FOSSIL CHIROPTERA COLLECTED BY H. E. ANTHONY IN JAMAICA, 1919–1920

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INTRODUCTION

In 1919–1920 H. E. Anthony made extensive collections of cave fossils in Jamaica. While not so phenomenally productive as his earlier explorations of Puerto Rico (Anthony, 1925–1926, and earlier titles) and Cuba (Anthony, 1919) this expedition gathered much material of value which unfortunately was never reported upon in full. The only publications describing the results of the expedition that have so far appeared are a preliminary note (Anthony, 1920b) recording the occurrence of four new genera of large rodents in Jamaican cave breccia and a popular article (Anthony, 1920a) giving only a very general account of the investigations. The value and interest of these collections have warranted their reëxamination, and the present paper will, it is hoped, be one of several to deal with them.

Anthony's coverage of Jamaica was remarkably thorough. In somewhat over three months he explored over 70 caves, visited at least briefly almost every section of the island, and brought back skins and skulls of living bats, owl pellet materials, and fossils. Only shortness of time prevented the collection in this way of an almost ideal vertical section (a time transect, so to speak) of the successive bat faunas of the island. The completion of this vertical section by additional material collected in the same thorough fashion is much to be desired.

We deal here with a record of only the evidence as collected by Anthony, leaving the filling in of details to future work.

We include also the evidence of non-chiropteran material when it adds to or clarifies the picture.

We are fortunate in having had made available to us Anthony's day-by-day field notes which have permitted a far more complete and adequate analysis than could otherwise have been possible, and we are grateful to Dr. Anthony for his permission to examine and to quote from this valuable record.

The principal caves visited by Anthony (in the order of his visit) are:

Healthshire Hills Caves, St. Catherine Parish	Non-fossiliferous
Oxford Cave, near Balaclava, St. Elizabeth Parish	Non-fossiliferous
Wallingford Main and Wallingford Roadside Caves, near Balaclava, St. Elizabeth Parish	Fossiliferous
Hutchinson's Meadow Cave, near Balaclava, St. Elizabeth Parish	Non-fossiliferous
Cambridge Cave, near Cambridge, St. James Parish	Fossiliferous
Sewell Cave, near Montego Bay, St. James Parish	Non-fossiliferous
Providence Cave, near Montego Bay, St. James Parish	Non-fossiliferous
Seven Rivers Cave, St. James Parish	Fossiliferous
Hounslow Money Cave, near Malvern, St. Elizabeth Parish	Non-fossiliferous
Early Cave, Windsor, Trelawney Parish	Fossiliferous
Long Mile Cave, Windsor, Trelawney Parish	Fossiliferous
Pen House Cave, Windsor, Trelawney Parish	?Fossiliferous
Fowl House Cave, Windsor, Trelawney Parish	Fossiliferous
Sheep Pen Cave, Windsor, Trelawney Parish	Fossiliferous
Dairy Cave, near Dry Harbour, St. Ann Parish	Fossiliferous
Thatchfield Cave, near Brownstown, St. Ann Parish	Non-fossiliferous
Peru Cave, near Goshen, St. Elizabeth Parish	?Non-fossiliferous
Portland Ridge Cave, Clarendon Parish	Fossiliferous

TENTATIVE STRATIGRAPHY OF THE FOSSILIFEROUS CAVES

Within caves in which Anthony collected fossils a number of different layers can be distinguished, the correlation of which in different caves and their real temporal sequence are in considerable part conjectural. It will be useful, however, to arrange these layers in some, apparently logical, fashion, and the temporal sequence we provisionally regard as probable is the following:

> *Rattus* layers
> *Oryzomys* strata
> "Lizard layers"
> Hard breccias

Omitted from this sequence are several formations which for

reasons mentioned below are not accurately to be placed in such an arrangement:

> Seven Rivers formation
> Loose breccia of Cambridge Cave
> Mixed breccias of Sheep Pen Cave

All these formations require at least a brief description if the deposits of the fossiliferous caves are to be properly understood.

The *Rattus* or surface layers are distinguished equally by their superficial position, their color (gray or black), by the freshness of the bones found in them, and by the occurrence of post-Columbian migrants—*Rattus, Mus, Herpestes,* etc. These strata, often only a few inches thick, may nevertheless represent a considerable time interval of at least hundreds of years.

The *Rattus* layers grade into, and are with difficulty distinguished from, the next or subsurface layers, the *Oryzomys,* which may represent an even longer time interval. In Pen House Cave, Windsor, Trelawney, where Anthony obtained a good series of *Oryzomys* skulls, he was able to distinguish the two layers. He states: "The *Oryzomys* were invariably old and rotten and not on the surface with the more recent *Epimys* (*Rattus*) material." A more brownish stain and a less fresh appearance of the bone tend to characterize the subsurface layers.

Orzomys, though abundant in certain localities in the subsurface, is doubtfully or infrequently present in the true surface layers. It seems now to be extinct. *Geocapromys,* at present restricted to the John Crow Mountains, an area in which caves were not examined by Anthony, occurs in the surface or subsurface layers of the investigated areas only in Wallingford Cave, Balaclava, St. Elizabeth Parish (a region in which *Geocapromys* is supposed only recently to have become extinct) and in the kitchen midden of Long Mile Cave, Windsor, Trelawney Parish. The genus is known from other kitchen midden deposits in widely scattered portions of the island (Duerden, 1897; Longley, 1914; Miller, 1916[1]). The bats of the surface

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[1] Miller's suggestion that two species of *Geocapromys* existed in Jamaica, *thoracatus* as well as *browni,* is not supported by the very considerable material we have seen. Small jaws of *Geocapromys* are to be found, but they grade insensibly upward into typical *browni,* i.e., the difference between large and small jaws is, on Jamaica, ontogenetic only.

and subsurface are recent forms: *Artibeus, Ariteus, Chilonycteris, Macrotus, Monophyllus, Glossophaga, Erophylla, Tadarida,* and *Molossus.*

Characteristically deeper are the "lizard layers." These are distinguished by the presence of a large number of bones, including the osteoscutes of a giant member of the lizard genus *Celestus.* These layers may be yellow, orange, or red brown in color, and we are tempted to believe that increasing darkness of color implies greater age. Most of the bones from these layers in any one cave can be recognized by their characteristic color. *Geocapromys* tends to occur in these layers wherever they are present. The fossil bats that have been recognized are from these layers; in fact, the most remarkable novelty among these fossils, a new endemic species of the genus *Tonatia,* receives its trivial name because of its association with the lizard so typical of these formations.

These layers are, of course, not everywhere faunally (and probably not temporally) precisely equivalent. The relative abundance of *Celestus* bones varies greatly with the individual deposit. In the Wallingford Caves they are probably the chief component. In the Dairy Cave, Dry Harbour, St. Ann Parish, bird bones tend to preponderate over lizard, but a second lizard, a huge fossil gecko, is an important element. In other localities *Geocapromys* may be the chief element of the fauna. A monkey jaw (with the other non-chiropteran novelties, to be described elsewhere) appears to belong to a layer of the latter type in Long Mile Cave, but it may be an intrusive from the kitchen midden which lay a foot above it.

The bones of the lizard layers are in no sense fossilized, nor are they typically even superficially mineralized. Rarely they may be heavily lime-encrusted.

Quite evidently much older are the very resistant breccias of Wallingford Roadside Cave (occurring also in Wallingford Main Cave) which are the type formation of *Clidomys* and the other genera of large rodents described by Anthony. In Wallingford Roadside Cave these breccias do not underlie the lizard layer; they form part of the wall and roof above the present floor. They are thus probably quite significantly older than any of the unconsolidated material of the cave floor.

The bones from these breccias are heavily mineralized, and the matrix is very solid and homogeneous. Much of this mate-

rial was brought back by Anthony, but the difficulty of its preparation resulted in its neglect. Abundant remains of the turtle genus *Pseudemys* occur in this breccia. A single crocodile vertebra was also obtained. No bats were found. The circumstances under which this formation was laid down were probably very different from those under which the other deposits mentioned were formed.

The layers thus far cited can all be found in Wallingford Roadside Cave, though in that cave the *Rattus* and *Oryzomys* strata were not distinguished. The hard breccias are not known in their typical state elsewhere, but the sequence of *Rattus*, *Oryzomys*, and lizard layers in that order from surface to a depth of 4 to 8 feet is a common one. In certain caves, which appear to have been recently formed or exposed, only the first two, or even only the first, of these unconsolidated layers was found.

The formations still to be mentioned are anomalous and do not fit readily into this general sequence:

In Seven Rivers Cave, St. James Parish, Anthony found a deposit in which *Rattus* was associated with *Geocapromys* and with the giant *Celestus*. It is possible to believe that this mixture of types is due to intermediate age, but the bones are white, very friable, and, according to Anthony's notes, distributed along the cave floor as if carried along by water. It seems probable to us that the association of *Rattus* and the lizard is a result of mechanical mixing and not an indication of intermediate time level. No extinct bats are known from this cave; only *Artibeus*, *Ariteus*, *Macrotus*, *Monophyllus*, and *Tadarida* occur in it.

Cambridge Cave, St. James Parish, contains a poorly consolidated breccia which has yielded one edentulous bat jaw (*Eptesicus*), much *Geocapromys*, and nothing else. The absence of all purely surface types, and even of *Oryzomys*, may be significant. Probably no great error is involved if this breccia is assumed to be approximately contemporaneous with the lizard layers. The bones obtained from the breccia are quite white, however, and have a fresh appearance.

In Sheep Pen Cave, Windsor, Trelawney Parish, an extraordinary situation was discovered by Anthony. The "cave" was really an overhang, on the face of which a bone-bearing breccia was discovered. Both *Geocapromys* bones and teeth of one of

the large rodents described by Anthony were found, *Geocapromys* in layers both above and below remains of the large rodent. The breccia was very heterogeneous, being in part granular and loose, in part very hard and homogeneous. From our own examination of the material brought back by Anthony it seems to us that the large rodent is localized in the hard breccia, and that quite possibly this was a reworked deposit in which the *Geocapromys* layers are distinctly younger and different in quality from those that contain the large rodent. No bats were found in this breccia.

THE FOSSIL BATS

The fossil bats here reported all occur in two localities, Wallingford Roadside Cave, Balaclava, St. Elizabeth Parish, and Dairy Cave, Dry Harbour, St. Ann Parish; in both cases the fossils are from the "lizard layers." A third locality might doubtfully be added (Cambridge Cave, St. James Parish) in which an edentulous *Eptesicus* jaw was found in the loose breccia, but this cave adds no new form; *Eptesicus* is also represented in the Wallingford Roadside Cave.

There are some peculiarities of preservation. The bats of the Wallingford Cave are known only from mandibles, while Dairy Cave includes also rostra. Edentulous jaws are common in Dairy Cave. The bones from Dairy Cave are also stained a lighter, redder color than the dark brown of the Wallingford remains.

The absolute age of the specimens is beyond present estimation. It is assumed, as indicated in the section on tentative stratigraphy, that the layers in which they occur are older than the *Oryzomys* strata and younger than the *Clidomys* formations.

The relative age of the two caves is perhaps more nearly determinable. The Wallingford Cave fauna may be older, the Dairy Cave fauna younger. The lighter color of the Dairy Cave fossils, the abundance of *Ariteus*, and the presence of *Mormoops* (see table 1) seem to us to indicate a faunal phase closer to the Recent. This opinion rests on the unsafe ground of assuming that the very small fossil bat faunas found in the two caves adequately mirror the faunas of their time, and that the observed differences are therefore real. On the other hand, there is no basis for assuming that the two cave faunas were strictly contemporaneous.

All fossils are listed in table 1, with mention of the remains by which they are known. Only the forms that are new (*Tonatia*), new to Jamaica (*Brachyphylla and Natalus*), or heretofore represented only by the type (*Reithronycteris*) are here discussed at length. *Eptesicus* is mentioned because of existing confusion in the literature as to the living form or forms present in Jamaica. The remaining fossils (*Mormoops* and *Ariteus*), not distinguishable from recent species, are cited only in the table.

TABLE 1

FOSSIL CHIROPTERA OF JAMAICA

	Wallingford Cave	Dairy Cave
Superfamily Phyllostomatoidea		
Family Phyllostomatidae		
Subfamily Chilonycterinae		
Mormoops blainvillei		2 partial mandibles
Subfamily Phyllostomatinae		
Tonatia saurophila, new species	2 partial mandibles	3 rostra
Subfamily Stenoderminae		
Brachyphylla pumila		8 partial mandibles 3 rostra
Ariteus flavescens		12 mandibles 3 rostra
Subfamily Phyllonycterinae		
Reithronycteris aphylla	1 mandible	3 mandibles 3 rostra
Superfamily Vespertilionoidea		
Family Natalidae		
Natalus major	1 mandible	
Family Vespertilionidae		
Subfamily Vespertilioninae		
Eptesicus sp.	1 mandible (also 1 mandible from Cambridge cave)	

Tonatia, new species

This hitherto undiscovered form is recognized from two mandibles from the lizard layer of Wallingford Roadside Cave and from three partial rostra from Dairy Cave. These specimens constitute the first record of the genus in the West Indies. Since this material is fragmentary, yet seems to represent a new form, reasons for its generic and specific allocation are given in

detail, and since rostra and mandibles were found in separate caves the analysis is made independently for the two sorts of elements.

The two mandibles include between them the whole dentary bone except for the end of the angular process (see fig. 1A–C). All three molars are present, together with the last premolar. The remainder of the dental formula can be determined from the alveoli. There are two rather small roots, a large canine root, and a single small incisor root in front of the last premolar. This dental-root formula excludes many families and additional genera immediately. The moderately high coronoid, the generalized tooth pattern, and the rather large size and straight robust form of the ramus restrict our attention to the subfamily Phyllostomatinae of the family Phyllostomatidae. Within this subfamily, however, *Macrotus* and *Vampyrum* (the only phyllostomatine genera previously recorded from Jamaica) and indeed all other genera except *Tonatia* and *Chrotopterus* are ruled out by a different number of dental roots. *Chrotopterus* is excluded because it, like *Macrophyllum*, *Lonchorhina*, and *Trachops*, has the middle or third premolar reduced to a minute vestige restricted to the labial side of the mandible.

The forms of the remaining genus, *Tonatia*, were compared with the fossil and are found to agree well at the generic level. Among living species all except *amblyotis*, *loephotis*, and *bidens* are considerably smaller than the fossil form. *T. amblyotis* and *T. loephotis* resemble each other and differ from both *T. bidens* and the fossil form in the shape of the last premolar. In the first-named forms this tooth has a large anterolingual lobe which considerably constricts the smaller middle premolar, while in *bidens* and in the fossil the same tooth is rather squared off in front, and the middle premolar hence is relatively larger. The Jamaican fossil is slightly smaller than *bidens* but otherwise very similar, differing principally in the shape of the talonid of the last molar (see fig. 1).

The rostral fragments include the entire rostrum, except the extreme anterior end, virtually the entire hard palate, and the roots of all teeth except the incisors. The last premolar is in place on one side in one specimen (fig. 2A–B). The upper dental formula was i? cl p2 m3. Dental formulas in agreement with this are found in a great variety of New World bats belonging to the families Emballonuridae, Furipteridae, Vespertilionidae,

and Molossidae, and all the seven subfamilies of the Phyllostomatidae. A number of forms can, however, be eliminated on the character of rostral shape, the rostrum in such forms being either too broad or too low. Thus we can eliminate the families Emballonuridae, Furipteridae, and Vespertilionidae, as well as the subfamilies Glossophaginae, Carollinae, Stenoderminae, and Phyllonycterinae of the family Phyllostomatidae. The subfamily Chilonycterinae can also be discarded from consideration because of the presence in that subfamily of a sharp angle be-
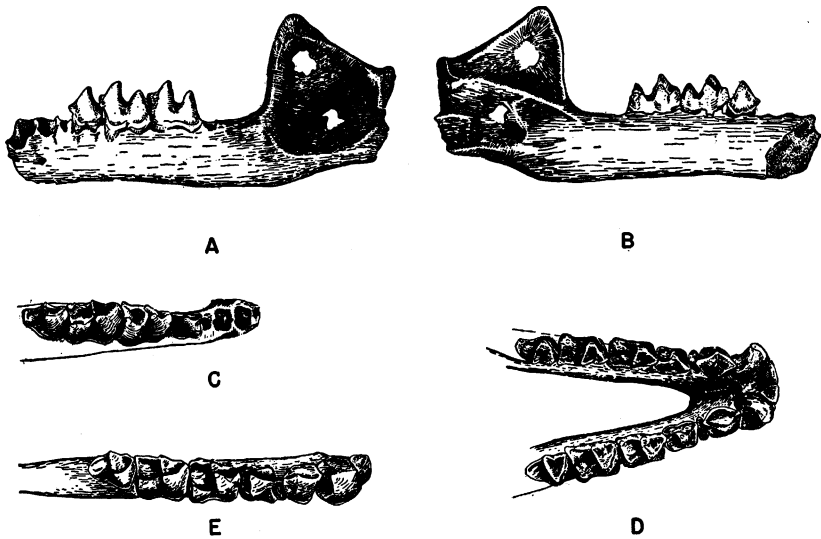

FIG. 1. *Tonatia* mandibles. A. *T. saurophila*, paratype, A.M.N.H. No. 147207, labial view. B. *T. saurophila*, paratype, A.M.N.H. No. 147207, lingual view. C. *T. saurophila*, type, A.M.N.H. No. 147206, crown view. D. *T. bidens* from Kartabo, British Guiana, A.M.N.H. No. 64164, crown view. E. *T. bidens* from Palmar, Costa Rica, A.M.N.H. No. 139440, crown view.

tween braincase and rostrum which the fossil lacks. In the family Molossidae the anterior border of the orbit rises almost vertically to join the dorsal border; in the fossil this junction is much more oblique. Finally the Sturnirinae have a much simpler premolar pattern than that observed in the fossil. This disposes of all groups except the Phyllostomatinae. All genera of this subfamily have been compared with the fossil. The genera *Macrotus*, *Vampyrum*, and *Micronycteris* (including *Xenoctenes*) need not be considered, since in all of these, apart

from other striking differences, the rostrum is too long.   In
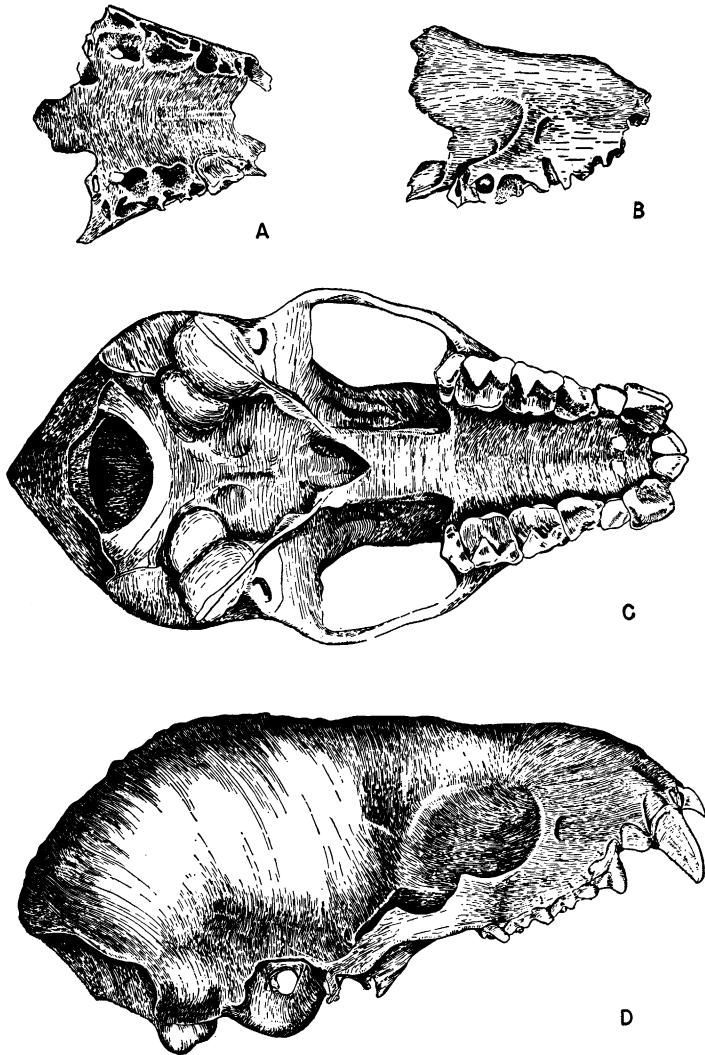the genera *Lonchorhina, Macrophyllum, Trachops, Phyllostomus,*

FIG. 2. A. *Tonatia saurophila*, A.M.N.H. No. 147205, rostrum, palatal view.
B.   *T. saurophila*, A.M.N.H. No. 147205, rostrum, lateral view.   C.   *T. bidens*,
A.M.N.H. No. 64164, from Kartabo, British Guiana, skull, palatal view.   D.
T. bidens, A.M.N.H. No. 64164, from Kartabo, British Guiana, skull, lateral view.

Phylloderma, Mimon, and *Anthorhina* an anterior lobe on the last
premolar is absent or poorly indicated; it is well developed in

the fossil. *Chrotopterus* lacks the prominent basin on the anterior lobe of the premolar seen in the fossil, and the anterior opening of the antorbital foramen is too close to the orbit. The species of *Tonatia*, however, agree with the fossil in all major characters. Again, all except *amblyotis*, *loephotis*, and *bidens* are considerably smaller than the fossil. The fossil differs from *amblyotis* and resembles *bidens* in the form of the posterior part of the rostrum and in the width and height of the ridge separating the anterior opening of the antorbital foramen from the orbit. The fossil differs from *bidens* in being of slightly smaller size and in having a somewhat more bulbous forehead and better developed posterior lobe on the last premolar (fig. 2).

Thus both rostra and mandibles, although from different caves, agree more closely with those of *Tonatia bidens* than with those of any other form, yet also differ slightly in several respects, including smaller size. The conclusion seems warranted that the two sets of elements represent the same species, namely, a close relative of *T. bidens*. The distinctness of the new form seems unquestionable. It has been compared with *T. bidens* from Costa Rica, Venezuela, British Guiana, and Brazil. While there is considerable variability within *bidens* as currently recognized, Costa Rican specimens represent the extreme of difference from the Jamaican type both in greater size and in the shape of the talonid of the last lower molar. While other specimens approach the latter more closely, all *bidens* differ significantly from the new species in both size and other characters. Since the new form is, however, allopatric to *T. bidens*, so far as known, the question of its status, whether as full species or as subspecies, arises. Because it appears to be slightly more distinct from *T. bidens* than *T. loephotis* is from *T. amblyotis*, both of which also have allopatric distributions and which Goodwin (1942), the last reviser of the genus, considered to be full species, we rank the fossil Jamaican form as a full species.

Tonatia saurophila, new species

TYPE: A partial mandible, A.M.N.H. No. 147206.

TYPE LOCALITY: Wallingford Roadside Cave, Balaclava, St. Elizabeth Parish, Jamaica, British West Indies.

PARATYPE: A second partial mandible, A.M.N.H. No. 147-207, from the same locality as the type.

REFERRED MATERIAL: Three rostra (A.M.N.H. Nos. 147-

205, 147211, 147212) from Dairy Cave, Dry Harbour, St. Ann Parish, Jamaica.

DIAGNOSIS: Closest to *T. bidens* but differing in having the axis of the talonid of m_3 running not obliquely in a lingual-labial direction but straight anteroposteriorly, in having a slightly lower coronoid, a slightly more bulbous forehead, and the labial posterior lobe of the last upper premolar better developed. Size slightly smaller than *T. bidens*.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF *Tonatia saurophila* AND *Tonatia bidens*

	Length of Tooth Row	Depth of Ramus Behind Last Molar	Coronoid Height
Tonatia saurophila			
Type, A.M.N.H. No. 147206	9.8	3.1	—
Paratype, A.M.N.H. No. 147207	9.5	2.9	6.3
Tonatia bidens			
A.M.N.H. No. 13446, from Costa Rica	11.8	3.4	7.7
A.M.N.H. No. 64164, from British Guiana	10.7	3.0	7.2

Brachyphylla pumila Miller

Brachyphylla pumila MILLER, 1918, Proc. Biol. Soc. Washington, vol. 31, p. 39.

Material referred to this Hispaniolan species is moderately abundant in the lizard layer of Dairy Cave, St. Ann Parish, where it is represented by three rostra, eight fragmentary mandibles, and some other barely recognizable fragments. Unfortunately most of the material is edentulous, but one rostrum has a last premolar and first molar. Except for the absence of teeth, the material is adequate, for the entire lower jaw and the rostral region, including the palate but not the braincase, are known. From the dental roots the dental formula is reconstructed as $1_2^2 \, c_1^1 \, p_2^2 \, m_3^3$ (see figs. 3, 4).

From the size and breadth of the rostra and from the dental cusp pattern in the one case in which it is preserved, all Western Hemisphere bats except the Stenoderminae are ruled out. Of the genera of this subfamily only *Brachyphylla, Vampyrops, Uroderma, Artibeus, Enchisthenes, Ardops, Phyllops,* and *Stenoderma* have the same dental formula. In all these genera except

Brachyphylla the rostrum is much shorter than in the fossil examples. This feature can be seen even in lateral rostral fragments, since rostral length is reflected in the distance between the antorbital foramen and the anterior border of the orbit.
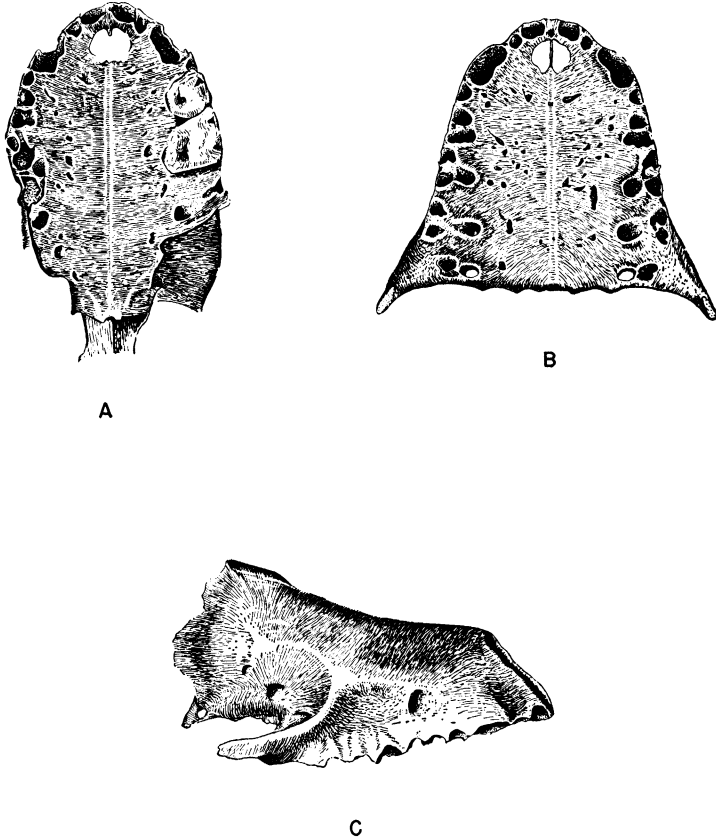

FIG. 3. *Brachyphylla pumila* rostra. A. A.M.N.H. No. 147202, palatal view. B. A.M.N.H. No. 147201, palatal view. C. A.M.N.H. No. 147201, lateral view.

The Jamaican material has been compared with all three Greater Antillean species of this genus. It is definitely smaller than *B. cavernarum* of Puerto Rico and the Lesser Antilles; it differs from *B. nanus* of Cuba and resembles *B. pumila* of Hispaniola in the presence of a distinct though shallow pit between

the orbit and the antorbital foramen. In *B. nanus* the pit is represented only by an indistinct depression. The Jamaican rostra cannot be distinguished from those of *pumila* and are therefore referred to that species.

The mandibles were not at first recognized as *Brachyphylla*, since, lacking teeth, they show no special stenodermine characters. A close study, however, revealed that in dental-root number and the general morphology of the coronoid and angle
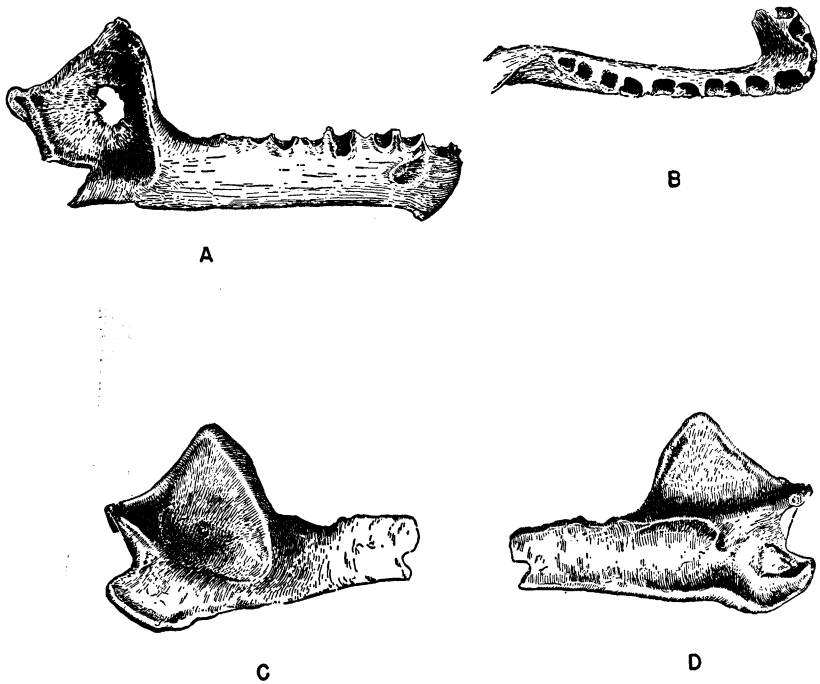

FIG. 4. *Brachyphylla pumila* mandibles. A. A.M.N.H. No. 147204, labial view. B. A.M.N.H. No. 147204, alveolar view. C. A.M.N.H. No. 147203, labial view. D. A.M.N.H. No. 147203, lingual view.

they agreed perfectly with *Brachyphylla* in general, and in size and in details of sculpturing of the inner surface of the angle with *B. pumila* in particular. The mandibles thus confirm the identification of the Jamaican *Brachyphylla* with *B. pumila*.

Reithronycteris aphylla Miller

Reithronycteris aphylla MILLER, 1898, Proc. Acad. Nat. Sci. Philadelphia, p. 334.

This endemic Jamaican form is known as a living animal only

from the unique type collected at an unknown locality in
Jamaica prior to 1898.[1] It appears to be represented in the lizard
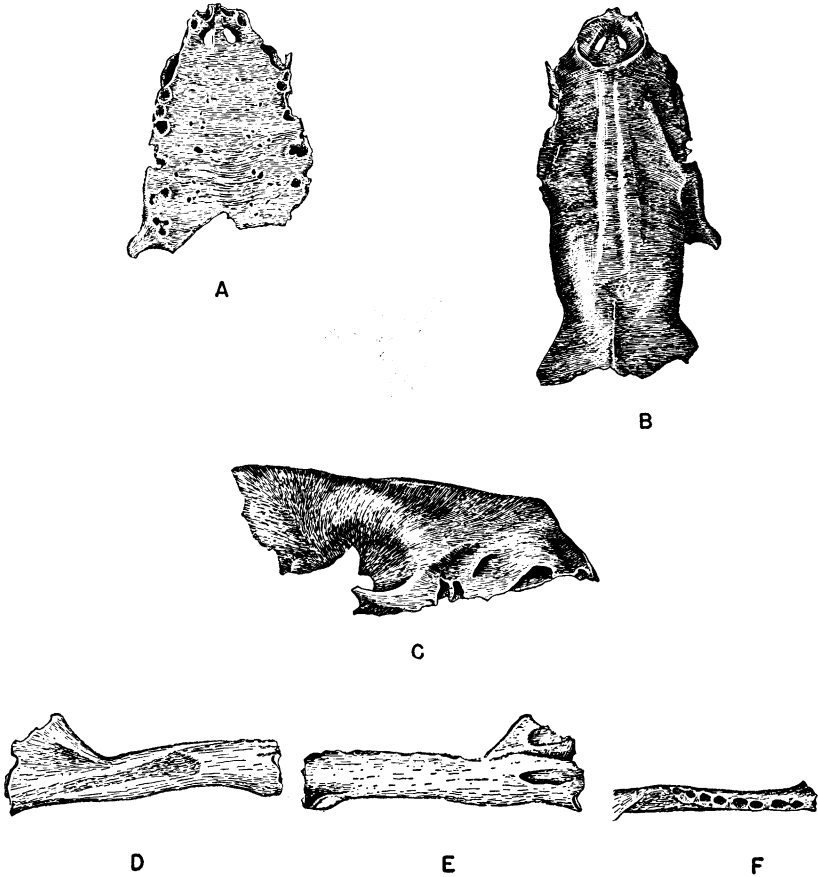layer of Dairy Cave, St. Ann Parish, by three rostra and three

FIG. 5. *Reithronycteris aphylla*. A. A.M.N.H. No. 147209, rostrum, palatal
view. B. A.M.N.H. No. 147209, rostrum, dorsal view. C. A.M.N.H. No.
147209, rostrum, lateral view. D. A.M.N.H. No. 147210, mandible, labial
view. E. A.M.N.H. No. 147210, mandible, lingual view. F. A.M.N.H. No.
147210, mandible, alveolar view.

partial mandibles, all without teeth, and in the lizard layer of

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[1] Recently, additional material has been obtained from a surface owl deposit.
This is the subject of another short paper by the senior author, in press.

Wallingford Cave, St. Elizabeth Parish, by a single, imper-
fect, edentulous mandible.

The rostra have the dental formula i2 c1 p2 m3 (fig. 5A–C).
New World forms having this upper dental formula are found
in the Furipteridae, Vespertilioninae, and all seven subfamilies
of the Phyllostomatidae. In all except the Glossophaginae and
Phyllonycterinae the posterior part of the rostrum is too broad,
too high, or forms too distinct an angle with the braincase to
permit close comparison with the fossil. The anterior end of the
rostrum is much more robust than in any glossophagine. Of
the Phyllonycterinae, *Erophylla* can be excluded for two reasons:
(1) in that genus the zygomatic arch is complete and on a level
with the base of the tooth row, whereas in the fossil the jugal
process of the maxillary is reduced to a stump which is dis-
tinctly bent upward; (2) the antorbital foramen is placed well
posterior to the root of the canine in *Erophylla*, whereas in the

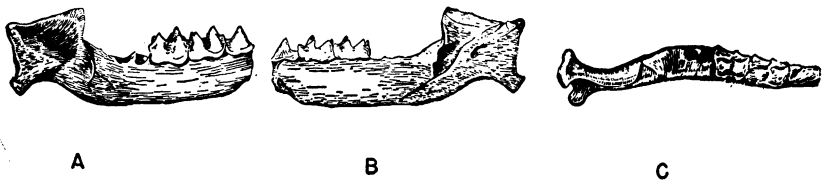A   B   C

FIG. 6. *Natalus major*, A.M.N.H. No. 147208, mandible. A. Labial view.
B. Lingual view. C. Crown view.

fossil this foramen is placed almost immediately behind the
canine. Of the two remaining closely related genera of the sub-
family, *Phyllonycteris* and *Reithronycteris*, the fossil resembles
both closely. Unfortunately the diagnostic differences between
these two genera are in the basicranial region, which is not
preserved in any of the fossil material. Decision in this problem
has been reached on the basis that since *Phyllonycteris* itself is
unknown from Jamaica and seems represented there by *Reithro-
nycteris aphylla*, the most conservative course is to refer the
fossil rostra to the known Jamaican form.

The mandibles are even more doubtfully referred here (fig.
5D–F). None is even approximately complete, and unfor-
tunately all lack very much the same parts. They show satis-
factorily only the posterior tooth row and the anterior coronoid
region. They appear to be assignable to the Phyllonycterinae

because of the slender ramus and the approximately 45° angle between the tooth row and the anterior edge of the coronoid. *Erophylla* seems to be eliminated by the height of the coronoid in those mandibles that show enough of this region, and also by the absence of the considerable interval between the last molar and the rise of the coronoid which distinguishes that genus. Again allocation to *Reithronycteris* rather than to *Phyllonycteris* is primarily on the basis of locality.

Natalus major Miller

Natalus major MILLER, 1902, Proc. Acad. Nat. Sci. Philadelphia, p. 398.

The single partial mandible referred to this species comes from the lizard layer of Wallingford Cave, St. Elizabeth Parish. It is complete to and including the last premolar, the last molar being lost (fig. 6). The pattern of the two remaining molars is a primitive tuberculo-sectorial one, with small accessory cusps between the main cusps. The last premolar is a simple triangular tooth, not caniniform and with no accessory cusps.

Apart from excluding the Desmodontidae, the dental formula so far as it can be made out is not restrictive. The dental pattern is much more useful in this regard. The family Noctilionidae and the subfamilies Glossophaginae, Phyllonycterinae, Carolliinae, Sturnirinae, and Stenoderminae of the family Phyllostomatidae can be immediately discarded from consideration since in these groups the dentition shows considerable specializations, usually in the direction of bunodonty, not found in the fossil. The family Thyropteridae and the subfamiles Chilonycterinae and Phyllostomatinae of the family Phyllostomatidae lack the small intermediate cusps on the molars. In the families Emballonuridae, Furipteridae, Vespertilionidae and Molossidae and in *Nyctiellus* of the Natalidae the last premolar is either caniniform or has additional cusps. Only *Chilonatalus*, *Phodotes*, and *Natalus* remain for discussion.

In both *Chilonatalus* and *Phodotes* the mandibular ramus is slender, not robust as in the fossil. *Chilonatalus* also differs in its hook-like angular process, which is straight in the fossil.

The Jamaican mandible has been compared with all the species of *Natalus* and seems indistinguishable from them generically. The compared forms are *mexicanus* from Mexico and Central America, *stramineus* from northern South America, *dominicensis*

from Dominica, material identified as *stramineus* from Anguilla, *major* from Hispaniola, and the fossil *primus* from Cuba. These forms constitute a series showing a gradual increase in size, *mexicanus* being the smallest, *primus* the largest. The Jamaican mandible is considerably smaller than that of *primus* but considerably larger than that of *dominicensis* or of the mainland forms; it is perhaps slightly larger than that of the compared *major* but in general agrees very well with *major*, and the Anguilla material which appears to be closer to *major* than to *stramineus*. The Jamaican form is therefore best considered for the present conspecific with *major*, though with more and better material it may eventually be found to be distinct (perhaps at the subspecific level) from the Hispaniolan form.

Eptesicus species

To this genus are referred two fragmentary mandibles, one small, edentulous, very fresh in appearance, from the "loose breccia" of Cambridge Cave, St. James Parish; the other larger and older in appearance, from the lizard layer of Wallingford Cave, St. Elizabeth Parish. Both are broken off behind the last molar, but the Wallingford jaw preserves all teeth except the incisors. The teeth of the Wallingford specimen are, however, peculiarly chipped and worn. Both jaws have been compared with modern *Eptesicus* and appear to be indistinguishable generically.

The specific identity of the living *Eptesicus* of Jamaica is at present in a confused state. Sanborn (1941) identified material from eastern Jamaica as *E. fuscus hispaniolae*. Shamel (1945) described a series from Montego Bay on the northwest coast as a new species, *E. lynni*, which he placed in an entirely different group of *Eptesicus* from *fuscus*. The two fossil jaws have been compared with material identified as *lynni* in the United States National Museum as well as with *fuscus hispaniolae* from Hispaniola. (No Jamaican material identified as *fuscus hispaniolae* has been seen.) Although the Wallingford jaw seems rather large and the Cambridge jaw rather small for *lynni*, both seem closer to the form described by that name than to *fuscus hispaniolae*. Unfortunately the character used by Shamel for separating the *fuscus* group from the *braziliensis* group, to which he ascribes *lynni*, that is, the cusp pattern of maxillary teeth, is of course unavailable in the fossils. In view of this

confusion and the poor quality of the fossils, specific identification has not been attempted.

COMPARISON OF RECENT AND FOSSIL FORMS

The value of any fossil material derives not from their discovery or description as such but from comparison of these fossil forms or faunas with the forms or faunas that precede and succeed them.   In this regard Anthony's collection of Recent bats in Jamaica, sometimes in the same caves with the fossils, permits a valuable contribution.

Table 3 compares in parallel columns the bats found fossil by Anthony, those found by him on the surface or just below the surface, and those collected by him alive.

The justice of the comparison depends upon the reliability of Anthony's recent and fossil collections as samples of these respective faunas.

The bats so far recorded alive from Jamaica are:

Noctilio leporinus mastivus
Chilonycteris parnellii parnellii
Chilonycteris macleayii grisea
Chilonycteris fuliginosus subspecies
Mormoops blainvillii
Macrotus waterhousii jamaicensis
Vampyrum spectrum
Carollia perspicillatum
Sturnira lilium
Ariteus flavescens
Artibeus jamaicensis jamaicensis
Reithronycteris aphylla
Erophylla sezekorni syops
Glossophaga soricina antillarum
Monophyllus redmani
Chilonatalus micropus
Eptesicus lynni
Eptesicus fuscus hispaniolae
Lasiurus degelidus
Tadarida murina
Tadarida molossus
Molossus fuliginosus
Eumops glaucinus

Of these, certain genera are recorded on very meager evidence: *Vampyrum* (one specimen), *Carollia* (one specimen), and *Sturnira* (two specimens).

There are several possible explanations of the rarity of these genera in Jamaican collections: (1) the locality records may be incorrect; (2) the individuals recorded may have been accidentals; (3) the genera may be present but genuinely rare; (4) they may not be rare but only local or may have peculiar habits and places of domicile which make them inaccessible to usual methods of collection.

In any event the absence of these genera from Anthony's collections does not argue against the general reliability of Anthony's sample of the Recent fauna.

In several other cases explanations of the last two sorts sug-

TABLE 3

BATS COLLECTED BY ANTHONY IN JAMAICA

Fossil	Surface and Subsurface	Living
Tonatia		
Natalus		
Brachyphylla		
Reithronycteris		
Ariteus	Ariteus	
Eptesicus		
Mormoops		Mormoops
	Artibeus	Artibeus
	Chilonycteris	Chilonycteris
	Macrotus	Macrotus
	Monophyllus	Monophyllus
	Glossophaga	Glossophaga
	Erophylla	Erophylla
	Tadarida	Tadarida
	Molossus	Molossus
		Chilonatalus

gested for the very rare bats probably hold for forms more certainly known to be Jamaican natives but not collected, or not collected both alive and in the surface debris by Anthony.

Thus the absence from the living collections of *Reithronycteris* known as a living form only from the type, of *Lasiurus* known from only four specimens, and of *Eumops* known from but very few more is not surprising. These forms seem to be rare; *Reithronycteris* may be extinct.

Similarly other anomalies of the record are to be regarded as explicable in terms of peculiarities of habit and habitat in the genera concerned. *Tadarida*, for example, was scarce or local

in caves in Anthony's experience of the living form. It occurs, however, in abundance in the surface layer of one cave—Peru Cave near Goshen, St. Elizabeth Parish. It seems to us that this genus may tend to be of very local distribution, restricting itself to caves not inhabited by other species, and that this cave was at one time favored by *Tadarida* but was later taken over by other types. Only *Artibeus, Chilonycteris,* and *Monophyllus* were taken alive by Anthony in this cave. Such localized habitat may account also for Anthony's failure to obtain *Noctilio* or *Eptesicus* at all and for his failure to obtain *Mormoops* (a small but not fragile species) in the surface or subsurface. Anthony mentions in his notes that in the Oxford Cave a certain section seemed reserved for *Mormoops.* In Puerto Rico Anthony reported both *Mormoops* and *Noctilio* to be very restricted in their occurrence.

Fragility may be the explanation of the absence of the smaller species of *Chilonycteris* from the surface and subsurface; only the large *C. parnellii* was obtained in these layers. A similar reason may account for the absence of *Chilonatalus* in the same layers.

No explanation so far stated accounts for Anthony's failure to obtain *Ariteus* living. It was ubiquitous in the surface and subsurface layers; it is recorded from all the caves in which such layers were collected, and it was wonderfully abundant in some of them. Sixty-five skulls (six with mandibles), four separate mandibles, and seven rostra come from Hounslow Money Cave, near Malvern, St. Elizabeth Parish, as against eight skulls, nine rostra, and three mandibles of *Artibeus.* Twenty-three skulls, three separate mandibles, and 12 rostra represent it in Peru Cave, in the same parish (compared with 13 skulls, one rostrum, and three mandibles of *Artibeus*); and 29 skulls, five mandibles, and nine rostra are from Seven Rivers Cave, St. James Parish (14 skulls, nine rostra, and five mandibles of *Artibeus*). Obviously the genus was neither rare nor localized when certain of the surface layers were laid down. Yet Anthony collected none alive, even though many *Artibeus* were obtained. It seems probable on the face of the record that this form was, like *Oryzomys,* a vanishing or already vanished form. However, the Institute of Jamaica has several specimens collected within the last decade within the neighborhood of Kings-

ton. It may nevertheless be suspected that the frequency of
Ariteus has diminished in recent times.

Thus the discrepancies that appear on first inspection of
table 3 between Anthony's two (living and surface-subsurface)
collections of Recent bats and the omission also of some forms
recorded previously from Jamaica seem to have in all cases a
plausible explanation. Anthony, collecting Recent bats in
caves very similar to those in which he collected fossils, se-
cured a very adequate representation of those bats that would
be expected in the fossil layers of these caves, if no phyletic or
faunal change had occurred since the deposits were laid down.

It seems then that the comparison in table 3 is in all major
respects valid, that the bat remains of the surface and sub-
surface are for the most part identical with those still found
living today, but that the list of these forms overlaps only very
incompletely that of the fossils from the lizard layers. In all
instances, too, the differences are not cases of phyletic change,
of the evolution of an ancestral species into a Recent form, but a
replacement at the generic level.

It will be noticed that no family or subfamily has been lost
so far as we know in the transition from the age of the lizard
layers to the Recent. All that were present (chilonycterines,
phyllostomatines, stenodermines, phyllonycterines, vespertilio-
nines, and natalids) are still present, though now mostly repre-
sented by different genera. One family (the molossids) may be a
recent addition; the "species" of *Tadarida* and *Molossus* are
weakly differentiated, and *Eumops* has no endemic form. Molos-
sid genera seem to be local (*Tadarida*) or only occasional (*Molos-
sus, Eumops*) cave dwellers, and their remains are thus not to
be expected in every cave deposit. Certain subfamilies may be
new (the glossophagines in particular, perhaps also the carol-
liines and sturnirines, if these latter are genuinely Jamaican),
but the absence of these may be chance defect in a fossil record
still very imperfectly known. In general the picture is one of
permanence at the family and subfamily level but with sub-
stitution of genus for genus within families and subfamilies.

It is an interesting speculation, whether or not this process of
substitution of forms is still continuing in Jamaica. Table 4
presents the evidence for this process as a continuing phenom-
enon. *Brachyphylla*, regarded as the most primitive steno-
dermine genus, has been for a considerable period extinct on

Jamaica. It was survived, perhaps replaced, in the near Recent by the specialized Jamaican endemic *Ariteus*. This appears now to be in process of being supplanted by the wide-ranging new

TABLE 4

NUMERICAL STATUS OF JAMAICAN BATS TODAY

Noctilionidae	
Noctilio	Rare or local
Phyllostomatidae	
Chilonycterinae	
Chilonycteris	Common
Mormoops	Rare or local
Phyllostomatinae	
Macrotus	Common
Tonatia	Extinct
Vampyrum	?Accidental
Glossophaginae	
Glossophaga	Rare or local
Monophyllus	Common
Carolliinae	
Carollia	?Accidental
Sturnirinae	
Sturnira	?Accidental
Stenoderminae	
Brachyphylla	Extinct
Ariteus	Rare or local
Artibeus	Abundant
Phyllonycterinae	
Reithronycteris	?Extinct
Erophylla	Rare or local
Natalidae	
Natalus	Extinct
Chilonatalus	Rare or local
Vespertilionidae	
Vespertilioninae	
Eptesicus	Rare or local
Lasiurus	Rare or local
Molossidae	
Tadarida	Common
Eumops	Rare or local
Molossus	Common

invader from the continent (not even subspecifically differentiated), *Artibeus*.

In the Chilonycterinae, *Mormoops* is recorded from the fossil layers and seems now to be relatively uncommon, while *Chilonyc-*

teris, unknown in the older layers, is now in several places extremely common. In the Phyllostomatinae, *Tonatia*, long extinct, appears to be replaced in the modern fauna by *Macrotus*. In the Phyllonycterinae the Jamaican endemic *Reithronycteris* may have given way to the genus *Erophylla*, of wide range in the West Indies. No evidence has appeared for generic replacement in the Glossophaginae. There seems to be a question whether or not the two genera *Monophyllus* and *Glossophaga* ever occur together.

The genus *Natalus* now has a distinctly relict distribution in the West Indies. It is extinct in Jamaica; *Chilonatalus* now represents the family Natalidae in that island. In the Vespertilionidae the situation is obscure. As mentioned above, it is not certain whether there are one or two species of *Eptesicus* on Jamaica.[1] *Lasiurus* is rare. Of the Molossidae, which may be recent arrivals, we know nothing of the earlier history, nothing of formerly successful, now extinct, or vanishing forms, thus nothing of a process of substitution of forms.

It would be unwise in the present incomplete state of the evidence to describe this apparent phenomenon as real. It is, however, a possibility worthy of further investigation. It is to be noted that generic substitution and faunal replacement need not be conceived naively in terms of the direct competition of two forms for one ecological niche but rather in terms of subtle shifts in ecology reflected by rather radical shifts in the fauna.

The geographical position of Jamaica, so close to both the mainland and the other Antilles, and the facility with which bats as flying mammals can cross water barriers are factors to be considered. Bats probably more frequently than any animals except birds might arrive as strays or migrants on the Antilles; the continental forms might thus be continually searching for foothold upon the Antillean islands (and especially upon one so close as Jamaica). Usually these new arrivals would be at a disadvantage as compared with the types already in possession. But any factor, or any ecological shift, that diminished the advantages of the natives would immediately find newcomers ready to exploit a land area now less efficiently utilized. In so

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[1] *Eptesicus* may have a different distribution now than formerly. Discovery of the genus in the very small fossil samples from Wallingford and Cambridge Caves certainly makes it probable that it was common in the regions of these caves at the time when the fossil layers were being laid down.

severely competitive a situation the native would be allowed no
time to evolve the type that could utilize the changing ecology;
its former place would be in whole or part usurped by an out-
side form before this evolution could occur.

Thus Jamaica, simply because of its proximity to the main-
land as well as to other Antilles, may subject its faunas to ex-
ceptional competition, restricting them to narrow ecological
niches.   Thus changes in faunal composition would be likely as
these rather narrow ecologies expand or contract, appear or dis-
appear.

Realization of the importance of the special geographic posi-
tion of Jamaica points up the observation that there are now a
number of forms known or reported from there that have come
to the island from Central America or the South American con-
tinent but that have not, so far as the evidence indicates, gone on
to the other Antilles.

In the rodents two such genera are known, of very different
age: *Alterodon,* known from a single tooth, contemporaneous
with *Clidomys* of the hard breccias, the single representative of
the Octodontidae *sensu* Simpson (1945) in the West Indies; and
Oryzomys of the sub-Recent extending into the Recent, the
only myomorph of the Greater Antilles.

In the bats the list is longer: *Tonatia; Vampyrum,* perhaps
an accidental;   *Carollia,* if truly Jamaican, the only representa-
tive of its subfamily in the Greater Antilles;   *Sturnira,* again,
if true, the only representative of its subfamily in the Greater
Antilles;   *Glossophaga,* certainly established in Jamaica, re-
corded by one skull, perhaps of an accidental, from New Provi-
dence in the Bahamas;   and *Eptesicus lynni,* if the Jamaican
species is correctly referred to the *brasiliensis* group.

It must be noted that while some of these forms may have
been accidentals or very temporary inhabitants of Jamaica,
several stayed long enough to speciate or subspeciate.   *Oryzomys
antillarum* seems on the material available to us to be a recog-
nizable form in which the characters cited by Goldman (1918),
on very slim evidence, seem to hold in the much more con-
siderable series we have examined.   *Glossophaga* in Jamaica is
regarded as subspecifically distinct, though closely similar to
G. soricina mutica of the Tres Marias Islands off the west coast
of Mexico (Miller, 1913b).

Such examples suggest the plausible hypothesis that Jamaica

may have been a way station on the road to the invasion of the West Indies. Such a hypothesis encounters a significant difficulty in the deficiencies of the Jamaican fauna in certain elements. Many elements (insectivores, ground sloths, and spiny rats among the mammals) that are common to two or more of the other Antilles are absent so far as known. It is a great puzzle how this way station can reveal so many forms that have stopped there and so few that can without doubt be said to have passed by way of this island to the other islands of the Antilles.

The two endemic Jamaican bat genera are of uncertain import. One, *Reithronycteris*, belongs to an endemic Antillean subfamily, the mainland derivation of which is not immediately evident. The other, *Ariteus*, has close relationship with specialized stenodermine genera on all the West Indies including the Lesser Antilles. Possibly it is a terminal endemic of a group that invaded the West Indies via the Lesser Antilles.

The close relationship of certain of the fossil bats with Hispaniolan species (*Natalus* and *Brachyphylla*) certainly indicates the passage of forms between Jamaica and Hispaniola, but the direction of passage is not indicated. It is, indeed, probable rather than otherwise, that the interrelations of the West Indian islands have been complex and never unidirectional in faunal migration.

In certain instances large-scale inferences seem possible as to the routes of invasion of genera. Thus in the genus *Natalus* there exists, as has been mentioned, a size gradient extending from Mexico with the smallest species, through northern South America, up the Lesser Antilles, and via Puerto Rico, Hispaniola, and Jamaica, to Cuba, where the largest member of the genus is known. Apparently we have here a chain of forms, at the northwest extremity of which the largest and smallest species occur in close proximity. It is reasonable to assume in these circumstances that the genus *Natalus* invaded the West Indies via the Lesser Antilles. In the same family the genus *Chilonatalus*, apparently descended from *Natalus*, a consistently smaller type, may well be derived from the ancestor of the Mexican species and thus may have invaded from Central America.

A parallel situation exists in the Glossophaginae. The endemic West Indian genus *Monophyllus* has in its eastern (Lesser Antillean) forms apparent affinities with *Glossophaga longirostris*

of South America, while the *Glossophaga* of Jamaica is probably derived from a Central American type.

But any speculation on these matters is at present based on our ignorance; critical fossil evidence is lacking.   Indeed, it can hardly be overemphasized that in discussing the relationships, sources, and directions of migration of all Antillean faunas, we have at present very insufficient grounds for opinion.   The bulk of the Antilles has been above water since the late Miocene or early Pliocene (Schuchert, 1935).   Our knowledge of the fossil history of this area does not, on the most liberal estimate, extend into more than the last twentieth of this time, and more probably it reflects a very inadequate coverage of a very much smaller fraction.   We have no knowledge of the date of invasion of any pre-Columbian form, nor is there any real ground for the frequent suggestion that a major fraction of the fauna arrived simultaneously.   There is a general lack of appreciation of the vicissitudes of the area which must, especially during the Pleistocene, have suffered very remarkable simultaneous changes in sea level and climate.   Add to this our ignorance of the fossil faunas of northern South America and of Central America, presumed sources of much of the Antillean fauna, and it must be admitted that our present conceptions founded on so little solid substratum of fact are certain to be defective in some part and are suspect in great part.

SUMMARY

The foregoing account has, in terms of described forms, not added any radical novelties to the West Indian faunal picture. *Tonatia saurophila* occurs as a Jamaican endemic, the genus being unknown elsewhere in the Antilles, and is quite comparable to the Jamaican *Oryzomys*.   The discovery of *Brachyphylla* and *Natalus* on Jamaica and the rediscovery of the phyllonycterine *Reithronycteris* round out a distributional pattern otherwise anomalous.

Very interesting are the hints presented by the fossil material of faunal replacement, of successive invasions, and successive extinctions.   The validity of this conception probably extends beyond the chiropteran order, but additional evidence is needed to translate the suggested picture into concrete terms not alone for Jamaica but for the other Antilles.

ACKNOWLEDGMENTS

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