928--15929.

548. Campamento Ucaima; Parque Nacional Canaima (6.24244, -62.83322, 422 m), **Ntu** (1): MHNLS 11002.

549. Parque Nacional Canaima Laguna, Canaima (6.24244, -62.83322, 422 m). **Ntu** (1): EBRG 22693.

550. Morichal; Aproximadamente 3.7 Km S De La Laguna De Canaima; Parque Nacional Canaima (6.20961, -62.85278, 378 m). **Ntu** (1): MHNLS 11617.

Carabobo

551. San Esteban, Venezuela (10.43528, -68.05639, 25 m). **Ntu** (8): AMNH 31510–31516; BMNH 5.11/12.25 (holotype of *Phodotes tumidirostris continentis* Thomas, 1911).

Delta Amacuro

552. unspecified locality. **Ntu** (Ochoa et al., 1993).

Falcón

553. Cueva Piedra Honda Cerca De San José De Cocodite, Paraguana Peninsula (11.93417, - 69.98167, 203 m). **Ntu**(56):EBRG 23554, 23555; MBUCV 2146-2180, 2225-2235, 2359-2362, ULA 429-432.

554. Cueva Guano, 49 Km N 34 Km W Coro (11.87860, -69.94140, 96 m). **Ntu**(27): AMNH (*P* 1–3, AT 113–115, colelction numbers); EBRG 13690-13693, 13046-13049; USNM 455968-455983, 494812-494818.

555. Cueva Ojo de Agua, Píritu (11.37389, -69.13722, 179 m). **Ntu** (7): AMNH (AT 118–124).

556. La Pastora, 11 km ENE Mirimiri (11.20000, -68.63333, 121 m). **Ntu**(2): USNM 441631, 494786.

557. Cueva el Zumbador15.5 km al ssw de Yaracal (10.85722, -68.61139, 459 m). **Ntu** (3):AMNH (Z 1–3, colletion numbers).

558. Cueva Copa de Oro (10.84086, -68.59375, 444 m). **Ntu** (1): AMNH (CO 1, collection numer).

559. Cueva Pararille, La Chara (10.73722, -69.42056, 474 m). **Ntu** (10): AMNH (AT 101–110, collection number).

Lara

560. Caserío Boro10 KM N el Tocuyo (9.88333, -69.78333, 803 m). **Ntu**(1): USNM 456549.

Miranda

561. Cueva Cajigal; Birongo (10.52028, -66.25306, 258 m). **Ntu** (5):MHNLS 1498, 2008-2011; MBUCV 3070.

562. Cueva en el Río Salmerón (10.48333, -66.36667, 556 m). **Ntu** (3): MHNLS 1155, 1156, 1211.

563. Quebrada de Caurimare, Petare Nueva Esparta (10.48333, -66.81667, 845 m). **Ntu** (1): MBUCV 1110.

564. Cueva Walter Dupouy, 5 Km S 60 Km E Caracas, 4 km SO Birongo (10.48111, -66.23944, 59 m). **Ntu** (9): EBRG 13686-13689, 2610, 2611; ULA 3158-3160.

565. Cueva del Indio, cerca del Hatillo (10.43333, -66.81667, 1289 m). **Ntu** (3): MBUCV 1659–1661.

566. Cueva Ricardo Zuloaga, 15 KM SE, Caracas cerca del Encanto (10.40250, -66.74059, 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.

567. Los Guayabitos; Caracas (10.30000, -66.51667, 616 m). **Ntu**(1):MHNLS 1188.

Nueva Esparta

568. Piedra de Rivero, Isla margarita (11.03700, -64.27500, 82 m). **Ntu**: AMNH (AT 213, fossil, field number).

Sucre

569. Parque Nacional Peninsula De Paria, Uquire (10.70000, -61.96667, 848 m). **Ntu**(6): EBRG 18674-18677, 20421, 20422.

570. Cueva de las Ánimas, Turimiquire (10.19722, -64.29111, 935 m). **Ntu** (13): AMNH (AT 85–97).

571. Represa Neverí (10.17444, -64.29722, 350 m). **Ntu**(2): EBRG 2644, 2645.

Yaracuy

572. Parque Bolivariano Minas De Aroa Mina San Antonio Aroa Municipio Bolivar, Aroa (10.43861, -68.89417, 257 m). **Ntu**(2): EBRG 23162, 23163.

573. Parque Bolivariano Minas De Aroa Tunel Detras Mina SANTA Barbara, Aroa (10.43861, -68.89417, 257 m). **Ntu**(1): EBRG 23394.

Zulia

574. Cueva de los gavilanes, Perija (10.93, -72.42, 328 m). **Ntu**(4): MBUCV 1577-1580.

575. Cueva de Toromo, Machiques (10.05556, -72.66667, 398 m). **Ntu**(12): AMNH (T 1–11, field numbers).

576. Kasmera, Perija (9.9525, -72.75083, 369 m). **Ntu** (1): MBUCV 169.

UNITED STATES

Florida

577. Thomas Farm, 12 km northeast of Bell. Ppr. FLMNH 108641–108647, 121136–121145.

APPENDIX II: PLATES

Plate legends

Plate 1. Observed pelage color variation in 8 species of the genus *Natalus*: A) *Natalus mexicanus*; B) *Natalus lanatus*; C) *Natalus jamaicensis*; D) *Natalus primus*; E) *Natalus tumidirostris*; F) *Natalus espiritosantensis*; G) *Natalus stramineus*; H) *Natalus major*.

Plate 2–10. Geographic and individual variation in skull morphology in 12 extant species of Natalidae. Plates: 2–4, dorsal view; 5–7, ventral view; 8–10, lateral view. Specimen numbers:

1–3) *Nyctiellus lepidus*: 1) AMNH 167133, male, Little Exuma, Bahamas; 2) AMNH 61169, male, Havana, Cuba; 3) FLMNH 4454, Long, The Bahamas

4–6) *Chilonatalus micropus*: 4) AMNH 216125, male, Samaná, Dominican Republic; 5) USNM 15849, Providencia Isl., Colombia; 6) BMNH 80.12.14.1, holotype, Kingston, Jamaica

7–9) *Chilonatalus macer*: 7) AMNH 186980, male, Isle of Pines, Cuba; 8) USNM 113724, holotype, female, Baracoa, Cuba; 9) AMNH 126161, La Habana, Cuba

10–12) *Chilonatalus tumidifrons*: 10) USNM 122024, male, San Salvador Isl., The Bahamas; 11) USNM 576614, male, Abaco, The Bahamas; 3) UF 24853, male, Abaco, The Bahamas

13–14) *Natalus primus*: 13) AMNH AT 1, field number, female, Pinar del Río, Cuba; 14) AMNH AT 2, collector number, female, Pinar del Río, Cuba

15–16) *Natalus jamaicensis*: 15) AMNH 182000, male, St. Catherine, Jamaica; 16) AMNH 246127, male, St. Catherine, Jamaica

17–20) *Natalus major*: 17) USNM 101395, holotype, male, Puerto Plata, Dominican Republic; 18) AMNH AT 51, field number, female, Maria Trinidad Sánchez, Dominican republic; 19) AMNH 97589, female, Barahona, Dominican Republic; 20) KU 150721, male, Department du L'Ouest, Haiti

21–28) *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

29–32) *Natalus lanatus*: 29) KU 39628, male, Nayarit, Mexico; 30) KU 39620, holotype, female, Nayarit, Mexico; 31) KU 82901, male, Veracruz, Mexico; 32) MSB

33–36) *Natalus mexicanus*: 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

37–40) *Natalus espiritosantensis*: 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

41–44) *Natalus tumidirostris*: 41) ROM 45239, male, Sucre, Colombia; 42) AMNH T 7, field number, male, Zulia, Venezuela; 43) USNM 102106, holotype, male, Curaçao; 44) female, Kaw, French Guiana

Figure legends

Fig. 1. 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.

Fig. 2. 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.

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.

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 outgrows on the muzzle.

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.

Fig. 6. Medial view of the feet in two species of *Natalus*: A) *Natalus lanatus*, showing ungual tufts; and B) *Natalus mexicanus*, showing lack of 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.

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

Fig. 11. Geographic distribution of *Nyctiellus lepidus*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

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.

Fig. 13. 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 bar = 5 mm.

Fig. 14. Location of type locality of *Primonatalus prattae*. Numbers correspond to entry in Appendix I.

Fig. 15. Holotype of *Chilonatalus macer* (USNM 113724, female, Baracoa, Cuba). Scale bar = 5 mm.

Fig. 16. Geographic distribution of *Chilonatalus macer*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 17. Holotype of *Chilonatalus micropus* (BMNH 80.12.14.1, "environs of Kingston", Jamaica). Scale bar = 5 mm.

Fig. 18. Geographic distribution of *Chilonatalus micropus*. Solid dots indicate collection localities where the species has been collected alive. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 19. 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.

Fig. 20. Holotype of *Chilonatalus tumidifrons* (USNM 122024, male, San Salvador, The Bahamas). Scale bar = 5 mm.

Fig. 21. Geographic distribution of *Chilonatalus tumidifrons*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I.

Fig. 22. Morphometric variation among to 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.

Fig. 23. Holotype of *Natalus espiritosantensis* (MBML 1801, male, Espirito Santo Brazil). Scale bar = 10 mm.

Fig. 24. Geographic distribution of *Natalus espiritosantensis*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 25. 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).

Fig. 26. Holotype of *Natalus jamaicensis* (AMNH 182000, male, Jamaica). Scale bar = 10 mm.

Fig. 27. Geographic distribution of *Natalus jamaicensis*. The solid dot indicates the only locality where the species is known to be extant. The open dot indicates a locality represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 28. Holotype of *Natalus lanatus* (KU 39628, female, Nayarit, Mexico). Scale bar = 10 mm.

Fig. 29. Geographic distribution of *Natalus lanatus*. Solid dots indicate collection localities. Numbers correspond to entries in Appendix I. Locality 71 is conjectural (see text). Light gray areas represent land above 600 m.

Fig. 30. 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); B) 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, $P < 0.05$).

Fig. 31. Holotype of *Natalus major* (USNM 101395, male, Hispaniola [Dominican Republic]). Scale bar = 10 mm.

Fig. 32. Geographic distribution of *Natalus major*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 33. Holotype of *Natalus mexicanus* (USNM 96496, Baja California Sur, Mexico). Scale bar = 10 mm.

Fig. 34. Geographic distribution of *Natalus mexicanus*. Solid dots indicate localities where the species has been collected alive. Numbers correspond to entries in Appendix I. Areas marked by numbered rectangles are shown in more detail in figs. 35 (areas 1, 2), 36 (area 3), and 37 (area 4). Some localities, especially those of the Mexico Basin and Veracruz highlands (rectangle 2), may represent *Natalus lanatus* (see text). Light gray areas represent land above 600 m.

Fig. 35. Geographic distribution of *Natalus mexicanus* in (1) northwest mainland Mexico and Baja California and (2) the central Mexican highlands and the northern Mexican Atlantic lowlands. Solid dots indicate collection localities. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m. Some localities (e.g. 294, 295, 333, and 446) of the Mexico Basin and Veracruz highlands (map 2) may represent *Natalus lanatus* (see text).

Fig. 36. Geographic distribution of *Natalus mexicanus* in western Mexico. Solid dots indicate collection localities. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m. Some localities may represent *Natalus lanatus* (see text).

Fig. 37. Geographic distribution of *Natalus mexicanus* in SE Mexico and N Central America. Solid dots indicate collection localities. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 38. 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 ten 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: S 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, W and NW Mexico (one-way ANOVA, $P < 0.01$). B) Plot of canonical scores for 7 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.

Fig. 39. A) Holotype of *Natalus primus* (AMNH 41009, fossil right dentary, Cuba). B) Second right dentary (unnumbered), designated by Anthony as a topotype, kept in the vial with the holotype. Scale bar = 10 mm.

Fig. 40. Skull and mandible of *Natalus primus* (AT 1, Pinar del Río, Cuba). Scale bar = 5 mm.

Fig. 41. Geographic distribution of *Natalus primus*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 42. 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.

Fig. 43. Holotype of *Natalus tumidirostris* (USNM 102106, male, Curaçao). Scale bar = 10 mm.

Fig. 44. A) Geographic distribution of *Natalus tumidifrons*. Rectangle corresponds to area enlarged in B. B) Geographic distribution of *Natalus tumidirostris* in Central N Venezuela. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 45. 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 21. 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.

Fig. 46. Holotype of *Natalus stramineus* (BMNH 70.2324, male, collection locality unknown).

Fig. 47. Geographic distribution of *Natalus stramineus*. Solid dots indicate localities where the species has been collected alive. Open dots indicate localities represented by bone remains only. Numbers correspond to entries in Appendix I. Light gray areas represent land above 600 m.

Fig. 48. 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 23).

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

Author	Genus	Subgenus	Species	Subspecies	Distribution	Current status
Gervais (1837)			*Vespertilio lepidus*		Cuba	distinct
Gray (1838)	***Natalus***					distinct genus
Gray (1838)			***Natalus stramineus***		unknown	distinct
Gervais (1855)	***Nyctiellus***					distinct genus
Dobson (1880)			*Natalus micropus*		Jamaica	distinct
Miller (1898)		***Chilonatalus***				distinct genus
Miller (1898)			*Natalus*		Providencia	syn. of *C. m.*
Miller (1900)			***Natalus***		Curacao	distinct
Miller (1902)			***Natalus major***		Hispaniola	distinct
Miller (1902)			***Natalus***		Mexico	distinct
Miller (1903)			***Chilonatalus tumidifrons***		Bahamas	distinct
Miller (1906)	*Phodotes*					syn. of
Thomas (1910)				*Phodotes tumidirostris continentis*	Venezuela	ssp. of *N.*
Miller (1914)			***Chilonatalus***		Cuba	ssp. of C.
Anthony (1919)			***Natalus primus***		Cuba	distinct
Shamel (1926)			*Natalus dominicensis*		Dominica	syn. of *N.*
Dalquest and Hall (1949)				*Natalus mexicanus saturatus*	SE Mexico	syn. of *N. mexicanus*
Ruschi (1951)			***Natalus espiritosantensis***		SE Brazil	distinct
Goodwin (1959)				*Natalus*	Jamaica	distinct
Goodwin (1959)				*Natalus*	NE Brazil	syn. of *N.*
Goodwin (1959)				*Natalus*	Trinidad	ssp. of *N.*
Linares (1971)				*Natalus stramineus tronchonii*	W Venezuela	syn. of *N. tumidirostris*
Morgan and Czaplewski (2003)	*Primonatalus*†					
Morgan and Czaplewski (2003)			***Primonatalus***		Florida	distinct
Tejedor (2005)			***Natalus lanatus***		Mexico	distinct

Table 2. Classifications of extant Natalidae

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

Table 2. Continuation

Hall 1981	Koopman 1994
North American Natalidae	Natalidae
Genus *Natalus*	Genus *Natalus*
N. stramineus stramineus	Subgenus *Natalus*
N. stramineus mexicanus	*N. stramineus stramineus*
N. stramineus saturatus	*N. stramineus mexicanus*
N. stramineus major	*N. stramineus tronchoni*
N. stramineus jamaicensis	*N. stramineus natalensis*
N. stramineus primus	*N. stramineus espiritosantensis*
N. micropus micropus	*N. stramineus major*
N. micropus tumidifrons	*N. stramineus jamaicensis*
N. micropus macer	*N. tumidirostris tumidirostris*
Subgenus *Nyctiellus*	*N. tumidirostris continentis*
N. lepidus	Subgenus *Chilonatalus*
	N. micropus micropus
	N. micropus macer
	N. tumidifrons
	Subgenus *Nyctiellus*
	N. lepidus

Table 2. Continuation.

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

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	occupies less than ½ the length of free edge of uropatagium	occupies about 2/3 of free edge of uropatagium	-	occupies 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 3/4 of tibia	from distal 2/3 to the proximal 1/3 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, seven or more	vestigial, 2–3	-	vestigial, 0–6
natalid organ, in 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	as high as condyloid	as high as condyloid	slightly higher than condyloid	slightly higher to as high as

process				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 humerous	higher than capitulum	higher than capitulum	as high as capitulun	as high as capitulun

Table 4. Diagnostic characters of species of the genus *Chilonatalus*

	C. *micropus*	**C. *tumidifrons***	**C. *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 the distal ½ of tibia (at about 2/3 of its length, measured from the knee to the ankle	on the proximal ½ of the tibia (at about 1/3 of its length, measured from the knee to the ankle)	on the proximal ½ of the tibia (at about 1/3 of its length, measured from the knee to the ankle)
in lateral view, braincase rises from rostrum	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 # 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

Table 5. Diagnostic characters of 8 species of the genus *Natalus.* Measurements: min.–max.

	N. espiritosantensis	***N. jamaicensis***	***N. lanatus***	***N. major***	***N. mexicanus***
forearm length	37.0–42.1	44.0–47	35.4–38.6	41.1–45.0	34.0–40.6
length of tibia	20.1–23.8	24.3–25.7	16.0–19.2	23.2–25.4	19.4–22.3
greatest skull length	15.9–17.0	17.2–18.1	15.0–16.4	17.0–18.1	14.9–16.8
breadth across canines	3.4–4.2	3.7–4.1	3.4–3.8	3.9–4.5	3.2–3.8
maxillary toothrow	6.5–7.0	7.8–8.1	6.3–6.9	7.5–8.0	6.3–7.1
medial margin of ear	deeply concave	straight	straight	straight	slightly concave
lateral margin of ear	deeply concave	deeply concave	deeply concave	deeply concave	deeply concave
number of ear folds	5–6	5–6	0–2	5–6	5–6
ventral pelage	monocolored	monocolored	hair bases dark than tips	monocolored	monocolored
ungual tuft	absent	absent	present	absent	absent
premaxilla	not inflated	not inflated	not inflated	not inflated	not inflated
maxilla dorsal to molars	convex, not inflated	concave	convex, not inflated	convex, not inflated	convex, not inflated
postorbital region in dorsal view	sides widely diverging rostrally	sides nearly parallel	sides widely diverging rostrally	sides widely diverging rostrally	sides widely diverging rostrally
palate between pterygoi	present	present	present	present	present

ds					
caudal margins of maxilla, in ventral view	forming an acute angle with longitudinal axis of skull	forming an acute angle with longitudinal axis of skull	almost perpendicular to longitudinal axis of skull	forming an acute angle with longitudinal axis of skull	forming an acute angle with longitudinal axis of skull
basisphenoid pits	shallow	shallow	shallow	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
I1 in ventral view	at level with I2	at level with I2	rostral to I2	at level with I2	rostral to I2
mesostylar crest on m3	absent	absent	absent	absent	absent

Table 5. Continuation.

N. stramineus	***N. primus***	***N. tumidirostris***
37.2–40.5	46.1–51.2	36.1–41.5
19.8–23.2	25.4–29.1	18.9–22.4
15.7–17.5	18.1–19.9	15.5–17.3
3.3– 4.2	3.8–4.5	3.4–4.2
6.8–7.5	7.8–10.3	6.5–7.3
slightly to deeply concave	straight	deeply concave
deeply concave	straight	deeply concave
5–6	4	5–6
monocolored	monocolored	monocolored

absent	absent	absent
inflated	not inflated	not inflated
convex, not inflated	convex, not inflated	inflated
sides widely diverging rostrally	sides widely diverging rostrally	sides widely diverging rostrally
present	present	absent
forming an acute angle with longitudinal axis of skull	almost perpendicular to longitudinal axis of skull	forming an acute angle with longitudinal axis of skull
shallow	deep and steep sided	shallow
perpendicular to alveolar plane	forming a 70° angle with alveolar plane	perpendicular to alveolar plane
at level with I2	rostral to I2	at level with I2
absent	present	absent

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 toothrow	5	5.2	(5.1–5.4)	0.1	21	5.3	(5.0–5.6)	0.1
Mandibular toothrow	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.

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 toothrow	3	6.1	(5.9–6.2)	0.1	3	6.1	(5.9–6.3)	0.2
Mandibular toothrow	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).

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 toothrow	7	5.8	(5.7–5.9)	0.1	19	5.8	(5.6–6.0)	0.1
Mandibular toothrow	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 (*).

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 toothrow	9	6.5	(6.4–6.7)	0.1	18	6.6	(6.3–6.8)	0.1
Mandibular toothrow	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 (*).

Table 10. Range of diameter of distal humerus in fossil and extant Natalidae.

Species	diameter of distal humerus	
	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

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 toothrow*	18	6.6	(6.5–6.9)	0.1	16	6.8	(6.5–7.0)	0.1
Mandibular toothrow*	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 (*).

Table 12. Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 5 geographic samples of *Natalus espiritosantensis*. CVA scores are plotted in fig. 25A.

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 toothrow	0.240	1.117
Eigen value	0.914	0.183
Percent explained	73.1	14.6

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 toothrow	4	7.9	(7.8–8.0)	0.1	8	7.9	(7.8–8.1)	0.1
Mandibular toothrow*	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 (*).

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 toothrow	13	6.5	(6.3–6.8)	0.1	14	6.7	(6.4–6.9)	0.2
Mandibular toothrow	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 (*).

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 toothrow	2	7.7	(7.6–7.7)	0.1	12	7.8	(7.6–8.0)	0.1
Mandibular toothrow	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 (*).

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 toothrow *	98	6.7	(6.4–7.1)	0.2	131	6.8	(6.3–7.2)	0.2
Mandibular toothrow*	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 (*).

Table 17. Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 9 geographic samples of *Natalus mexicanus*. CVA scores are plotted in fig. 38B.

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 toothrow	0.005	0.987
Postorbital toothrow	0.484	-0.210
Depth of skull	0.058	-0.607
Eigen value	1.045	0.716
Percent explained	45.5	31.7

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 toothrow	6	8.6	(8.4–8.8)	0.1	6	8.8	(8.6–9.0)	0.1
Mandibular toothrow	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 (*).

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, $P < 0.01$)

Table 20. 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 toothrow *	73	7.0	(6.5–7.2)	0.2	103	7.1	(6.7–7.4)	0.2
Mandibular toothrow*	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 (*).

Table 21. Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 9 geographic samples of *Natalus tumidirostris*. CVA scores are plotted in fig. 45.

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 toothrow	0.447	-0.075
Postorbital toothrow	-0.106	-0.053
Depth of skull	-0.650	0.351
Eigen value	2.638	1.888
Percent explained	48.0	34.3

Table 22. 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 toothrow	14	7.0	(6.8–7.5)	0.2	24	7.3	(6.9–7.5)	0.2
Mandibular toothrow	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 (*).

Table 23. Loadings of the first two canonical axes of two canonical variates analyses (CVA) performed with 4 geographic samples of *Natalus stramineus*. CVA scores are plotted in fig. 49.

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 toothrow	0.886	0.723
Postorbital width	-0.670	-0.149
Eigenvalues	8.938	2.976

Phylogeny of Natalidae based on morphology and gene sequences

ABSTRACT

The evolutionary history of Natalidae has received intense attention in recent years, both concerning its relationships to other bat families and as a mean to answer questions of distribution and extinction among Neotropical bats. As a consequence, the position of Natalidae within the phylogeny of Chiroptera and its geographic origin are known with a high degree of certainty. Nonetheless, all studies that have addressed natalid relationships thus far have been limited by an incomplete understanding of the diversity of the family. Recent taxonomic revisions have refined the knowledge of taxonomic and geographic limits among natalid species and have increased the number of recognized taxa, revealing that existing phylogenies for the family still suffer from a coarse resolution. Therefore, despite the significant advances in our understanding of natalid evolution many questions concerning basic intrafamilial relationships remain unanswered. Such uncertainties are an obstacle for studies of the biogeography and for conservation assessments of the group. In this study, I provide the most complete phylogeny of Natalidae generated to date in terms of number of taxa and diversity of phylogenetic characters. A total of 12 ingroup taxa were compared on the basis of 119 morphological characters and complete cytochrome *b* gene sequences, using partitioned and combined cladistic analyses. The phylogenies generated are notable in their greater explanatory power and robustness of some branches compared to previous studies. Also, novel relationships were recovered, including a sister relationship of *Primonatalus* with *Natalus*/*Chilonatalus*, and a “picket

fence" topology of the genus *Natalus* with *Natalus primus* diverging from the base and *Natalus stramineus* and *Natalus tumidirostris* at the crown. The molecular results indicate that the diversity of the family was still being underestimated, and that *Chilonatalus* from Hispaniola should be elevated to species status. Relative to previous studies, the phylogenies generated in this work provide a much finer-grained framework for investigations on the ecological evolution, biogeography, and conservation of Natalidae.

INTRODUCTION

The evolutionary history of Natalidae has been the subject of numerous studies in the last decade. Recent phylogenetic studies, based on either morphological or molecular data, have confirmed the monophyly of the family, have illuminated the position of Natalidae among other bat families, and have made great strides in elucidating intrafamilial relationships (Dávalos, 2005; Morgan and Czaplewski, 2003; Simmons and Geisler, 1998; Van den Bussche and Hoofer, 2001; Teeling et al., 2005). These studies have shown that Natalidae is more diverse both at the species and genus level than previously supposed (Dávalos, 2005; Morgan and Czaplewski, 2003), have pointed toward southeastern North America as the most likely ancestral area of the family (Dávalos, 2005; Morgan and Czaplewski, 2003), and have suggested that several broad morphological traits of Natalidae, such as funnel-shaped ears (Simmons and Geisler, 1998), have evolved independently in other bat lineages (e.g. Furipteridae; Van den Bussche and Hoofer, 2001; Teeling et al., 2005).

The study of the evolution of Natalidae has focused mainly on its relationships to other bat families. Although since the description of the genus *Natalus* (Gray, 1838), Natalidae has occasionally been associated to bat families now considered distantly related to it (e.g. Phyllostomidae; Gervais, 1855; Miller, 1898), relationships with Vespertilionidae have been overwhelmingly favored (e.g. Dobson, 1878; Van Valen, 1979). Recent phylogenetic studies (Simmons, 1998; Simmons and Geisler, 1998; Teeling et al., 2005; Van den Bussche and Hoofer, 2001) have confirmed the placement of this family at the base of Vespertilionoidea, a clade including two highly diverse families, Vespertilionidae and Molossidae, both of worldwide distribution and together comprising 507 species (45 % percent of all bats). Phylogenies based on morphology place Natalidae as sister to Furipteridae within the Nataloidea clade (also including Thyropteridae and Myzopodidae; Simmons, 1998; Simmons and Geisler, 1998) branching off at the base of Vespertilionoidea. Conversely, molecular-based phylogenies indicate that Natalidae stands alone as the sister group of Vespertilionidae/Molossidae and that the remaining families of Nataloidea belong within the Noctilionoidea clade (Van den Bussche and Hoofer, 2001; Teeling et al., 2005; Figure 1). The strong support for either the monophyly or polyphyly of Nataloidea, depending on the type of data (morphology or molecules) examined, remains one of the areas of greatest conflict of the evolutionary tree of the order Chiroptera (Simmons, 2005a).

By contrast, studies of intrafamilial relationships of Natalidae, using either morphological (Morgan and Czaplewski, 2003) or molecular evidence (Arroyo-Cabrales et al., 1997; Dávalos, 2005) have been less conflicting, essentially differing only in the number of phylogenetic terminals used (Figure 2). When *Nyctiellus* is included, it appears at or near the base of the family, with *Chilonatalus* and *Natalus* as reciprocally monophyletic sister genera. When the Miocene fossil, *Primonatalus prattae* Morgan and Czaplewski, 2003 is included, it is recovered as the basal-most member of the family (Morgan and Czaplewski, 2003). Similarly, relationships recovered within *Natalus* have depended on the terminals used. The *Natalus* from Mexico and Central America (under the name *N. stramineus*) has been found to be sister to *Natalus* from the Lesser Antilles (Arroyo-Cabrales et al., 1997) or to *Natalus tumidirostris* (Morgan and Czaplewski, 2003). Still, in the more comprehensive study of Dávalos (2005), the Mexican-Central American taxon (called *N. saturatus*) appeared as the basal-most *Natalus* and sister to two monophyletic groups: Greater Antillean *Natalus*, and a clade composed of Lesser Antillean *Natalus* and *Natalus tumidirostris* (Figure 2).

Despite their substantial contributions, all of the studies mentioned above have been significantly limited by an incomplete understanding of the diversity of the family and a lack of an explicit and comprehensive approach to address the evolutionary history of Natalidae. Those studies that have addressed the relationships of Natalidae to other bat families have focused on the evolutionary tree of Chiroptera as a whole, and have often included only one or two terminals to represent Natalidae. Studies that have explored relationships within Natalidae, on the other hand, have sampled its diversity poorly due to a long history of conservative taxonomy in the family (Arroyo-Cabrales et al., 1997), or never attempted a full-fledged phylogenetic assessment of this group (Dávalos, 2005; Morgan and Czaplewski, 2003). The phylogeny of Morgan and Czaplewski (2003), for example, was produced mainly with the aim to determine the position of the fossil *Primonatalus*; therefore it was based exclusively on osteological characters. Likewise, the molecular phylogeny of Dávalos (2005) aimed to illuminate bat biogeography in the Caribbean, and therefore did not sample natalid populations spread over vast areas of South America and northern Mexico. Also, Dávalos (2005) could not include Caribbean populations for which tissue samples were unavailable.

As a consequence, several questions concerning the evolution of Natalidae have remained open. Among these, the relationships of several Caribbean taxa (*Natalus primus*, *Chilonatalus* from Cuba and Hispaniola) and *Natalus* from Northern Mexico and mainland South America are outstanding. Moreover, recent taxonomic advances have added one new species (*Natalus lanatus*; Tejedor, 2005) and revalidated another (*Natalus espiritosantensis*; Tejedor, in press) previously sunk into synonymy, for neither of which there are hypotheses of relationships. With four species and several widespread populations still unsampled, high uncertainty remains concerning the pattern of diversification of the family. Furthermore, the data needed for a thorough assessment of the uniqueness of many natalid lineages and their conservation needs are far from complete.

In this study, I provide the most complete phylogenetic hypotheses for Natalidae proposed thus far. These new estimates of the evolutionary history of Natalidae are based on combined and separate analyses of morphology and molecular data. The phylogenetic matrix presented here includes the most comprehensive representation of the diversity of the family examined to date, and is based on new analyses of morphological characters and several newly obtained genetic sequences. The results of this study clarify significantly the history of diversification of Natalidae, provide novel information essential for evaluating the taxonomic and conservation status of this family's taxa, and represent a much needed framework for the study of the ecological evolution and biogeography of the group.

METHODS

TAXONOMIC SAMPLING

Ingroup terminals for the morphological and combined analyses include all species of Natalidae defined in Chapter 2. A denser sampling was used in the molecular analyses to test the genetic distinctiveness of named taxa that were synonymized in Chapter 2, and to explore patterns of genetic variation within species. Taxa and individuals sampled for morphological and molecular analyses are listed in Appendix I. Because of conflict between phylogenies based on morphology (Simmons, 1998; Simmons and Geisler, 1998) and gene sequences (Van Den Bussche and Hoofer, 2001; Teeling et al., 2005) regarding the position of Natalidae among bat families, multiple outgroups were selected to explore the degree of congruence between the morphological and molecular characters used in this study, and to maximize the stability of ingroup relationships. Outgroups include representatives of six bat families: *Saccopteryx* (family Emballonuridae), *Pteronotus* (Mormoopidae), *Furipterus* (Furipteridae), *Thyroptera* (Thyropteridae), *Myotis* (Vespertilionidae), and *Tadarida* (Molossidae). Ingroup and outgroup designations were not constrained for any of the analyses with the exception of *Saccopteryx* which was used to root the tree.

MORPHOLOGICAL CHARACTER SCORING AND CHARACTER SAMPLING

A matrix of 119 characters (40 cranial, 26 dental, 17 postcranial, 36 external) was assembled (Appendices II and III). Osteologic and dental characters were scored from cleaned skeletons and skulls, and external characters from fluid-preserved specimens, using exclusively adult individuals. Scoring was based on the observation of at least 5 individuals (although the number usually exceeded 10 for each terminal), except for skeletons, of which only one was available for *Natalus primus*, *Natalus major*, *Natalus espiritosantensis*, and none for *Natalus lanatus*.

Characters were obtained by surveying character lists reported by Morgan and Czaplewski (2003), Simmons and Conway (2001) and by direct observation of the specimens. Characters describing relative position or shape were included only if discrete states could be established. All characters were treated as unordered and no distinction was made between putatively plesiomorphic or apomorphic state in the assignation of a state number (e.g. “0”). Polymorphisms, where present, occurred in only one taxon per character, therefore to maximize the number of hypotheses of homology they were represented by ambiguity coding. Missing data were scored as ? if due to lack of appropriate material or as – if due to inapplicable comparisons.

MOLECULAR CHARACTERS

A total of 32 new ingroup sequences were obtained for this study, and 21 other ingroup sequences and all outgroup sequences were obtained from GenBank (Table 1).

Complete mitochondrial cytochrome *b* gene sequences (1140 bp) were obtained for all taxa with the exception of 2 outgroups for which only incomplete sequences (*Saccopteryx bilineata*, AF044664, 402 bp; *Tadarida brasiliensis*, L19734, 528 bp) were available from GenBank.

Genomic DNA was extracted from wing clip, muscle, or liver tissue preserved in ethanol or lysis buffer using a Qiagen DNeasy Tissue Extraction Kit. The entire cytochrome *b* gene was amplified using the primers MVZ05 and UMMZ04 and then reamplified into two separate fragments using MVZ05 in combination with NEW12, and UMMZ13 in combination with UMMZ04. All primers were obtained from Dávalos and Jansa (2004) and their sequences are listed in Table 1. All amplifications used AmpliTaq and two-step PCR cycling: initial denaturation at 94 °C for 5 minutes, followed by 5 cycles of denaturation at 94 °C for 15 seconds, annealing at 53 °C for 15 seconds, and extension at 72 °C for 30 seconds; this was followed by 33 cycles of denaturation at 94 °C for 30 seconds, annealing at 50 °C for 30 seconds, and extension at 72 °C for 1 minute; the 38th cycle was followed by extension at 72 °C for 10 minutes. Amplification products were sequenced with the same primers used for PCR amplification on an automated ABI 3730XL sequencer. Sequences were edited and compiled using Sequencher 4.2 software (Gene Codes). Base-calling ambiguities were resolved by choosing the call on the cleanest strand or using the appropriate IUB ambiguity code if two or more strands were equally clean. Gene sequences generated by this study will be deposited in GenBank.

DATA ANALYSIS

Cytochrome *b* sequences were aligned by eye and translated into aminoacids using the mammalian mitochondrial code as implemented in Sequencher 4.1 (GeneCodes) to ensure that a coding sequence had been obtained. Uncorrected pairwise divergence among cytochrome *b* sequences were calculated using PAUP* v.4.0b10 (Swofford, 2001).

Analyses were performed on three data sets: 1) the morphological matrix; 2) the cytochrome *b* gene sequences; and 3) the combined molecular and morphological data sets. For the combined analysis, an arbitrary cytochrome *b* sequence exemplar of each species was chosen and appended to that species' morphological character string. One species (*Natalus tumidirostris*), treated as monophyletic in the morphological analyses, was recovered as diphyletic in the molecular tree. Therefore, this species was split into two terminals for the combined analyses by duplicating its morphological character string and appending to each duplicate an arbitrary sequence exemplar from each of the two clades resulting from the molecular analyses. Parsimony analyses searched for trees using 200 different addition sequences followed by branch swapping using tree bisection-reconnection (TBR) as implemented in NONA (Goloboff, 1993). Maximum parsimony analyses of individual data sets and the combined data sets were performed with all characters unordered. Morphology analyses were performed with all characters equally weighted. Clade stability was assessed using Bremer support (BS) plus bootstrap support using 1000 replicates.

RESULTS

MOLECULAR CHARACTERS

Two individuals from Saba (TK 117119, 117622) had identical cytochrome *b* sequences, as also did three individuals from Falcón, Venezuela (P1, P3, Z1). In addition, the cytochrome *b* sequence of an individual from Sucre, Venezuela (AT 88), was identical to that of an individual from Trinidad, Trinidad and Tobago (AMNH 275518). Uncorrected pairwise divergences in cytochrome *b* among individuals are shown in Figure 3. Of the 1140 base pairs of cytochrome *b*, 512 characters (45%) were variable, and 399 (35%) were parsimony informative.

PHYLOGENETIC ANALYSES

MORPHOLOGICAL ANALYSES: Maximum parsimony searches resulted in 2 trees of 346 steps. The degree of homoplasy in the morphological partition was moderate (CI = 0.60, RI = 73). A strict consensus tree (Figure 4) had 13 resolved nodes and 2 trichotomies: 1) among basal relationships of outgroups, mostly due to character conflict (i.e. with low relative Bremer support); and 2) near the crown of the genus *Natalus*, mostly due to lack of synapomorphies. Two clades in the tree were highly supported (BS > 7, bootstrap 100): one defining the family Natalidae and the other comprising all species of *Natalus* except *Natalus primus*. The remaining support values varied between 1 and 3.

Among the outgroups, the relationship (Thyropteridae (Furipteridae + Natalidae)) traditionally recovered in analyses based on morphology (e.g. as part of the clade

Nataloidea *sensu* Simmons, 1998) was also recovered in the morphology tree reported here. Also, as found by previous authors, Vespertilionidae appeared as sister to Molossidae, but the relationship of this clade to "Nataloidea" and Mormoopidae was not resolved.

The topology of the morphology tree was similar to previous morphology trees (compare fig. 2B with fig. 4). Natalidae was recovered as monophyletic with *Nyctiellus* as sister to the remaining genera. *Chilonatalus* and *Natalus* were also monophyletic. *Natalus* consisted of one well-defined crown group and a markedly plesiomorphic member: *Natalus primus*. The genus *Primonatalus*, recovered in the morphological analyses of Morgan and Czaplewski (2003) as the basal-most member of Natalidae, moved one node up in the morphology tree reported here. Its sister relationship to *Chilonatalus* and *Natalus*, as well as the sister relationship of the latter two genera, however, are poorly supported (Bremer values = 1–2, bootstrap < 50). Relationships were poorly supported among crown *Natalus*, with the exception of the sister relationship of the two South American members of the genus, *Natalus tumidirostris* and *Natalus espiritosantensis* (Bremer = 3, bootstrap = 97).

MOLECULAR ANALYSES: Parsimony searches based on the cytochrome *b* sequences recovered 26 shortest trees of 1416 steps. The degree of homoplasy in the molecular partition (CI = 47, R = 78) was roughly similar to that of the morphological partition. The resolution of the consensus tree was relatively low with 23 resolved nodes and 10 polytomies (Figure 5). Resolution was greatest at the terminal branches and least along the backbone of the tree.

The position of Natalidae among other bat families in the molecular tree was similar to that found by other molecular analyses, although outgroup relationships included nodes not reported before (e.g. in Hoofer et al., 2003; Hulva and Horacek, 2002; Teeling et al., 2005; Van Den Bussche and Hoofer, 2001). Natalidae branched out from an unresolved node containing *Myotis* and a *Pteronotus*/*Furipterus* clade, of which *Tadarida* and *Thyroptera* were successive sister outgroups. Branch support was low for most outgroup relationships.

As in the morphology tree, the monophyly of the family Natalidae and of the genus *Natalus* was well supported (BS ≥ 7, bootstrap values were 82 and 100, respectively), but compared to the morphology tree, relationships among species of *Natalus* were almost entirely unresolved and the only interspecies clade recovered within this genus, containing *Natalus espiritosantensis*, *Natalus tumidirostris*, and *Natalus stramineus* had relatively low support (BS = 1, bootstrap = 86). By contrast, the monophyly of most species-level taxa was highly supported (Bremer values ≥ 7, bootstrap = 100) with the notable exception of *Natalus tumidirostris*, which was split into two clades: one, containing populations of west and central Venezuela (Zulia-Miranda; from here after referred to as the *N. tumidirostris* "West" clade); and the other, containing populations from eastern Venezuela (Sucre) and Trinidad (from here after referred to as the *N. tumidirostris* "East" clade). The West clade was well supported (Bremer >7, bootstrap = 100), whereas the East clade nested within a well supported (Bremer >7, bootstrap = 100) but internally unresolved clade containing populations assigned to *Natalus stramineus* (Central and Northern Lesser Antilles). All branches within this later clade, including the *Natalus tumidirostris* East clade and a northern Lesser Antilles (Saba and Barbuda) *Natalus stramineus* clade were poorly supported.

Among the species with the widest geographic representation in the analyses, *Natalus mexicanus* populations were more highly structured and had greater support values than those of *Natalus tumidirostris* (west clade). The latter consisted mostly of a large politomy that included individuals from the state of Falcón (both from the continental portion of the state and from Peninsula de Paraguaná) and two poorly supported clades that correspond to two haplotypes confined to two caves: Toromo, Zulia (locality 573 in Chapter 2, Gazetteer), and Ricardo Zuloaga (locality 559 in Chapter 2, Gazetteer). The geographic area represented by the populations of *Natalus mexicanus* sampled here, however, is over four times larger (linear distance between the two furthest localities) than that of the *Natalus tumidirostris* West clade. Therefore the internal levels of divergence found for these two taxa may not be comparable. Among Caribbean taxa, Jamaican and Hispaniolan populations of *Chilonatalus micropus* were reciprocally monophyletic and well supported (BS >7, bootstrap = 100).

COMBINED ANALYSES: Two shortest trees of 1655 steps were recovered with the combined analysis of 119 morphological characters and complete cytochrome *b* sequences. The degree of homoplasy in the combined matrix (CI = 51) was similar to that of the morphological and molecular partitions. With respect to the partitioned analyses, the combined analyses consensus tree (Figure 6) showed a significant increase in the overall resolution and the support for both backbone and terminal relationships (e.g. the clade containing *Chilonatalus tumidifrons* and *Chilonatalus macer*, with BS > 7 and bootstrap = 100). The superior performance of the combined analysis resulted in the resolution of the relationship between *Natalus major* and *Natalus jamaicensis* which was unresolved in both the morphology-only and cytochrome *b*-only trees. The only unresolved node in the combined tree resulted from the collapse of the sister relationship between *Primonatalus* and a *Chilonatalus*/*Natalus* clade that had been recovered (although with very low support; Bremer = 1, bootstrap < 50) in the morphology-only tree.

The topology of relationships among outgroups in the combined tree was a combination of the topologies of the morphology only and the cytochrome *b*-only tree. The clade formed by *Furipterus* and *Pteronotus* in the cytochrome *b*-only tree was retained in the combined tree, but with *Thyroptera* as sister taxon to this clade instead as basal to almost all taxa (with the exception of *Saccopteryx*) as in the molecular tree.

Although the addition of the morphological data greatly improved the resolution and clade support in the combined analyses, the topology of the combined tree was dominated by the molecular signal. Among ingroup taxa, changes in the topology of the combined tree with respect to that of the morphology-only tree (in addition to the collapse of the *Primonatalus*/*Chilonatalus*/*Natalus* node) include the recovery of a "picket fence" topology of the genus *Natalus*, in which a crown group formed by *N. stramineus* and *N. tumidirostris* is followed by a succession of more basal members of the genus down to *N. primus*. Internal readjustments within *Natalus* included the movement up the tree of *Natalus mexicanus* to become sister of the south American/lesser Antillean *Natalus*. In addition, the combined tree includes one more taxon relative to the morphology tree, which resulted from splitting *Natalus tumidirostris* into two terminals (*Natalus tumidirostris* West and *Natalus tumidirostris* East) to reflect their lack of monophyly in the molecular tree. As in the partitioned analyses, the monophyly of Natalidae and the genus *Natalus* (to the exclusion of *N. primus*) were highly supported (Bremer > 7, bootstrap = 100) in the combined tree.

DISCUSSION

Compared to previous systematic investigations of Natalidae the results of this study are notable for the greater explanatory power of the phylogenetic hypothesis resulting from the inclusion of a larger number of taxa. This more inclusive approach was made possible by the use of combined analyses of morphological and molecular data with the aim of including as many species-level terminals as defined by morphology (see Chapter 2). Because of the greater overall resolution and branch support of the combined analysis tree relative to the partial analyses presented here, the interpretations of this study are based on the topology of the combined tree, but are complemented by the much more fined grained information provided by the cytochrome *b* tree.

The topology of the combined tree proposed here includes several significant changes, relative to relationships recovered in previous natalid phylogenies. Whereas Morgan and Czaplewski (2003) found that the early Miocene fossil *Primonatalus prattae* was sister to all extant natalids, the morphological and combined analyses of this study recovered *Nyctiellus* in that position, with *Primonatalus* nested within an unresolved clade containing *Chilonatalus* and *Natalus*. This is a consequence of a different character coding used in this study compared to that of Morgan and Czaplewski (2003). Whereas

Morgan and Czaplewski scored 26 characters for this taxon, 42 are scored here. *Primonatalus* shares four apomorphies with *Chilonatalus* and *Natalus* (nearly vertical anterior rim of orbit; wide diameter of rostral half of p3 in occlusal view; p3 constricted at level of cusp in occlusal view; slender maxillary branch of zygomatic arch), two with *Chilonatalus* and *Natalus primus* (labial side of p3 indented between roots; mesostylar crests of M1 and M2 long and broadly curved [Figure 7]), and 2 with *Natalus* (capitulum of humerus wide; spinous process of humerus small; Figure 8). The placement of *Primonatalus* up in the Natalidae tree implies that the lineage leading to *Nyctiellus* originated in the early Miocene or earlier.

In contrast with the cytochrome *b* tree of Dávalos (2005), *Chilonatalus* was monophyletic in the cytochrome *b* tree reported here. This result may be due to the addition of data (including sequences of *Chilonatalus* from Cuba). Nonetheless, the low Bremer support for this genus still highlights the deep divergence between the *Chilonatalus micropus* clade and the *tumidirostris*/*macer* clade. It is notable that *Chilonatalus* had been thought in the past to comprise a single species, since, contrary to Dávalos' (2005) assumption of little morphological differentiation within the genus, the two main lineages within *Chilonatalus* are distinguished by four external an five internal morphological characters, including shape of the natalid organ (Chapter 2: Figure 5), attachment of plagiopatagium to tibia, shape of the ear, length of the penis (Chapter 4: Figure 10), degree of fusion of the ribs (Figure 9), degree of fusion of thoracic vertebrae, size of the ectotympanic, shape of anterior margin of orbit, and presence of a tubercle on the caudal margin of the dentary between the angular process and the condyle (Figure 10).

The close association of the 'nataloid' outgroups (*Furipterus* and *Thyroptera*) to Mormoopidae in the combined tree is similar to that found by previous molecular-based studies (e.g. Hoofer et al., 2003; Hulva and Horacek, 2002; Teeling et al., 2005). Although the nataloid-mormoopid topology found here is dominated by the molecular signal, their relationships were also defined by 12 morphological characters. Most of these were synapomorphies only of *Thyroptera* and *Furipterus*, with the *Furipterus*/*Pteronotus* relationship being overwhelmed by molecular synapomorphies (38). A notable apomorphy shared by Thyroptera and Furipterus is the shape of the ear that superficially resembles that of Natalids and with which it has been homologized in the past (e.g. Simmons, 1998). The ear pinna of Thyroptera and Furipterus, however, is characterized by a dermal flap in its basal or ventral portion that is lacking in natalids but is similar to a dermal ridge present in other bat families (Figure 11). This difference in structure may indicate a different developmental origin and independent acquisition of a funnel-shaped pinna in Natalidae and Furipteridae/Thryopteridae.

Independently of the relatively high compatibility in topology between the morphological and the cytochrome *b* trees concerning ingroup relationships, the molecular results of this study indicate that genetic differentiation in Natalidae is not entirely congruent with morphological differentiation. Both within *Chilonatalus* and *Natalus*, there are examples where notable morphological differences are not supported by significant gene sequence divergence and vice versa. Among *Chilonatalus*, the differences in size and body proportions between *Chilonatalus tumidifrons* and *Chilonatalus macer*, which have traditionally being considered indicative of species level status for these two taxa (Ottenwalder and Genoways, 1982; Koopman, 1993, Chapter 2 of this thesis), are underlain by an average cytochrome *b* divergence of 2.2 %. The much slighter morphological differentiation between populations of *Chilonatalus micropus* from Hispaniola and those of Jamaica, on the other hand, are underlain by a greater average cytochrome *b* divergence (3.2 %). In *N. tumidirostris*, the morphometrically divergent populations of Zulia and Paraguaná (Chapter 2, Figures 45), relative to populations of mainland Falcón and Miranda, are nearly indistinguishable from the latter in cytochrome *b* sequences. Most populations of the *N. tumidirostris* East clade, on the other hand, are indistinguishable on the basis of morphology from those of the genetically divergent West clade (mean divergence = 3.4 %). Finally, populations of *Natalus mexicanus* from west-northwest Mexico show a moderate mean sequence divergence (2.1 %) from those of eastern Mexico and Central America, from which they appear almost undistinguishable morphologically.

In addition to the incongruence between genetic divergence and apparent morphological differentiation, sequence divergence and number of fixed character differences in cytochrome *b* are not exactly correlated among natalid lineages (Figure 12). This discrepancy is most evident between two pairs: *Chilonatalus macer* vs. *Chilonatalus tumidifrons* and *Natalus mexicanus* from west-northwest Mexico (or *N. mexicanus mexicanus*, Villa-R, 1966; Table 3) vs. other *Natalus mexicanus*. *Chilonatalus macer*, 2.2 % divergent from *Chilonatalus tumidifrons* in cytochrome *b*, is defined by 10 molecular synapomorphies unique within *Chilonatalus*. *Natalus mexicanus* from the pacific versant of Mexico is also about 2% genetically divergent from other *N. mexicanus* but is defined by only 4 synapomorphies. Such a pattern might be expected if taxa differ in their amount of internal genetic variation, which may be related to the geographic distance among localities representing a given clade. The data, however, indicate that this relationship does not seem to be influencing the observed genetic uniformity of the lineages under study. The amount of cytochrome *b* divergence (1.2 %) between two individuals of *Chilonatalus macer* from the same locality (AT81, AT82; Table 1) was considerably larger than that (0.8 %) between two individuals of *N. mexicanus* (AY621010, AT 210; Table 1) separated by a distance of nearly 1000 km, including a 200 km stretch of open sea. This suggests that among the natalids sampled in this study the number of fixed molecular character differences are reliable indicators of lineage distinctiveness.

Discrepancies as those listed above highlight the difficulty of selecting an unambiguous threshold of genetic divergence above which populations should be considered different species. Although Baker and Bradley (2006) proposed a 2 % divergence in cytochrome *b* as the limit below which two populations are unlikely to represent different species, they themselves pointed out that taxa differing markedly in morphology and behavior such as white tail deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) can have less than 2% genetic divergence. Therefore, criteria to distinguish between species should rely less on genetic distance and more on the strength of clade support, which is a direct reflection of the number of synapomorphies, both morphological and molecular, that define a taxon.

Among natalid taxa not recognized as species by Simmons (2005b) but recovered as monophyletic in this study there are two noticeable breaks in a continuum of genetic variation: one occurring between 1% and 2% divergence in cytochrome *b*, and the other between 5 and 8 fixed character differences in cytochrome *b* (Figure 12). Most taxa that combine 8 or more fixed character differences with a greater than 2% divergence in cytochrome *b* coincide with those recognized as distinct species in Chapter 2 on the basis of morphological distinctiveness (the exception being *Chilonatalus micropus* from Hispaniola). In addition, these taxa occupy well defined geographic regions, in many cases separated by topographic or water barriers. Therefore it is reasonable to postulate a significant degree of genetic isolation among these taxa. Eight or more fixed character differences together with a divergence in cytochrome *b* higher than 2% are therefore selected here as the molecular criteria to designate taxa as distinct species. Still, these criteria should be evaluated in concert with morphological and geographical discontinuity among populations for a more confident assessment.

Under these criteria, four taxa deserve discussion either as potentially distinct species, or because they have been described in the past as distinct. These include *Chilonatalus micropus* from Hispaniola, genetically distinct from that of Jamaica but without noticeable discrete morphological character differences; the *N. tumidirostris* East clade, genetically close to *N. stramineus* and distant from *N. tumidirostris* West, but undistinguishable from the latter morphologically; *N. stramineus tronchonii*, described from the eastern versant of Sierra de Perijá, Venezuela (Linares, 1971) but now included within *N. tumidirostris* and very similar genetically to *N. tumidirostris* West; and *N. mexicanus mexicanus*, 2% divergent from other *N. mexicanus* (roughly corresponding to *N. saturatus* of Dávalos, 2005) yet with few character differences and almost undistinguishable in morphology from other *N. mexicanus*.

Individuals of *Chilonatalus* from Hispaniola are proposed here to comprise a species distinct from *C. micropus*. Although no discrete morphological character has been observed to distinguish Hispaniolan and Jamaican *Chilonatalus*, these two insular populations are defined by 13 (Hispaniola) and 10 (Jamaica) fixed character differences, which results highly supported (BS > 7) reciprocal monophyly. In addition, these two populations are more divergent in cytochrome *b* (3.2 %) than are *Chilonatalus macer* (Cuba) and *Chilonatalus tumidifrons* (Bahamas), two species traditionally considered distinct on the basis of their divergent morphology. Cranial differences do exist, nonetheless, between *C. micropus* from Hispaniola and *C. micropus* from Jamaica. Relative to the Jamaican taxon, *C. micropus* from Hispaniola is characterized by a more swollen and globular braincase and a more slender and dorsoventrally depressed rostrum. The two populations are also morphometrically distinct (Ottenwalder and Genoways, 1982; Chapter 2, Fig. 19), with bats from Hispaniola being smaller on average. There is no name available for *Chilonatalus* from Hispaniola as it has always been referred to the nominate subspecies of *C. micropus* (Table 1). Therefore a new name should be proposed to assign this taxon full specific status.

Chilonatalus from the islands of San Andrés and Providencia, Colombia, were not sampled for the molecular part of this study (Table 1). This taxon was named originally as the distinct species *Chilonatalus brevimanus* (Miller, 1898) on the basis of its shorter forearm. The overall smaller body size and relatively uninflated skull of *C. m. brevimanus* suggest that further genetic investigations may find this taxon to be a distinct lineage meriting revalidation to species status.

Natalus tumidirostris was recovered as diphyletic or paraphyletic depending on the character weight regime used. These two distinct “phylogroups” (i.e. the *N. tumidirostris* East and West clades; *sensu* Baker and Bradley, 2006) are genetically divergent (mean cytochrome *b* divergence of 3.4 %). Allocation into genetically divergent phylogroups was considered sufficient evidence of species level differentiation by Baker and Bradley (2006). Under that principle, *N. tumidirostris* east should be considered a distinct species under the name *N. haymani*, an epithet proposed originally at the subspecies level for the Trinidadian population (Goodwin, 1959). As mentioned above, however, cytochrome *b* sequences of *Natalus tumidirostris* east are very similar (0.7 % divergent) to those of *Natalus stramineus*, despite the obvious identity between *N. tumidirostris* east with *N. tumidirostris* West on the basis of morphology. Such a slight genetic divergence is comparable to that occurring within most natalid species-level clades (e.g. *N. tumidirostris* West). The existence of phylogroups in *N. tumidirostris*, then, does not seem to result from an ancestral relationship of *N. tumidirostris* East to *N. stramineus*, in which case the genetic divergence of the two should be expected to be much higher. Such a close relatedness is most likely the result of mitochondrial introgression from the lesser Antillean *Natalus stramineus* into eastern populations of *Natalus tumidirostris*. Provisionally, therefore, the population of *N. tumidirostris* bearing the name *N. t. haymani* is not considered here to be a distinct species. Future tests of the introgression hypothesis should address whether the morphological similarity of the East and West clades of *N. tumidirostris* is congruent with phylogenies based on fast evolving or paternally inherited nuclear genes, and should include the nominal subspecies *N. t. tumidirostris* from Curaçao and Bonaire.

Populations of *Natalus* from sierra de Perijá, Zulia, Venezuela, were described by Linares (1971) as the distinct subspecies *N. stramineus tronchonii*, on the basis of its palatal morphology. As shown in Chapter 2 the palate of this taxon represents one extreme a continuous range of variation in palatal fenestration present in *N. tumidirostris*, and for this reason it was synonymized with the latter taxon. The *Natalus* from Perijá form a clade defined by three synapomorphies and their cytochrome *b* of is very similar (0.4 % divergent) to that of other *N. tumidirostris* (West) populations, justifying the synonymization of this taxon with *N. tumidirostris*.

Populations of *Natalus* from Mexico and Central America have been considered by some authors to comprise two allopatric taxa: *Natalus mexicanus mexicanus* Miller, 1902 (northwest Mexico and Baja California) and *Natalus mexicanus saturatus* Dalquest and Hall, 1949 (eastern and southern Mexico plus Central America; e.g. Álvarez, 1963; Goodwin, 1959; Hall, 1981; Hall and Dalquest, 1963; Villa-R, 1966). The putative limit between the subspecies was placed in the state of Nayarit (by Hall, 1981) and in the state of Guerrero (Villa-R, 1966). Although the recognition of these two taxa has been put in doubt (Handley, 1966; Koopman, 1993; Linares, 1971; Tejedor, in press), Dávalos (2005) elevated *N. saturatus* to species level to include populations from Michoacán, Mexico to Nicaragua, in accord with the definition of Hall (1981). The results of the present study support a genetic split between Central American and west Mexican *Natalus* that corresponds to the limit between *mexicanus* and *saturatus* proposed by Villa-R (1966; Figure 7). The west Mexican *Natalus* (Michoacán to Baja California) formed a clade and was 2.1 % divergent in cytochrome *b* from *Natalus* from Central America, which did not form a clade. If the individual from Michoacán is excluded from the west Mexican clade to conform to the definition of Hall (1981), the genetic distance between the culled west Mexican clade and the remaining *N. mexicanus* drops to 1.8 %. Nonetheless, the west Mexican clade (including the individual from Michoacán) is supported by only four molecular synapomorphies and is less distinct in morphology from ‘*saturatus*’ than are some ‘*saturatus*’ populations between themselves (Chapter 2, Figure 38). Therefore, *N. saturatus* is not considered a valid taxon here.

CONCLUSIONS

The combination of cytochrome *b* sequences and morphology produced a well resolved and robust hypothesis of phylogeny for Natalidae. *Nyctiellus* is the most basal genus of the family. The Miocene fossil genus *Primonatalus* is sister to *Natalus*/*Chilonatalu*s implying an older than early Miocene origin for the *Nyctiellus* lineage. Relationships within *Natalus* formed a picket-fence topology of successive branching of species with *Natalus primus* branching off the most basal node and *Natalus stramineus*/*Natalus tumidirostris* at the crown. The synonymization of *Natalus saturatus* with *N. mexicanus* and of *Natalus tumidirostris haymani* and *Natalus stramineus tronchonii* with *Natalus tumidirostris* is supported by the molecular data. The morphologically distinctive species *Natalus tumidirostris* was not monophyletic in the cytochrome b tree, with populations from eastern Venezuela and Trinidad nesting together with *N. stramineus*. This striking result may be the consequence of introgression of *N. stramineus* mitochondrial genome into parapatric populations of *N. tumidirostris.* This hypothesis should be tested using paternally inherited genes. Future molecular phylogenetic studies should include the nominal subspecies of *N. tumidirostris* and the isolated *Chilonatalus micropus brevimanus*, and should test the congruence of relationships based on nuclear genes with the cytochrome *b* results of this study.

APPENDIX I. TAXA AND LOCALITIES

The taxa studied are listed below, including named synonyms (subspecies) of ingroup taxa, and their localities and sequences available. Area of distribution, instead of specific locality, is listed for taxa for which sequences were not obtained. Sequence numbers with prefixes AT, P, T, and Z were newly obtained for this study. Sequence numbers with prefixes AF, AY, and L were obtained from GenBank. Country abbreviations: AB, Antigua and Barbuda; BA, Bahamas; BE, Belize; BR, Brazil; BO, Bolivia; CO, Colombia; CU, Cuba; DO, Dominica; GD, Guadeloupe; GT, Guatemala; TT, Trinidad and Tobago; NA, Netherlands Antilles; CR, Costa Rica; ME, Mexico; DO, Dominican Republic; JA, Jamaica; US, United States; NI, Nicaragua; VE, Venezuela. *Listed as Natalus saturatus by Dávalos (2005).

Taxon (ingroup)	Named synonym (subspecies)		Sequences
Nyctiellus lepidus		Industrious Hill, Cat, BA	AY621006
Chilonatalus micropus	*C. m. micropus*	Los Patos, Barahona, DR	AT158
	C. m. micropus	Arroyo Chico, Samaná, DR	AT188
Chilonatalus micropus	*C. m. micropus*	Polly Ground, St. Catherine, JA	AY621025 AY621026
Chilonatalus micropus	*C. m. brevimanus*	San Andrés and Providencia Is., CO	
Chilonatalus tumidifrons		San Salvador, BA	AY621027 AY621028
Chilonatalus macer		Guanahacabibes, Pinar del Rio, CU	AT82
		Guanahacabibes, Pinar del Rio, CU	AT81
		Galalón, Pinar del Rio, CU	AT80
Primonatalus prattae		Thomas Farm, Florida, US	
Natalus primus		CU	
Natalus major		La Entrada, Maria Trinidad Sanchez, DR	AY261021
		Platanal, Sanchez Ramirez, DR	AY261020
Natalus jamaicensis		Polly Ground, St. Catherine, JA	AY261022 AY261023
Natalus mexicanus	*N. m. mexicanus*	Las Cuevas, Baja California Sur, ME	AT210
	N. m. mexicanus	Batopilas, Chihuahua, ME	AT206
	*N. m. mexicanus**	Colola, Michoacán, ME	AY621010
	N. m. saturatus	Noh-Bec, Quintana Roo, ME	AY621012
	N. m. saturatus	San Cristóbal Acasaguastlán, El Progreso, GT	AY621013
	N. m. saturatus	Rivas, NI	AY621014
	N. m. saturatus	Las Cuevas Research Station, Belmopan, BE	AY621011
Natalus lanatus		ME, CR	
Natalus tumidirostris	*N. t. tumidirostris*	Bonaire, Curaçao, NA	
	N. t. continentis	Paraguana, Falcón, VE	P1, P2, P3, AT113,

			AT115
	N. t. continentis	Yaracal, Falcón, VE	Z1, Z2, Z3
	N. t. continentis	La Chara, Falcón, VE	AT103, AT106, AT108
	N. t. continentis	Lagunita, Miranda, VE	AT132 AT133 AT134 AT136
	N. t. continentis	Turimiquire, Sucre, VE	AT88 AT96
	N. t. haymani	Mt. Tamana, St. Andrew, TT	AY AY
	N. stramineus tronchonii	Machiques, Zulia, VE	T2, T4, T11
Natalus stramineus	*N. s. stramineus*	Mary's Point, Saba, NA	TK117119 TK117622
	N. s. stramineus	Dark Cave, Barbuda, AB	TK117558 TK117559
	N. s. stramineus	Marie Galante, GD	AY621019
	Natalus dominicensis	Toucari, St. John, DO	AT621015
		Calihaut, St. Peter, DO	AY621016
Natalus espiritosantensis	*N. s. espiritosantensis*	Southeast Brazil	
	N. s. natalensis	Northeast Brazil, BR	
	unassigned	Santiago de Chiquitos, Santa Cruz, BO	AT211
(outgroups)			
Myotis nigricans			AF376864
Tadarida brasiliensis			L19734
Furipterus horrens			AY621004
Thyroptera tricolor			AY621005
Pteronotus parnelli			AY604456
Saccopteryx bilineata			AF044664

APPENDIX II: LIST OF CHARACTERS

Character 1. Height of coronoid above alveolar plane of mandible: *(0) greater than 3/2 the height of condyle above alveolar plane;(1) subequal to the height of condyle (including slightly less or slightly higher than condyle); (2) much less than height of condyle (less than 2/3 of height of condyle)* (Morgan and Czaplewski, 2003: character 1)

Character 2. Angle between anterior ridge of ascending ramus and alveolar plane: *(0) straight; (1) obtuse (>90°).*

Character 3. Anterior ridge of ascending ramus: *(0) straight; (1) concave rostrally.*

Character 4. Rotation of caudal portion of ascending ramus with respect to rostral portion of ascending ramus, in caudal view: *(0) slight, less than 20 degrees; (1) moderate, >24 degrees and < 27 degrees; (2) pronounced, > 32 degrees, and < 40 degrees; (3) very pronounced, > 50 degrees.*

Character 5. Shape of articular surface of mandibular symphysis in medial view: *(0) rounded oval, small ventral projection; (1) elongate oval, long posteroventral projection; (2) elongate oval, no projection; (3) elongate oval, small posteroventral projection* (Morgan and Czaplewski, 2003; character 9).

Character 6. Angular process: *(0) longer than it is broad; (1) broader than it is long.*

Character 7. Apophysis of angular process: *(0) curved dorsally; (1) curved anterodorsally; (2) not curved; (3) curved anteriorly, with minute pointed anterior projection.*

Character 8. Shaft of angular process in lateral view: *(0) with straight ventral and dorsal margins; (1) with dorsally curved dorsal and ventral margins.*

Character 9. Ridge along margin of angular process in dorsal view: *(0) uniformly thin or absent; (1) thickened at the distal tip of angular process.*

Character 10. Pointed tip on ridge on medial margin of angular process: *(0) present; (1) absent.*

Character 11. Shape of distal tip of angular process in lateral view: *(0) acute; (1) markedly hooked; (2) rounded or quadrate.*

Character 12. Posterior edge of ascending mandibular ramus: *(0) rising from base of angular process in an angle between 70 and 50° with the alveolar plane; (1) rising from base of angular process in an angle between 70 and 90°, relative to the alveolar plane.*

Character 13. Very small tubercle on posterior margin of ascending ramus, dorsal to angular process: *(0) present; (1) absent.*

Character 14. Ventral base of angular process: *(0) at level with alveolar plane; (1) dorsal to alveolar plane; (2) ventral to alveolar plane.*

Character 15. Mandibular angle: *(0) present; (1)polymorphic ,often present and rudimentary but sometimes absent; (2) absent.*

Character 16. Base of dentary between first molar and region ventral to ascending ramus: *(0) slightly curved to almost straight; (1) markedly curved.*

Character 17. Braincase: *(0) inflated; (1) uninflated; (2) greatly inflated (globular)* (Morgan and Czaplewski, 2003; character 25).

Character 18. Sagittal crest: *(0) low and split in two crests along its rostral* *third; (1) low and of uniform height along its entire length; (2) moderately high and most pronounced at anterior half: (3) very low; (4) markedly and uniformly high around its entire length; (5) absent.*

Character 19. Degree of rostral flexion : *(0) pronounced, angle between occlusal and zygomatic planes about 30°; (1) moderately pronounced, angle between occlusal and zygomatic planes about 20°; (2) slight, angle between occlusal and zygomatic planes about 10°; (3) almost absent, angle between occlusal and zygomatic planes less than 3°* (Simmons and Conway, 2001: character 5).

Character 20. Point of flexion between dorsal plane of nasals and frontal plane of braincase, in lateral view: *(0) dorsal to anterior edge of orbit; (1) posterior to the anterior edge of orbit.*

Character 21. Relative length of rostrum: *(0) long, distance between anterior edge of orbit and incisors > 1/3 of skull length; (1) short, distance between anterior edge of orbit and incisors < 1/4 of skull length* (Morgan and Czaplewski, 2003: character 30).

Character 22. Anterior rim of orbit: *(0) with a rather straight section that is almost perpendicular to the occlusal plane of upper toothrow; (1) curved or straight but forming a markedly acute angle with occlusal plane.*

Character 23. Height of anterior base of zygomatic arch: *(0) greater than one and one half the height of third molar; (1) about the same as the height of third molar* (Morgan and Czaplewski, 2003: character 34).

Character 24. Edge of maxilla at level of M2, in ventral view: *(0) obscured from view by M2; (1) visible beyond labial side of M2.*

Character 25. Sulcus between nasals: *(0) shallow or absent; (1) deep.*

Character 26. Lacrimal fossa: *(0) absent; (1) present* (Morgan and Czaplewski, 2003: character 39).

Character 27. Infraorbital canal: *(0) extends from P4 to M1; (1) from P2 to M2; (2) P4 to M2; (3) M1 to M2* (Morgan and Czaplewski, 2003; character 38).

Character 28. Premaxillary region of rostrum: *(0) anteriorly projected so that I2-C diastema is visible in lateral view; (1) not projected anteriorly, I2-C diastema not visible in lateral view.*

Character 29. Posterior margin of maxilla in ventral view: *(0) nearly perpendicular to longitudinal axis of skull ;(1) forming an angle greater than 90° with midline; (2) forming an angle smaller than 90° with midline.*

Character 30. Pterygoid processes: *(0) convergent; (1) almost parallel; (2) divergent.*

Character 31. Posterior margin of palate: *(0) at level of last molar; (1) at < 1/4 the distance from base to tip of pterygoids; (2) at about 1/3 the distance from base to tips of pterygoids; (3) at 1/2 the distance from base to tip of pterygoids; (4) at > than 2/3 the distance from base to tip of pterygoids; (5) polymorphic, at level of last molar or at level of second molar*

Character 32. Tips of pterygoids: *(0) tips sinusoid, converge first and then diverge distally; (1) straight and divergent; (2) convergent.*

Character 33. Medial bases of pterygoids: *(0) widely separated; (1) close together.*

Character 34. Position of caudal base of pterygoid process: *(0) caudal to foramen ovale; (1) rostral to foramen ovale.*

Character 35. Basioccipital furrows: *(0) absent; (1) present.*

Character 36. Basisphenoid immediately posterior to pterygoid processes: *(0) with deep, steep-sided concavity; (1) flat or with very shallow concavity* (Morgan and Czaplewski, 2003: character 36).

Character 37. Medial longitudinal ridge in basisphenoid: *(0) absent; (1) present.*

Character 38. Ridge between basisphenoid and alisphenoid: *(0) thick, extends to cochlea; (1) absent, or, if present, short or thin, does not extend to cochlea; (2) thin, extends caudally ventral to cochlea.*

Character 39. Elongated styliform process of ectotympanic: *(0) absent; (1) present, extends anteromedially and contacts pterygoid* (Morgan and Czaplewski, 2003; character 33).

Character 40. Size of ectotympanic in caudal view: *(0) medium, diameter about as large as depth of visible portion of cochlea; (1) large, covers most of the periotic; (2) small, diameter about 2/3 as large as depth of visible portion of cochlea.*

Character 41. Diastema between i3 and canine: *(0) absent; (1) present.*

Character 42. Diastema between i2 and i3: *(0) absent; (1) present.*

Character 43. Crown of lower canine: *(0) higher than p4; (1) subequal to p4; (2) smaller than p4.*

Character 44. p2: *(0) about equal to p3, both small relative to p4; (1) greatly reduced; (2) larger than p3; (3) about equal to p3, both subequal to p4; (4) absent* (Morgan and Czaplewski, 2003: character 50).

Character 45. Oclusal outline of p3: *(0) elongated, length much greater than* *width; (1) not elongated, length similar to width* (Morgan and Czaplewski, 2003: character 11).

Character 46. Diameter of rostral half of p3: *(0) smaller than diameter of caudal half; (1) similar to diameter of caudal half; (2) greater than diameter of caudal half.*

Character 47. Diameter of p3, in oclusal view: *(0) wider at level of roots, constricted at level of cusp; (1) widest at level of cusp.*

Character 48. p3 labial cingulum in lateral view: *(0) slightly indented between the roots, indented portion lies ventral to rostral and caudal extremes of cingulum; (1) straight, not indented between the roots; (2) markedly indented between the roots, indented portion lies at same level as rostral and caudal extremes of cingulum.*

Character 49. Notches in cristid oblicua and postcristid of lower molars: *(0) absent; (1) little developed; (2) large, carnassial like* (Morgan and Czaplewski, 2003: character 13).

Character 50. Distance from lingual cingulum to protoconid of m3: *(0) greater than distance from lingual cingulum to hypoconid; (1) same as distance from lingual cingulum to hypoconid; (2) less than distance from lingual cingulum to hypoconid.*

Character 51. Entoconid of m2: *(0) about twice as wide as metaconid; (1) about the same size as metaconid*

Character 52. Lingual talonid crest of m3: *(0) straight; (1) concave*

Character 53. Lingual cingular cusp caudal to entoconid of m3: *(0) present; (1) absent*

Character 54. Height of lower molar protoconids in lingual view: *(0) progressively decreasing in size from m1 to m3; (1) about the same on all molars.*

Character 55. I1 in lateral view: *(0) visible in front of I2; (1) not visible.*

Character 56. I2 in lateral view: *(0) long and narrow, sickle-shaped; (1) short and broad, nearly triangular; (2) I2 absent.*

Character 57. Crown of upper canine: *(0) higher than that of P4; (1) similar in height as that of P4* (Morgan and Czaplewski, 2003: character 27).

Character 58. Crown of P2*: (0) similar in height to that of P4; (1) very small; (2) p2 absent* (Morgan and Czaplewski, 2003: character 29).

Character 59. Crown of P3: *(0) similar in height to that of P4; (1) greatly reduced; (2) p3 absent* (Morgan and Czaplewski, 2003: character 49).

Character 60. Labial cingular cusp of P4: *(0) absent; (1) small; (2) well developed and short; (3) well developed, long and pointed* (Morgan and Czaplewski, 2003: character 14).

Character 61. Oclusal outline P4: *(0) indented anterolingually; (1) not indented anterolingually; (2) indented anteriorly* (Morgan and Czaplewski, 2003: character 15).

Character 62. P4 protocone: *(0) present; (1) absent.*

Character 63. Mesostylar crest of M1: *(0) short and straight; (1) long, straight anteriorly and ending in an abrupt curve; (2) short and curved; (3) very long and rather uniformly curved; (4) absent.*

Character 64. Mesostylar crest of M2: *(0) short and straight; (1) long, straight anteriorly and ending in an abrupt curve; (2) very long and sickle-shaped; (3) absent.*

Character 65. Mesostylar crest on M3: *(0) present; (1) absent.*

Character 66. Shape and orientation of mesostylar crest of M3: *(0) short and oriented anterolabially; (1) long and oriented anterolingually; (2) short and oriented anterolingually.*

Character 67. Position of capitulum of humerus: *(0) centrally located, aligned with longitudinal axis of humerus; (1) displaced dorsally, aligned with dorsal margin of humerus; (2) aligned with plane set midway between axis and dorsal margin of humerus.*

Character 68. Capitulum of humerus: *(0) capitulum rather cylindrical and narrow, its diameter less than 2/5 the width of the entire distal humerus; (1) capitulum swollen in the middle and wide, diameter about the same as height of spinous process + height of lateral process.*

Character 69. Distal spinous process of humerus: *(0) separated from medial edge of trochlea by small notch; (1) not separated from trochlea by notch; (2) separated from trochlea by large notch* (Morgan and Czaplewski, 2003: character 23).

Character 70. Tip of spinous process of humerus distal to capitulum: *(0) located distal to capitulum, height of spinous process greater than radius of capitulum; (1) located distal to capitulum, height of spinous process smaller than 1/2 the radius of capitulum; (2) located proximal to distal surface of capitulum.*

Character 71. Size of head of humerus: *(0) much larger than greater tuberosity; (1) same size as greater tuberosity.*

Character 72. Orientation of largest axis of head of humerus: *(0) posteroventral to longitudinal axis of humerus; (1) posterodorsal to longitudinal axis of humerus; (2) aligned with longitudinal axis of humerus.*

Character 73. Height of lesser tuberosity of humerus : *(0) almost as high as* *greater tuberosity and higher than head; (1) much lower than greater tuberosity and at level with head.*

Character 74. Head of humerus separated from ventral tip of lesser tuberosity by: *(0) wide notch; (1) minuscule or no notch.*

Character 75. Anterior thoracic vertebrae: *(0) C7- T6 unfused; (1) C7- T1 fused; (2) C7-T2 fused; (3) C7-T3 fused; (4) C7-T6 fused* (Morgan and Czaplewski, 2003: character 40).

Character 76. Lumbar tube (structure formed by the fusion of 10th and 11th thoracic vertebrae with all but the last 1-2 lumbar vertebrae): *(0) absent; (1) present* (Morgan and Czaplewski, 2003: character 41).

Character 77. Posterior lumbar vertebrae: *(0) all not fused; (1) last not fused; (2) last not fused* (Morgan and Czaplewski, 2003: character 42).

Character 78. Manubrium of sternum: *(0) not expanded laterally; (1) expanded laterally into plate like structure* (Morgan and Czaplewski, 2003: character 43).

Character 79. Ribs: *(0) normal; (1) broadly expanded; (2) completely coalesced with each other and with sternum so that individual ribs are not discernible in frontal view; (3) coalesced with each other and with sternum, individuals ribs discernible in frontal view* (Morgan and Czaplewski, 2003: character 44).

Character 80. Caudal vertebrae: *(0) short; (1) long* (Morgan and Czaplewski, 2003: character 45).

Character 81. Proximal end of femur: *(0) straight; (1) bent laterally* (Morgan and Czaplewski, 2003: character 46).

Character 82. Trochanters of femur: *(0) lesser trochanter of about the same* *size as greater trochanter; (1) lesser trochanter much smaller than greater trochanter.*

Character 83. Lesser trochanter in proximal view (aligning greater trochanter with shaft of femur): *(0) not projected beyond head of femur, axis of lesser trochanter forming an angle of about 90° with axis of greater trochanter; (1) not projected beyond head of femur, axis of lesser trochanter forming an angle greater than 100° with axis of greater trochanter; (2) projecting beyond head of femur away from axis of greater trochanter; (3) not projectiong beyond head of humerus, its axis forming and angle of about 45° with axis of greater trochanter.*

Character 84. Position of nostrils: *(0) set almost on margin of upper lip; (1) set markedly dorsal to upper lip.*

Character 85. Orientation of nostril openings : *(0) anteroventrolaterally, at end of a longitudinal nasal ridge that may bifurcate as two separate short tube-like structures on upper lip; (1) ventrolaterally, on rostrally projecting subcilindrical tubercle; (2) anteroventrally, on a thick anterodorsally projected upper lip; (3) anterolaterally, at unmodified tip of snout.*

Character 86. Small longitudinal ridge between nostril tubes: *(0) present; (1) absent.*

Character 87. Nostril bifid tuberculae : *(0) sunk into shallow pit of upper lip; (1) not sunk into shallow pit on upper lip.*

Character 88. Lower lip: *(0) simple; (1) with pad(s) and/or outgrowths.*

Character 89. Central lower lip skin pad: *(0) absent; (1) small and inconspicuous; (2) large.*

Character 90. Paired lower lip skin pad (on both sides of central lower lip

pad): *(0) absent; (1) smooth; (2) with numerous grooves.*

Character 91. Upper lip in lateral view: *(0), projects markedly rostrally to lower lip; (1) is nearly at level with lower lip.*

Character 92. Tubercle on dorsum of rostrum: *(0) absent; (1) transversal and dorsal to nostrils; (2) transversal and caudal to nostrils; (3) longitudinal and caudal to nostrils.*

Character 93. Ear ridges: *(0) well developed, raised and long, transversally occupying 1/3 or more of pinna; (1) vestigial, transversally occupying less than 1/5 of ventral surface of pinna; (2) absent.*

Character 94. Number and location of ear ridges: *(0) 7 or more, distributed longitudinally along 2/3 of pinna; (1) 6-5, confined to distal 1/4 of pinna; (2) 4; (3) 3.*

Character 95. Ear pinna: *(0) simple and lanceolate, either narrow or very wide (funnel shaped); (1) ear quadrate and convoluted, shaped as an airfoil.*

Character 96. Distal pinna: *(0) narrow; (1) wide; (2) very wide.*

Character 97. Lateral extension of pinna: *(0) narrow; (1) wide; (2) very wide.*

Character 98. Ventral extension of pinna (proximal pinna): *(0) narrow; (1) wide.*

Character 99. Ear tip: *(0) rounded; (1) pointed.*

Character 100. Medial edge of ear: *(0) convex; (1) straight; (2) slightly concave but much less concave than lateral margin of pinna; (3) markedly concave, nearly as concave as lateral margin of pinna.*

Character 101. Ridge delineating the contact between lateral and ventral portions of pinna: *(0) absent; (1) present but inconspicuous; (2) present and markedly* *developed, forming a pronounced flap overlapping the ventral portion of pinna.*

Character 102. Bidimensional shape of tragus: *(0) lanceolate; (1) spatulate; (2) bifurcated.*

Character 103. Tridimensional shape of tragus: *(0) linear; (1) curled rostrally, forming an incomplete cilinder or ring; (2) base flaring laterally, tip bent medially; (3) bent rostrally, with an angle along its basal half.*

Character 104. Natalid organ: *(0) absent; (1) elliptical; (2) hemispherical; (3) wedge-shaped; (4) rather rectangular and flat* (fig. 13).

Character 105. Position of natalid organ: *(0) on dorsum of rostrum; (1) on forehead covering part of dorsal base of rostrum* (fig. 13).

Character 106. Facial pelage: *(0) profuse, forming thick mustaches; (1) sparse*

Character 107. Labial portion of mustache: *(0) formed by rigidly parallel hairs; (1) formed by lax hairs that are not arranged in parallel.*

Character 108. Portion of mustache on dorsum of rostrum: *(0) formed by hairs as long as those of labial portion; (1) formed by hairs shorter than those of labial portion; (2) absent.*

Character 109. Superciliary vibrissae: *(0) absent; (1) two; (2) one* (Simmons and Conway, 2001: character 100).

Character 110. Mystacial vibrissae: *(0) forming a single cluster; (1) dispersed or forming two clusters* (Simmons and Conway, 2001; character 101).

Character 111. Number of mistacial vibrissae: *(0) 5 vibrissae; (1) 6 vibrissae; (2) 7 vibrissae; (3) 8 vibrissae; (4) 9 vibrissae.*

Character 112. Number of interramal vibrissae: *(0) no vibrissae; (1) 1* *vibrissa; (2) 2 vibrissae* (Simmons and Conway, 2001: character 97).

Character 113. Number of ramal vibrissae: *(0) no vibrissae; (1) 2 vibrissae; (2) 3 vibrissae; (3) 4 vibrissae; (4) 6 vibrissae.*

Character 114. Ramal vibrisal tuberculae: *(0) absent; (1) high and coalesced, forming dermal ridge; (2) low and separated.*

Character 115. Number of genal vibrissae: *(0) no vibrissae; (1) 1 vibrisa; (2) 2 vibrissae* (Simmons and Conway, 2001: character 99).

Character 116. Attachment of plagiopatagium to leg: *(0) at proximal 3/4 of tibia; (1) at ankle; (2) at foot; (3) at toe; (4) attaching at distal 3/4 of tibia .*

Character 117. Length of tail: *(0) greater than length of legs; (1) same as length of legs; (2) smaller than length of legs.*

Character 118. Tip of tail: *(0) enclosed in uropatagium but does not extend to distal edge; (1) slightly protruding from uropatagium; (2) extensively protruding from uropatagium; (3) terminating at edge of uropatagium.*

Character 119. Fringe of fine hairs at edge of uropatagium : *(0) present; (1) absent.*

APPENDIX III. MORPHOLOGICAL CHARACTER MATRIX

Natalus jamaicensis

1002301001 2110212210 0010011101 4000110012 1003010011 0000110002 11111-1111 0001111111

Natalus major

1012301001 2110212210 0010011101 4000110012 1003010011 0000110002 11111-1111 0001111111

Natalus stramineus

1012301001 2110212210 0010011111 4000110012 1003010011 0000110002 11111-1111 0001111111

Natalus tumidirostris

1010301001 2110212210 0010011111 5000110012 1003010011 0000110002 11111-1111 0001111111

Natalus espiritosantensis

1010301001 2110212210 0010011111 4000110012 1003010011 0000110002 11111-1111 0001111111

Natalus mexicanus

1012301001 2110112210 0010011111 4000110012 1003010011 0000010002 11111-1111 0001111111

Natalus lanatus

1012301001 2110112210 0010011101 4000110012 1003010011 0000000002 11111-???? ??????????

Natalus primus

1101301011 2000112211 0010111000 3000101010 1003010211 0000000002 1132011101 0001111111

Chilonatalus micropus

1101100111 1000002111 0010111000 3000101012 1103010211 0000000003 1132011010 1111312131

Chilonatalus tumidifrons

1101100111 1010002111 0110111000 3000101010 1103010211 0000000003 1132011010 1111412121

Chilonatalus macer

1101100111 1010002111 0110111000 3000101010 1103010211 0000000003 1132011010 1111412121

Nyctiellus lepidus

110100000[01] 0002000411 0101111020 2000000011 1011001112 0001001101 0100001010 1111111111

Primonatalus prattae

1101000000 000200???? ?010?1???? ?????????? 11??010211 0000?????1 0132011101 ??????????

Furipterus horrens

2013313001 2111012001 1110100000 0100110102 0021111121 1101001200 00431-1001 1211112010

Thyroptera tricolor

2002212001 2111012501 1100000002 1111001102 0010010210 1111000000 0043021002 1111200010

Pteronotus parnelli

1002312001 2110010310 0001103-02 1111000102 0002101100 1111010020 00031-1121 0001000000

Myotis nigricans

0000200001 0002201520 1100102011 2200110100 0010101110 0101001110 00431-0012 0111000000

Tadarida brasiliensis

0103202001 211221133- 1100102-01 0100011100 0004121100 0101-21210 00431-0010 0111000000

Saccopteryx bilineata

0113302001 2012210421 1101000-02 0111001202 0004011111 1111-20210 20431-2022 0110000000

APPENDIX III. MORPHOLOGICAL CHARACTER MATRIX (continued)

Natalus jamaicensis	1020000112	1011021111	0015101100	314221030
Natalus major	1020000112	1011021111	0015101100	314021030
Natalus stramineus	1020000112	101102111[23]	0015101100	314221030
Natalus tumidirostris	1110000112	1011021113	0015101100	314221030
Natalus espiritosantensis	1110000112	1011021113	0015101100	314221030
Natalus mexicanus	1020000112	1011021112	0015101100	314221030
Natalus lanatus	???0000112	1011021111	0013101100	314221030
Natalus primus	1020000112	1012022101	001?101200	323221030
Chilonatalus micropus	1010001112	1313022100	0012000200	223124030
Chilonatalus tumidifrons	1010001112	1313022100	0011000200	222120030
Chilonatalus macer	1010001112	1313022100	0011000200	222120030
Nyctiellus lepidus	1100011112	1010011000	0014000000	121024031
Primonatalus prattae	??????????	??????????	??????????	?????????
Futipterus horrens	11012--120	002-022100	2210-01000	0222?1201
Thyroptera tricolor	00?01--120	0110011111	2020-01200	414211111
Pteronotus parnelli	00312--120	0200000101	1030-01000	322104211
Myotis nigricans	00200110--	0000010001	1000-01220	322212031
Tadarida brasiliensis	0??00110--	00001---01	0100-1--00	121021121
Saccopteryx bilineata	00113--101	0000000001	0100-1--11	0?0021211

Figure legends

Figure 1. Relationships of Natalidae to other bat families on the basis of (A) morphological data (Simmons and Geisler, 1998) and (B) molecular data (Teeling et al., 2005). Clades: a, Noctilionoidea; b, Nataloidea; c, Vespertilionoidea. In the morphology tree, Natalidae nests within the Nataloidea clade, which branches off the base of Vespertilionoidea. In the molecular tree, Natalidae remains at the base of Vespertilionoidea, but the remaining “nataloids” move into Noctilionoidea.

Figure 2. Phylogenies of Natalidae based on different data sets: A, allozymes (Arroyo-Cabrales et al., 1997); B, osteological characters (Morgan and Czaplewski, 2003); C, gene sequences (Dávalos, 2005). Nomenclature follows Chapter 2 of this thesis. Taxa that appeared under different names in the original publications are identified by superscript numerals: 1, *Natalus stramineus*; 2, *Natalus stramineus*; 3, *Natalus major*; 4, *Natalus stramineus*; 5, *Natalus saturatus*.

Figure 3. Plot of divergence in cytochrome *b* sequences vs. taxonomic rank. Numerals: 1 among *Natalus mexicanus*, 2 Between the West and East clades of *Natalus tumidirostris*; 3, East clade of *Natalus tumidirostris* vs. *Natalus stramineus*; 4, *Chilonatalus tumidifrons* vs. *Chilonatalus macer*; 5, *Chilonatalus micropus* (Jamaica) vs. *Chilonatalus micropus* (Hispaniola); 6, *Natalus espiritosantensis* vs. *Natalus tumidirostris* and *Natalus stramineus*; 7, *Natalus mexicanus*, *N. major*, and *N. jamaicensis* vs. other *Natalus*; 8,

among species of *Chilonatalus*; 9, *Chilonatalus* vs. *Natalus*; 10 *Nyctiellus* vs. other Natalidae; 11, *Tadarida brasiliensis* vs. Natalidae; 12, *Nyctiellus* vs. *Furipterus*

Figure 4. Strict consensus of 2 most parsimonious trees of 346 steps based on 119 morphological characters, recovered using the unweighted character regime. Numbers above branches are Bremer support values and numbers below branches are bootstrap support values.

Figure 5. Strict consensus of 26 most parsimonious trees of 1416 steps based on complete sequences of the cytochrome *b* gene, recovered using the unweighted character regime. Numbers above branches are Bremer support values and numbers below branches are bootstrap support values. Dashed vertical lines indicate taxa not recovered as monophyletic.

Figure 6. Strict consensus of 2 most parsimonious trees of 1655 steps based on a combined analysis of 119 morphological characters and complete cytochrome *b* gene sequences. Numbers above branches are Bremer support values and numbers below branches are bootstrap support values.

Figure 7. Left upper molar toothrow in 6 species of Natalidae: A, *Nyctiellus lepidus*; B, *Chilonatalus tumidifrons*; C, *C. micropus*; D, *Natalus primus*; E, *Primonatalus prattae*; F, *Natalus mexicanus*.

Figure 8. 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).

Figure 9. 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*.

Figure 10. Lateral view of the ascendant ramus of the left dentary of *Myotis* (A) 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*.

Figure 11. Anteroventral view of the maximally extended ear pinna in six bat species with lanceolate ear pinna (A, *Saccopteryx bilineata*; B, *Myotis nigricans*; C, *Pteronotus pranelli*; D, *Thyroptera tricolor*; E, *Furipterus horrens*; F, *Kerivoula hardwickei*) and in five species of Natalidae (G; *Nyctiellus lepidus*; H, *Chilonatalus micropus*; I, *Natalus primus*; J, *Natalus major*; K, *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

Figure 12. Plot of fixed character differences vs. mean sequence divergence in cytochrome *b* of natalid taxa not given species status by Simmons (2005b) but recovered as monophyletic in this study. Mean sequence divergences were determined by pair wise comparisons between sister taxa if a sister relationship was recovered or, if the taxon was part of an unresolved node, between the taxon in question and all lineages branching off the politomy. Letters correspond to taxa listed in Table 3.

Figure 13. Dorsal (top), frontal (middle), and lateral (bottom) views of the natalid organ (shaded in gray) in four species of Natalidae (A–*Nyctiellus lepidus*; B–*Chilonatalus macer*; C–*Chilonatalus micropus*; D–*Natalus tumidirostris*) showing variation in the shape and position of the natalid organ. Character states: A) natalid organ rather rectangular and on dorsum of muzzle; B) natalid organ elliptical and centered at dorsal point of flexion of skull; C) natalid organ hemispheric and centered at dorsal point of flexion of skull; D) natalid organ wedge-shaped and centered on forehead.

Ecomorphological evolution and biogeography of Natalidae

ABSTRACT

Given that natalids were long considered to be a monogeneric family comprising a few uniform species, intriguing patterns of morphological diversity within this group have been overlooked. Likewise, the assumption that the few traditionally recognized species were geographically widespread has obscured a complex pattern of distribution in this family that demands explanation. Armed with a deeper understanding of the diversity and evolutionary history of the family, gained from a new revision and phylogeny of this group, some of these patterns can now begin to be explored. Here, I examine variation within Natalidae in body size, the morphology of wings, skulls, teeth, and genitals as well as distributional patterns in a phylogenetic and ecologic context. I use the most complete phylogeny available for the family to estimate the evolution of morphological characters and discuss their possible functional value. Also, I present results of vicariance-dispersal analysis that illuminate natalid biogeographic history. Natalids show significant trophic differentiation within the family in terms of use of flying space and food processing. In Natalidae, male genital morphology appears to be correlated to the morphology of the natalid organ, and both traits appear to be sexually selected. A much finer-grained historical explanation of the biogeography of family than those previously available indicate that the pattern of distribution of Natalidae resulted from a counter-clockwise sequence of dispersal events around the Caribbean basin beginning in Cuba and The Bahamas, passing through Central and South America, and ending in the Lesser Antilles.

INTRODUCTION

Until recently, traditional taxonomists (with the notable exception of G. S. Miller) had failed to detect the subtle yet significant morphological differentiation that is present among members of the family Natalidae. As a consequence, intriguing patterns of the ecological evolution and biogeography of this group had been overlooked. With new taxonomic interpretations of the diversity of the family and a deeper understanding of their evolutionary history, these patterns can now be examined under a clearer focus.

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

Among New World bats, the pattern of distribution of Natalidae is also unique. The family is most diverse in the West Indies both at the genus and species level, but also includes a few species that range almost throughout the entire tropical belt of the New World. An early Miocene fossil natalid, *Primonatalus prattae*, has been described from northern Florida, USA, a currently extra-tropical locality where the family no longer occurs. In addition, late Quaternary fossils of extant Natalidae indicate widespread extirpation events of island populations throughout the West Indies. Thus far, no natalids, extant or fossil, have been found in two Caribbean island groups: 1) the Puerto Rican Bank (including Puerto Rico and the Virgin Islands); and 2) the southern Lesser Antilles (islands to the south of the St. Lucia Channel).

Investigations on the historical biogeography of Natalidae have determined that the family probably originated in southeastern North America, diversified in the West Indies, and only reached the mainland in recent geologic history (Dávalos, 2005; Morgan and Czaplewski, 2003). Nonetheless, because of limited taxonomic resolution at the species level, previous studies could not determine the likely ancestral areas of natalid genera, the point (or points) of entry of the family into the continent, and the routes of dispersal within the continent or among the islands. Gaps in the West Indian distribution of the family (i.e. the Puerto Rican bank and the southern Lesser Antilles) also remained unexplained.

In this chapter, the most complete phylogeny available of the family and information (although limited) on natalid ecology are used to address questions on the morphological diversification and the historical biogeography of Natalidae. Four main questions are addressed in this chapter: 1) do different natalid species correspond to different ecomorphs? 2) is the structure of natalid faunas influenced by competition? 3) is genital morphology sexually selected in Natalidae? 4) what is the most likely sequence of events that has led to the current pattern of distribution of the family? The patterns and hypotheses discussed here provide a starting point for studying the process of bat faunal formation in the insular and mainland Neotropics.

METHODS

The interpretations proposed in this chapter are based on data presented on Chapters 2 and 3 of this thesis. The taxonomy follows that of Chapter 2. In particular, the populations of *Chilonatalus micropus* found to be genetically divergent in Chapter 3 are treated here *sensu lato* in all discussions. 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 hereafter treated as the "*Natalus stramineus* group". Similarly, a distinction is made between *Chilonatalus micropus* and a *Chilonatalus* "*tumidifrons* group" (= *C. tumidifrons* + *C. macer*). In some graphs and figures, 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*; and Ppr, *Primonatalus prattae*.

Ecological 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 indexes 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) 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*; 3) small (mean forearm length of 29–34 mm), including *Nyctiellus* and *Chilonatalus*.

Canonical analyses were preformed using STATISTICA 5.0 (1995). Character optimization and ancestral area reconstruction analyses were performed with T.N.T. (Goloboff et al., 2004). Ancestral area reconstruction analyses used a single optimization downpass to generate ancestral-area-states at internal nodes. This parsimony procedure minimizes the cost of vicariance-dispersal events in the tree and produces results similar to those obtained using the software DIVA (Ronquist, 1997: figs. 1, 3, 4, 6). Areas of endemism used in biogeographic analyses are shown in Table 1. Given the geologic time frame involved (post early-Miocene, see Discussion) all range-extension events discussed in this chapter were considered to result from dispersal.

RESULTS AND DISCUSSION

FLIGHT MORPHOLOGY: The aerodynamic design (i.e. relative size and shape) of flight surfaces (wings plus uropatagium) is highly variable among bats and has a profound influence on their ecology. Bats with pointed wing tips and narrow flight surfaces (high aspect ratio) 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, as it 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 maneuverability and 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 shape of wing tip, 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. 1, 2). With regard to size of the uropatagium natalids also fall into three categories: 1) bats with small uropatagia (*Nyctiellus*); 2) bats with large uropatagia (*Natalus*, *Chilonatalus tumidifrons* and *C. macer*); and 3) bats with intermediate sized uropatagia (*Chilonatalus micropus*, *Natalus lanatus*; figs. 1, 2). Narrow wing tips seem to be the ancestral conditions in natalids, with broad wing tips evolving within *Natalus* (i.e., in the *Natalus stramineus* group; figs. 3). The ancestral condition of uropatagium size, on the other hand, is ambiguous in Natalidae but intermediate size uropatagia appear to have evolved twice from ancestors with large uropatagia (fig. 4).

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 the natural history information that could 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 moth like (Goodwin, 1970; Jennings et al., 2004; Miller, 1905; Tejedor et al., 2004; Tejedor et al., 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; Chapter 2).

Despite the difficulty of interpreting the flight morphology of natalids in the absence of ecological data, the differences found among genera and species are notable and suggest the existence of five distinct ecomorphs. Most sympatric species belong to separate ecomorphs (Table 1). 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*) the same ecomorph is shared between 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; Chapter 3: fig. 7). Bat genera from other families, including *Thyroptera* (Thyropteridae), *Furipterus* (Furipteridae), and *Kerivoula* (Vespertilionidae) also show mesostylar crests, usually with 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, occupying more than a third of the labial side of the oclusal 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* (to the exclusion of *N. primus*) lack a mesostylar crest in M3. The ancestral type of mesostylar crest in Natalidae is ambiguous in optimization analyses, but it seems that short mesostylar crests have appeared twice in the family either at or before the divergence of *Nyctiellus* and once again within the genus *Natalus* (fig. 5).

Long, sharp edges in the molars appear within several predatory mammalian lineages (e.g. carnivorans; Butler, 1946; insectivorans, and microchiropterans; Strait, 1993). The dilambdodont tooth with multiple shearing crests of insectivorous bats 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 coarse 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-bodied 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 as a family natalids select very 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 rostrum geometry: 1) bats with longer, narrower rostra (*Chilonatalus* and *Natalus primus*); and 2) bats with shorter, wider rostra (*Nyctiellus* and the remaining species of *Natalus*; fig. 6). 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 extremely scant but hints at the existence of 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 (orders Homoptera, Diptera, and Hymenoptera; Silva-Taboada, 1979). Accounts of the diet of narrow skull species mention a marked predominance of moths (*Chilonatalus macer*; Silva-Taboada, 1979) and of 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 1). A second sympatric species pair, *N. mexicanus* and *N. lanatus* also fall within the same ecomorph.

EVOLUTION OF BODY SIZE: For a small family, Natalidae has a wide variation of body sizes. The largest member of the family, *Natalus primus*, is five times heavier and has almost twice the length of the forearm of *Nyctiellus lepidus*, the smallest natalid and one of the smallest bats in the world. Body sizes in Natalidae appear to have a strong phylogenetic component, with medium to large body sizes occurring only in the genus *Natalus* and small body sizes in *Chilonatalus* and *Nyctiellus*. A small body size appears to be the ancestral condition in the family (fig. 7)

The distribution of body size in Natalidae appears to be related to sympatry among species (fig. 8). 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 Greater Antilles 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; Chapter 2).

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 to avoid competition (Brown and Wilson, 1956). Rigorous demonstration for 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 hallmark evidence for independent assortment with regards to body size is that members of each size class are monophyletic, whereas that for character displacement is that taxa that occur both allopatrically and sympatrically are more divergent between themselves when they occur sympatrically than when they occur allopatrically (Losos, 1990).

Both patterns are present in Natalidae. The consistent partition of body size classes between *Natalus* (always large) and *Chilonatalus* (always small) in all islands where small and large natalids are found, suggests the influence of species assortment. By contrast, the unidirectional changes in body size of the large (*Natalus*) and small (*Chilonatalus micropus*) natalids on the islands of Hispaniola, Jamaica, San Andrés, and Providencia, suggest the effect of character displacement. In Jamaica, where the largest *Natalus* (*N. jamaicensis*) of those islands occurs, *C. micropus* reaches its maximum body size, whereas in Hispaniola, where the smaller *N. major* occurs, *C. micropus* is also smaller (fig. 8). In San Andrés and Providencia, moreover, a member of the Antillean fauna (*Chilonatalus*) coincides with a medium-sized member of the continental fauna (*N. mexicanus*). In these two islands, *N. mexicanus* seems to reach its largest body size and C. *micropus* its smallest, in agreement with the requisites of character displacement. Although the size difference between *C. micropus* and *N. mexicanus* in San Andres and Providencia is much smaller than those between *C. micropus* and greater Antillean *Natalus*, the apparent lack of differentiation 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 *Natalus primus* and *Chilonatalus macer* in Cuba) and a second of lack of difference (between *Natalus mexicanus* and *Natalus 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 *Chilonatalus 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 narrow 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. 9A,B).

The pair *Natalus lanatus* and *Natalus mexicanus* represents 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. 9B). 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 in Chapter 2, 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 EVOLUTION: The relative length of the penis (length of the penis/forearm length) is markedly variable among natalids (Chapter 2). Three classes of penis length relative to body size can be distinguished in Natalidae: 1) penis long (*Chilonatalus micropus*); 2) penis intermediate (*Natalus* and *Nyctiellus*); and 3) penis short (*Chilonatalus macer* and *Chilonatalus tumidifrons*; fig. 10). The mean relative penis length of *Chilonatalus tumidifrons* (5.4% of the forearm length) is more than ten standard deviations shorter than that of *Chilonatalus micropus* (14.6% of the forearm length). An intermediate sized penis seems to be the primitive condition in the family, with short and long penises having evolved only in the genus *Chilonatalus* (fig. 11).

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; Hosken, 1998; Wilkinson and McCracken, 2003). Investigations of the 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.

Natalids are an interesting group 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. 12). 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% (fig. 13). Interestingly, across

Natalidae, relative penis length does appear to be negatively associated with relative length of the natalid organ (fig. 14). This unexpected association does not seem to be affected by phylogenetic history, given that the natalid species at the extremes of the variation in both penis length and natalid organ are members of the genus *Chilonatalus*.

The natalid organ, a unique synapomorphy of Natalidae, 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 is widely variable among natalid genera (Chapter 3; figure 13), reaching its maximum development (8.5 mm; 53% of the skull length) in *Chilonatalus tumidifrons*. Although the function of the natalid organ is unknown, its exclusive presence in males suggests it has a sexual function. When manipulated, males of the genus *Natalus* may 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 the secretion from the natalid organ functions as a quality 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.

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 *Chilonatalus 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 *Chilonatalus tumidifrons* and *Chilonatalus* *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 increased access to females, as it occurs among harem-keeping or lekking species with exaggerated secondary sexual dimorphism (Andersson, 1994). The lack of body size dimorphism between males and females in *Chilonatalus macer* and *C. tumidifrons*, suggests that lekking is a most likely strategy. These intriguing hypotheses remain to be tested with behavioral data.

BIOGEOGRAPHY: The pattern of distribution of the family Natalidae is unique among new world bats. Natalidae is the only Neotropical bat family that is most diverse in the insular portion of the region, and in which species and generic richness decreases from north to south. This north-south decline in richness is marked by limits between well defined natalid faunas (fig. 15).

The richest fauna occurs in the northern Greater Antilles (Cuba and The Bahamas), and is characterized by the genus *Nyctiellus*, *Natalus primus*, and *Chilonatalus* (*tumidifrons* group), and a maximum of three sympatric species (Table 1). Even though in The Bahamas *N. primus* is extinct and *Chilonatalus* and *Nyctiellus* no longer occur in sympatry, the Pleistocene natalid fauna of those islands was essentially identical to that of Cuba (Morgan, 2001). The Cayman Islands also harbor Pleistocene remains of a subset of this fauna (*Natalus primus* and *Chilonatalus macer*; Morgan, 1994; Chapter 2).

The next richest fauna is that of the central Greater Antilles (Hispaniola and Jamaica), characterized by *Chilonatalus* (of the *micropus* group), and two species of

Natalus (*Natalus* group), with a maximum of two species occurring in sympatry (Table 1). At least until the late Pleistocene part of this fauna also extended to the Turks and Caicos, where remains of *N. major* have been found (Morgan, 1989).

In the continent, Natalidae is represented by two distinct faunas containing only the genus *Natalus*: 1) the Mexican-Central American fauna, with two sympatric species of dissimilar morphology (*N. mexicanus* and *N. lanatus*); and 2) the South American-Lesser Antillean fauna with three allopatric species of similar morphology (*N. tumidirostris*, *N. espiritosantensis*, and *N. stramineus*; Table 1). In the Caribbean islands of San Andrés and Providencia (both about 200 km off the coast of Nicaragua), the fauna of Mexico-Central America merges with that of the central Greater Antilles, combining the insular derived *Chilonatalus micropus* with the continental derived *N. mexicanus*.

Two major discontinuities in natalid fauna do not correspond to faunal geographic turnover but to gaps in the distribution of the family (fig. 15). These are the islands of the Puerto Rican Bank (Puerto Rico and the Virgin Islands), and the southern Lesser Antilles (islands south of the St. Lucia Channel), where neither extant nor fossil natalids have ever been found.

Ancestral-area analyses optimized five ancestral nodes of Natalidae to Cuba and the Bahamas, the region containing the greatest generic diversity and the most plesiomorphic natalid lineage: *Nyctiellus* (fig. 16). Three of these nodes were exclusive to Cuba and the Bahamas, including the most recent common ancestor of the family, the ancestor of the genera *Primonatalus*, *Chilonatalus*, and *Natalus*, and the ancestor of the species pair *Chilonatalus tumidifrons* and *Chilonatalus macer*. The remaining two nodes were shared with the central Greater Antilles (the ancestor of *Chilonatalus*) and with

Mexico and Central America (the ancestor of *Natalus*). By contrast, the ancestor of the *Natalus* group clade was optimized exclusively to Mexico and Central America, from where at least two separate range expansions seem to have taken place: one to the central Grater Antilles and another to South America. Finally, the ancestral area of the closely related *N. tumidirostris*, *N. espiritosantensis*, and *N. stramineus* was optimized to South America and the Lesser Antilles.

The optimal ancestral areas of basal natalid nodes recovered in this study are notable in their greater exclusivity compared to those recovered by Dávalos (2005). The ancestor of all Natalidae was previously thought to range through the Greater Antilles (excluding Puerto Rico) and Florida (Dávalos, 2005) because of the basal-most divergence recovered for *Primonatalus* by Morgan and Czaplewski (2003). Likewise, Dávalos (2005) could not resolve the point of entry of *Natalus* into the continent. The results of this work indicate that the invasion of the continent coincided either with the divergence of the genus *Natalus* or of the *Natalus stramineus* group clade, and that the event took place between Cuba/Bahamas and Mexico/Central America. Therefore, the divergence of *Natalus primus* from the *Natalus* group clade was either the result of an invasion of the continent by the lineage leading to the *Natalus* group or a reinvasion of Cuba by the lineage leading to *Natalus primus*.

All hypothesized vicariance events between subaerial lands in the Caribbean basin are thought to have ended by late Oligocene (Iturralde-Vinent and MacPhee, 1999). All lineage divergence events of Natalidae that include regions outside the ancestral area of the family (Cuba and the Bahamas), on the other hand, appear to have taken place after the early Miocene, the age of *Primonatalus* (Morgan and Czaplewski, 2003). Therefore, all range extension and lineage divergence events of Natalidae are assumed here to result from dispersal. Under this mechanism, a most parsimonious diversification/dispersal history of Natalidae can be deduced from the results of ancestral area analyses.

The most recent ancestor of Natalidae was distributed in Cuba and/or the Bahamas. Later on, the lineage leading to *Primonatalus* dispersed into Florida and that leading to *Chilonatalus* diverged in the area encompassing the northern and central Greater Antilles. The genus *Natalus* may have originated in Cuba/Bahamas from where it dispersed to Mexico/Central America. An origin of *Natalus* in Mexico/Central America would require a reinvasion of the islands, hence one more step. With the tree available, however, two separate dispersals into the central Greater Antilles, one to Hispaniola and a second to Jamaica, are required to explain the presence of *Natalus* there, unless the relationships between *N. major* and *N. jamaicensis*, weakly supported here, are found to be that of monophyly with the addition of more data. South America, on the other hand, was most likely colonized from Central America and the Lesser Antilles from South America. It is striking that no dispersal events of *Natalus* seem to have taken place between the northern and central Greater Antilles.

The diversification and dispersal in Natalidae, therefore, seems to have proceeded in counterclockwise sequence around the Caribbean basin, coming almost full circle, but without reaching the islands of the Puerto Rican Bank. Such a history explains the apparent absence of Natalidae from Puerto Rico but not that from the southern Lesser Antilles. Compared, to Puerto Rico, the extant and fossil bat faunas of the Lesser Antilles have been much less intensely investigated, and new island records continue to appear in the literature (e.g. *Natalus stramineus* for Martinique; Timm and Genoways, 2003).

Future surveys of the islands spanning the arc between St. Lucia and Grenada may reveal a taxonomic connection between *Natalus stramineus* and *Natalus tumidirostris*.

CONCLUSIONS

Despite the fact that Natalidae was traditionally considered a rather homogeneous family of little diversity, the results of this study indicate otherwise. Natalidae appears to comprise bats with distinct trophic ecomorphs in terms of food acquisition, given by potential different uses of foraging space, and of food processing, given by potential different masticatory capabilities. Some natalids, in addition, appear to have widely different mating systems, as indicated by differences in genital morphology and secondary sexual traits. Natalid faunas differ in their phylogenetic and ecomorphological composition, with that of the northern Greater Antilles being dominated by long-winged/narrow-skulled plesiomorphic lineages, and that of the continent by more derived broad-winged/broad-skulled lineages. The structuring of natalid faunas seems to have involved competition, reflected either in species sorting or size adjustments as members of the family dispersed around the Caribbean basin reinvading the Antilles multiple times.

Figure legends

Fig. 1. 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/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.

Fig. 2. Wing outlines of four species of Natalidae: A) *Chilonatalus micropus*; B) *Natalus lanatus*; C) *Natalus primus*; and D) *Nyctiellus lepidus*. *Nyctiellus lepidus* has the narrowest wing of all natalids.

Fig. 3. Evolution of wing-tip shape in Natalidae. A narrow wing tip is the ancestral condition with intermediate and broad wing tips evolving within the genus *Natalus*.

Fig. 4. Evolution of the relative size of the uropatagium in Natalidae. The ancestral condition of the relative size of the uropatagium is uncertain in Natalidae, but a large uropatagium evolved early in the history of the family and intermediate size uropatagia evolved twice in two separate lineages.

Fig. 5. Evolution of mesostylar crests in Natalidae. Regardless of the ambiguity in the ancestral condition of the mesostyle in natalids, short mesostylar crests appear to have evolved secondarily within the genus *Natalus*.

Fig. 6. 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 toothrow (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.

Fig. 7. Evolution of body size in Natalidae. A small body size is the ancestral condition in the family. Large body sizes arose with the evolution of *Natalus* and intermediate body sizes evolved twice in continental species of the genus.

Fig. 8. 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.

Fig. 8. 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. 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.

Fig. 9. 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.

Fig. 10. Evolution of penis length in Natalidae. An intermediate penis length is optimized as the ancestral condition, with large and small penis lengths evolving only within *Chilonatalus*.

Fig. 11. Relationship of penis length with length of the tibia in Natalidae. Family wide, 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*.

Fig. 12. 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 relatively large natalid organ and a second containing species with a relatively small natalid organ.

Fig. 13. 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*.

Fig. 14. Quaternary faunal composition of Natalidae around the Caribbean Basin. Dashed lines indicate the limits of three distinct assemblages of natalid genera: A) *Nyctiellus*, *Chilonatalus*, *Natalus*; B) *Chilonatalus*, *Natalus*; C) *Natalus*. Natalid faunal richness decreases from the northern Greater Antilles to South America and the Lesser Antilles. No extant or fossil Natalidae are known from the Puerto Rican Bank and the southern

Lesser Antilles. The islands of San Andrés and Providencia combine insular (*Chilonatalus*) and continental (*Natalus mexicanus*) fauna.

Fig. 15. Ancestral area optimizations for six basal nodes of Natalidae. Cuba and the Bahamas contain four ancestral nodes, including that of all known species of Natalidae (A). Mexico and Central America contain three ancestral nodes, including that of the "*Natalus*" group. The ancestral area of *Natalus* from Hispaniola and Jamaica does not include Cuba and Bahamas.

Fig. 16. Probable routes of dispersal of *Natalus* around the Caribbean basin based on the results of the ancestral area analysis. These potential routes of dispersal offer a parsimonious explanation for the apparent absence of both extant and fossil Natalidae in Puerto Rico and predict that either living or fossil *Natalus* might be found with further survey of the Southern Lesser Antilles.

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