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Taxonomic and Distributional Notes on Lesser Antillean Bats

By Karl F. Koopman¹

The present paper reports additional records of bats from the Lesser Antillean islands, from Barbados and St. Vincent north to Anguilla. The specimens are mainly from three collections: the first made by G. G. Goodwin in 1926 on Anguilla and St. Martin; the second made by Clayton E. Ray in 1963 on St. Martin, St. Eustatius, St. Kitts, Barbuda, Antigua, and Barbados; and the third made by Harry Beatty and Peter Martin in 1967 on Martinique. The Goodwin collection, which also contains material from West Indian islands (Puerto Rico, Mona, Virgin Islands) not in the Lesser Antilles, is at the American Museum of Natural History. Ray's collection, which also includes extralimital (Dominican Republic) material, has been divided between the American Museum of Natural History and the Florida State Museum at Gainesville. The Beatty-Martin collection is at the American Museum, and the trip was supported by a grant from the Explorers Club and by Mr. Martin. In addition to several smaller collections at the American Museum, certain critical specimens from the Museum of Comparative Zoology, Cambridge, the United States National Museum, Smithsonian Institution, Washington, the Field Museum of Natural History, Chicago, the British Museum (Natural History), London, the Academy of Natural Sciences of Philadelphia, and the Bruce Museum, Greenwich, Connecticut, are included in this study. I thank the mammalogists and other staff members at all these institutions for permission to study specimens in their

 $^{^{\}rm 1}\,{\rm Associate}$ Curator, Department of Mammalogy, the American Museum of Natural History.

care. I am particularly indebted to Mr. Paul Griswold Howes, Director of the Bruce Museum, for lending his entire collection of mammals collected on Dominica.

I have previously reported on the bats of Grenada (Koopman, 1958), and, as no additional records of bats from this island have since appeared, no comments on Grenadian bats are presented in this paper, except as they relate to the zoogeographical pattern of the Lesser Antilles as a whole.

SPECIES ACCOUNTS

Noctilio leporinus: The subspecific status of the populations of Noctilio in the Lesser Antilles has been unclear. I am inclined, however, to refer all Lesser Antillean populations to the large N. l. mastivus, originally described from St. Croix in the Virgin Islands. Goodwin and Greenhall (1961, p. 219) referred material from Trinidad to N. l. leporinus, originally described from Surinam. A comparison of my measurements of Trinidad specimens with those of Surinam specimens given by Husson (1962, p. 68), however, shows that skulls of the former are distinctly larger and agree better in measurement with skulls of N. l. mastivus. The problem of drawing subspecific boundaries for N. leporinus is due mainly to the paucity of specimens from many critical areas, plus the rather extreme sexual dimorphism which demands that males be compared only with males and females with females. As well as the islands listed by Hall and Kelson (1959), N. leporinus is known from at least the following islands: St. Martin (specimen in the Academy of Natural Sciences of Philadelphia), Barbuda (Husson, 1960), Antigua (J. A. Allen, 1890), and Martinique (G. M. Allen, 1937; also three specimens in the American Museum collected by Beatty and Martin). Actually this large, strongflying, fish-eating bat is likely to occur anywhere in the Lesser Antilles where fresh or salt water is calm enough to allow it to catch fish.

Pteronotus davyi: In the area here considered, this species is still known only from Dominica. The American Museum has a single female from this island with a forearm length of 48 mm. Clearly this species has reached the Lesser Antilles from the south and represents the typical subspecies, P. d. davyi.

Glossophaga longirostris: Hall and Kelson (1959) record this species in the Lesser Antilles only from Grenada and the Grenadines (G. l. rostrata). The American Museum, however, has three specimens in alcohol from St. Vincent, collected by David O. Hill, June 3, 1964. The two adults, male and female, both have forearm lengths of 36 mm. The single extracted skull (of the female) has a condylobasal length of 21.1 mm.

Farther north, G. l. rostrata has been recorded from Dominica (Miller, 1913c), but with some doubt as to precise identity owing to the unsatisfactory condition of the two available specimens (one too young, the other too mutilated). The species has clearly entered the Lesser Antilles from the south.

Monophyllus: Two Lesser Antillean species of this genus are currently recognized. The earlier-described (1900) plethodon from Barbados is still known only from the type. This specimen is in alcohol, with the skull extracted. It was evidently in formalin long enough for some decalcification of the skull to take place, which caused the dried skull to shrivel in a way that makes comparison with other Lesser Antillean material difficult. The somewhat later-described (1902) luciae is currently recorded only from St. Lucia. There are other specimens, however, that extend its known range to three other islands. The Bruce Museum of Greenwich has a male skin and skull from Dominica (forearm, 40 mm.; condylobasal length, 21.4 mm.). The Museum of Comparative Zoology has a specimen in alcohol (with the extracted skull) from Antigua (forearm, 42; condylobasal length, 22.6). The American Museum of Natural History has a female skin and skull from Anguilla collected by Goodwin, April 8, 1926 (forearm, 42; condylobasal length, 21.5). Although all these specimens appear to represent the same form, no systematic comparison among all of them has been made. Albert Schwartz, of Miami, Florida, is currently revising Monophyllus and presumably will clarify the taxonomic situation.¹

Carollia perspicillata: Hall and Kelson (1959) recorded this species in the Lesser Antilles only from Grenada. Quite surprisingly, however, Hahn (1907) recorded three specimens from the tiny island of Redonda far to the north between Montserrat and Nevis. I have seen the specimens in the Academy of Natural Sciences of Philadelphia, and they are indeed Carollia, collected by R. E. Van Rijgersma, who is known to have visited several adjacent islands. Redonda, however, is very small (ca. 1 mile in diameter) and, according to Howard (1962), supports only scrubby xerophytic vegetation, with an abundance of cactus. In view of these facts and the large hiatus (ca. 300 miles) between Redonda and Grenada, with a number of much larger and better-collected islands between, it would be most surprising if Redonda really supported a population of Carollia. The record should, therefore, be regarded as

¹ Since the present paper was submitted for publication, the anticipated revision has appeared (Schwartz and Jones, 1967). A single species of *Monophyllus* is recognized in the Lesser Antilles, with two subspecies, *M. p. plethodon* and *M. p. luciae*. The latter is recorded from St. Vincent, in addition to the above-mentioned islands.

doubtful. Carollia has clearly reached the Lesser Antilles from the south. Sturnira: Until recently, Sturnira in the Lesser Antilles had been recorded only from Dominica and was identified as S. lilium. Recently, de la Torre (1966) and de la Torre and Schwartz (1966) have considerably extended the known Lesser Antillean range of the genus. Their material is allocated to three endemic species: paulsoni (St. Vincent), angeli (Martinique, Dominica), and thomasi (Guadeloupe). De la Torre is currently revising this genus, and it is hoped that he will clarify the relationships among the three Lesser Antillean forms and the relation of these to the various mainland species. Beatty and Martin recently obtained a series of 20 specimens of Sturnira from Martinique, and I have recently collected four more specimens from Martinique and two from Dominica, so a few observations on these series seem in order. I have extracted the skulls of two from Martinique and the two from Dominica and compared them with skulls of lilium and tildae, the two species known from Trinidad. I have also compared them with skulls of *lilium* from various parts of its mainland range and with those of members of the ludovici group. The Martinique specimens agree reasonably well with de la Torre's (1966) description of angeli, but only in the absence of a sharp metaconid-entoconid separation and a slight difference in size can I see any clear distinction from lilium. Furthermore, the degree of this separation agrees better with the photograph of the type of paulsoni (de la Torre and Schwartz, 1966) from St. Vincent than with that of the type of angeli from Dominica. I am inclined to regard paulsoni, angeli, and even thomasi as successive modifications of lilium out of contact with other species of Sturnira. In addition to the lessening of the degree of separation of metaconid and entoconid, there also seems to be some tendency in the Martinique series for one or both of the pairs of lower incisors to be lost. In any case, there seems to be no doubt that the genus entered the Lesser Antilles from the south.

Brachyphylla cavernarum: Two allopatric species of this genus are currently recognized in the Lesser Antilles: minor from Barbados and cavernarum from most of the remaining Lesser Antillean islands from St. Vincent to Puerto Rico. Miller (1913a), in the original description of B. minor, distinguished it from cavernarum solely on the basis of its somewhat smaller size. The only measurement given by Miller in which a comparison with cavernarum was made is the condylobasal length. He gave a measurement of 26.6 mm. for the type female and 27.8 mm. for his only other specimen, a male. Males tend to be larger in the B. cavernarum group, and Miller mentioned that his measurement of the condylobasal length of the male is the same as that of his smallest

(female) specimen of cavernarum. The skulls of two specimens in alcohol (a male and a female) of the series of minor in the American Museum chosen for relatively large size have been extracted and cleaned. Each has a condylobasal length of 27.5. Series of cavernarum in the American Museum from Anguilla and St. Martin have condylobasal lengths of 27.7–29.9 (males) and 27.4–28.8 (females). Thus there is some overlap between cavernarum and minor among both males and females. The length of the forearm shows an overlap at least as great. I therefore regard minor as a subspecies of B. cavernarum.

Hall and Kelson (1959) recorded Brachyphylla in the Lesser Antilles only from Barbuda, St. Vincent, and Barbados. The following specimens were examined in this study: Anguilla (11 specimens in the American Museum collected by Goodwin); St. Martin (33 specimens in the American Museum collected by Goodwin); St. Eustatius (seven specimens collected by Ray); Martinique (one specimen in the American Museum collected by Beebe, and a large series collected by Beatty and Martin): Barbados (two specimens in the American Museum collected by R. A. and S. P. Montgomery, 18 collected by Ray). There are literature records for the following additional islands: Saba (Husson, 1960); Antigua (Miller, 1913a); Montserrat (Miller, 1913a); Dominica (Miller, 1913a); and St. Lucia (Miller, 1913a). The Museum of Comparative Zoology has specimens from Guadeloupe and the small adjacent islands of Saintes. It seems probable that Brachyphylla will eventually be found to occur on all larger islands and even on some very small ones in the area under discussion.

Artibeus jamaicensis: There are two closely related species of Artibeus in the area under consideration: the widespread West Indian A. jamaicensis, and A. lituratus which occurs only in the southern Lesser Antilles. Of the former, all populations in the area under discussion are currently allocated to the nominate subspecies, with two Lesser Antillean synonyms. Of the two named forms currently allocated to A. lituratus, A. l. palmarum is clearly correctly identified as a member of this large species and ranges from South America north to St. Vincent. The other form, praeceps, is supposed to be confined to Guadeloupe and Dominica. The current allocation of forms to A. jamaicensis and A. lituratus dates from Hershkovitz (1949). In his paper the two species were distinguished solely on size, but praeceps was allocated to the larger A. lituratus. It was, in fact, stated to be doubtfully distinct from A. l. palmarum. A study of the type of praeceps in the United States National Museum, however, shows it to be clearly jamaicensis by Hershkovitz' characters (forearm, 58; condylobasal length, 25.2). Other specimens from Guadeloupe and Dominica give a range of 58-63 for forearm length and 25.2-25.8 for condylobasal length. A series of seven specimens in alcohol of A. lituratus from St. Vincent in the Field Museum of Natural History have a forearm range of 62-67, indicating some overlap with praeceps. However, only one of these measures less than 65, and its skull, when extracted, measured 27.5 mm., larger than that of any Lesser Antillean jamaicensis or praeceps I have studied. Specimens from Guadeloupe and Dominica, together with Barbados, tend to be slightly larger than A. j. jamaicensis from the northern Lesser Antilles (58-64 versus 56-62 in forearm length, 24.9-25.8 versus 24.2-25.2 in condylobasal length), but there is so much overlap that I cannot see the validity of recognizing praeceps even as a subspecies. This name therefore joins the long list of synonyms of A. j. jamaicensis. Besides the islands from which Hall and Kelson (1959) recorded this species under the names of jamaicensis and praeceps (including Anguilla where Goodwin collected a series now in the American Museum, Dominica where I recently collected a series now in the American Museum, and Barbados where Ray collected a large series), the species is known from the following islands: St. Martin (a large series in the American Museum collected by Goodwin); Saba (15 specimens in the Field Museum of Natural History); St. Eustatius (four specimens collected by Ray); Montserrat (three specimens in the United States National Museum); and Martinique (a large series in the American Museum collected by Beatty and Martin). There is also a specimen in the American Museum labeled as from St. Lucia, collected by Beebe, but the data are unfortunately questionable.

If all populations of Artibeus from Barbados north belong to A. j. jamaicensis, then derivation from Central America through the Greater Antilles is the most probable. There is another subspecies on Trinidad, Tobago, and Grenada, A. j. trinitatis, which differs most conspicuously from A. j. jamaicensis in having a third upper molar. Artibeus j. trinitatis is probably most closely related to A. j. planirostris of eastern South America. Thus in the Lesser Antilles, we have A. j. jamaicensis moving southward and reaching Barbados, A. j. trinitatis moving northward and reaching Grenada, but neither subspecies reaching St. Vincent, which is occupied only by the related A. lituratus.

Artibeus lituratus: With the removal of praeceps, A. lituratus is known in the area under discussion only from St. Vincent, from which Hall and Kelson (1959) listed it. The species, represented by the subspecies A. l. palmarum, has clearly reached the Lesser Antilles from the south.

Ardops: As compiled by Hall and Kelson (1959), there are four species recognized in this genus, each confined to a single island: montserratensis

(Montserrat), annectens (Guadeloupe), nichollsi (Dominica), and luciae (St. Lucia). J. Knox Jones of the University of Kansas and Albert Schwartz of Miami are currently revising this genus, and it seems pointless at present to comment on the taxonomy except to say that all four "species" appear to be quite similar to one another and that Ardops seems rather closely related to, and possibly congeneric with, Phyllops of Cuba and Hispaniola.¹ Three additional islands can, however, be added to the known range. The Field Museum of Natural History has a single specimen in alcohol from St. Vincent. Unfortunately the skull is fragmentary, but it appears to be referable to A. luciae. Clayton Ray obtained two specimens, a male and a female, from St. Eustatius. The forearms measure, respectively, 50 and 51 mm., the condylobasal lengths, 20.5 and 21.3. These specimens are tentatively identified as Ardops montserratensis. Beatty and Martin obtained two males and three females from Martinique that Jones (in litt.) informs me he is describing as new. The forearm length ranges from 45 to 49, and the condylobasal lengths of the two extracted skulls are 18.9 (male) and 20.8 (female). Judged by the characters given by Hall and Kelson (1959, p. 142), the Martinique form shows greater resemblance to the more southern luciae of St. Lucia than to the more northern nichollsi of Dominica.

Natalus stramineus: I have nothing to add to the taxonomy of the Lesser Antillean forms of this species beyond what was given by Goodwin (1959), who recorded it from the islands of Anguilla, Antigua, and Dominica. More material from eastern Brazil is needed to establish whether or not Goodwin was justified in setting aside Cabrera's previous type locality fixation of Lagoa Santa, Brazil, and replacing it with Antigua. Two islands can be added to the list, however, since the Field Museum of Natural History has specimens from Saba and Montserrat. The species clearly has reached the Lesser Antilles from the south.

Myotis nigricans: Within the area considered, Hall and Kelson (1959) recognized only a single form (M. n. dominicensis), confined to Dominica. Although clearly some overlap exists in all characters between this subspecies and the widespread M. n. nigricans, it may be tentatively maintained pending further study of Lesser Antillean populations. There are at least five of these. In addition to the population on Dominica and one on Grenada (currently referred to M. n. nigricans), this species has been recorded from St. Martin (Husson, 1960). The latter, a single

¹ Since this paper was submitted for publication, the anticipated revision by Jones and Schwartz (1967) has appeared. A single species, *Ardops nichollsi*, is recognized, with five subspecies covering the seven islands from which it is here recorded.

specimen, was identified, with some question, as M. n. nesopolus, the form on Curação and Bonaire. Such an allocation seems geographically improbable. On Barbados Clayton Ray collected a single male that appears to be too large for M. n. dominicensis, as is evidenced from the following measurements of his specimen compared with those of four males in the American Museum from Dominica (one collected by myself and the other three by Paul Griswold Howes, only one skull extracted): forearm length, 35 (32-35); condylobasal length, 13.3 (12.2). The measurements of the Barbados specimen are even larger than those of a small series of M. n. nigricans from Trinidad. Its measurements are equaled, however, by some mainland specimens (see Miller and Allen, 1928), and it is therefore referred to the widespread M. n. nigricans. A series of nine specimens of Myotis collected by Beatty and Martin on Martinique are still more divergent from dominicensis (forearm, 36-38; condylobasal length of the two extracted skulls, 13.5). Even these, however, are matched by measurements of some mainland specimens of M. n. nigricans given by Miller and Allen, and the Martinique series is therefore allocated to this subspecies with some hesitation. Clearly this species has entered the Lesser Antilles from the south.

Eptesicus fuscus: The only record of this species in the Lesser Antilles is a specimen from Barbados listed by Dobson (1878, p. 194). This species is otherwise known from no closer than Puerto Rico and the coastal region of central Venezuela, each more than 500 miles from Barbados. Another smaller species is known from Tobago (Goodwin and Greenhall, 1961, pp. 277–278), but if the Barbados specimen were referable to this form, one would expect that Dobson would have identified it as hilarii rather than fuscus. It seems likely that the Barbados specimen was either mislabeled or represents an accidental occurrence.

Tadarida brasiliensis: All Lesser Antillean populations of this species are referable to T. b. antillularum. Hall and Kelson (1959, p. 205) recorded the species from Barbuda, Dominica, and St. Lucia. Shamel (1931) recorded it in addition from St. Kitts, Antigua, Montserrat, and Guadeloupe. G. M. Allen (1911, p. 245) gave a St. Bartholemew record; Husson (1960, p. 78), one from St. Martin. The American Museum has two virtual topotypes from Dominica, collected by R. C. Murphy in 1912, and a large series from Martinique collected by Beatty and Martin. Ray obtained a good series on St. Kitts. The United States National Museum has material from St. Eustatius. Probably it occurs throughout the Lesser Antilles with the possible exception of Barbados, since it is also known from Tobago. In view of the presence of the same subspecies in Puerto Rico, of other subspecies in the rest of the West Indies, and the apparent

absence of the species from Trinidad and the lowlands of northern South America, or its great rarity there, it is probable that *T. brasiliensis* reached the Lesser Antilles from the northwest.

Molossus molossus: Miller (1913b) recognized three species of Molossus from the Lesser Antilles (major, debilis, and obscurus). I concur with Husson (1962, p. 258) in regarding major and obscurus as synonyms of M. molossus which would then be the form from the islands south of Guadeloupe. Molossus debilis, from the islands north of Guadeloupe, was compared only with major and distinguished solely by the claim that the "crown area of molars [was] decidedly reduced," but no comparable measurements were given to support this statement. Comparisons of skulls of two specimens from St. Martin, one from St. Kitts (the type locality of debilis), one from Dominica (a locality of major), one from Martinique (the type locality of molossus, major, and obscurus), three from Barbados (a locality for obscurus), and four from Tobago show no consistent difference between those of the northern islands and those of the southern islands and no clear-cut distinction between large and small molars. Although I have not assembled enough material to demonstrate that debilis is an absolute synonym of molossus, it is clear to me that debilis is at most a subspecies of M. molossus. Hall and Kelson (1959, p. 217) recorded Molossus from the following islands in the area under consideration: Barbados, St. Lucia, Martinique, Dominica, Montserrat, Antigua, Nevis, and St. Kitts. G. M. Allen (1911, p. 250) mentioned specimens from St. Vincent, and the Museum of Comparative Zoology has a large series from Guadeloupe. In addition to three specimens from Barbados collected by R. C. Murphy, seven from Martinique collected by Beatty and Martin, and 16 from Dominica collected by E. Kirsteuer, Ray collected two from Antigua, four from Barbuda, 10 from St. Kitts, and five from St. Eustatius. Goodwin collected two each from St. Martin and Anguilla, specimens from the former island having also been recorded by Husson (1960, p. 81). This common house bat probably occurs on virtually every Lesser Antillean island. Because all Lesser Antillean populations belong either to the same subspecies that occurs on the north coast of South America or to one very much like it, the most plausible invasion route for Molossus into the Lesser Antilles is from the south.

ZOOGEOGRAPHICAL DISCUSSION

Of the 13 species and species groups of bats definitely known from the Lesser Antilles south to St. Vincent and Barbados (not including Eptesicus fuscus and Carollia perspicillata), six (Pteronotus davyi, Glossophaga

TABLE 1 Distribution Pattern of Lesser Antillean Bats from South (Left) to North (Right)

Greater Antilles

	Grenada	St. Vincent	Barbados	Central Lesser Antilles ^a	Guadeloupe	Northern Lesser Antilles b
Perohiemy marratic 3	+ 4				1	1
Martin Istanian	. 4	+	+	+	1	+
lvociiiio teporinus	+	-	<u>-</u>			-
Pteronotus davyi→	+	1	1	+	I	ı
Micronycteris megalotis—→	+	1	1	[1	ı
Glossophaga longirostris	+	+	1	+	1	1
Monophyllus plethodon	J	+	+	+	1	+
Carollia perspicillata→	+	-	1	l	I	د.
Sturnira	↑	+	1	+	+	J
Brachyphylla cavemarum	1	+	+	+	+	+
Artibeus jamaicensis	+	ı	+	+	+	+
Artibeus literatus→	+	+	1	1	1	I
Artibeus cinereus—→	+	I	1	1	I	1
Ardops nichollsi	I	+	1	+	+	+
Natalus stramineus—→	1	1	Ì	+	1	+
Myotis nigricans→	+	1	+	+	1	+
Tadarida brasiliensis	ļ	\	1	+	+	+
Molossus molossus-→	+	+	+	+	+	+
^a Central Lesser Antilles include St. Lucia, Martinique, and Dominica. ^b Northern Lesser Antilles include all the islands from Montserrat and Antigua to Saba and Anguilla. ^c An organization the direction of directions of presumed passage.	le St. Lucia, M ade all the islar	artinique, and Donds from Montser	ominica. rat and Antigua	to Saba and	Anguilla.	
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^c An arrow indicates the direction, or directions, of presumed passage.

^d A plus sign indicates a definite record.

longirostris, Sturnira, Artibeus lituratus, Natalus stramineus, and Myotis nigricans) have clearly entered the Lesser Antilles from the south, and for a seventh (Molossus molossus) such a derivation is the most plausible. Two species (Artibeus jamaicensis and Tadarida brasiliensis) probably came into the main Lesser Antilles from the Greater Antilles. The derivation is uncertain for the remaining species or species groups (Noctilio leporinus, Monophyllus plethodon, Brachyphylla cavernarum, and Ardops nichollsi). These include all three endemic West Indian genera occurring in the Lesser Antilles. Noctilio leporinus has an extensive circum-Caribbean distribution, but many populations are too poorly known for one to say from which direction invasion of the Lesser Antilles occurred. Monophyllus is more diversified in the Greater than in the Lesser Antilles, but its closest relative appears to be the South American Glossophaga longirostris, so its derivation is uncertain. Brachyphylla is a very distinct genus of uncertain affinities, widespread in both the Greater and Lesser Antilles. Just where it originated is uncertain. Ardops nichollsi is closely related to three endemic Greater Antillean genera (Phyllops, Ariteus, and Stenoderma). All four are allopatric, and the derivation of the group is somewhat obscure, though probably from some form of Artibeus or a close relative.

Both species of Greater Antillean origin (Artibeus jamaicensis and Tadarida brasiliensis) have spread widely through the Lesser Antilles, A. jamaicensis having reached Barbados and T. brasiliensis apparently being absent from Barbados, but having reached Tobago, possibly only as an accidental. Of the seven species of probably Lesser Antillean origin, one is not known north of St. Vincent (Artibeus lituratus), two (Pteronotus davyi and Glossophaga longirostris) reach Dominica, Sturnira reaches Guadeloupe, and Myotis nigricans reaches St. Martin, whereas both Natalus stramineus and Molossus molossus reach Anguilla and also have closely related and probably derivative forms in the Greater Antilles. It should be pointed out that four and probably five species coming from South America, Trinidad, or Tobago have reached Grenada but not St. Vincent or the islands farther north (see Koopman, 1958). These are Peropteryx macrotis, Micronycteris megalotis, Artibeus jamaicensis trinitatis, Artibeus cinereus, and probably Carollia perspicillata. Obviously, as expected, there is a rapid decline in the number of species as the first few water gaps are hopped, followed by a much slower decline as one goes farther north. Barbados, which is somewhat isolated from the main Lesser Antillean chain, apparently lacks several species (Pteronotus davyi, Glossophaga longirostris, Sturnira, Artibeus lituratus, Ardops, Natalus stramineus, and Tadarida brasiliensis) known from the islands of Dominica, Martinique, St. Lucia, or St. Vincent. The reason may be at least in part ecological, since Barbados is relatively flat and heavily agriculturalized. I have tried to summarize these zoogeographical patterns in table 1.

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