

Brachyphylla cavernarum. By Pierre Swanepoel and Hugh H. Genoways

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Brachyphylla Gray, 1834

Fruit-eating Bats

Brachyphylla Gray, 1834:122. Type species *Brachyphylla cavernarum* Gray.

CONTEXT AND CONTENT. Order Chiroptera, Family Phyllostomidae, Subfamily Brachyphyllinae. The genus *Brachyphylla* consists of two species. The following will aid in identification (measurements in mm):

Mandibular length 18.9 or longer; length of maxillary toothrow 10.0 or longer; occurs east of Mona Passage (Puerto Rico and Lesser Antilles) *Brachyphylla cavernarum*
Mandibular length 18.2 or shorter; length of maxillary toothrow 9.9 or shorter; occurs west of Mona Passage (Greater Antilles except Puerto Rico) *Brachyphylla nana*

DIAGNOSIS. *Brachyphylla* resembles the other brachyphyllines externally in all respects except for having a more stocky build and shorter snout; lower lip with median groove ridged by papillae; nodular ridges on chiropatagium; calcar absent or very small; five lumbar vertebrae, fifth lacking spine; skull relatively long, narrow; upper incisors markedly different in size and shape, inner one large, higher than long, recurved, outer one rounded, minute, flat-crowned; anterior upper premolar minute; posterior upper premolar high and short; crowns of upper and lower molars heavily wrinkled; first lower molar with distinct posteriointernal cusp, differing markedly from last premolar; interpterygoid space not extending forward as a palatal emargination; posterior palatal emargination narrow, V-shaped; nasal region without emargination; ears small, separate; nose-leaf rudimentary; pectoral process of the humerus low and not developed into a flange; tail very short if present and wholly enclosed by interfemoral membrane. Dentition is i 2/2, c 1/1, p 2/2, m 3/3, total 32. Karyotype is $2n = 32$; FN = 60.

Brachyphylla cavernarum Gray, 1834

Lesser Antillean Fruit-eating Bat

Brachyphylla cavernarum Gray, 1834:123. Type locality St. Vincent, Lesser Antilles.

Brachyphylla minor Miller, 1913:32. Type locality Cole's Cave, St. Thomas Parish, Barbados.

CONTEXT AND CONTENT. Context is given in the generic account above. Three subspecies currently are recognized (Swanepoel and Genoways, 1978) as follows:

- B. c. cavernarum* Gray (1834:123), see above.
- B. c. intermedia* Swanepoel and Genoways (1978:38). Type locality 1 mi W Corozal, Puerto Rico.
- B. c. minor* Miller (1913:32), see above.

DIAGNOSIS. Size large for the genus in external and cranial measurements. See also aid to identification above. The cranium and mandible of *B. cavernarum* are illustrated in Fig. 1.

GENERAL CHARACTERISTICS. Color in the genus *Brachyphylla* does not exhibit a great deal of variation. Typically the hair is white to yellowish white at the base with the tips darker in some areas on the dorsum. These darker areas, which vary in size, occur as a distinct patch on top of the head and neck and a V-shaped mantle starting approximately at the shoulders and meeting posteriorly in the middle of the dorsum. The flanks are usually lighter colored. The darker areas may be blackish gray, blackish brown, grayish brown, or dark brown in color (see Fig. 2).

In a morphometric analysis of chiropteran wings, Smith and Starrett (1979) found that members of the Brachyphyllinae have the shortest wings, relatively, among the phyllostomids. They re-

semble phyllostomines in possessing relatively long forearms and have the shortest relative length of digit III as compared to the other members of the family. Smith and Starrett (1979) gave a number of statistical values for the wings of *Brachyphylla*.

Secondary sexual dimorphism is present. Males exceeded females significantly in size in all 16 measurements tested, except length of ear from one or more localities, whereas females proved to be significantly larger than males only in length of hindfoot in the sample from eastern Puerto Rico, and in breadth across upper molars in specimens from St. Lucia (Swanepoel and Genoways, 1978).

Brachyphylla cavernarum minor is distinguished by its small size, and occurs on Barbados. It is phenetically the most distinct of

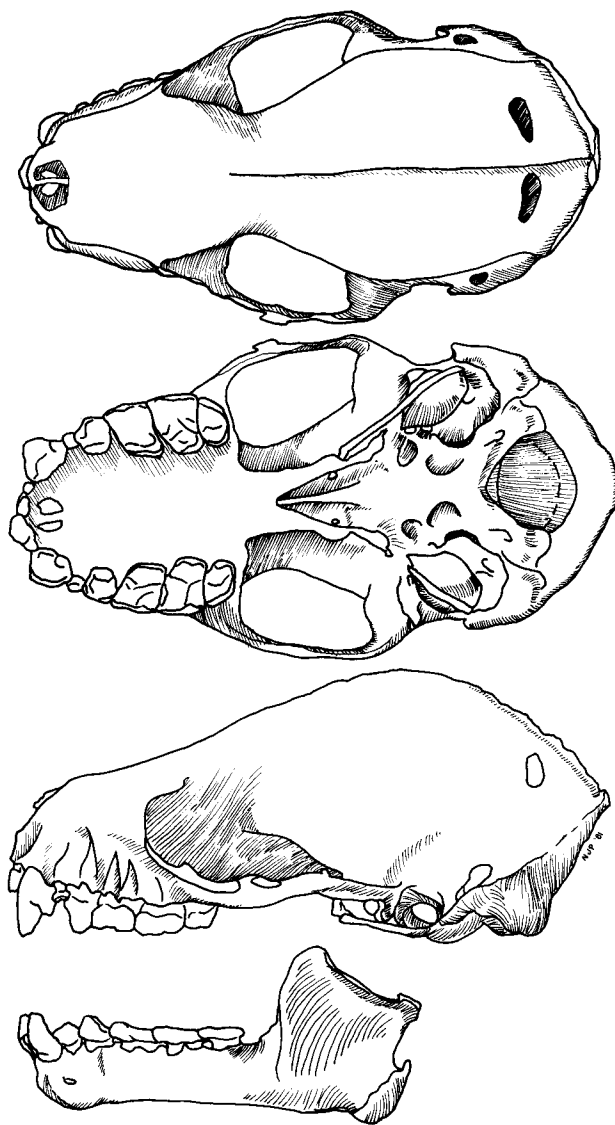


FIGURE 1. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of *Brachyphylla cavernarum intermedia* (♂, CM 44708) from Puerto Rico. Greatest length of skull is 32.5 mm. Drawn by Nancy J. Perkins.

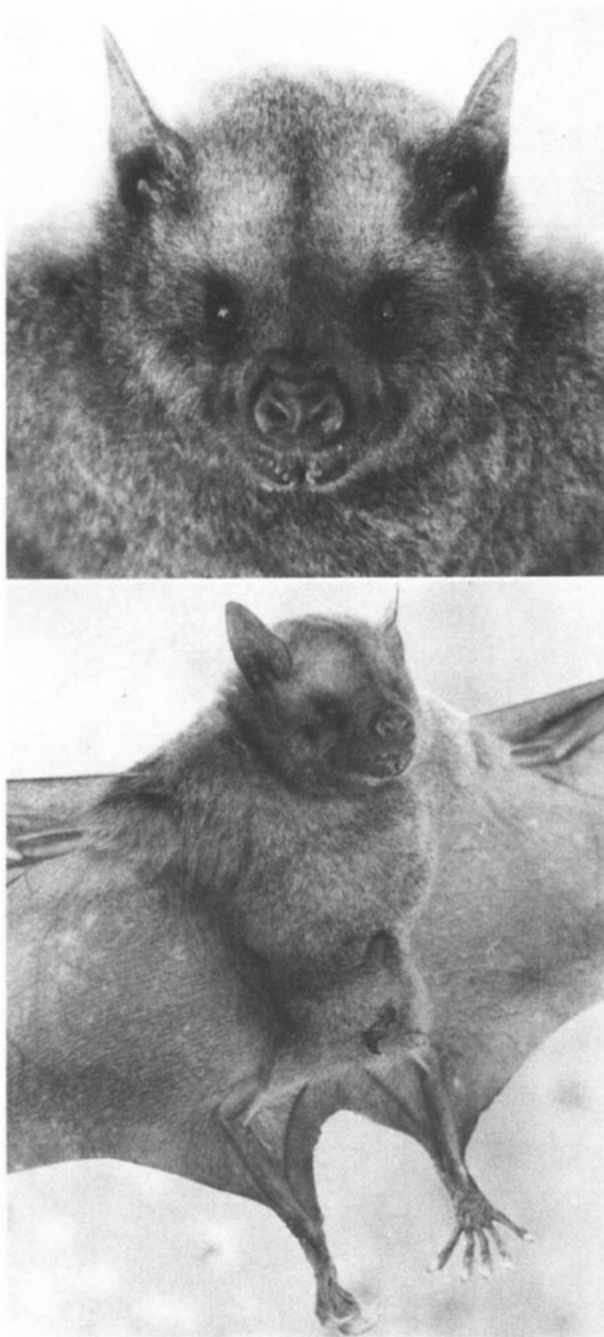


FIGURE 2. Male *Brachyphylla cavernarum cavernarum* photographed on Guadeloupe Island by Robert J. Baker.

all the subspecies. The nominate subspecies, *Brachyphylla cavernarum cavernarum*, includes the largest individuals, and occurs on St. Croix in the Virgin Islands and Anguilla southward through the Lesser Antilles to St. Vincent. The third subspecies, *Brachyphylla cavernarum intermedia*, is intermediate in size and occurs on Puerto Rico and most of the Virgin Islands (St. John, Norman, and St. Thomas, excluding St. Croix). This subspecies is not distinguished by any one single character, but its overall size as measured in multivariate analyses indicates that 80% to 90% of the individuals in this population are distinguishable from Lesser Antillean populations.

The range and sample size of external and cranial measurements (in mm) of males and females for *B. c. minor* are as follows: total length, 90 to 92 (3), 86 to 94 (8); length of hindfoot, 20 to 22 (3), 20 to 23 (8); length of ear, 22 to 23 (3), 22 to 23 (8); length of forearm, 59.2 to 63.1 (6), 59.3 to 62.4 (12); greatest length of skull, 30.0 to 31.2 (7), 29.6 to 30.9 (11); condylobasal

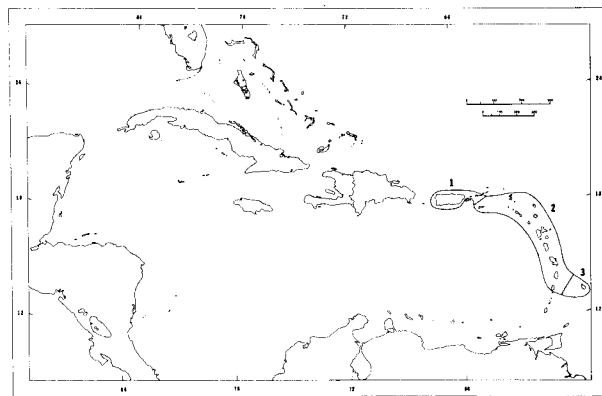


FIGURE 3. Geographic distribution of *Brachyphylla cavernarum*: 1, *B. c. intermedia*; 2, *B. c. cavernarum*; and 3, *B. c. minor*. The upper scale is in kilometers and the lower in miles.

length, 26.3 to 27.7 (7), 26.3 to 27.6 (12); palatal length, 10.7 to 12.0 (7), 10.7 to 12.3 (12); depth of braincase, 13.0 to 13.2 (6), 12.2 to 13.3 (12); zygomatic breadth, 16.2 to 16.7 (8), 16.0 to 17.2 (10); breadth of braincase, 12.2 to 12.7 (8), 11.9 to 12.7 (12); mastoid breadth, 13.7 to 14.8 (7), 13.7 to 14.6 (12); postorbital breadth, 6.1 to 6.6 (8), 5.8 to 6.5 (12); length of maxillary toothrow, 10.3 to 10.9 (8), 10.0 to 10.8 (12); rostral width at canines, 6.6 to 7.2 (8), 6.3 to 7.0 (12); breadth across upper molars, 10.9 to 11.5 (8), 10.8 to 11.9 (11); mandibular length, 18.9 to 20.0 (7), 19.1 to 20.3 (11).

Values for *Brachyphylla c. cavernarum* are as follows: total length, 80 to 98 (37), 86 to 103 (30); length of hindfoot, 18 to 23 (37), 17 to 23 (19); length of ear, 18 to 24 (23), 18 to 23 (14); length of forearm, 59.6 to 68.9 (94), 60.4 to 71.1 (68); greatest length of skull, 30.9 to 33.0 (96), 30.4 to 33.3 (85); condylobasal length, 27.1 to 29.8 (93), 26.8 to 29.4 (81); palatal length, 10.6 to 13.1 (97), 11.1 to 13.1 (81); depth of braincase, 12.3 to 14.4 (92), 12.4 to 14.1 (82); zygomatic breadth, 16.0 to 18.2 (91), 16.3 to 18.3 (79); breadth of braincase, 12.2 to 13.4 (98), 12.1 to 13.4 (85); mastoid breadth, 14.1 to 15.6 (93), 14.0 to 15.9 (82); postorbital breadth, 5.9 to 6.9 (99), 6.0 to 6.7 (86); length of maxillary toothrow, 10.5 to 11.6 (97), 10.5 to 11.4 (83); rostral width at canines, 6.7 to 8.1 (97), 6.7 to 7.7 (85); breadth across upper molars, 11.0 to 12.4 (96), 10.9 to 12.4 (85); mandibular length, 19.7 to 21.5 (90), 19.4 to 21.3 (79).

DISTRIBUTION. *Brachyphylla cavernarum* occurs on Puerto Rico, the Virgin Islands, and down the Lesser Antillean chain as far as St. Vincent and Barbados (Fig. 3).

FOSSIL RECORD. Fossils of *Brachyphylla cavernarum* are known on Puerto Rico from Cueva Cathedral (Anthony, 1918), at a late Pleistocene level according to Smith (1976); from Cueva Monte Grande at an unspecified time level (Reynolds et al., 1953); from Cueva de Clara, Cueva del Perro, and Cueva de Silva in sub-Recent times (Choate and Birney, 1968); and from Antigua in sub-Recent times (Wing et al., 1968).

FORM AND FUNCTION. Baker and Genoways (1978) ascribed the success of *B. cavernarum*, which occurs on at least 13 of the 19 major islands in its range, to its large, robust size and varied diet.

Wing loading was found to be in the range of 16 g/cm² (Nellis and Ehle, 1977). Nellis (1971) reported *B. cavernarum* carrying sapidilla fruits (*Manilkara zapota*). These fruits weighed 30 to 34 g, whereas the bats weighed 34.4 to 49.2 g. However, in captivity Nellis and Ehle (1977) found that these bats were unable to carry fruit half their body weight. These authors reported that the intestinal transit time was 15 min, which agrees with the findings of Klite (1965) for other bats.

In a study of thermoregulation in *B. cavernarum* from St. Croix, McManus and Nellis (1972; see also McManus, 1977) found this species to be a good thermoregulator, showing greater resistance to cold stress than *Artibeus jamaicensis* and *Molossus molossus*. The 20 test animals, which had a mean weight of 40.1 g (range 31.1 to 45.1), had rectal temperatures of 39.8 ± SD 0.40°C. Exposure to ambient temperature of 10.6 ± SD 3.13°C (range 4.5 to 14.3) caused a continuous decrease in body temperature throughout the period of exposure. After 24 h, body temperature was still

above 25°C. None of the test animals died during exposure. Nellis and Ehle (1977) concluded that body temperature in young animals seemed to be lowered during sleep in contrast with that of adults.

Benedict (1957) provided a detailed description and photographs of the hair structure of *B. cavernarum*. The overhair was found to average 9 mm in length and to have a maximum diameter of 30.6 microns and a diameter of 25.5 microns at the midpoint of the hair. The maximum diameter of hair is in the distal portion. Melanin granules were generally dispersed in the distal two-thirds of the filament, with most in the distal third. The scale form was of the medium and short, erose coronal type.

The results of hematological determinations by Valdivieso and Tamsitt (1971) showed polychromatophilia in *B. cavernarum* in 65% of the samples, normoblasts in 33%, and cabot rings, usually seen in stained erythrocytes of severe anemias, in 22%. Hemograms (percentages of leucocytes of each type) for two males, three females, and four gravid females from St. Croix, respectively, were given by Valdivieso and Tamsitt (1971) as follows (mean \pm 1 SE, range): neutrophils, 70.5 (70 to 71), 60.0 (55 to 65), 56.8 ± 2.8 (51 to 64); lymphocytes, 24.0 (24), 34.7 (32 to 37), 38.5 ± 2.4 (32 to 42); eosinophils, 2.0 (1 to 3), 2.0 (1 to 3), 3.0 ± 1.1 (1 to 6); basophils, 0.5 (0 to 1), 0.3 (0 to 1), —; monocytes, 3.5 (3 to 4), 2.3 (2 to 5), 1.8 ± 0.5 (1 to 3); hemoglobin concentration (g/100 ml) was 18.3 (18.2 to 18.4), 17.6 (16.8 to 18.6), 15.5 (15.3 to 15.7). These authors also gave the diameter in microns (mean \pm 1 SE, range) of erythrocytes of nine adult *B. cavernarum* (sexes combined) and eight pregnant females as follows: 5.5 ± 0.4 (4.1 to 7.7), and 5.5 ± 0.06 (4.1 to 7.6).

Valdivieso and Tamsitt (1974) presented data on the serum proteins of a single lactating female from Puerto Rico. This individual had a total serum protein of 6.03 g/100 ml. Of the bats tested, this individual had the greatest percentage of protein in the gamma region. The overall serum pattern of *B. cavernarum* was found to be unlike that of *Erophylla* and to be more similar to that of the vespertilionid bat *Eptesicus fuscus*.

McDaniel (1976) studied both the external and internal morphology of the brain of *Brachyphylla cavernarum*. Externally it was characterized by having relatively smooth and massive cerebral hemispheres. "The major cerebral sulci are well developed, including the sulcus anterior to the pseudocentral sulcus. The pseudotemporal lobes are ventrally angular, but do not protrude ventrally. The inferior colliculi are not visible from above. The vermiform body of the cerebellum is laterally enlarged and constitutes half of the dorsal exposure of the cerebellar tissues." An additional external character of the brain of *Brachyphylla cavernarum*, not found in any other phyllostomid brain, was the greatly enlarged uvular portion of the cerebellum which formed a prominent lobe at the posterior edge of the vermiform body along the dorsal surface of the medulla.

The internal structure of the brain of *B. cavernarum* differs in some ways from that of other phyllostomids (McDaniel, 1976). The cerebrum is remarkably circular in cross section. "Anteriorly, the interhemispheric sulcus includes only a well-developed cingulate sulcus. Posteriorly, there is a shallow cingulate sulcus and a callosal sulcus similar to that of the Desmodontinae. Cortical cells dorsal to the corpus callosum and substantia alba do not form a dense layer distinct from the overlying cortex." Of all the brains of phyllostomid species studied, that of *B. cavernarum* is the only one in which the lateral olfactory tracts are located on the lateral aspects of the cerebrum. "The lateral thalamic nuclei project no higher than the habenular nuclei. The amygdaloid nuclei are large as in the phyllostomatines. The pons is deep, wide, and ventrally flattened."

According to McDaniel (1976) the magnitude and nature of the differences between the structure of the brains of *B. cavernarum* and *Erophylla bombifrons* indicate a greater divergence than within any other subfamily of phyllostomids. He did not examine the brain of *Phyllonycteris*. On the basis of brain anatomy, McDaniel (1976) concluded that the affinities of *Brachyphylla cavernarum* are with the Desmodontinae or possibly the Stenoderminae rather than with the other brachyphyllines.

The structure of the alimentary tract of *B. cavernarum* was reported on by Rouk (1973) and Forman et al. (1979). The esophagus enters the stomach near the gastroduodenal junction with the result that the lesser curvature between the esophagus and duodenum is extremely short. The fundic caecum is well developed, forming a bag-like structure that appears to be nearly compartmentalized into a two-chambered structure. The caecum bends abruptly anteriorly about midway along its length. Here there is a constriction in the muscularis externa which has not been found to function as a sphincter. The duodenum is enlarged where it enters the stomach,

which is separated from the intestine by a distinctive construction. The stomach of *Brachyphylla* is distinctive among the phyllostomids; however, no other brachyphylline stomach has been studied.

The valve flap of the pyloric sphincter of bats that feed on plant material, including fruit, nectar, and pollen, is nearly always longer and thinner than valves of bats that feed on animal material. This feature is particularly well developed in *B. cavernarum*, and in the stenodermines (Forman et al., 1979). *B. cavernarum* is among the species of phyllostomids with the longest intestines relative to body length (Forman et al., 1979).

The mucus-producing glands of Brunner are generally restricted to an extremely narrow submucosal ring at the gastroduodenal junction of the stomach. Several unusual conditions with respect to Brunner's glands occur within the phyllostomids. In *B. cavernarum*, the only brachyphylline examined by Forman et al. (1979), these glands were absent.

Forman and Genoways (1979) found the head of the sperm of *B. cavernarum* to be of moderate length, and narrow. The symmetrically-shaped acrosome is considerably shorter than the nucleus, and has its posterior limit well anterior to the midpoint of the nucleus. The nucleus is more ovoid than that of *Ardops*, *Arteus*, and *Artibeus*. The base of the head is slightly concave. The neck is short and the junction with the head is near the center. The midpiece is of moderate width, long, and tapers posteriorly; the junction with the tail is distinctive. Measurements (in microns) of sperm of two specimens from Guadeloupe are as follows: head length, 4.60, 5.12; acrosome length, 2.79, 2.79; nuclear length, 3.26, 3.53; width of head, 2.79, 1.98. The sperm of *B. cavernarum* was found to be unlike that of other brachyphyllines examined (for example, it differs in shape and size of the acrosome, relative length of midpiece, and symmetry of the head), and based on sperm morphology, *B. cavernarum* could be distinguished by its long midpiece.

ONTOGENY AND REPRODUCTION. Anthony (1918) reported that nursing females were collected on 5 July on Puerto Rico but no young were noted. During December 1956, Bond and Seaman (1958) examined 25 females from St. Croix, none of which showed enlarged uteri and ovarian follicles, nor grossly apparent corpora lutea. In males the testes measured from 4 to 6 mm long. All specimens examined were adult or subadult. Walker et al. (1964) reported lactating females from Puerto Rico in July, and Walker et al. (1975) reported pregnant females from there in February, and a lactating one in April, and on St. Croix pregnant females were observed in March. Nellis (1971) reported a lactating female from St. Croix during April.

Nellis and Ehle (1977) observed parturition to occur within a 3-week period during late May and early June on St. Croix. During this time the colony was almost exclusively composed of mothers and their single young together with only a few adult males or barren females. These authors also concluded that because simultaneous apparent population declines just prior to parturition occur throughout St. Croix, females may become solitary during this time.

Baker et al. (1978) captured 15 adult females on Guadeloupe during July of which none was pregnant, three were lactating, and four were postlactating. These authors surmised that *B. cavernarum* probably has a more synchronized reproductive cycle than, for instance, *Artibeus*. In 10 males captured during the same time the testes length was 4 mm for one individual, 5 for five, and 6 for four.

Of nine *B. cavernarum* taken from Montserrat, Jones and Baker (1979) reported six to have been adult females, four of which were lactating. Two adult males had testes measuring 6 and 7 mm in length. One individual was a volant young.

Based upon the available data, Wilson (1979) suggested a synchronized reproductive cycle in *B. cavernarum*. He also suggested that a second period of parturition occurred annually in at least some populations.

ECOLOGY. Bats of the species *Brachyphylla cavernarum* have been reported to roost in the following situations: in small colonies in old disused buildings or in dense tree tops on St. Croix (Beatty, 1944); in large numbers in suitably sized caves, frequently in well-lighted areas near the entrance, even in extensive caves on Puerto Rico (Anthony, 1918, 1925); in caves and in an underground unused sugar house on St. Croix, always in complete darkness (Koopman, 1975); in a deep crevice on St. Croix (Valdivieso and Tamsitt, 1971). On St. Croix, Nellis and Ehle (1977) found that they generally roosted in large colonies in dark sites; however, a colony of 5,000 bats illuminated by direct sunlight was found in a large well (4 m in diameter and 50 m deep), another colony was in a sea cliff cleft with subdued lighting, and another small colony was hanging from the wooden beam ceiling of a dimly lighted ware-

house. In captivity Nellis and Ehle (1977) found *B. cavernarum* selecting the darkest area of the cage to roost. They concluded that the use of lighter roosts is atypical and ascribed this behavior to a lack of more suitable locations in an otherwise favorable environment. On St. Croix, roosts were found to be monospecific.

The microclimate in Coles Cave on Barbados inhabited by *B. cavernarum* was described by Schwartz (*in* Buden, 1977) as being "moist and humid but not extremely hot" as were caves inhabited by *B. nana* on Cuba. Individuals of *B. cavernarum* have been taken on St. Eustatius on a steep-sided volcanic crater in a net placed across a path at the rim of the crater. Other bats taken in this net were of the species *Ardops nichollsi* and *Artibeus jamaicensis* (Ray, pers. comm., *in* Jones and Schwartz, 1967). On Dominica *B. cavernarum* was netted together with *Ardops*, *Artibeus*, *Monophyllus*, and *Sturnira* over a rock-strewn gravel bar in the Layou River (Jones and Schwartz, 1967; Schwartz and Jones, 1967). Homan and Jones (1975) also reported *Myotis dominicensis* being taken with *B. cavernarum* on Dominica.

B. cavernarum occurs in "dry arborescent vegetation" on St. John together with *Stenoderma rufum*, *Noctilio leporinus*, *Artibeus jamaicensis*, *Tadarida brasiliensis*, and *Molossus molossus* (Hall and Bee, 1960). In the Laquillo National Forest on Puerto Rico, bats of the species *B. cavernarum* were netted above the forest canopy together with those of *S. rufum* and *A. jamaicensis*. However, *B. cavernarum* was not found under the canopy of the broad-leaved forest at this place (Jones et al., 1971). Anthony (1918) noted that *A. jamaicensis* and *B. cavernarum* are often associated and are very similar in habits.

Although *B. cavernarum* occurred at six of the nine collecting localities sampled on Guadeloupe, it was common only at one on Grande-Terre in a dry canyon containing low dry scrub where netting took place under native trees. The limestone nature of Grande-Terre, which may provide caves and rock crevices for roosting, might be the reason that these bats are more common there (Baker et al., 1978). Elsewhere on Guadeloupe, these bats were taken over a boulder-strewn river in rain forest over a large stream lined with gallery forest, and high on the southwest slopes of the Soufriere volcano where banana groves gave way to tall native forest. Other bats taken at these same locations include those of the species *A. jamaicensis*, *Ardops nichollsi*, and *M. molossus* (Genoways and Jones, 1975).

Six wheelbarrow loads of dead *B. cavernarum* were removed after about 2,000 bats were gassed in an old sugar house on St. Croix during December 1956. The bats consisted of both adult and subadult animals. One load yielded a sex ratio of 63 males to 276 females (Bond and Seaman, 1958).

The diet of *B. cavernarum* is pollen, fruit, and insects (Bond and Seaman, 1958; Gardner, 1977; Nellis, 1971; Nellis and Ehle, 1977). Nellis (1971) found this bat on St. Croix eating the fruit of *Manilkara zapota*, and Nellis and Ehle (1977) found it feeding on papaya (*Carica papaya*), mango (*Mangifera indica*), West Indian almond (*Terminalia catappa*), manjack (*Cordia* spp.), royal palm (*Roystonea beringuena*), and sapodilla (*Manilkara zapota*). The latter authors also found captive bats to feed on bananas, apples, pears, melons, peaches, but not citrus, and the flowers of silk cotton (*Ceiba pentandra*), sausage tree, royal palm, portia tree (*Thespesia populnea*), and locust (*Hymenaea courbaril*).

Nellis and Ehle (1977) were unable during their field observations to distinguish between pollen and nectar consumption. Droppings from roosts mainly showed pollen. They found stomach contents from specimens collected while feeding on locust flowers to contain pollen and fluid that might have been nectar. Coprophagy was observed when sticky feces adhered to the fur and were removed by grooming.

Although individuals of *B. cavernarum* were netted while carrying ripe sapodilla fruit (*Manilkara zapota*), these were never carried to the roosts (Nellis, 1971). Bats were found to feed in the upper parts of the tree canopy. However, they were also observed feeding on the ground on fallen fruit or flowers (Nellis and Ehle, 1977).

One species of mite (Macronyssidae), two species of batfly (Streblidae), one species of tick (Argasidae), and two species of labidocarpid are known from *B. cavernarum* as follows (Cruz et al., 1974; Tamsitt and Fox, 1970a, 1970b; Webb and Loomis, 1977): *Redfordiella oudemansi* (Puerto Rico), *Nycterophilina coxata* (British West Indies), *Trichobius truncatus* (Puerto Rico), *Ornithodoros hasei* (Guadeloupe, Martinique), *Lawrenceocarpus micropilus* (Puerto Rico), and *L. puertoricensis* (Puerto Rico). In addition Bond and Seaman (1958) observed fleas and batflies (Streblidae) on these bats from St. Croix. Valdivieso and Tamsitt (1971) observed no hemoparasites in specimens from St. Croix. No endo-

parasites have been recorded from *B. cavernarum* (Ubelaker et al., 1977).

BEHAVIOR. *Brachyphylla cavernarum* was described as being quarrelsome and petulant by Anthony (1918), and belligerent and pugnacious both towards conspecifics and other species by Nellis and Ehle (1977). The latter authors observed fighting to be so severe at times that broken wings resulted. In spite of this Nellis and Ehle (1977) and Fenton and Kunz (1977) found them in tight groups during the day with individual bats frequently moving from one group to another. In a large roost the general appearance was that the bats were active most of the day, grooming, quarreling, or moving around. Individuals or groups appear to sleep only for short intervals.

Initial emergence from roosts was found to be synchronous at more than an hour after sunset and at least 20 minutes after the emergence of *A. jamaicensis* from similar roosts. A similar synchrony with a sharp drop in activity just before the first evidence of dawn was found for the returning bats.

The following observations on the feeding behavior of *B. cavernarum* were reported by Nellis and Ehle (1977). When feeding on flowers they mouth the anthers and extend their tongues into the nectaries. On juicy fruit, they rapidly lick, stopping every few seconds to swallow. Firm fruit is chewed until the pulp is dry, after which it is discarded by shaking the head with the mouth open. In captivity, the bats treat flies and mealworms in a similar manner.

Individuals of *Brachyphylla cavernarum* usually tolerated conspecifics feeding on the same or nearby fruit or flowers, but hostility was shown towards any *A. jamaicensis* in the vicinity. When *B. cavernarum* began feeding in the upper parts of the canopy, *A. jamaicensis* moved to the lower areas. As *B. cavernarum* started feeding lower, *A. jamaicensis* gave way completely. *A. jamaicensis* never succeeded in displacing *B. cavernarum* at a feeding site (Nellis and Ehle, 1977). An individual of *B. cavernarum* often landed on or near a feeding *A. jamaicensis* and would then chase it. *B. cavernarum* was found to be much better at clambering about on trees than *A. jamaicensis*, usually climbing to nearby flowers, whereas *A. jamaicensis* flew there (Nellis and Ehle, 1977).

In a captive colony, immatures became active first. Self-grooming was the first activity on arousal. Mutual grooming was observed infrequently between adults but more commonly between mother and young (Nellis and Ehle, 1977).

Recognition of roostmates or parent-child recognition is based primarily on smell. The first few weeks of life, the young mostly groom, sleep, and nurse. First free flight occurs at about 2 months of age. During a year of severe drought, mortality of both mother and young was found to be very high. Some roosts were abandoned and it was surmised that this might have been because of the stench of dead and rotting bats (Nellis and Ehle, 1977).

GENETICS. *Brachyphylla cavernarum* has a diploid chromosomal number of 32; there are 60 autosomal arms. All the autosomes are metacentric or submetacentric. The X chromosome is subtelocentric and the Y is a minute element. There is a secondary constriction on one of the smallest pairs of autosomes (Baker and Lopez, 1970).

Baker et al. (1981) suggested that a karyotype similar to that of *B. cavernarum* and characteristic of *Glossophaga* was primitive for a clade including the Brachyphyllinae and the glossophagine genera *Anoura*, *Glossophaga*, *Monophyllus*, *Leptonycteris*, *Phyllonycteris*, and *Choeronycteris*.

REMARKS. The genus *Brachyphylla* was erected by Gray in 1834. Gray (1838) placed the genus in the tribe Phyllostomina of the family Vespertilionidae. Gervais (1855-1856) placed the genus in the tribe Stenodermina, which subsequently was recognized as the subfamily Stenoderminae of the family Phyllostomidae. In 1866, Gray erected the tribe Brachyphyllina with *Brachyphylla* as the sole genus. Later, Dobson (1878) included *Brachyphylla* in his group Stenodermata but stated that it was the most closely related of all known genera of phyllostomids to the desmodontines. In fact, Winge (1892) arranged it as a desmodontine, and McDaniel (1976), in his study of the brain anatomy, also thought the *Brachyphylla* was most closely allied to the desmodontines, or possibly the stenoderminae. Allen (1898) placed *Brachyphylla* in the subfamily Glossophaginae, but separated it in a group termed Brachyphyllina along with *Phyllonycteris* and *Erophylla*. Miller (1898), in describing *Reithronycteris* (= *Phyllonycteris*), followed this arrangement but clearly allied *Reithronycteris* with *Brachyphylla*, *Phyllonycteris*, and *Erophylla*. Miller later changed his opinion and stated that he could detect no indication that *Brachyphylla* was a phyllonycterine and placed it in the subfamily Stenoderminae

(Miller, 1907). Here it remained until Silva-Taboada and Pine (1969) presented evidence based on osteology, behavioral characteristics, and host-parasite specificity for considering *Brachyphylla* a member of the subfamily Phyllostercinae. However, as Baker (1979) pointed out, Brachyphyllinae is the oldest available family-group name for the subfamily. Slaughter (1970) reflected on the similarity between this genus and *Sturnira* and thought it possible that these two genera, in addition to the glossophagines and stenodermines, were related to some unknown common ancestor, and concluded that the dentition offered no evidence that *Brachyphylla* was any more closely related to the stenodermines than *Sturnira*. The latter is now included in the Stenoderminae by most authorities. Analysis of the chromosomes of *Glossophaga soricina*, *Monophyllus redmani* (Glossophaginae), *Phyllonycteris aphylla*, *Erophylla sezekorni*, and *Brachyphylla nana* (Brachyphyllinae), indicated no detectable differences in the G- and C-band patterns among the karyotypes of these species (Baker and Bass, 1979). These taxa have been found not to be closely allied to the Stenoderminae on the basis of chromosomal data (Baker et al., 1979). Baker and Bass (1979) surmised that if the primitive karyotype for the family Phyllostomidae is similar to that of *Macrotus waterhousii*, then the above members of the Glossophaginae and Brachyphyllinae shared a common ancestor after evolving their highly derived karyotypes. This evidence casts doubt on the validity of the subfamily Brachyphyllinae, which perhaps should be placed in the Glossophaginae. However, Baker et al. (1981) found that both electrophoretic and immunological data sets supported the hypothesis that the Brachyphyllinae forms a natural evolutionary unit.

In erecting the genus *Brachyphylla*, Gray (1834) described *cavernarum* from St. Vincent as the first species. Subsequently three additional species were described, *nana* by Miller (1902) from Cuba, *minor* by Miller (1913) from Barbados, and *pumila* by Miller (1918) from Haiti. Koopman (1968) presented evidence for considering *minor* a subspecies of *cavernarum*. Varona (1974; see also Hall, 1981), without presenting any evidence, recognized only one species, *B. cavernarum*, with all other previously recognized species as subspecies thereof. Jones and Carter (1976) and Silva-Taboada (1976, 1979) recognized two species, *B. cavernarum* and *B. nana*, with *minor* as a subspecies of the former and *pumila* of the latter. Buden (1977), studying geographic variation in Greater Antillean populations, agreed with Varona's (1974) arrangement. Swanepoel and Genoways (1978), in a revision of the genus, showed it to consist of two species, *B. cavernarum* and *B. nana*. The former species consists of three subspecies, one of which was described as new, and the latter is a monotypic species.

Zoogeographically, the genus *Brachyphylla* is an endemic to the Antillean islands. It is a member of the otherwise Greater Antillean subfamily Brachyphyllinae. The probability that *B. cavernarum* originated in the Greater Antilles and subsequently invaded the Lesser Antilles is greater than the reverse (Baker and Genoways, 1978; Koopman, 1975).

The generic name, formed from the Greek words *brachys* and *phyllon*, means "short leaf" in reference to the short, broad nose-leaf of members of the genus. The specific name is from Latin and refers to caves or grottos in which this species typically roosts. The subspecific epithets *intermedia* and *minor* refer to the general overall size, intermediate and small, respectively, of the individuals of the two subspecies.

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