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A Revision of Extant Greater Antillean Bats of the Genus *Natalus*

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ABSTRACT

The taxonomy of the genus *Natalus* in the Greater Antilles has been controversial for decades. Although as many as three taxa of *Natalus* (sensu stricto) were described for the Greater Antilles, the main source of disagreement was whether *Natalus major* (thought to be distributed in Cuba, Hispaniola, and Jamaica) is a species distinct from *Natalus stramineus*. The Cuban form of *Natalus*, previously known only from incomplete fossils, has been largely excluded from the debate surrounding the taxonomic status of *N. major*. The discovery of an extant population of the Cuban *Natalus* prompted a reanalysis of species limits among *Natalus* in the Greater Antilles. In this paper, we show that the genus *Natalus* is represented in the Greater Antilles by three distinct extant species, each endemic to a single island. We also summarize information about the natural history of these species and emphasize the importance of taking immediate conservation action for their protection.

RESUMEN

Durante décadas, la taxonomía del género *Natalus* en las Antillas Mayores ha sido controvertida. A pesar de que tres taxa han sido descritos para *Natalus* (sensu stricto) en las Antillas Mayores, la controversia se ha concentrado en la validez de *Natalus major* (supuestamente distribuida en Cuba, La Española y Jamaica) como especie distinta de *Natalus stramineus*. La forma cubana de *Natalus*, previamente conocida solo a partir de fósiles incompletos, ha sido prácticamente excluida del debate concerniente a *N. major* y *N. stramineus*. El descubrimiento de una colonia viviente de *Natalus* en Cuba ha estimulado un reanálisis taxonómico de *Natalus* en las Antillas Mayores. En este trabajo, demostramos que el género *Natalus* está representado en las Antillas Mayores por tres especies vivientes, cada una endémica a una sola isla. También presentamos información acerca de la historia natural de estas especies y enfatizamos la importancia de tomar acción inmediata para su protección.

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INTRODUCTION

The New World family Natalidae comprises a small assemblage of insectivorous, cave-dwelling bats characterized by funnel-shaped ears, very long legs and tail, and the natalid organ, a saclike glandular structure located in the dorsum of the muzzle in males. The family was long considered monogeneric (e.g., Koopman, 1994; Varona, 1974), with the genus *Natalus* having three subgenera: *Natalus*, *Chilonatalus*, and *Nyctiellus*. A recent morphological analysis led Morgan and Czaplewski (2003) to suggest that the three previously recognized subgenera are best treated as genera. Six species of Natalidae are currently recognized: *Natalus major, Natalus stramineus, Natalus tumidirostris, Chilonatalus micropus, Chilonatalus tumidifrons*, and *Nyctiellus lepidus* (Morgan and Czaplewski, 2003).

The family Natalidae occurs widely throughout the lowlands of tropical America, having its highest diversity in the Caribbean island of Cuba (Tejedor et al., 2004). The genera *Chilonatalus* and *Nyctiellus* are restricted to the West Indies, and the genus *Natalus* is distributed throughout the Neotropics, from northwestern Mexico (Baja California and Sonora) and the West Indies (Greater and Lesser Antilles) to southeastern Brazil, Bolivia and Paraguay (Koopman, 1994; López-Gonzales et al., 1998; Taddei and Uieda, 2001). In the Greater Antilles, the genus *Natalus* occurs on the three largest islands in the region (Cuba, Hispaniola, and Jamaica) and is known from fossil remains from the Bahamas and the Cayman Islands (Morgan, 1989, 1994, 2001). Historically, the taxonomy of *Natalus* in the Greater Antilles has been controversial. Depending on the author, the taxa of Cuba, Hispaniola, and Jamaica have been recognized as one or two Greater Antillean endemic species, or as insular subspecies of *Natalus stramineus* Gray, 1838, a widespread continental species with a distribution congruent with that of the genus *Natalus* (Koopman, 1994).

The genus *Natalus* was first known in the Greater Antilles through the description of *Natalus major* Miller, 1902, from Hispaniola, a taxon diagnosed as having a larger skull and a more inflated braincase than the already known form, *Natalus stramineus*. Years later, Anthony (1919) described *Natalus primus*, from Cuba, on the basis of two fossil mandibular rami that were much larger and had heavier teeth than mandibles of *N. major*. By the middle of the 20th century, Koopman and Williams (1951) reported the first record of *Natalus* from Jamaica (and tentatively referred it to *N. major*), based on a single partial mandible collected by H. E. Anthony on that island during 1919–1920. Living specimens of the Jamaican *Natalus* were first reported almost a decade later, with Goodwin's (1959) description of *Natalus major jamaicensis*. Surprisingly, although Goodwin (1959) diagnosed the Jamaican *Natalus* on the basis of more than five discrete characters he still considered it to be only subspecifically distinct from the Hispaniolan population. In his paper, Goodwin (1959) also treated the Cuban *N. primus* as a subspecies of *N. major*, thereby recognizing a single, endemic species of *Natalus* for all Greater Antillean islands. Living representatives of *Natalus* in Cuba were not known until 1991, when a colony was found in a cave in the westernmost tip of the island (Tejedor et al., 2004).

Traditionally, taxonomic decisions involving Greater Antillean *Natalus* (and all of the Natalidae, in general) have been conservative, and often have lacked appropriate support. Cabrera (1957), for example, suggested, without providing justification, that most populations of *Natalus*, both insular and continental (with the exception of *Natalus tumidirostris* Miller, 1900, from northern South America), represented the single species *Natalus stramineus*. This point of view was formalized in the 1970s in a series of publications (Linares, 1970, 1971; Linares and Löbig-A, 1973) that, based on limited character observation, collectively argued that morphological variation among all populations of *Natalus*, including West Indian species, was clinal, and that therefore should all be referred to *Natalus stramineus* (even though the name *N. tumidirostris* was tentatively retained for Venezuelan populations). Later, Varona (1974) also assigned all Greater Antillean *Natalus* to *N. stramineus*, but similarly did not provide justification for his decision. Subsequently, with the exceptions of

Hoyt and Baker (1980) and McFarlane (1997), which retained *N. major* as a valid Greater Antillean species, most authors (e.g., Hall, 1981; Koopman, 1989, 1993, 1994; McFarlane, 1986; Silva-Taboada, 1979) have followed Linares' (1971) and Varona's (1974) arrangement.

Despite the historic prevalence of conservative treatment regarding the systematics of Greater Antillean *Natalus*, taxonomic discordance has continued until the present. In recent years, several works have argued for the revalidation of full specific status for *Natalus major* on the basis of the larger size of Greater Antillean *Natalus* (Tejedor et al., 2004) and of divergent discrete cranial morphology between Greater Antillean and other populations of *Natalus* (Morgan, 1989, 1994, 2001; Morgan and Czaplewski, 2003). Nonetheless, a recent monograph on the bats of Dominica (Genoways et al., 2001) favored the inclusion of all insular *Natalus* within *Natalus stramineus*. This point of view was further supported by Timm and Genoways (2003: 30), who stated that, other than size, there were no ''structural'' differences between *N. major* and other insular and continental taxa of *Natalus*.

Besides the fact that influential taxonomic decisions involving Greater Antillean *Natalus* have often been based on insufficient evidence, the few truly detailed morphological studies of the genus *Natalus* in the West Indies (e.g., Goodwin, 1959; Morgan, 1989, 2001) have been limited by specimen sampling and availability (for instance, most of Morgan's morphological arguments for the recognition of *N. major* as a distinct species apply only to the Jamaican form of *Natalus*). In particular, the lack of neontological material of the Cuban form of the genus reduced the breadth of any morphological study that aimed at understanding the diversity of *Natalus* in the Greater Antilles. Recent material of *Natalus* made available from Cuba (Tejedor et al., 2004) prompted the reanalysis of the taxonomic status of the three Greater Antillean populations of *Natalus*. As our study shows, we find that the three populations of the subgenus *Natalus* that inhabit the three largest Greater Antillean Islands are divergent in many morphological traits and therefore merit recognition as three distinct species.

MATERIALS AND METHODS

MUSEUM SPECIMENS

We examined most of the specimens of Greater Antillean *Natalus* currently available in museum collections in Cuba, the United Kingdom, and the United States. Museums visited and specimens examined are listed in the appendix.

MEASUREMENTS

All observations reported here are based on adults with closed epiphyses. Cranial and external measurements follow Silva-Taboada (1979) and Handley (1988). Cranial measurements and length of tibia were taken to the nearest 0.1 mm with digital or dial calipers. Ear length, and forearm length of dry specimens were taken from specimen tags. Weight was measured in the field or taken from specimen tags.

Forearm length: Maximum distance between elbow and wrist, taken dorsally with the wing folded.

Length of tibia: Maximum length of the tibia taken with the femur and foot flexed in an angle smaller than 90°.

Ear length: Greatest distance from the basal notch of the ear to the tip of the ear.

Greatest skull length: Maximum length of the skull taken from the anterior edge of the premaxilla to the posterior edge of the occiput.

Zygomatic breadth: Maximum distance between the exterior sides of the zygomatic arches, taken perpendicular to the longitudinal axis of the skull.

Postorbital breadth: Distance between the lateral walls of the frontals, taken dorsally at the level of the least postorbital width.

Braincase breadth: Maximum distance between the lateral walls of the braincase, taken perpendicular to the longitudinal axis of the skull.

Breadth across molars: Maximum distance between the labial margins of the molar tooth rows, taken perpendicular to the longitudinal axis of the skull.

Maxillary tooth row length: Maximum distance between anterior edge of maxillary canine and posterior edge of last maxillary molar.

STATISTICAL ANALYSES

Statistical analyses were performed with STATISTICA (1995, version 5). Six two-way ANOVAs and Tukey's Test for unequal sample sizes were used to compare measurements between species for six variables with sample sizes (per species) ≥ 10. Given a previous report of sexual dimorphism in a Greater Antillean *Natalus* (Tejedor et al., 2004), we used T tests to compare measurements between sexes in our samples. Due to the small size of samples of females from Hispaniola and Jamaica, and given that significant differences between the sexes of *Natalus* from Cuba showed no interaction with differences between island samples, we pooled both sexes in most statistical analyses. Nonetheless, we performed a separate one-way ANOVA for zygomatic breadth including only males because it was the only character for which differences among males (potentially significant due to relatively large sample sizes) seemed obscured by differences among females. Probabilities were compared to a significance level of $\alpha = 0.01$ for all the ANOVAs and T tests (in which several tests were performed on the same all-species sample), and to a significance level of $\alpha = 0.05$ for the Tukey's comparisons. Within-island geographic variation was not tested because there is only one known extant locality for two of the three species treated in this paper (i.e., *Natalus jamaicensis* and *Natalus primus*), and the sizes of the available samples of *Natalus major* with different geographic provenience were generally very small. Finally, we performed a principal components analysis (PCA) of the variables with sample sizes (per species) ≥ 10, and used the first two extracted principal components to generate a plot of specimen scores.

SYSTEMATICS

Our analyses of qualitative and quantitative morphological characters reveal the presence of three separate evolutionary lineages of the genus *Natalus* in the Greater Antilles, with a degree of morphological divergence characteristic of fully differentiated species. The three species are distinct in cranial morphology, and can be distinguished by size and external characters. Accordingly, we redescribe them here.

Natalus major Miller, 1902
Figures 1–4

Natalus major major Goodwin, 1959.
Natalus stramineus major Linares, 1971.

HOLOTYPE: USNM 101395, adult male skull and skin in fluid, collected by W. M. Gabb between 1869 and 1871 "near Savaneta [locality 10 in the appendix], Dominican Republic". The skull is complete and the skin is in good condition.

DISTRIBUTION: Hispaniola, including the Dominican Republic and Haiti (fig. 5).

DIAGNOSIS: Forearm length relatively small (42.1–44.8 mm); ear tip pointed, with a shallow notch on the outer margin; rostrum relatively short, with the point of flexion between rostrum and braincase dorsal to the anterior edge of orbit; braincase not rising abruptly from the rostrum, with an angle smaller than 55° between dorsal plane of rostrum and frontal plane of forehead; braincase oval-shaped in dorsal profile, its breadth smaller than its length; postorbital constriction relatively wide, its sides markedly diverging anteriorly; maxillary convex dorsal to molars; one pair of small palatal fenestra sometimes present between last molars; basisphenoid pits shallow, and raised above plane of basisphenoid furrows, in ventral view; posterior edge of ascending ramus of mandible straight and vertical, forming an angle close to 90° with basal plane of dentary, and lacking notch below condyloid process (table 1).

DESCRIPTION: *Natalus major* has a relatively short forearm (42.0–44.8 mm) and a relatively short ear (ear length 15.8–17.9 mm). The braincase breadth and greater skull length means of males of *N. major* appear to average larger than those of females (fig. 6), but these differences were not statistically significant in our sample.

The hair is long (7 mm) and lax, both ventrally and dorsally. Dorsal hairs are bicolored, with bases lighter than tips, and ventral hairs are monocolored. There are two morphs of pelage color, one bright yellowish and another grayish, with a few intermediate individuals. In the bright-yellowish morph, dor-

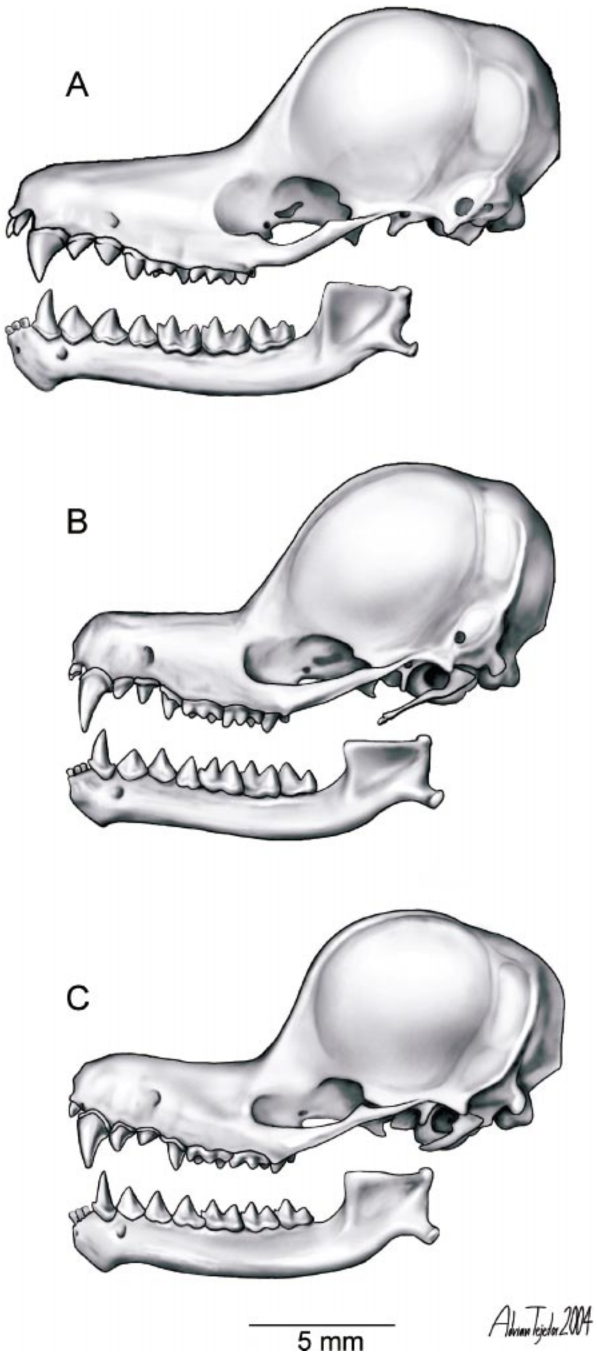

Fig. 1. Lateral view of the skull of three species of Greater Antillean bats of the genus *Natalus*: **A,** *N. primus* (Cuba; MNHN 51, field number); **B,** *N. major* (Hispaniola; AMNH AT 51, field number); **C,** *N. jamaicensis* (Jamaica; AMNH 246127).

sal hair bases are buff and the tips are sepia, and ventral hairs are entirely cream buff (fig. 4). In the grayish morph, the dorsal hairs are drab to smoke gray with fuscous tips, and ventral hairs are pale smoke gray. Most individuals have a darker-colored patch on the forehead. There is a fringe of hairs along the free border of the uropatagium. Mustachelike facial hair is sepia to fuscous, connected across dorsum of muzzle by a narrow band of dark hairs. The pelage extends slightly into both faces of the plagiopatagium, dorsally to 6 mm, and ventrally to 10 mm.

The muzzle is relatively short and dorsoventrally flattened. The nostrils are small, oval, and open ventrolaterally. In ventral view, the tip of the muzzle between the nostrils projects slightly beyond the upper lip. The lower lip is thickened and with a shallow central groove. The ears are rather square-shaped. The inner edge of the ear is straight below the tip and has a shallow notch on the outer edge, giving the tip a pointed appearance. The ears of *N. major* show five to seven rudimentary folds, though they may be entirely absent in some individuals.

The skull is relatively broad and robust. The braincase of *Natalus major* is not markedly inflated, nor very abruptly elevated above the rostrum, forming an angle smaller than 55° with the dorsal plane of the nasals. The postparietal region is relatively wide in dorsal view. A conspicuous ridge separates the postparietal and occipital regions. The sagittal crest is well developed. The postorbital region is wide, with sides markedly diverging anteriorly, in dorsal view. The rostrum is relatively short and broad. The dorsal point of flexion between the rostrum and the braincase is dorsal to the anterior edge of the orbit. There is a moderately deep sulcus between the nasal bones. The premaxillary region does not project anteriorly, so that in lateral view the small diastema between canines and incisors is not particularly noticeable. The maxillary is convex above molars. The rostrum does not tip downward, or does so only slightly. The anterior palatal foramina are very small and near the palatine emargination, and their anterior margin is posterior to the anterior edge of the canines. Two pairs of small palatal fenestra are present at the level of the last molar in some

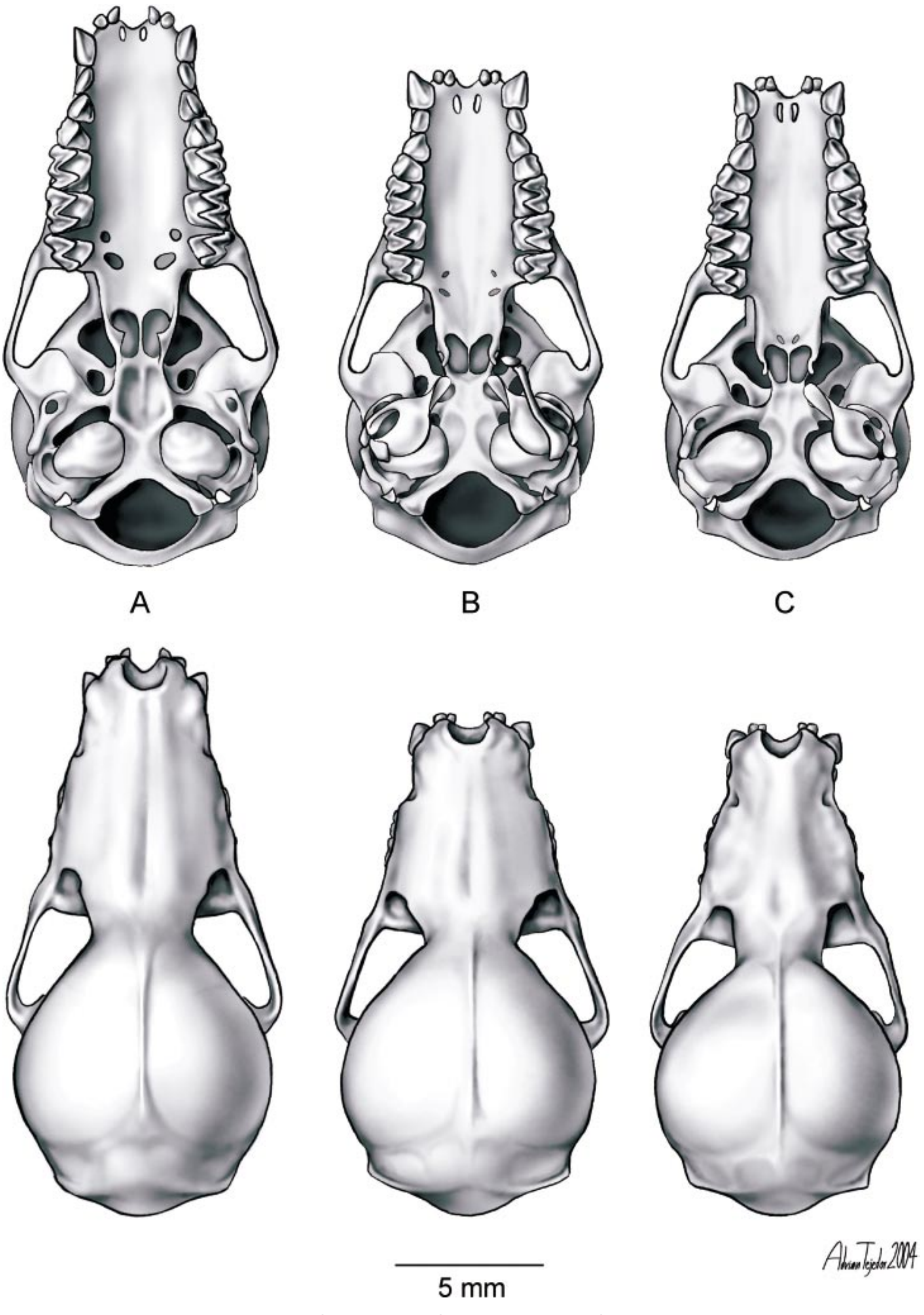

Fig. 2. Dorsal and ventral views of the skull of three species of Greater Antillean *Natalus*. **A,** *Natalus primus* (MNHN 51, field number); **B,** *Natalus major* (AMNH AT 51, field number); **C,** *Natalus jamaicensis* (AMNH 246127).

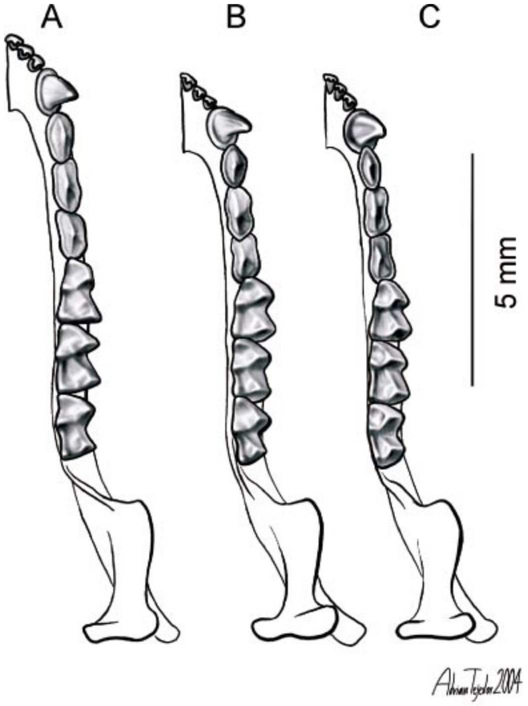

Fig. 3. Dorsal view of the right mandibular ramus of three species of Greater Antillean *Natalus*. **A,** *Natalus primus*, **B,** *Natalus major*, **C,** *Natalus jamaicensis*.

individuals. The bony palate extends more than half the distance between the posterior edge of the last molar and the tip of pterygoids. The pterygoid processes are slightly convergent and markedly hooked in lateral view. In ventral view, the inner edge of each pterygoid is smoothly convex. In ventral view, the basisphenoid pits, between the maxillary articular facets, are shallow and raised above the level of the basisphenoid furrows.

The dentary is curved (upturned) and thick. The angular process is thick, rather straight, and with a blunt spatulate end. The base of the angular process is dorsal to the alveolar plane. The coronoid process is at about the same height than the condyle, above the alveolar plane. The ascending ramus of the mandible is markedly upturned, with its anterior border concave and raising from the alveolar plane at an angle greater than 80°. The posterior border of the ascending ramus rises from the base of the angular process at a nearly straight angle with the base of the dentary, giving a rectangular appearance to the ascending ramus. The mental foramen is between the canine and the first premolar.

The upper incisors of *Natalus major* are small, with a hooked point in lateral view. The first incisor is situated more posteriorly than the second, so that in lateral view the first incisor is not visible. The base of the upper canines is robust, in occlusal view, with a well-developed cingulum that is about as wide as it is long. The upper premolars are successively larger, in occlusal view, and relatively short and crowded. The upper molar row is relatively slender, its width less than half the width of the palate. The first and second molars are approximately equal in size, with the third slightly smaller.

The lower incisors are small, tricuspid, and subequal. The lower canine is large and rather curved, with a large cingulum that is slightly longer than it is wide. The canine and premolars are longitudinally short in occlusal view, and the first premolar is shorter than the canine and the other two premolars. The first two molars are larger and wider than the third; the first projects more labially than the other two. The last premolar and first molar are relatively crowded (fig. 3).

COMPARISONS: *Natalus major* can be distinguished from most other species of *Natalus* (with the exception of *Natalus jamaicensis*) on the basis of body size and external characters. The forearm length of *N. major* (42.0–45.0 mm) is smaller than that of *Natalus primus* (46.1–51.2 mm; $P < 0.001$; fig. 6), and is larger than those of *Natalus stramineus* (35.0–41.0 mm; Tejedor et. al., 2004) and *Natalus tumidirostris* (37.2–41.5 mm; Tejedor, unpublished data). Externally, the ear of *N. major* has a straight anterior margin and a pointed tip, whereas that of *N. primus* has a relatively rounded tip and those of *N. stramineus* and *N. tumidirostris* have slightly to deeply concave anterior margins. The dorsum of the muzzle of *N. major* shows a thin band of dark, long hairs connecting the labial mustaches, which is absent in *N. primus*.

Natalus major is morphometrically distinct from *Natalus jamaicensis* (figs. 6, 7), but both species overlap in size and are similar in external characters. Nonetheless, *N.*

Fig. 4. Photograph of an adult male *Natalus major* (showing a bright yellowish pelage) captured in Cueva Grande de Julián, Sánchez Ramírez province, Dominican Republic, in January 2002. Photograph by A. Tejedor.

major can be unambiguously distinguished from *N. jamaicensis* on the basis of cranial characters (table 1, figs. 2–3). In *N. major* the maxillary bone is convex dorsal to the molars, and in *N. jamaicensis* it is markedly concave. In *N. major*, the sulcus between the nasal bones is moderately deep and long, whereas it is short and shallow in *N. jamaicensis*. In *N. major*, the upper molar series is narrower than half of the palate width, whereas in *N. jamaicensis* it is thicker than half of the palate's width. In *N. major*, the postorbital constriction is wider than in *N. jamaicensis* ($P < 0.001$, fig. 6), with sides markedly diverging anteriorly, in dorsal view, as opposed to sides almost parallel in *N. jamaicensis*. Also, in *N. major*, the braincase is much less inflated than in *N. jamaicensis*, and it is oval-shaped in dorsal profile, instead of almost circular as in *N. jamaicensis*. Finally, in *N. major*, the braincase does not rise very abruptly from the rostrum (angle between dorsal plane of rostrum and frontal plane of braincase less than 55°), whereas it rises very abruptly from the rostrum in *N. jamaicensis* (angle between dorsal plane of rostrum and frontal plane of braincase greater than 60°).

Cranially, *Natalus major* can also be distinguished from *Natalus primus*, by its smaller skull size (greatest skull length 17.0–18.1 mm; $P < 0.001$), and shallow basisphenoid pits, whereas in the latter the basisphenoid pits are very deep and the skull is larger (greatest skull length 18.1–19.9 mm; $P < 0.001$; table 2, figs. 2–3). From *Natalus tumidirostris*, *N. major* can be distinguished by its convex yet uninflated maxillary bones, which are markedly inflated in the former, so that the molars are not easily seen in dorsal view. *Natalus major* differs from *Natalus stramineus*, as it is currently defined, by its larger skull (greatest skull length: 17.0–18.1 mm, 15.0–17.1 mm in *N. stramineus*) and by a larger and more voluminous braincase, relative to the overall size of the skull.

TABLE 1

Diagnostic Characters of Greater Antillean Species of the Genus *Natalus*

Character	*N. major*	*N. jamaicensis*	*N. primus*
Braincase breadth	< 90% of zygomatic breadth	> 92% of zygomatic breadth	< 90% of zygomatic breadth
Postorbital constriction	relatively wide, diameter > 34% zygomatic breadth	relatively narrow, diameter < 34% zygomatic breadth	relatively wide, diameter > 34% zygomatic breadth
Maxillary bone	convex above molars	concave above molars	convex above molars
Posterior border of ascending ramus of the mandible	rising vertically (angle close to 90°) from base of angular process	rising vertically (angle close to 90°) from base of angular process	rising obliquely (angle < 70°) from base of angular process
Angular process	short and thick, with broad spatulate tip	short and thick, with broad spatulate tip	long and slender, with slightly hooked tip
Cranial flexion	slight, angle between dorsum of rostrum and frontal plane of braincase < 55°	pronounced, angle between dorsum of rostrum and frontal plane of braincase > 60°	slight, angle between dorsum of rostrum and frontal plane of braincase < 55°
Point of flexion between dorsal plane of rostrum and frontal plane of forehead	dorsal to anterior edge of orbit, in lateral view	dorsal to anterior edge of orbit, in lateral view	well posterior to anterior edge of orbit, in lateral view
Basisphenoid pits	small and shallow, their bottoms ventral to plane of basisphenoid furrows	small and shallow, their bottoms ventral to plane of basisphenoid furrows	large, deep and steep sided, their bottoms dorsal to plane of basisphenoid furrows
Ear tip	pointed, with shallow notch on outer margin	pointed, with shallow notch on outer margin	rounded, notch on outer margin almost imperceptible

REMARKS: Fossil *Natalus* collected in the eastern Bahamas (Grand Caicos) were referred to *N. major major* by Morgan (1989). We tentatively include these fossils within *N. major* until they can be reexamined.

Natalus primus Anthony, 1919
Figures 1–3

Natalus major primus Goodwin, 1959.
Natalus stramineus primus Linares, 1971.

HOLOTYPE: AMNH 41009, a fossil right dentary, collected by H. E. Anthony in 1917, Cueva de Los Indios (locality 29 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 is missing all teeth except the third premolar and the first molar).

DISTRIBUTION: Cuba, Isle of Pines, and the Bahamas (Abaco, Andros, New Providence). There is only one known extant locality (Cueva La Barca, Cuba; Tejedor et al., 2004) and 14 fossil localities (fig. 5).

DIAGNOSIS: Largest extant species in the genus *Natalus* (forearm length 46.1–51.2 mm, greatest skull length 18.1–19.9 mm); ear tip rounded, notch on outer margin of ear almost imperceptible; rostrum longer than in any other Greater Antillean *Natalus*, point of flexion between rostrum and braincase posterior to anterior edge of orbit; braincase not rising abruptly from rostrum, forming an angle smaller than 55° with dorsal plane of rostrum; braincase oval-shaped in dorsal profile,

TABLE 2

Summary of Measurements[a] of Greater Antillean *Natalus*

	Males			Females		
	Number	Mean ± SD	Range	Number	Mean ± SD	Range
			Natalus jamaicensis			
Weight	4	6.3 ± 0.4	5.9–6.7	2	—	6.8–7.3
Forearm length	10	45.2 ± 0.9	44.0–47.0	2	—	45.5–46.0
Length of tibia	4	24.4 ± 0.4	23.8–24.8	1	—	23.1
Greatest skull length	9	17.7 ± 0.2	17.4–18.0	2	—	17.6–18.1
Zygomatic breadth	8	9.3 ± 0.2	9.1–9.5	2	—	9.2–9.5
Braincase breadth	9	8.8 ± 0.1	8.6–9.0	2	—	8.6–8.7
Breadth across molars	9	6.1 ± 0.1	5.9–6.2	2	—	5.9–6.1
Maxillary toothrow length	8	7.9 ± 0.1	7.8–8.1	1	—	8.0
Postorbital breadth	9	2.8 ± 0.1	2.7–3.0	2	—	2.7–3.0
Ear length	2	16.2 ± 1.3	15.3–17.1	—	—	—
			Natalus major			
Weight	6	7.9 ± 1.4	6.2–10.0	1	—	7.6
Forearm length	17	43.3 ± 1.0	42.0–45.0	7	43.8 ± 0.7	42.6–44.8
Length of tibia	15	23.3 ± 0.8	21.9–24.3	5	22.6 ± 1.1	21.3–23.5
Greatest skull length	12	17.7 ± 0.3	17.3–18.1	3	17.2 ± 0.3	17.0–17.6
Zygomatic breadth	12	9.4 ± 0.2	8.8–9.6	3	9.2 ± 0.3	8.9–9.4
Braincase breadth	12	8.8 ± 0.2	8.5–9.0	3	8.6 ± 0.1	8.5–8.7
Breadth across molars	13	6.2 ± 0.1	5.9–6.4	3	6.1 ± 0.3	5.9–6.4
Maxillary toothrow length	13	7.8 ± 0.1	7.6–8.0	3	7.6 ± 0.1	7.5–7.7
Postorbital breadth	13	3.3 ± 0.1	3.1–3.5	3	3.3 ± 0.1	3.2–3.4
Ear length	14	16.1 ± 1.4	13.0–17.9	5	16.0 ± 2.1	14.0–18.9
			Natalus primus			
Weight	26	9.8 ± 1.2	7.8–12.6	24	8.4 ± 1.0	6.0–10.1
Forearm length	26	48.8 ± 1.2	46.1–51.2	24	48.5 ± 0.8	47.0–50.1
Length of tibia	26	27.3 ± 0.8	26.0–29.1	24	26.4 ± 0.6	25.4–27.1
Greatest skull length**	18	19.2 ± 0.4	18.5–19.9	17	18.8 ± 0.3	18.1–19.5
Zygomatic breadth*	13	9.6 ± 0.2	9.2–10.0	11	9.3 ± 0.1	9.1–9.5
Braincase breadth	14	8.5 ± 0.1	8.3–8.7	11	8.4 ± 0.2	8.1–8.7
Breadth across molars	12	6.7 ± 0.2	6.5–6.9	7	6.8 ± 0.2	6.6–7.0
Maxillary toothrow length	6	8.8 ± 0.1	8.6–9.0	3	8.7 ± 0.1	8.6–8.8
Postorbital breadth	18	3.4 ± 0.1	3.2–3.5	18	3.3 ± 0.1	3.0–3.4
Ear length	1	—	20.2	2	—	20.6–21.2

[a] Weight is given in grams; all other measurements are given in millimeters. See text for description of measurement methods. Significance of differences between sexes: * = $P \leq 0.05$, ** = $P \leq 0.01$.

breadth smaller than length; postorbital constriction relatively wide, its sides markedly diverging anteriorly; postorbital sphenoid fenestra present; maxillary convex above molars; two pairs of relatively large fenestra on palate, between molars; basisphenoid pits deeply concave; posterior edge of ascending ramus of mandible forming an angle smaller than 70° with basal plane of dentary, and often with a notch below condyloid process (table 1).

DESCRIPTION: *Natalus primus* is the largest of the Greater Antillean *Natalus* in mean forearm length, greatest skull length, and breadth across molars ($P < 0.001$; table 2, fig. 6). Its mean braincase breadth, however, is relatively small compared to those of *N. jamaicensis* and *N. major* ($P < 0.001$; fig. 6). The ears of *N. primus* are very large (20.2–21.2 mm). Males of *N. primus* are significantly, although only slightly, larger than females in body weight, length of tibia, greatest skull length, and zygomatic breadth ($P < 0.01$; table 2; fig. 6).

The hair is long and lax. Dorsal and ventral hairs are 8 mm long. The dorsal hairs are bicolored, with bases lighter than tips, and the ventral hair is monocolored. There are two pelage-color morphs, one bright yellowish and another grayish, with some individuals showing intermediate coloration. In the bright-yellowish phase the bases of the dorsal hairs are buff and the tips are sepia, and the ventral hair is entirely cream buff. In the grayish phase the dorsal hairs are drab to smoke gray with fuscous tips and the ventral hairs are pale smoke gray. There is a fringe of hairs along the free border of uropatagium. *Natalus primus* has mustachelike facial hair tufts that are sepia to fuscous in color, and are not connected across the dorsum of the muzzle by a band of dark hairs. The pelage extends slightly into both faces of the plagiopatagium, dorsally to 6 mm, and ventrally to 10 mm.

The muzzle is long and dorsoventrally flattened. The small, oval nostrils open ventrolaterally. The tip of the muzzle, between nostrils, projects slightly beyond upper lip, a feature that is most noticeable in ventral view. The lower lip is thickened and has a shallow central groove. The ears are rather square-shaped, with a straight anterior margin and lacking a notch on the posterior margin, giving the tip a relatively round appearance. The ears of *Natalus primus* show rudimentary folds, varying in number from five to seven.

The braincase of *Natalus primus* is moderately inflated, and does not rise abruptly from the rostrum, forming an angle smaller than 55° with the dorsal plane of the nasals. The sagittal crest is pronounced and its interparietal region is slightly higher than its supraoccipital region. The postparietal region is relatively narrow in dorsal view and the ridge formed between this region and the occipital is relatively low. The postorbital constriction is relatively wide, with sides markedly diverging anteriorly. The rostrum is very long and moderately broad. The sulcus between the nasals is long and deep. The premaxillary region projects anteriorly, so that in lateral view the diastema between canines and incisors is conspicuous. The maxillary is convex dorsal to the molars. The rostrum tips slightly downward. The infraorbital foramen opens laterally, close to the alveolar margin. The anterior palatal foramina are very small and near the palatine emargination, at the level of the anterior edge of the canines. There are two relatively large palatal fenestra at the level of the last two molars. The bony palate extends for less than half the distance between posterior edge of last molars and tip of pterygoids. The pterygoid processes are convergent posteriorly, and vary from broadly triangular to acutely pointed in lateral view. The inner edge of each pterygoid has a prominent right-angled point visible in ventral view. The basisphenoid pits are deep, forming a large, double concavity that is conspicuously deeper than the basisphenoid furrows between the auditory bullae.

The dentary bone is thin and not markedly curved. A rudimentary mandibular angle is sometimes present. The angular process is long and thin, rather straight, and with a hooked end. The base of the angular process is at the level of the alveolar plane. The coronoid process is at about the same height or slightly higher than the condyle above the alveolar plane. The ascending ramus is not markedly upturned. The anterior border of the ascending ramus is slightly concave, rising from the alveolar plane in an angle of about 80°. The posterior border of the ascending ramus rises from the base of the angular process in an angle smaller than 70°. Usually the posterior edge of the ascending ramus is not straight, having a shallow notch immediately above the base of the angular process. The mental foramen is between the canine and the first premolar.

The superior incisors are relatively long and slightly hooked in lateral view. The first incisor is situated more anteriorly than the second, so that in lateral view the first incisor is easily visible. In occlusal view, the base of the canine is slender, its width comprising about two thirds of its length. The cingulum of the canine is well developed. The premolars are successively larger, in occlusal view, and relatively long and not crowded. The molar row is relatively slender, its width less than half the width of the palate. The first and second molars are approximately equal in size, with the third slightly smaller.

The inferior incisors are small, tricuspid, and subequal. The canine is relatively small and straight. In occlusal view, the canine and premolars are longitudinally elongate, with the first premolar longer than the canine and about as long as the other two premolars. The molars are approximately equal in size and shape, with the first more projected labially than the other two. The last premolar and the first molar are not markedly crowded (fig. 3).

COMPARISONS: *Natalus primus* is the largest of all extant *Natalus*, and overlaps in range of forearm length only with *Natalus jamaicensis* (mean forearm length, however, is significantly different between the two species; $P < 0.001$; table 2). *Natalus primus*, therefore, can be distinguished by size alone from most other species of the genus.

Externally *N. primus* can be identified by its rather rounded ear tip that lacks a notch or emargination along the posterior margin of the ear, whereas in all other species of *Natalus* the ear tip is markedly pointed and the lateral ear margin has a notch below the ear tip. Similarly, *N. primus* lacks the band of dark hairs that in all other species of *Natalus* connects the labial mustachelike hair tufts characteristic of the genus.

Cranially, *Natalus primus* is unlike any other species of *Natalus* in that its basisphenoid pits are very deep and steep-sided, whereas 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 greater length of the rostrum in *N. primus* is concomitant with (1) the elongation of the premaxillary region, resulting in an anterior projection of the incisors, and (2) the position of the dorsal point of flexion of the skull, which, in lateral view, lies posterior 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. In *N. primus*, the posterior edge of the ascending ramus of the mandible is not perpendicular to the basal plane of the dentary, and usually shows a distinctive notch, absent in all other species of *Natalus*, that is dorsal to the angular process.

REMARKS: Fossil *Natalus* collected in the western Bahamas were referred to *N. major primus* by Morgan (1989), but were reported by him to be noticeably larger than those of Cuba. Although it is possible that the Bahamian fossils represent a species distinct from *N. primus*, we refrain from excluding them from the Cuban taxon until specimens from both island groups are compared in greater detail.

Natalus jamaicensis (Goodwin), 1959

Figures 2–4

Natalus major jamaicensis Goodwin, 1959.
Natalus stramineus jamaicensis Linares, 1971.

HOLOTYPE: AMNH 182000, skull and skin in fluid, collected by C. B. Lewis in St. Clair Cave (locality 1 in the appendix), 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. 5).

DIAGNOSIS: A relatively large representative of Greater Antillean *Natalus* with a long forearm (44.1–44.8 mm) relative to its skull length (17.4–18.1 mm); ear tip pointed, with a shallow notch on the outer margin of ear; point of flexion between rostrum and braincase dorsal to anterior edge of orbit; 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 narrow, its sides almost parallel; maxillary distinctly concave above molars; one pair of small palatal fenestrae near the posterior edge of palate; basisphenoid pits shallow and almost imperceptible; posterior edge of ascending ramus of mandible straight and vertical, forming an angle close to 90° with basal plane of dentary, and lacking notch below condyloid process (tables 2, 3).

DESCRIPTION: *Natalus jamaicensis* has a long forearm (44.0–47.0 mm; $P < 0.001$, compared to *Natalus major* and *Natalus primus*) but a relatively small skull (greatest skull length smaller than that of *N. primus*, $P < 0.001$; table 2; fig. 6). Its ears are large (20.2–21.2 mm). No significant secondary

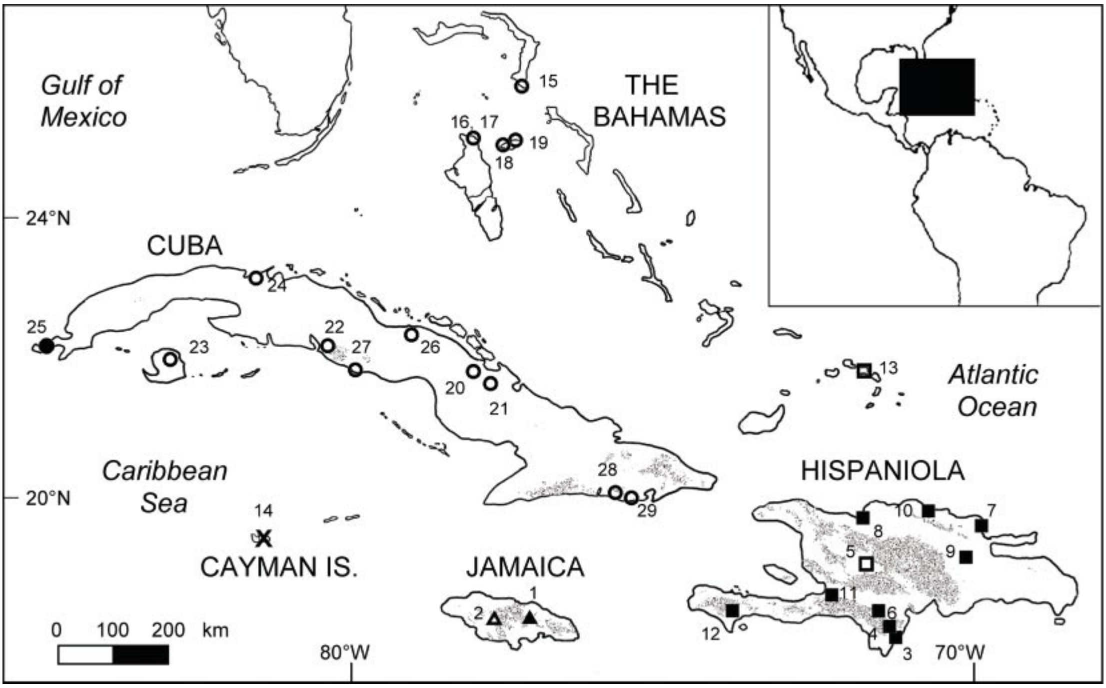

Fig. 5. The Greater Antilles (excluding Puerto Rico) and adjacent archipelagoes, showing collection localities for bats of the genus *Natalus*. Symbols: (■) *Natalus major*, extant; (□) *Natalus major*, fossil; (●) *Natalus primus*, extant; (○) *Natalus primus*, fossil; (▲) *Natalus jamaicensis*, extant; (△) *Natalus jamaicensis*, fossil; (×) *Natalus* cf. *Natalus major*. Numbers correspond to localities in the Gazetteer. Stippled areas show land above 600 m.

sexual dimorphism in size was found in our sample of *N. jamaicensis*.

The hair of *Natalus jamaicensis* is long, lax, dense, and slightly woolly. The dorsal hairs are longer (9–11 mm) than the ventral hairs (6–7 mm). The dorsal hairs are bicolored, with bases lighter than tips, and the ventral hair is also slightly bicolored, with bases darker than tips. The dorsal hair bases are buff and the tips are light sepia to tawny olive. The ventral hair bases are buff and the tips are pale pinkish-buff. Dorsally, there is a faint lighter-colored band across the shoulders. The pelage extends slightly into the plagiopatagium, dorsally to 6 mm, and ventrally to 10 mm. The uropatagium is sparsely furred in microscopic view. There is a sparse fringe of hairs along the free edge of the uropatagium.

The muzzle is long and dorsoventrally flattened. The small, oval nostrils open ventrolaterally. In ventral view, the tip of the muzzle, between the nostrils, projects slightly beyond the upper lip. The lower lip is thickened and has a shallow central groove. The ears are rather square-shaped with a straight anterior edge and a shallow notch on the distal third of the posterior margin, below the tip, giving it a pointed appearance. The ears of *N. jamaicensis* show rudimentary folds varying in number from five to seven.

The skull is relatively narrow and delicate. The braincase is greatly inflated and abruptly elevated above the rostrum in an angle greater than 60°. The postparietal region is relatively wide in dorsal view, and is separated from the occipital region by a conspicuous ridge. The sagittal crest is greatly developed and, in the interparietal region, it is noticeably higher than in the supraoccipital region. The postorbital region is very narrow with nearly parallel sides. The rostrum is markedly flattened dorsoventrally, so that the orbits appear relatively narrow in lateral view. The sulcus between the nasal bones is short and shallow, being restricted to the posterior

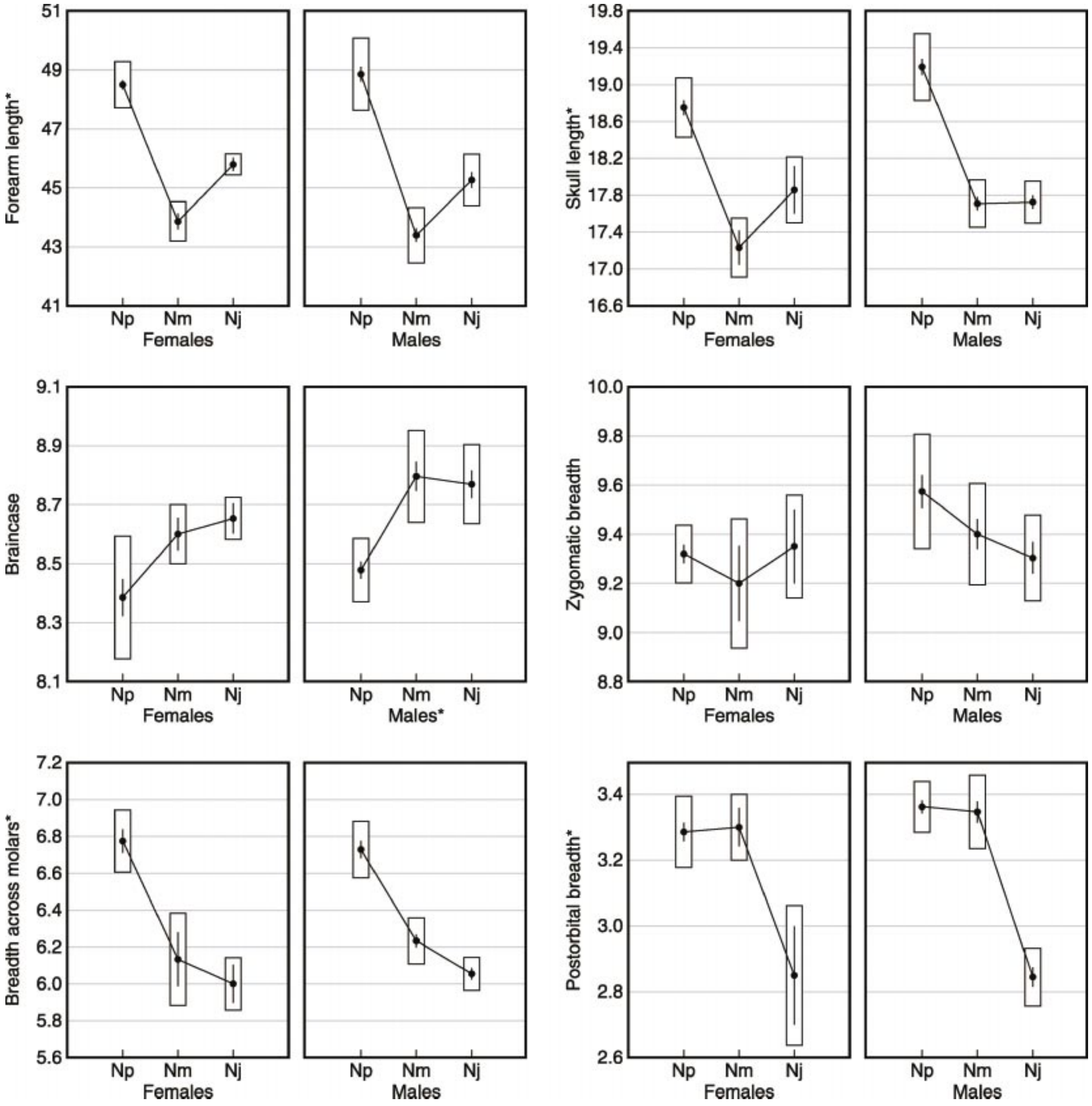

Fig. 6. Plot of observed arithmetic mean (dots), one standard deviation on each side of the mean (vertical rectangles), and one standard error on each side of the mean (vertical line) for one external and five cranial dimensions of Greater Antillean *Natalus*. Males and females are plotted separately. **Np**: *Natalus primus*; **Nm**: *Natalus major*; **Nj**: *Natalus jamaicensis*. * = statistically significant difference ($P \leq 0.01$) detected by an ANOVA within the whole sample (if following a measurement) or among male-only samples (if following the word ''males''). See text for results of pair-wise Tukey's comparisons.

end of the rostrum. The premaxillary region does not project anteriorly, so that in lateral view the diastema between canines and incisors is not particularly noticeable. The maxillary bone is concave above the molars. The rostrum tips downward. The anterior palatal foramina are very small, and near the palatine emargination, their anterior edges lie posterior to the anterior edge of the canines. The bony palate extends more than half the distance between the posterior edge of last molars and the tip of pteryogids. The pterygoid processes are not markedly convergent, and are conspicuously hooked in lateral view. In ventral view the inner edge of each pterygoid is smooth and convex. The basisphenoid pits are very shallow, in contrast with the basisphenoid furrows, which are relatively deep.

The dentary bone is markedly curved (upturned) and thick. The angular process is relatively short, rather straight, and with a blunt spatulate end. The coronoid process is at about the same height as the condyle above the alveolar plane. The ascending ramus is markedly upturned, being relatively tall and square-shaped, with its anterior border concave at the base and rather straight for most of its length, rising from the alveolar plane in an angle close to 90°. The posterior border of the ascending ramus rises from the base of the angular process in a nearly straight angle with the base of the dentary. The mental foramen is between the canine and the first premolar.

The upper incisors are small and with slightly hooked tips. The inner incisors are transversally aligned with the outer ones, so that the inner incisors are not visible in lateral view. The base of the canine is robust in occlusal view, with a well-developed cingulum that is slightly longer than it is wide. In occlusal view, the premolars are successively larger, and are relatively short and crowded. The molar row is relatively thick, its width about half the width of the palate. The first and second molar are approximately equal in size, with the third slightly smaller.

The lower incisors are small, tricuspid, and subequal. The canine is curved, relatively short, and with a well-developed cingulum. In occlusal view, the canine and the premolars are relatively short longitudinally, with the first premolar slightly shorter than the canine and the other two premolars. The first two molars are larger and wider than the third, the first more projected labially than the other two. The last premolar and the first molar are relatively crowded (fig. 3).

COMPARISONS: The large body size (forearm length 44.0–47.0 mm) of *Natalus jamaicensis* readily separates this species from *Natalus stramineus* (35.0–41.0 mm; Tejedor et. al., 2004) and *Natalus tumidirostris* (37.2–41.5 mm; Tejedor, unpublished data). From *Natalus primus* and *Natalus major*, *N. jamaicensis* is best distinguished by discrete external and/or cranial characters because, although clearly distinct in morphometry from the former two species (as shown by our principal component analysis [PCA] results; fig. 7), *N. jamaicensis* overlaps in size with the other two Greater Antillean species.

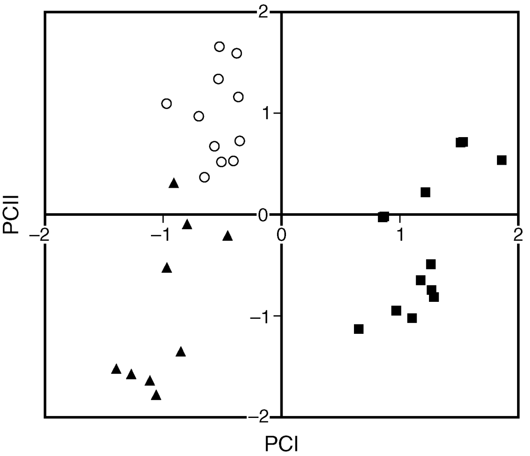

Fig. 7. Plot of specimen scores on the first two axis of the principal component analysis (PCA) based on forearm length and five variables of cranial dimensions of Greater Antillean *Natalus*. Breadth across molars had the greatest loading on axis PCI, increasing from the negative to the positive end of the axis. Zygomatic breadth had the greatest loading on axis PCII, increasing from the negative to the positive end of the axis. (○) *Natalus major*, (▲) *Natalus jamaicensis*, (■) *Natalus primus*.

Natalus jamaicensis differs externally from *Natalus primus* by its pointed ear tips (rounded in *N. primus*), and from *Natalus stramineus* and *Natalus tumidirostris* by its straight anterior ear margin (slightly to deeply concave in the latter two species). From *Natalus major* and all remaining species of the genus, *N. jamaicensis* is best distinguished on the basis of cranial characters. Most conspicuously, *N. jamaicensis* shows several cranial modifications concomitant with its high degree of cranial flexion. First, in *N. jamaicensis* the frontal plane of the braincase rises 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 it is long, hence it has an almost circular profile in dorsal view. In all other species of *Natalus* the braincase is longer than wider and thus appears oval-shaped. Third, the postorbital constriction of the skull of *N. jamaicensis* is proportionally narrower than in all other species of *Natalus* (mean postorbital breadth is significantly smaller than in *N. major* and *N. primus*; $P < 0.001$; fig. 6), with sides almost parallel in dorsal view, whereas in all other species of *Natalus* the sides of the postorbital constriction markedly diverge anteriorly. Also, 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, a rather dorsal location of the infraorbital foramen, and a concave shape of the maxillary in the area dorsal to the molars. The concave maxillary bone is sufficient to diagnose *N. jamaicensis* because all other species of *Natalus* have markedly convex to markedly inflated maxillary bones.

REMARKS: Fossil mandibles of *Natalus* from Grand Cayman were described by Morgan (1994) as being smaller than any other Greater Antillean *Natalus*, and as having a relatively large last premolar. Morgan referred to these fossils as *Natalus* cf. *N. major* and remarked that they may represent and undescribed form. Given the geographical proximity of the Cayman Islands to Jamaica and Cuba, it is probable that either of the populations of these two larger islands may be the closest relative of the Grand Cayman *Natalus*. Future examination of these fossils should shed light on this question.

NATURAL HISTORY

The natural history of Grater Antillean bats of the genus *Natalus* is poorly known. Even though the differences in morphology between Greater Antillean *Natalus* may be related to ecological differences, as it has been found to be the case among closely related bat species (e.g., *Pipistrellus*, Barlow et al., 1997), the information available on their habits is scant. Therefore, we treat the three species together here. Below, we summarize the few accounts that exist on the habits of *N. primus* and *N. jamaicensis*, and include Tejedor's unpublished observations of *N. major*. Most of the available information concerns roosting habits.

Natalus primus and *Natalus jamaicensis* are known extant from a single cave each. *Natalus major* has been found almost exclusively in caves, the exception being one report of nine individuals (2 females and 7 males) found roosting inside a large hollow tree in semiarid lowlands in the northern Dominican Republic (Timm and Genoways, 2003). All caves where Greater Antillean *Natalus* have been found are ‘‘hot caves’’, caves housing large bat communities, and with poor ventilation and nearly constant high temperatures (26–40°C) and humidity (> 90%; Silva-Taboada, 1977, 1979; Rodríguez-Durán, 1998). *Natalus primus* and *N. major*, however, are rarely found in the hottest parts of hot caves, preferring better-ventilated corridors and chambers that adjoin the areas of maximum temperature (Tejedor et al., 2004; Tejedor, personal obs.). Caves where *Natalus* have been found often contain open bodies of water (Tejedor et al., 2004). Greater Antillean *Natalus* are moderately to highly gregarious with cave colonies estimated at fewer than 100 individuals (*N. jamaicensis*, Goodwin, 1970; *N. major*, Tejedor, personal obs.), to a few thousand (*N. primus*, Tejedor et al., 2004). All three species of Greater Antillean *Natalus* usually roost in close association with many other bat species that often occupy cave chambers with climatic conditions similar to those selected by *Natalus*: *Pteronotus parnellii*, *Mormoops blainvillii*, *Brachyphylla nana*, *Erophylla sezekorni*, *Monophyllus redmani*, *Chilonatalus micropus*, and more rarely *Artibeus jamaicensis* (Goodwin, 1970; Tejedor et al., 2004). Individuals of *Natalus* usually hang on the lower part of walls (mostly at about 1 m high) or from very low ceilings and solution cavities. In contrast, other species generally roost higher up, so that mixed groups rarely occur. As in other species of Natalidae, individuals of Greater Antillean *Natalus* hang from one or both feet, usually without ventral contact with the substrate, and roost regularly spaced out, keeping a distance greater than the width of one or two bats between individuals (Goodwin, 1970; Hoyt and Baker, 1980; Tejedor et al., 2004). Individuals may be alert or quiet, sometimes taking flight at the slightest sign of disturbance or allowing the extreme close proximity of the observer for a few seconds. When retreating from disturbance, the bats invariably fly extremely close to the cave walls and to the floor (at about 1 m high), sometimes in tight flocks (Goodwin, 1970; Tejedor et al., 2004). Copulation in *Natalus primus* has been observed to take place in April, and pregnant females of this species have been captured in May (Tejedor et al., 2004).

Natalus major, the only Greater Antillean *Natalus* known to occur in more than one locality, does not seem to have any association with a particular kind of habitat. This species is found throughout Hispaniola both in dry areas (e.g., Pepillo Salcedo, locality 8 in the Gazetteer) and moist areas (e.g., La Entrada, locality 7 in the Gazetteer), spanning an annual precipitation gradient of 700–2000 mm (Bolay, 1997). *Natalus primus* and *Natalus major* fly very slowly and are highly maneuverable. They probably forage in rather cluttered vegetation and over relatively small home ranges (Tejedor et al., 2004). *Natalus primus* have been found to feed mostly on moths, crickets, and beetles, and less frequently on other insect orders: Hymenoptera (Formicidae), Neuroptera, Diptera, Homoptera, and Hemiptera. As is apparently common among natalids, Greater Antillean *Natalus* dehydrate very rapidly when taken outside the caves where they roost (Hoyt and Baker, 1980; Tejedor et al., 2004). This propensity for dehydration, together with a slow flight, probably restricts the ability of species of *Natalus* for long-distance dispersal and colonization, a condition that would limit gene flow across the water gaps that separate the Greater Antilles, thus promoting the independent evolution of the genus on different islands.

CONSERVATION

The taxonomic changes we propose increase the recognized diversity and endemism of the West Indian bat fauna. Each of the three largest islands within the Greater Antilles hosts an endemic extant species of *Natalus*. By recognizing three species within what was previously treated as a single species, the range of each is reduced to a single island, which has profound implications for their conservation status. One of these species, *Natalus major*, is known from extant colonies from at least eight localities, and thus seems of less concern. The remaining two species, *Natalus jamaicensis* and *Natalus primus*, however, are each apparently confined to a single locality (St. Clair Cave in Jamaica and Cueva La Barca in Cuba, respectively) and thus seem highly vulnerable to extinction. Treated as *Natalus stramineus*, none of the three species of Greater Antillean *Natalus* is listed in the 2003 IUCN Red List of Threatened Species (IUCN, 2003a) or in the IUCN/SSN Chiroptera specialist action plan (IUCN/SSC Chiroptera Specialist Group, 2001). The reduced population estimates given for *N. jamaicensis* (Goodwin, 1970), taken together with its restricted range, puts this species in the critically endangered IUCN category (IUCN 2003b). In the case of *N. primus*, populations estimates are greater (Tejedor et al., 2004), but this species is known to have become extirpated throughout most of Cuba apparently beginning in the late Pleistocene and into the Holocene (Silva-Taboada, 1974, Tejedor et al., 2004), suggesting a population decline that may have continued until the present. These conditions also put *N. primus* in the critically endangered IUCN category (IUCN, 2003b).

Because of their specialized roosting requirements, species of Natalidae seem more dependent on caves for survival than on other ecological factors (Emmons, 1997; Tejedor et al., 2004; Timm and Genoways, 2003). Given their limited potential of dispersal (Silva-Taboada, 1979; Tejedor et al., 2004), the destruction of roost sites by erosion throughout geologic history may be responsible for the high number of extirpated populations of natalids in the West Indies (Morgan, 2001; Tejedor et al., 2004). Current anthropogenic disturbance of roost sites, found to be highly threatening to cave-bat species worldwide (Kunz and Pierson, 1994), may also imperil species of *Natalus*.

Of the three species of *Natalus* in the Greater Antilles, *Natalus jamaicensis*, considered the rarest of Jamaican bats (Goodwin, 1970; McFarlane, 1986), seems to be in the most dire situation. Its only known roost site, St. Clair Cave, has resident populations of feral domestic cats that feed on the bats (species not specified) and rats of the cave (McFarlane, 1997). Domestic cats are known to be highly effective predators of bats (e.g., *Myotis*, Barbour and Davis, 1969; *Mystacina*, Daniel,1985; *Phyllonycteris*, Tejedor and Tavares, personal obs.), and if they feed on the *Natalus* of St. Clair their effect on its population could be considerable. Moreover, given the habit of *Natalus* species of roosting low on wall surfaces, they may be more vulnerable to cave cats than other bats. Unfortunately, with the exception of Windsor Great Cave in the Jamaican Cockpit Country, no other cave in Jamaica, including St. Clair Cave, receives any form of official protection (Dávalos and Eriksson, 2003).

Natalus primus may also face grave threats in the near future, when Cueva La Barca (thus far protected by its remoteness in Guanahacabibes Peninsula) becomes more accessible as Cuba opens its remote areas to tourism (Díaz-Brisquets and Pérez-López, 2000). The protection of Cueva La Barca is important not only because it harbors the only known colony of *N. primus*, but also because its cave life is the most diverse in Cuba (Armas et al., 1989). The impact of its rich bat fauna on the ecology of the Guanahacabibes deciduous forest, the largest of its kind in Cuba (Dinerstein et al., 1995), must be considerable, thus potentially placing a whole ecosystem at risk if the cave is overdeveloped.

The fact that *Natalus major* is known from more localities than the other two Greater Antillean *Natalus* does not mean that this species is adequately protected. Practices highly disturbing to cave biota, such as intensive guano extraction and cave modification for tourist use (Silva-Taboada, 1979; Trajano, 2000), are widespread in the Dominican Republic (K. Christenson, personal commun.; Tejedor, personal obs.). Unless these activities become controlled and directed to areas of least importance for the survival of cave-bat colonies, their long-term practice can deteriorate the future conservation status of *N. major*.

The reduced geographic range and low population numbers of *Natalus* species in the Greater Antilles makes these bats highly vulnerable to extinction. Programs of population status assessment and monitoring are urgently needed to ensure that these unique West Indian endemic species do not become extinct as a consequence of human activity.

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APPENDIX

GAZETTEER AND SPECIMENS EXAMINED

The gazetteer below provides locality information for all specimens of Greater Antillean *Natalus* examined by us or reported in literature known to us. Collection localities are listed by country: italic type identifies secondary political units (states, provinces, etc.) and boldface identifies locality names as cited in the text. Latitude and longitude, obtained from original published references or the United States Office of Geography (USOG 1963) and the United States Defense Mapping Agency (USDMA 1972, 1973) are given in parentheses, followed by supplementary information (when available) including museum catalog number, sex of specimen, and the earliest published reference to each specimen. Specimens measured are in boldface. Locality numbers refer to figure 5.

The following institutional abbreviations are used: **AMNH,** American Museum of Natural History, New York, New York, USA; **BMNH,** The Natural History Museum, London, the United Kingdom; **DZSJRP,** Department of Zoology, Universidade Estadual Paulista, São José do Rio Preto, Brazil; **FLMNH,** Florida Museum of Natural History, Gainesville, Florida, USA; **FMNH,** Field Museum, Chicago, Illinois, USA; **IES,** Instituto de Ecología y Sistemática, Havana, Cuba; **JI,** Jamaica Institute, Kingston, Jamaica; **ISEZ,** Institute of Systematic and Experimental Zoology, Krakow, Poland; **KU,** University of Kansas Natural History Museum, Lawrence, Kansas, USA; **MBML,** Museu de Biologia Mello-Leitão, Santa Teresa, Espirito Santo, Brazil; **MCZ,** Museum of Comparative Zoology, Cambridge, Massachusetts, USA; **MNHN,** Museo Nacional de Historia Natural, Havana, Cuba; **ROM,** Royal Ontario Museum, Toronto, Ontario, Canada; **USNM,** National Museum of Natural History (Smithsonian), Washington, DC, USA.

Gazetteer

Natalus jamaicensis

JAMAICA

St. Catherine Parish

1. **St. Clair Cave,** Linstead (18°07′N, 77°01′W). 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).

St. Elizabeth Parish

2. **Wallingford Cave,** Balaclava (18°10′N, 77°39′W). AMNH **147208** (fossil), Koopman and Williams (1951).

Natalus major

DOMINICAN REPUBLIC

Barahona

3. **Los Patos** (17°58′N, 71°10′W). AMNH **97590** (male).
4. **Maniel Viejo (**17°58′N, 71°19′W, 278 m). AMNH **97589** (female).

Elias Piña

5. **Cerro de San Francisco,** Bánica (19°04′N, 71°42′W). FLMNH (fossil), Morgan (2001).

Independencia

6. **Puerto Escondido** (18°19′N, 71°34′W), 9.9 km S, North slope Sierra de Bahoruco. USNM **542274** (female, mummy).

María Trinidad Sánchez

7. **Cueva de Murciélagos,** Entrada (19°33′N, 69°54′W), Cabrera. **AMNH 238148, 238149** (2 females); (AMNH, 4 males, 1 female) **AT 44, 45, 49, 51, 52** (field numbers).

Montecristi

8. **Pepillo Salcedo** (19°42′N, 71°45′W), 5 km SE. KU **150713–20,** KU **152361** (7 males, 2 females), Timm and Genoways (2003).

Sánchez Ramírez

9. **Cueva Grande de Julián,** Don Miguel, 4 km E Platanal (19°07′N, 70°05′W). (AMNH, field numbers) AT 70 (female), AT 77 (male).

Santiago

10. **Savaneta** (possibly Sabaneta [19°40′N, 70°22′W] ‘‘near the north coast’’; see Timm and Genoways 2003). USNM **101395a** (male, holotype), **101395b** (female, paratype), Miller (1902).

unknown locality FLMNH **5517** (male); USNM **49362, 96496,** Goodwin (1959).

HAITI

Departement du L'Ouest

11. **Port-au-Prince** (18°34′N, 72°17′W). BM (1 specimen, unspecified), Sanborn (1941).

Departement du Sud

12. **Camp Perrin** (18°19′N, 73°52′W, 246 m), Les Cayes. KU **150721** (male), Timm and Genoways (2003).

TURKS AND CAICOS

Grand Caicos

13. **Conch Bar Cave.** FLMNH 246 (fossil), Morgan (1989).

Natalus cf. *N. major*

CAYMAN ISLANDS

Grand Cayman

14. Bodden Cave, Bodden Town (19°16′N, 81°15′W). FLMNH (fossil), Morgan (1994).

Natalus primus

THE BAHAMAS

Abaco

15. Hole in the Wall Cave, (fossils), Morgan (2001).

Andros

16. Coleby Bay Cave, Morgans Bluff (25°10′N, 78°02′W). FLMNH 79324 (fossil), Morgan (1989).

17. King Cave, Morgans Bluff (25°10′N, 78°02′W). FLMNH 79110 (fossil), Morgan (1989).

New Providence

18. Banana Hole (25°01′N, 77°33′W). FLMNH 79986–79990 (fossils), Morgan (1989).

19. Hunts Cave (25°02′N, 77°22′W). FLMNH 27694, 79751–79759, 79761–79766, 79843–79848 (fossils), Morgan (1989).

CUBA

Camagüey

20. Cueva de los Portales de Pinto, Jaronú (21°48′N, 77°57′W), Esmeralda. MCZ (fossil), Koopman and Ruibal (1955).

21. Cueva del Círculo, Cairije (21°36′N, 77°40′W), Tomás Betancourt. IES (fossil), Silva-Taboada (1979).

Cienfuegos

22. Cueva de la Macha [= Cueva de los Machos, Cueva de Vilches], Cantera de San Antón, Soledad (22°07′N, 80°19′W). AMNH (fossil), Goodwin (1959).

Isla de la Juventud

23. Cueva del Abuelo, Sierra de Caballos (21°52′N, 82°46′W). IES (fossil), Silva-Taboada (1979).

Matanzas

24. Cueva de la Eloísa, Bellamar (23°01′N, 81°33′W), Guanábana. IES (fossil), Silva-Taboada (1979).

Pinar del Rio

25. Cueva La Barca, 20 km E of Cabo de San Antonio (21°50′N, 84°56′W), Guanahacabibes Peninsula, Manuel Lazo. MNHN **1–26** G. Silva-Taboada field numbers (male), **27–51** G. Silva-Taboada field numbers (female), Tejedor et al. (2004). FLMNH 26810 (female).

Sancti Spiritus

26. Lomas de Judas (22°6′N, 78°27′W), Yaguajay. IES (fossil), Silva-Taboada (1974). ISEZ (fossil), Wolozyn and Silva-Taboada (1977).

27. Sistema Cavernario Masones-Jagüey, Trinidad (21°48′N, 79°59′W). IES (225 fossil specimens), Silva-Taboada (1974); ROM 59133–59135 (fossils).

Santiago de Cuba

28. Cueva de la Cantera, Siboney (19°57′N, 75°42′W), Damayajabo. IES (fossil), Silva-Taboada (1979).

29. Cueva de Los Indios, Daiquirí (19°55′N, 75°39′W), AMNH 41009 (fossil, holotype), Anthony (1919).

Other Specimens Examined

Natalus stramineus—**Antigua and Barbuda,** Antigua (2): BMNH 18.4.1.1, 18.4.1.4. **Belize** (5) FLMNH 9844, 9845, 9847; FMNH 121072, 121073. **Bolivia** (1): DZSJRP 14507. **Brazil** (16): DZSJRP 12118, 12124, 12125, 12251, 12261, 12265, 16748, 16750, 16751; MBML 1801 (holotype of *Natalus espiritosantensis*); USNM 242828, 242829, 245517, 536442, 555711, 242830 (holotype of *Natalus stramineus natalensis*), 549504. **British Virgin Islands,** Anguilla (3): AMNH 72368, 72369; USNM 544834. **Dominica** (10): USNM 62850, 361906–361908, 362100–362104. **Costa Rica** (1): USNM 566451. **Guatemala** (2): FMNH 64809, 64810. **Mexico** (20): AMNH 147903–147911, 171570–171580; KU 23815 (holotype of *Natalus stramineus saturatus*); USNM 96496 (holotype of *Natalus mexicanus*) **Panama** (8): USNM 319065–319072. **Unknown locality** (1): BMNH 70.2324 (holotype of *Natalus stramineus*)

Natalus tumidirostris—**Colombia** (2): AMNH 183854, 183855. **Netherlands Antilles,** Curaçao (1): USNM 102106 (holotype *Natalus tumidirostris*). **Trinidad and Tobago** (12): AMNH 176587–176589, 176590 (holotype *Natalus tumidirostris haymani*), 176591–176598. **Venezuela** (6): BMNH (1) 5.11/12.25 (holotype *Phodotes tumidirostris continentis*); USNM 405774–405778.

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