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Genetic relationships of Caribbean lowland spiny pocket mice (*Heteromys desmarestianus*: Rodentia; Heteromyidae): evidence of a distinct mitochondrial lineage

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Genetic studies provide important insights into the evolutionary history and taxonomy of species, allowing us to identify lineages difficult to distinguish morphologically. The relationships among species in the genus *Heteromys* have been in flux as new species have been described, and candidate species have been suggested in the *H. desmarestianus* group. One new potential species may be in Costa Rica's Caribbean lowlands. Herein, we test the phylogenetic relationships of individuals from Costa Rica's Caribbean lowlands to individuals from throughout the species' range using mitochondrial sequences from cytochrome-*b* (*cytb*). We captured 116 individuals from the lowlands, sequenced their *cytb* gene, and incorporated 74 GenBank sequences from throughout the species' range to test if individuals from Costa Rica's Caribbean lowlands potentially constitute an undescribed species. Our results document a distinct mitochondrial lineage in the Caribbean lowlands of Costa Rica. Our results from extensive sampling within the lowlands show a unique mitochondrial DNA lineage, which suggests the presence of an undescribed species. The Caribbean lowlands of Costa Rica may hold other cryptic diversity, and further phylogenetic studies should incorporate samples from this area, as it may have a unique evolutionary history.

Los estudios genéticos proporcionan información importante sobre la historia evolutiva y la taxonomía de las especies, lo que nos permite identificar linajes difíciles de distinguir morfológicamente. Las relaciones filogenéticas entre las especies del género *Heteromys* han estado cambiando a medida que se han descrito nuevas especies y se han sugerido especies candidatas en el grupo *H. desmarestianus*. Una nueva especie potencial podría encontrarse en las tierras bajas del Caribe de Costa Rica. En este trabajo analizamos las relaciones filogenéticas entre individuos de las tierras bajas del Caribe de Costa Rica con individuos de todo el rango de la especie utilizando secuencias mitocondriales del citocromo-b (*cytb*). Capturamos 116 individuos de las tierras bajas, secuenciamos su gen *cytb* e incorporamos 74 secuencias GenBank de todo el área de distribución de la especie para probar si los individuos de las tierras bajas del Caribe de Costa Rica constituyen potencialmente una especie no descrita. Nuestros resultados indican la presencia de un linaje distinto basado en el ADN mitocondrial, que sugiere que los individuos de las tierras bajas del Caribe de Costa Rica probablemente son una especie distinta. Las tierras bajas del Caribe de Costa Rica pueden tener una diversidad críptica significativa. Por ello sugerimos que estudios filogenéticos adicionales deberían incorporar muestras de esta área, ya que puede tener una historia evolutiva única.

Key words: Central America; cryptic species; cytochrome *b*; Heteromyidae; species boundaries.

Introduction

Understanding the relationships among evolutionary lineages is critical to estimating species diversity at varying spatial scales, reconstructing the evolutionary history of taxa, delineating ecological communities, and in making informed conservation decisions (Crozier 1992; Faith 1992; Crandall *et al.* 2000; Sinclair *et al.* 2005; Chave *et al.* 2007). Molecular data are increasingly used for evaluating relationships among species, identifying potential species-level clades, and identifying so-called cryptic species and thus can have significant impact on our understanding of evolutionary relationships (Sinclair *et al.* 2005; Beheregaray and Caccone 2007; Bickford *et al.* 2007; Mort *et al.* 2015).

With the continual improvement of molecular techniques and analyses, and broader sampling of natural populations, our understanding of phylogenetic relationships is often in flux. A group that has proven particularly difficult to delineate with traditional morphological characters are the species of spiny pocket mice of the genus *Heteromys* (Rodentia: Heteromyidae; see Anderson 2015 and references therein). Goldman (1911), in the first revision of the genus, recognized 13 species of *Heteromys* dividing them into two subgenera: *Heteromys* containing 12 species and *Xylomys* with a single species. This author further recognized the subgenus *Heteromys* as comprising two distinct species groups with the *H. desmarestianus* group containing eight species, including the first named *Heteromys* and most widely distributed species, *H. desmarestianus* (Gray, 1868). Recent research based on mitochondrial DNA indicates, however, that the lowland dry forest spiny pocket mice that were long recognized as a separate and sister genus, *Liomys*, are paraphyletic with respect to the species of *Heteromys*, thus should either be recognized as species of *Heteromys* or as another generic level clade (see Anderson *et al.* 2006; Hafner *et al.* 2007; Anderson and Gutiérrez 2009; and references therein). The current trend is to consider all species as belonging in the genus *Heteromys*.

Heteromys desmarestianus has remained a recognized taxon through several revisions (Hall 1981; Rogers and Schmidly 1982; Williams *et al.* 1993; Patton 2005; Rogers and González 2010), although new species have since been recognized (Anderson and Jarrín-V 2002; Anderson 2003; Anderson and Timm 2006; Anderson and Jansa 2007; Anderson and Gutiérrez 2009). Recently, Rogers and González (2010) suggested four additional clades within *H. desmarestianus* should be recognized. This research focuses on one of those four proposed clades that is located within the Caribbean lowlands of Costa Rica.

Heteromys desmarestianus, as currently defined, is common and widespread, ranging from southern Mexico to Colombia (Reid 2009). This species is found in evergreen and semideciduous forests, from sea level to high elevation cloud forests (Timm *et al.* 1989; Reid 2009). In Central America's Caribbean lowlands, the forest spiny pocket mouse is difficult to study because populations are often found at low densities (Fleming 1974; Timm *et al.* 1989), and anthropogenic disturbances often have negative impacts on density and species diversity (Romero, pers. obs.). Based on molecular evidence from mitochondrial and nuclear DNA of three individuals from Caribbean lowlands of Costa Rica, Rogers and González (2010) suggested that these individuals may actually represent a separate species from what is recognized as *H. desmarestianus*. Herein, we test across multiple sites in the lowlands, if individuals from the Caribbean lowlands of Costa Rica are genetically distinct from what is recognized as *H. desmarestianus* and how this population(s) and others of the *H. desmarestianus* species complex are related to each other. In order to build a better understanding of the species diversity in this lineage and to test the hypothesis that there is greater diversity than is currently recognized we, herein, evaluate the relationship within the lineage currently recognized as the species *H. desmarestianus*.

Materials and methods

We trapped mice in several locations throughout the Caribbean lowlands of Costa Rica from 2007–2010 (Figure 1, Table 1). The Caribbean lowlands have similar ambient temperature throughout, but annual precipitation can vary from 2,400 to 4,800 mm per year (McClearn *et al.* 2016). Our localities (Table 1) ranged in elevation and size of forested area; our individuals from the highest elevation were from the Berlin property (Destierro) ranging from 210 to 280 masl. Samples from Berlin also represented our southern-most sample. Our northern-most samples were from the Refugio Nacional de Vida Silvestre Mixto Maquenque, close to the Costa Rica–Nicaragua border on the Río San Juan (Figure 1).

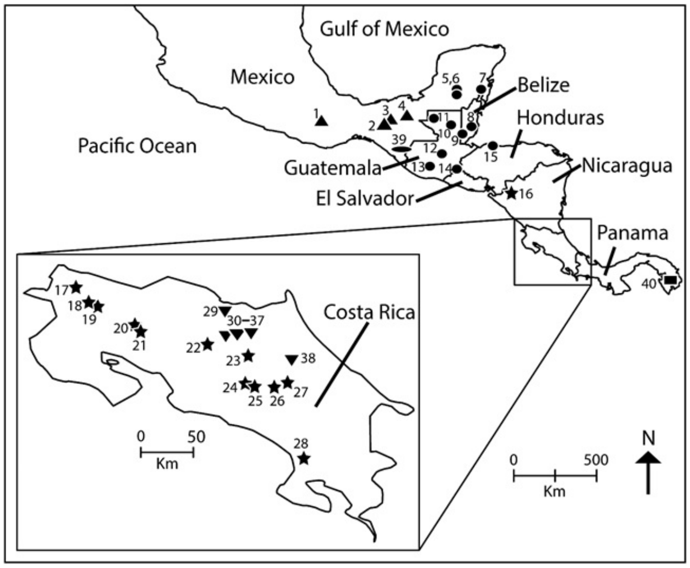

Figure 1. Map of localities for all specimens used in the study. Localities 29–38 represent specimens from Costa Rica's Caribbean lowlands. Symbols correspond to lineages depicted in the maximum likelihood tree (Figure 2). *H. anomalus* from Venezuela not depicted herein. Specific data regarding localities can be obtained from Appendix 1.

We used Sherman live traps (8 cm × 9 cm × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, FL) placed at ground level and baited with cracked corn, oats, and mixed bird seed. Traps were checked daily, and when an individual was caught, a toe was removed with surgical scissors and immediately placed in 95 % ethanol. All vials with tissue and ethanol were stored frozen within hours of collection. Voucher specimens of both complete specimens and toe samples are deposited at the University of Kansas Natural History Museum, Lawrence, Kansas. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with the guidelines of the American Society of Mammalogists (Sikes *et al.* 2016).

Laboratory procedures—116 samples from 10 sites in the Caribbean lowlands were used (Table 1) for genetic comparisons. Tissues were soaked in deionized water for one hr prior to beginning the digestion process. Standard digestion and DNA extraction were conducted following the protocol for mouse tails in Sambrook *et al.* (1989). The mitochondrial

Table 1. Sampling areas in the Caribbean lowlands of Costa Rica. Locality numbers refer to numbers from Figure 1.

Site (locality)	Max elevation (m)	Min elevation (m)	Latitude	Longitude
Maquenque (29)	70.1	47	10° 40′ 48.96″ N	-84° 10′ 39.65″ W
Water Tower (34)	98	42	10° 27′ 52.90″ N	-84° 00′ 29.47″ W
Agrícola Sofía (35)	68.58	51.21	10° 27′ 32.01″ N	-83° 58′ 41.40″ W
Juan Enriques (31)	189.59	45.72	10° 27′ 20.46″ N	-84° 04′ 01.70″ W
Selva Verde (30)	164.59	84.43	10° 26′ 46.36″ N	-84° 04′ 00.62″ W
Starky (36)	69	43	10° 26′ 31.73″ N	-83° 59′ 09.16″ W
Fragment A (37)	162	131	10° 26′ 03.92″ N	-84° 07′ 42.76″ W
La Selva (32)	146	22	10° 25′ 47.90″ N	-84° 00′ 55.15″ W
Tirimbina (33)	224.03	149.35	10° 24′ 45.58″ N	-84° 07′ 02.55″ W
Berlin (38)	280	210	10° 07′ 59.73″ N	-83° 36′ 18.38″ W

cytochrome-*b* (*cytb*) gene was amplified in full using the primers 765 and 766 (Bickham *et al.* 2004). Polymerase chain reaction (PCR) was performed using 50 µl reactions of the following reagents: 5 µl of 10× buffer, 5 µl of 10× $MgCl_2$, 5 µl of 10× solution of dNTP, 0.5 µl of Taq DNA polymerase, 5 µl of a 10× solution of each primer, 25 µl of deionized water, and 1–2 µl of extracted DNA. Thermal cycle conditions consisted of initial heating at 94°C for 3 min, then 36 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 30 s, and extension at 70°C for 2.5 min. PCR products were purified using the QiAquick PCR purification kit (Qiagen, Valencia, CA) and were subsequently used in standard sequencing reactions using Big Dye version 3.0 (Applied Biosystems, Foster City, CA). Sequencing reactions were cleaned using Sephadex spin columns and analyzed with an ABI 3100 automated genetic analyzer (Applied Biosystems, Forster City, CA). Sequence data were manually aligned using Sequencher v. 4.9 (Gene Codes Corporation, Ann Arbor, MI). We used the complete *cytb* gene, and all flanking regions were discarded prior to phylogenetic analysis.

To expand our dataset, we used *cytb* sequences of *H. desmarestianus* available from GenBank (Benson *et al.* 2013). We incorporated 74 individuals representing samples from throughout the range of the species, including specimens from near the type locality of *H. desmarestianus*, Cobán, Guatemala. *Heteromys anomalus*, *H. australis*, and *H. nelsoni* were used as outgroups (Appendix 1). We aligned all sequences with Muscle v.3.8.31 (Edgar 2004) implemented in Jalview 2.8 (Waterhouse *et al.* 2009).

Phylogenetic analysis—Phylogenetic relationships were obtained by performing a maximum likelihood (ML) analysis. We estimated models of molecular evolution using jModelTest v.2.1.1 with the corrected Akaike information criterion test (Guindon and Gascuel 2003; Darriba *et al.* 2012). We used GARLI v. 2.0 (Zwickl 2006) for ML analyses, using two independent search runs, with a maximum of five million generations each. Support values were calculated using bootstrap with 500 replications in GARLI, and results visualized and edited in FigTree v.1.4 (Rambaut 2007).

Results

The aligned data set comprises 1,142 characters of which 738 were constant, 335 characters were parsimony-informative, and 69 variable characters were parsimony-uninformative. The model of DNA substitution inferred from jModeltest 2.1.1 is TIM2+I+G.

The ML tree topology (Figure 2) shows two highly supported lineages for all individuals currently considered *H. desmarestianus*. One clade comprises all samples from the Caribbean lowlands of Costa Rica and had very strong (99 %) bootstrap support. The other lineage comprises all of the *H. desmarestianus* sequences obtained from Belize, Costa Rica (in part), El Salvador, Guatemala, Honduras, México, and Nicaragua and also have strong bootstrap support (83%). Within the clade containing samples from the Caribbean lowlands of Costa Rica (not shown in Figure 2), the individuals from two sites, Berlin and Maquenque, formed clades supported by strong bootstrap support (90 % and 86 %, respectively). Two individuals from the eight sampled at Maquenque were placed elsewhere within the tree, and thus the nonexclusive nature of the branching pattern complicates lower level population patterns from these data. Maquenque is biologically quite interesting being in the floodplain of the Río San Juan and our continued studies there are elucidating other unexpected patterns with other rodent species.

Specimens collected near Baja Verapas, Guatemala (GU646966, GU646967, GU646968; Appendix) ~30 km from the type locality, Cobán, cluster with specimens from Belize, El Salvador, Honduras, and parts of México, but not with specimens from the Caribbean lowlands of Costa Rica (Figure 2). The specimen that clustered closest to Cobán from our Costa Rican lowland dataset was from the Costa Rica–Nicaragua border region ~ 850 km away. Genbank accession numbers of new sequences are reported in the Appendix.

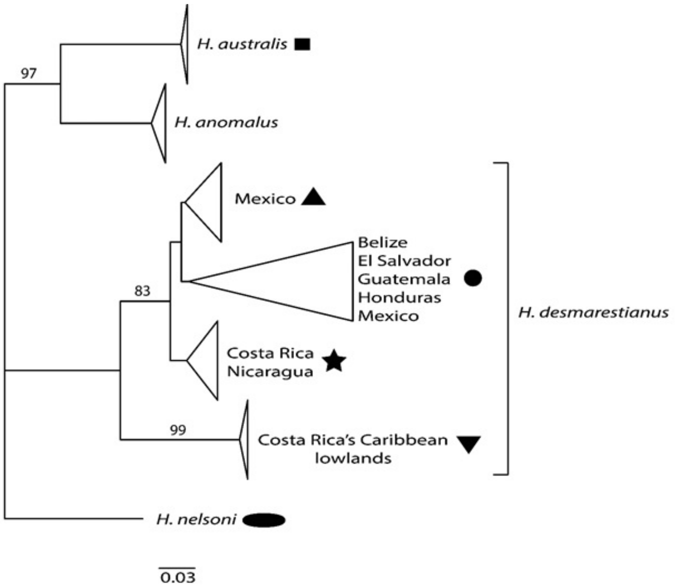

Figure 2. Maximum likelihood tree of our *Heteromys* dataset, based on *cytb* sequences. The maximum likelihood tree is collapsed for visual clarity, and shows the results with bootstrap values. These results indicate that individuals from Costa Rica's Caribbean lowlands harbor unique mitochondrial lineages that could reflect reproductive isolation. Symbols in tree are used in Figure 1 to show the geographic range of lineages. Tree is rooted with *H. golmani*.

Discussion

The results of this study strongly support the hypothesis that what is currently called *Heteromys desmarestianus* in Central America and northern-most South America comprises two very distinct clades, one being found in the Caribbean lowlands of Costa Rica and the other comprising all other populations. Our results show a clear geographic pattern; individuals currently considered *H. desmarestianus* in the Caribbean lowlands of Costa Rica harbor distinct mtDNA haplotypes from individuals considered *H. desmarestianus* found elsewhere in the Neotropics, including other areas in Costa Rica (Figure 2). The specimens from near the type locality of *H. desmarestianus*, Cobán, Guatemala form a well-supported clade with specimens from southern México, Belize, El Salvador, and Honduras. Specimens from western Costa Rica and one specimen from western Nicaragua all form another distinct clade.

Costa Rica is only ~51,000 km^2, yet its variable topography and climate result in diverse habitats with unique flora and fauna (Janzen 1983). Currently, four main mountain ranges divide the country into the Pacific and Caribbean sides. These mountain ranges span southeast to northwest, and are of diverse ages and origins (Anderson and Timm 2006). Extending from western Panama to northern Costa Rica, the Cordillera de Talamanca, Cordillera Central, and Cordillera de Tilarán form an expansive mountain range with peak elevations of over 3,000, 2,500, and 2,000 masl, respectively. The Cordillera de Guanacaste is the northern-most range in Costa Rica, and is comprised of several isolated volcanoes, with passes of ~500 to 700 masl in elevation that connect the Pacific and Caribbean sides (Anderson and Timm 2006). The historical and current topography of these mountain ranges probably shaped the diversification and speciation patterns in the flora and fauna observable today.

The family Heteromyidae originated on the North America continent (Wood 1935; Schmidly *et al.* 1993), and fossil remains for the subfamily Heteromyinae are known from the Pliocene, Pleistocene, and Holocene (Rogers 1990). Rogers (1990) estimated that the major groups within this subfamily diverged ~12 to 13 mya, yet the historical events that produced the *H. desmarestianus* group are largely unknown. The geologic history of the Caribbean, and Central and South America has been a debated topic (Bartoli *et al.* 2005; Montes *et al.* 2012a, 2012b, 2015; Bacon *et al.* 2015; O'Dea *et al.* 2016), but it is thought that islands of volcanic origin between Central and South America may have allowed faunal exchanges prior to the formation of a permanent land bridge (Bartoli *et al.* 2005; Woodburne 2010; O'Dea *et al.* 2016). The time of the emergence of a permanent Panamanian land bridge is disputed, and estimates range from 2 to 7 mya (Montes *et al.* 2012b; but see Bacon *et al.* 2015). Because of the widespread distribution pattern of the *H. desmarestianus* group, a hypothesis similar to the one suggested for other rodent groups has been proposed for this clade (Patterson and Pasqual 1972; Baskin 1978; Simpson 1980; Rogers 1990; Almendra and Rogers 2012; Pine *et al.* 2012); It is thought that considerable radiation occurred in the Miocene and Pliocene throughout Central America, with a subsequent entry to South America via the Panamanian land bridge (Rogers 1990; Schmidly *et al.* 1993).

Our results herein document a broad distribution of this distinct and unrecognized Costa Rican lowland lineage. The northern-most samples within this clade are from the Costa Rica–Nicaraguan border, while the southern-most are ~86 km southeast of there. Unfortunately, little is known about spiny pocket mice in the lowlands of Nicaragua and southern Costa Rica, and we are unable to demarcate northern and southern boundaries of this mtDNA lineage. In terms of elevation, the lowland specimens came from forests that ranged in elevation from ~22 to 280 masl. In our analysis, we included a single GenBank sequence from Cerro Honduras in Parque Nacional Braulio Carrillo. The park, along with privately owned reserves and biological stations, is part of a continuously forested transect that expands from the lowlands at La Selva Biological Station and reaches elevations > 2,700 masl. Although we do not have specific data on the elevation from which this particular specimen came, our results do show that this higher elevation specimen is a member of the clade with *H. desmarestianus* proper from throughout Central America and does not group with our samples from the lowlands, including specimens from the nearby La Selva Biological Station. While our results suggest two distinct clades, we are unable to delineate at this time limits of their specific elevational range, or if there are areas of overlap or hybridization that await discovery.

Our results expand upon, compliment, and confirm Rogers and González (2010), who used both *cytb* and nuclear data, and identified three individuals from the Caribbean lowlands of Costa Rica as a potential candidate species. Although useful to characterize species that are difficult to establish based on morphological data, DNA sequence data do have limitations, particularly when a single marker is used (Farias *et al.* 2001; Rogers and González 2010). Now that we provide more extensive sampling of individuals from the Caribbean lowlands of Costa Rica, we recommend that future studies determine if population structure based on nuclear markers correlates with the distinctive mtDNA lineage of the Costa Rican lowland. Further investigation focused on nuclear DNA is also important because mitochondrial DNA and nuclear DNA can be discordant (Lack *et al.* 2010, Bernardo *et al.* 2019). This can result in distinct mitochondrial DNA lineages within a population or species that are not supported by nuclear DNA.

The diversity of rodent communities in the Caribbean lowlands of Costa Rica have been vastly understudied and we believe underestimated, in part, because of low densities resulting in low trap success (Romero, pers. obs.). Consequently, the lack of data and specimens has hindered our understanding of the basic phylogenetic relationships and biogeographic patterns of species in the area. Other widespread rodent species have been found to hold similar patterns reported herein, where individuals from the Caribbean lowlands of Costa Rica are genetically distinct and potentially new species (Timm, unpublished data). These data suggest that there may be significant cryptic diversity in the lowlands, and that more phylogenetic studies should include samples from this region to identify potential biogeographic patterns for rodents in the Neotropics. This information is necessary not only to understand phylogenetic relationships, but also to have a grasp on the patterns and levels of diversity for the area, and make large-scale conservation decisions based on this information. We believe that our results, in conjunction with future studies that aim to identify and delineate diversity in the *H. desmarestianus* species complex, and the relationships between these species, will allow for a greater understanding of the historical events leading to speciation in this group.

Clearly much remains to be learned about the diversity of these widespread and common rodents that are considered keystone species in the Neotropics.

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Appendix 1.

Localities and specimen information for samples utilized in the study. Map numbers correspond to numbers on Figure 1. Data for specimens not from the Caribbean lowlands of Costa Rica were obtained from GenBank and the published papers associated with the GenBank accession numbers.

Map	Species	Specimen information	GenBank	Locality	Country
N/A	*H. anomalus*	CM 78170 = MDE 2087 = AK 3468	GU646919	Miranda, 25 km N Altagracia de Orituco, 500 m	Venezuela
N/A	*H. anomalus*	CM 78168 = MDE 2034 = AK3437	GU646924	Sucre, 40 km NW Caripito, 250 m	Venezuela
40a	*H. australis*	LSUMZ 35452 = MSH 1187 = TK 22565	GU646926	Darién, approximately 6 km NW Cana, E. slope Cerro Pirre, 1,200 m	Panama
40b	*H. australis*	ROM 104356 = F38215	GU646927	Darién, Cerro Pirre, Parque Nacional Darién	Panama
8a	*H. desmarestianus*	CM 91988 = AK7663	GU646929	Stann Creek District, 3.4 km WNW Quam Bank, Cockscomb Basin	Belize
8b	*H. desmarestianus*	CM91980 = AK7688	GU646930	Stann Creek District, 6.8 km WNW Quam Bank, Cockscomb Basin	Belize
8c	*H. desmarestianus*	CM 91951 = AK 7665	GU646932	Stann Creek District, 7.7 km WNW Quam Bank, Cockscomb Basin	Belize
9a	*H. desmarestianus*	CM 91991 = AK 7540	GU646933	Toledo District, 1.0 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9b	*H. desmarestianus*	CM 91989 = AK 7555	GU646934	Toledo District, 2.4 km NNW Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91993 = AK 7588	GU646935	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91994 = AK 7586	GU646936	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
9c	*H. desmarestianus*	CM 91995 = AK 7589	GU646937	Toledo District; 2.1 km NNE Salamanca, Forestry Camp, Columbia Forest Reserve	Belize
18	*H. desmarestianus*	KU 158615 = MK 00-112	DQ450094	Guanacaste, Area de Conservación Guanacaste, approximately 20 km NNE Liberia, Pailas, Sendero Pailas, near Rio Colorado, 800 m	Costa Rica
17	*H. desmarestianus*	KU 158508 = MK 99-088	DQ450095	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Orosilito	Costa Rica
17	*H. desmarestianus*	KU 158509 = MK 99-090	DQ450096	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Orosilito	Costa Rica
17	*H. desmarestianus*	KU 158512 = MK 99-093	DQ450097	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla	Costa Rica
17	*H. desmarestianus*	KU 158513 = MK 99-094	DQ450098	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla	Costa Rica
17	*H. desmarestianus*	KU 158514 = MK 99-102	DQ450099	Guanacaste: Área de Conservación Guanacaste, ca. 39 km N Liberia, Pitilla, Sendero Carica	Costa Rica
22	*H. desmarestianus*	ROM 113310 = F 48617	GU646938	Alajuela; 10 km E of Sucre, Parque Nacional, Juan Costro Blanco	Costa Rica
22	*H. desmarestianus*	ROM 113311 = F 48618	GU646939	Alajuela; 10 km E of Sucre, Parque Nacional, Juan Costro Blanco	Costa Rica
24	*H. desmarestianus*	ROM 113130 = F 48436	GU646940	Cartago, Iztaru, Cerros de la Carpintera	Costa Rica
24	*H. desmarestianus*	ROM 113131 = F 48437	GU646941	Cartago, Iztaru, Cerros de la Carpintera	Costa Rica
27	*H. desmarestianus*	MVZ 164823 = DSR 2153	GU646942	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164823 = DSR 2154	GU646943	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164825 = DSR 2166	GU646944	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164826 = DSR 2167	GU646945	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
27	*H. desmarestianus*	MVZ 164827 = DSR 2246	GU646946	Cartago, Rio Reventazón, 5.6 km SE (by road) Turrialba, 450 m	Costa Rica
26	*H. desmarestianus*	ROM 97324 = FAR 111	GU646947	Cartago, 4 km SE of Turrialba by road, Catie, 600 m	Costa Rica
26	*H. desmarestianus*	ROM 97325 = FAR 112	GU646948	Cartago, 4 km SE of Turrialba by road, Catie, 600 m	Costa Rica
20	*H. desmarestianus*	MVZ 164828 = DSR 2123	GU646949	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164829 = DSR 2124	GU646950	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164831 = DSR 2134	GU646952	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164833 = DSR 2124	GU646953	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
20	*H. desmarestianus*	MVZ 164835 = DSR 2143	GU646954	Guanacaste, 4.1 km NE (by road) Tilarán, 650 m	Costa Rica
21	*H. desmarestianus*	MVZ 164839 = DSR 2121	GU646955	Guanacaste: 5.0 km NE (by road) Tilarán, 675 m	Costa Rica
21	*H. desmarestianus*	MVZ 164840 = DSR 2122	GU646956	Guanacaste: 5.0 km NE (by road) Tilarán, 675 m	Costa Rica
19	*H. desmarestianus*	ROM 113244 = F 48551	GU646957	Guanacaste: Volcán Santa Maria	Costa Rica
19	*H. desmarestianus*	ROM 113245 = F 48552	GU646958	Guanacaste: Volcán Santa Maria	Costa Rica
28	*H. desmarestianus*	LSUMZ 28354 = MSH 1260	GU646959	Puntarenas, 1 km N, 5 km W Palmar Norte, 33 m	Costa Rica
25	*H. desmarestianus*	BYU 15197 = EA 21	GU646960	San José, Bajo de Iglesia, SW Volcán Irazu, Cascajal de Coronado	Costa Rica
25	*H. desmarestianus*	BYU 15198 = EA 22	GU646961	San José, Bajo de Iglesia, SW Volcán Irazu, Cascajal de Coronado	Costa Rica
23	*H. desmarestianus*	BYU 15195 = EA 78	GU646962	San José, Parque Nacional Braulio Carillo, Moravia, Cerro Honduras	Costa Rica
23	*H. desmarestianus*	BYU 15196 = EA 79	GU646963	San José, Parque Nacional Braulio Carillo, Moravia, Cerro Honduras	Costa Rica

29	*H. desmarestianus*	No specimen available	MN335341	Alajuela: Maquenque, 10°40′48.96″N, 84°10′39.65″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335416	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335415	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335420	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335369	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335417	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335429	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335422	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335368	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
30	*H. desmarestianus*	No specimen available	MN335428	Heredia: Selva Verde, 10°26′46.36″N, 84°04′00.62″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335344	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335353	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335356	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335351	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335379	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335345	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335412	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335382	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335405	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335363	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335404	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335411	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335403	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335350	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335389	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335362	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335383	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335336	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335381	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335343	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335387	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335354	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335386	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335407	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335359	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335376	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335391	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335357	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335361	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335349	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335399	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335350	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335355	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335390	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335380	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335358	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335384	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335352	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335342	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335347	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335340	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
32	*H. desmarestianus*	No specimen available	MN335346	Heredia: La Selva Biological Station, 10°25′47.90″N, 84°00′55.15″W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335392	Heredia: Tirimbina, 10°24′45.58″N, 84°07′02.55″W	Costa Rica

33	*H. desmarestianus*	No specimen available	MN335378	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335395	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335364	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335371	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335365	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335367	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335338	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335337	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335394	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335372	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
33	*H. desmarestianus*	No specimen available	MN335385	Heredia: Tirimbina, 10°24'45.58"N, 84°07'02.55"W	Costa Rica
38	*H. desmarestianus*	No specimen available	MN335406	Limon Province: Berlin, 10°07'59.73"N, 83°36'18.38"W	Costa Rica
38	*H. desmarestianus*	No specimen available	MN335397	Limon Province: Berlin, 10°07'59.73"N, 83°36'18.38"W	Costa Rica
38	*H. desmarestianus*	No specimen available	MN335398	Limon Province: Berlin, 10°07'59.73"N, 83°36'18.38"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335409	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335348	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335334	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335410	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335402	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335401	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335333	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335370	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
35	*H. desmarestianus*	No specimen available	MN335414	Heredia: Agrícola Sofía, 10°27'32.01"N, 83°58'41.40"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335332	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335413	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335385	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335393	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335335	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335375	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335332	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335419	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335388	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335360	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335373	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
36	*H. desmarestianus*	No specimen available	MN335374	Heredia: Starky, 10°26'31.73"N, 83°59'09.16"W	Costa Rica
37	*H. desmarestianus*	No specimen available	MN335424	Heredia: 10°26'03.92"N, 84°07'42.76"W	Costa Rica
37	*H. desmarestianus*	No specimen available	MN335418	Heredia: 10°26'03.92"N, 84°07'42.76"W	Costa Rica
14	*H. desmarestianus*	ROM 101369 = F 35547	GU646964	Santa Ana, Parque Nacional Montecristi, Bosque Nebuloso, 2,200 m	El Salvador
14	*H. desmarestianus*	ROM 101389 = F 35567	GU646965	Santa Ana, Parque Nacional Montecristi, Bosque Nebuloso, 2,200 m	El Salvador
11	*H. desmarestianus*	LVT 5499	AY926358	Tikal, El Peten	Guatemala
12	*H. desmarestianus*	ROM 98405 = FN 31394	GU646966	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
12	*H. desmarestianus*	ROM 98406 = FN 31395	GU646967	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
12	*H. desmarestianus*	FN 31402	GU646968	Baja Verapaz: 5 km E of Puruhla, 1,550 m	Guatemala
10a	*H. desmarestianus*	ROM 99603 = FN 32272	GU646969	El Peten: Biotope, Cerro Cahui, El Remate	Guatemala
10a	*H. desmarestianus*	ROM 99604 = FN 32273	GU646970	El Peten: Biotope, Cerro Cahui, El Remate	Guatemala
10b	*H. desmarestianus*	ROM 99469 = FN 32318	GU646971	El Peten: Campo los Guacamayos, Biotopo Laguna del Tigre, 40 km N El Naranjo	Guatemala
11	*H. desmarestianus*	ROM 99292 = FN 31842	GU646973	El Peten, Tikal	Guatemala
11	*H. desmarestianus*	ROM 99293 = FN 31843	GU646974	El Peten, Tikal	Guatemala
13	*H. desmarestianus*	ROM 98266 = FN 31252	GU646975	Sacatepequez, 5 km W San Miguel Duanas, 1,765 m	Guatemala
13	*H. desmarestianus*	ROM 98265 = FN 31254	GU646976	Sacatepequez, 5 km W San Miguel Duanas, 1,765 m	Guatemala
15	*H. desmarestianus*	TCWC 52259 = BEL 865 = AK 9696	DQ168466	Atlántida, Lancetilla	Honduras
1a	*H. desmarestianus*	MVZ 161229 = DSR 1685	DQ168467	Oaxaca; Distrito Ixtlán, Vista Hermosa, 1,000 m	Mexico
5	*H. desmarestianus*	ROM 97050 = FN 30853	GU646977	Campeche, 10 km N El Refugio	Mexico

5	*H. desmarestianus*	ROM 97051 = FN 30854	GU646978	Campeche, 10 km N El Refugio	Mexico
6	*H. desmarestianus*	ROM 96089 = FN 29880	GU646979	Campeche: 25 km N Xpujil	Mexico
2	*H. desmarestianus*	ASNHC 3515 = LAF 1689	GU646980	Chiapas, 12 km N (by road) Berriozábal	Mexico
2	*H. desmarestianus*	ASNHC 1424 = ASK 660	GU646981	Chiapas, 12 km N (by road) Berriozábal	Mexico
2	*H. desmarestianus*	ASNHC 1425 = ASK 689	GU646982	Chiapas, 12 km N (by road) Berriozábal	Mexico
4a	*H. desmarestianus*	ASNHC 1426 = ASK 51	GU646983	Chiapas, 6.6 km S Palenque	Mexico
4b	*H. desmarestianus*	ASNHC 5826 = ASK 49	GU646984	Chiapas, 9.0 km S Palenque	Mexico
4c	*H. desmarestianus*	ROM 96096 = FN 29887	GU646985	Chiapas, 12.5 km S Palenque	Mexico
4c	*H. desmarestianus*	ROM 96105 = FN 29896	GU646986	Chiapas, 12.5 km S Palenque	Mexico
4d	*H. desmarestianus*	ASNHC 1440 = ASK 29	GU646987	Chiapas, 1.2 km E Ruinas de Palenque	Mexico
4d	*H. desmarestianus*	ASNHC 1441 = ASK 31	GU646988	Chiapas, 1.2 km E Ruinas de Palenque	Mexico
3a	*H. desmarestianus*	ROM 97542 = FN 33018	GU646989	Chiapas, 6 km E of Rayon, 1,560 m	Mexico
3b	*H. desmarestianus*	ASNHC 1431 = ASK 589	GU646990	Chiapas, 9 km SE Rayon	Mexico
3b	*H. desmarestianus*	ASNHC 1432 = ASK 591	GU646991	Chiapas, 9 km SE Rayon	Mexico
7	*H. desmarestianus*	ROM 97520 = FN 30995	GU646992	Quintana Roo, 1 km N Noh-Bec	Mexico
7	*H. desmarestianus*	ROM 97521 = FN 30996	GU646993	Quintana Roo, 1 km N Noh-Bec	Mexico
1b	*H. desmarestianus*	CM 79530 = DSR 934 = AK 3108	GU646994	Oaxaca, Vista Hermosa, 1,000 m	Mexico
1b	*H. desmarestianus*	MVZ 161230 = DSR 1686	GU646995	Oaxaca; Distrito Ixtlán, Vista Hermosa, 1,000 m	Mexico
16	*H. desmarestianus*	ROM 112284 = F 48170	GU646996	Esteli, Esteli	Nicaragua
39	*H. nelsoni*	BYU 20644 = DSR 7189	GU647014	Chiapas, Cerro Mozotal, 15º25.866’N, 92º20.274’W, 2,930 m	Panama