

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2742, pp. 1-45, figs. 1-33, table 1 August 2, 1982

Systematics of the New World Nectar-Feeding Bats (Mammalia, Phyllostomidae), Based on the Morphology of the Hyoid and Lingual Regions

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ABSTRACT

Dissection and histological examination of the hyoid and lingual regions of the New World nectar-feeding bats reveal marked modification of the tongue retractor musculature (Mm. sternohyoideus, geniohyoideus, hyoglossus, styloglossus, and genioglossus) and modification of the internal and external tongue structure from the conditions found in non-nectar-feeding bats. Use of these derived characters in a cladistic analysis leads to the phylogenetic hypothesis that nectivory evolved twice independently in the family Phyllostomidae. One group of nectar-feeding phyllostomids, comprising the genera *Lonchophylla*, *Lionycteris*, and *Platalina* (traditionally considered glossophagines) deserves separate subfamilial status based on the markedly different adaptations for necti-

vory observed. The other group, comprising the remaining 10 glossophagine genera (Glossophaginae, *sensu stricto*), plus *Phyllonycteris*, *Erophylla*, and perhaps *Brachyphylla* form a monophyletic group. Within the newly restricted subfamily Glossophaginae there are two major clades. One clade is composed of *Glossophaga*, *Monophyllus*, and surprisingly, *Lichonycteris*. The other is composed of the more derived nectar-feeding genera: *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and probably *Scleronycteris* and *Musonycteris*. Interestingly, both karyotypic evidence, and evidence from dental and basicranial studies, can be interpreted to support the phylogeny presented here.

INTRODUCTION

For almost 15 years the systematic status of the New World nectar-feeding bats (subfamily Glossophaginae) has been disputed. Baker (1967) first suggested that the subfamily Glossophaginae might not be a monophyletic group on the basis of his karyotypic studies of several genera of the group. Since then Baker and others (see Baker, 1970,

1973; Baker and Lopez, 1970; Gerber and Leone, 1971; Phillips, 1971; Stock, 1975; Gardner, 1977; Baker and Bass, 1979; Baker et al., 1981) have continued to examine this question, but while many investigators agree that the group is probably not monophyletic, there is little agreement as to exactly how the group should be properly divided.

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In addition to the comparatively large subfamily Glossophaginae, there is a smaller group of endemic Antillean genera that are at least partly nectivorous. These genera have been traditionally placed in a separate subfamily, the Brachyphyllinae (=Phylloonycterinae, Miller, 1907). However, recent karyological work (Baker and Bass, 1979) and immunological work (Baker et al., 1981) indicated that the Brachyphyllinae may be closely related to *Glossophaga* and *Monophyllus* (both glossophagines). This finding led Baker and Bass (1979) to question the validity of the subfamily Brachyphyllinae, and to once again suggest that the Glossophaginae might not be a monophyletic group.

The hyoid and lingual regions of the glossophagine bats are highly modified (Sprague, 1943; Wille, 1954; Winkelmann, 1971; Greenbaum and Phillips, 1974; Howell and Hodgkin, 1976; Griffiths, 1978a) presumably to permit the hyperextension of the tongue required for nectar-feeding. These modifications are complex and extensive, and thus are ideal for use as derived characters (apomorphies, Hennig, 1966) in a cladistic study. The main purpose of this paper is to attempt to resolve the question of the monophyly of the subfamily Glossophaginae via dissection of the hyoid region and histological examination of the tongue. Secondary purposes include resolving the exact systematic relationship of the three genera of the other nectar-feeding subfamily (Brachyphyllinae) to the Glossophaginae, and determining the relationships of the genera within each subfamily to one another. To accomplish these goals, representative species of each genus of glossophagine (except *Musonycteris* and *Scleronycteris*, which were unavailable) were dissected and compared with representative species of each genus of brachyphylline bat, and with a variety of species of non-nectar-feeding phyllostomid bats.

HISTORY OF THE PROBLEM

The first attempt at a unified classification of a large number of New World bats was that of Dobson (1878). Dobson recognized two subfamilies within the family Phyllostomidae: the Lobostominae (=Mormoopidae, Smith, 1972) and the Phyllostominae.

Within the Phyllostominae, he recognized four "groups": the Vampyri, the Glossophagae, the Stenodermata, and the Desmodontes. The Glossophagae contained 10 species in seven genera. These genera were *Glossophaga*, *Phylloonycteris*, *Monophyllus*, *Ischnoglossus* (= *Leptonycteris*), *Lonchoglossa* (= *Anoura*), *Glossonycteris* (= *Anoura*), and *Choeronycteris*.

The "group" Glossophagae was considered distinct from all other phyllostomids on the basis of: (1) the long, narrow muzzle; (2) the long, extensible tongue "clothed with filiform papillae"; and (3) the deep groove in the lower lip. Except for the inclusion of *Phylloonycteris*, today considered to be grouped with *Brachyphylla* and *Erophylla* in a separate, endemic Antillean subfamily, the "group" Glossophagae includes all the bats then known that are today considered to belong to the subfamily Glossophaginae.

Miller (1907) reexamined the species known to Dobson, plus specimens in the United States National Museum and museums in Paris, Leiden, and Berlin. Basing his classification on the structure of the wing, sternum, shoulder girdle, and tooth cusps, Miller divided the Chiroptera into two suborders, 17 families, and 19 subfamilies. All subsequent classifications of the Chiroptera are based on Miller's work, including Simpson (1945), Hall and Kelson (1959), Koopman and Cockrum (1967), Koopman and Jones (1970), Smith (1976), and Hall (1981). Miller (1907) divided the family Phyllostomidae into seven subfamilies: the Chilonycterinae (=family Mormoopidae, Smith, 1972), Phyllostominae, Stenodermatinae, Phylloonycterinae (=Brachyphyllinae, Baker, 1979), Hemiderminae, Sturnirinae, and Glossophaginae. Miller (1907) recognized that *Phylloonycteris*, "*Reithronycteris*" (= *Phylloonycteris*, Koopman, 1952), and *Erophylla* deserved separate subfamilial status on the basis of the "peculiar" tooth structure and the modified noseleaf. Miller also added the genera *Lonchophylla*, *Hylonycteris*, and *Lichonycteris* to the subfamily Glossophaginae, and recognized Dobson's "*Ischnoglossa*" and "*Glossonycteris*" as *Leptonycteris* and *Anoura*, respectively. With the addition of five more genera (*Scleronycteris*, Thomas, 1912;

Lionycteris, Thomas, 1913; *Choeroniscus*, Thomas, 1928; *Platalina*, Thomas, 1928; and *Musonycteris*, Schaldach and McLaughlin, 1960), the subfamily Glossophaginae was generically complete as it is traditionally recognized today.

However, recent investigations in the areas of chromosome morphology, immunological reactions of blood sera, and hard morphology of the basicranial skull and teeth have given rise to speculation that the classic "Glossophaginae" may not be a monophyletic group. Baker (1967, 1970), on the basis of chromosome morphology, suggested that *Leptonycteris sanborni*, *Glossophaga soricina*, *G. alticola*, and *G. commissarisi* form a distinct group which may be more closely related to *Phyllostomus hastatus*, *Macrotus waterhousii*, and *Trachops cirrhosus* (all subfamily Phyllostominae) than to two other glossophagines: *Choeronycteris mexicana* and *Choeroniscus godmani*. Baker (1967) hypothesized that the Glossophaginae may actually be an artificial grouping of nectar-feeders, evolved from two or more independent lines. *Choeronycteris* and *Choeroniscus* karyotypically showed great similarity to *Carollia subrufa* and *Carollia perspicillata* (subfamily Carollinae), whereas another glossophagine, *Anoura geoffroyi*, showed similarities to both the *Leptonycteris-Glossophaga* group and the *Choeronycteris-Choeroniscus* group, but was karyotypically distinct from each. Baker and Lopez (1970) added *Monophyllus redmani* to the *Leptonycteris-Glossophaga* group. They also, however, examined the karyotypes of bats of the other New World nectar-feeding subfamily, the Brachyphyllinae (=Phyllonycterinae) and found that the chromosomes of *Erophylla* and *Brachyphylla* (both brachyphyllines according to Silva Taboada and Pine, 1969; and Nagorsen and Peterson, 1975) are similar to each other, and to those of the *Leptonycteris-Glossophaga-Monophyllus* group. Further work by Baker (1973), Gardner (1977), and Baker and Bass (1979), confirmed this finding, and both Gardner (1977) and Baker and Bass (1979) suggested that the Brachyphyllinae (=Phyllonycterinae) be grouped with the *Glossophaga-Monophyllus* group within the Glossophaginae (see fig. 1).

Gerber and Leone (1971), studying the

immunologic reactions of sera of glossophagine bats, also suggested that the Glossophaginae were an artificial grouping of nectar-feeders. They too suggested that there was a distinct *Glossophaga* group and a distinct *Choeronycteris* group. However, relationships of these groups to non-glossophagines were directly opposite to those suggested by Baker (1967). *Glossophaga soricina* and *Glossophaga commissarisi* were immunologically more closely related to *Carollia* than to *Choeronycteris*; *Choeronycteris mexicana* was most closely related to *Phyllostomus*, *Chrotopterus* (both phyllostomines), and surprisingly, to *Desmodus*, the vampire bat. Recent electrophoretic and albumin immunological work by Baker et al. (1981) seem to contradict the karyotypic studies further. Baker et al. (1981) presented evidence that *Anoura*, *Glossophaga*, *Monophyllus*, *Leptonycteris*, *Hylonycteris*, and *Choeroniscus* form a clade. This suggestion directly contradicts the karyotypic studies (see Baker, 1967; Baker and Bass, 1979) that suggest the Glossophaginae are not monophyletic.

Stock (1975) contributed to the Baker/Gerber and Leone controversy by reexamining chromosomes of *Carollia* and *Choeroniscus* using G and C banding techniques. Stock showed that although the gross chromosomal morphology of *Carollia* and *Choeroniscus* is similar, banding patterns show that there is no relationship between *Carollia* and *Choeroniscus* [refuting half of Baker's (1967) hypothesis].

Slaughter (1970) examined dentitions of a number of bats, including a few glossophagines. Although he did not divide the Glossophaginae into two formal groups, Slaughter did observe that "primitive" glossophagines such as *Glossophaga* and phyllostomines such as *Macrotus* may have shared a recent common ancestor. Slaughter (1970) also noted the similarity between "advanced" glossophagine (*Choeroniscus*-type) teeth, and the teeth of carollines and desmodontines (vampires). Phillips (1971) examined the dentitions of the glossophagines, although in a much more rigorous manner. Phillips also split the Glossophaginae into two groups (see fig. 2). In regard to the origins of these two groups, he suggested that the teeth of *Choeronycteris* resemble those of *Phyllostomus*,

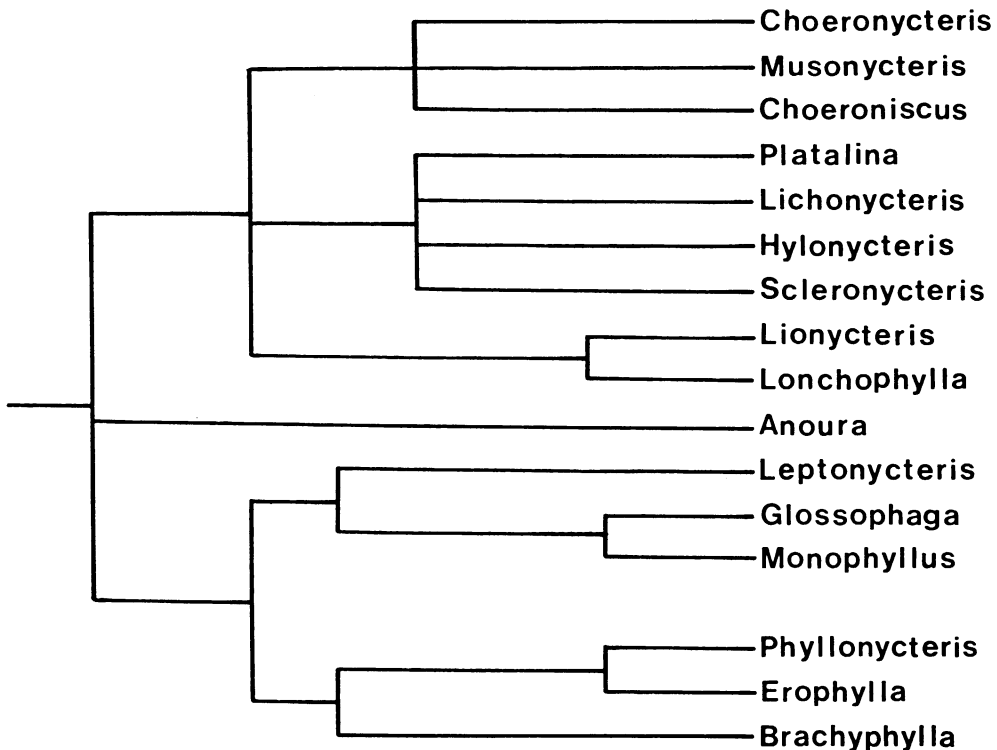


FIG. 1. Relationships among the genera of the Glossophaginae. Redrawn from Gardner (1977).

Mimon, *Chrotopterus* (all phyllostomines), and *Carollia* (Carolliinae), whereas the teeth of *Glossophaga* and *Leptonycteris* resemble those of *Macrotus* and *Artibeus* (a phyllostomine and a stenodermatine).

There are a number of other, less rigorous works that have made reference either to the origin (or origins) of the Glossophaginae, or to the possibility of a polyphyletic, false grouping of the nectar-feeders into a single subfamily. Walton (1967), on the basis of postcranial osteology, suggested that the glossophagines arose as a group from a *Vampyrops*-like stenodermatine ancestor. Walton did not suggest a polyphyletic origin for the Glossophaginae, although he did mention that *Glossophaga*-like bats resemble stenodermatines much more than do *Choeronycteris*-like bats. Interestingly, Walton (1967) believed that the Brachyphyllinae arose from a primitive *Macrotus*-like ancestor. Walton, in suggesting that the relationship between the brachyphyllines and glossophagines is not close, was at variance with the proposals of

Baker (1967), Baker and Bass (1979), and Gardner (1977) to include the brachyphyllines with *Glossophaga*, *Monophyllus*, and *Leptonycteris*.

Other workers have also supported a schism within the Glossophaginae, although they have not always suggested that the glossophagines are a polyphyletic group. Forman, Baker and Gerber (1968), Forman (1971) on the stomach morphology of bats, and Wille (1954) on glossophagine tongues, observed basic morphological differences between *Glossophaga*-like and *Choeroniscus*-like glossophagines. Forman, Baker and Gerber tentatively suggested that there was a relationship between *Choeronycteris* and several non-glossophagines (*Chrotopterus*, *Phyllostomus*, and *Desmodus*).

Only two works deal comprehensively with the relationships within the subfamily Glossophaginae. These are the work of Phillips (1971) on tooth and basicranial morphology, and the work by Gardner (1977) on karyology. Both papers divide the Glossophaginae

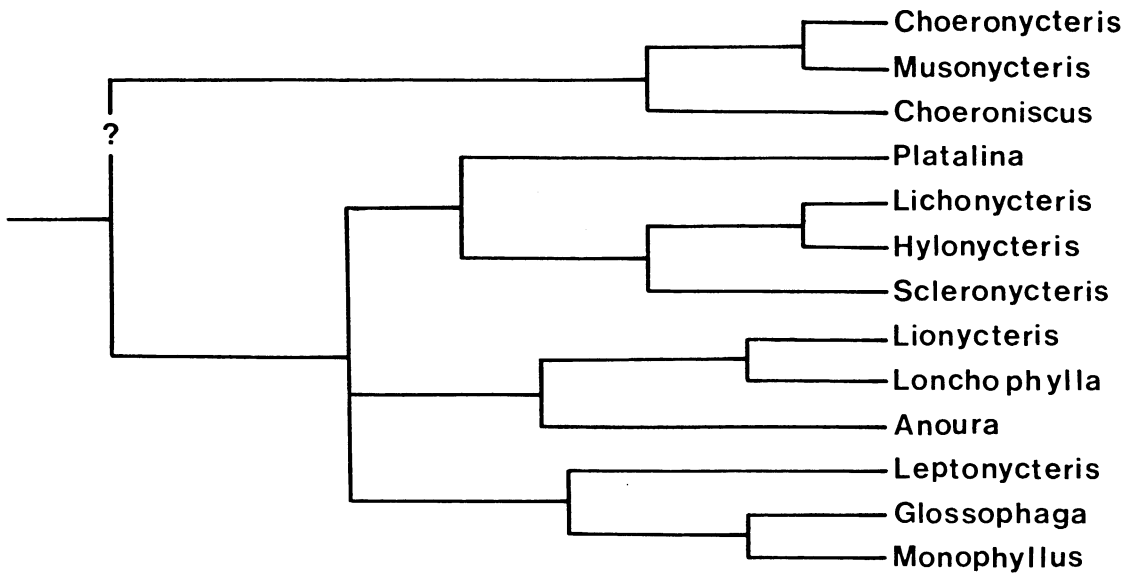


FIG. 2. Relationships among the genera of the Glossophaginae. Redrawn from Phillips (1971).

into essentially the same discrete groups (see figs. 1 and 2), but in the proposed relationship of these groups to one another, these two papers differ considerably. Phillips (1971) divided the Glossophaginae into two major groups: (1) a group containing *Choeroniscus*, *Choeronycteris*, and *Musonycteris* which he called the “*Choeronycteris*-group”; and (2) a large group containing the remaining 10 glossophagine genera which he called the “*Glossophaga*-group.” On the basis of molar configurations, he then divided the latter group into three subgroups: (1) *Glossophaga*, *Monophyllus*, and *Leptonycteris*; (2) *Lonchophylla*, *Lionycteris*, and *Anoura*; and (3) *Scleronycteris*, *Lichonycteris*, *Hylonycteris*, and *Platalina*. Of these three subgroups, the *Anoura* subgroup was considered most primitive, or most like the hypothetical glossophagine ancestor that Phillips proposed. The *Platalina* subgroup was considered most derived.

Gardner (1977) generally followed Phillips (1971) in his breakdown of the Glossophaginae into subgroups (see fig. 1). There were two basic differences. First, *Anoura* was placed in its own group, separate from other glossophagines. This placement reflected Gardner's belief that *Anoura* has had a separate evolutionary history from the other

genera of glossophagines. Second, and of great interest, *Platalina*, *Lichonycteris*, *Hylonycteris*, *Scleronycteris*, *Lionycteris*, and *Lonchophylla* were placed with the *Choeronycteris*-group, whereas Phillips (1971) placed these bats with the *Glossophaga*-group. Both researchers agreed that the subfamily Glossophaginae might not be monophyletic. It is of further interest that Gardner (1977) tentatively placed the Brachyphyllinae with the glossophagine genera *Leptonycteris*, *Glossophaga*, and *Monophyllus* in his phylogeny. If the Glossophaginae are monophyletic, however, Gardner (1977) concluded that all modern glossophagine karyotypes could have been derived from a primitive karyotype similar to the present day *Lonchophylla thomasi* karyotype.

The use of the hyoid and lingual regions: It is obvious from the preceding discussion that there are differences of opinion on the phylogeny of the Glossophaginae. Much of the confusion has resulted from lack of recognition of the fact that it is incorrect to use shared primitive characters (symplesiomorphies) to unite taxonomic groups. With few exceptions (e.g., Baker and Bass, 1979), no effort has been made to differentiate derived from primitive character states. Unfortunately, the few studies that have done

so have been hampered by a lack of suitable specimens of some of the rarer glossophagine genera.

Previous work on the hyoid region of bats (Sprague, 1943; Wille, 1954; Winkelmann, 1971; and Griffiths, 1978a, 1978b) demonstrated that the hyoid muscles controlling the tongue are markedly modified in the Glossophaginae, apparently to permit the tongue to be extended and manipulated for nectar-feeding. Work on the tongue structure of the *Leptonycteris-Glossophaga-Monophyllus* group (Wille, 1954; Winkelmann, 1971; Greenbaum and Phillips, 1974; Howell and Hodgkin, 1976; and Griffiths, 1978a) and the *Choeronycteris* group (Wille, 1954; Winkelmann, 1971) has demonstrated that intrinsic and extrinsic tongue structure is distinctly different in the two groups of glossophagines, and that in both groups these structures are very different from those of non-glossophagine bats. Until the current study, however, the majority of the genera of glossophagines had not been examined.

Modifications for nectar-feeding are so marked (Griffiths, 1978a) that they appear to be irreversible without abandoning the nectar-feeding niche. Stated another way, all modifications for nectar-feeding are clearly apomorphies, and thus ideal for use in a taxonomic study. The sole problem, then, is to determine which are true shared, derived characters (synapomorphies, and useful in taxonomy) and which are convergent characters (misleading unless recognized as such). Specialized mechanisms for tongue hyperextension have evolved independently in the Mammalia several times (Doran and Baggett, 1971), and although the overall mechanism in every known case is similar, there are observable morphological differences among them. Thus the question of the monophyly of the taxon Glossophaginae should be resolvable by observations of the hyoid and lingual regions to answer the question: did a morphology facilitating nectar-feeding evolve more than once in the phyllostomid bats?

MATERIALS AND METHODS

Fluid preserved specimens of the following species were dissected (species are listed here in the traditional taxonomic classification for

ease to the reader, but see the Systematic Conclusions for my arrangement):

Family Phyllostomidae

Subfamily "Glossophaginae"

Glossophaga soricina: Texas Tech University (TTU) Nos. 3326, 3327, 3328, 3329, 3330. All from Mexico, Tamaulipas, La Gruta de Quintero. University of Michigan Museum of Zoology (UMMZ) 111278, 111280, 111294, 111300, 111301, 111302. All from Costa Rica, Cartago, 1 mi. S Cartago, Agua Caliente.

Monophyllus redmani: University of Massachusetts (UMA) 2252, 2258. Both from Haiti, Dept. du Sud, Reynolds Station above Miragoâne, 2000 ft.

Leptonycteris sanborni: UMMZ 122935, 122936, 122937, 122938, 122939. All from Arizona, Cochise Co., 9 mi. SW San Simon.

Lichonycteris obscura: National Museum of Natural History, Smithsonian Institution (NMNH) 519892. From Panama, Darien, Tacarcuna Village, 1900 ft. NMNH 432194. Collection locality unknown.

Anoura geoffroyi: UMMZ 108640, 108641, 108653, 108655, 108680, 108681. All from Chiapas, 1 mi. S Tuxtla Gutierrez.

Hylonycteris underwoodi: American Museum of Natural History (AMNH) 238199. From Panama, Darien, Cerro Mali, 1400 m. NMNH 506578. From Costa Rica, Heredia Prov., Finca La Salva, Rio Puerto Viejo.

Choeromiscus godmani: NMNH 522934. From Venezuela, Yaracuy, San Felipe, Puente Marroquina.

Choeronycteris mexicana: UMMZ 77750, 77751. From Mexico, Sonora, Pilaes. UMMZ 77755, 77756. From Mexico, Sonora, El Tigre Mtns. UMMZ 77760. From Mexico, Sonora, St. Marie Mtns.

Lonchophylla robusta: UMMZ 114923, 114927, 114928, 114929, 114930, 114933. All from Costa Rica, Limon, Los Diamantes, 4 mi. N Headquarters, 250 m.

- Lionycteris spurrelli*: NMNH 499771. Colombia, Antioquia, Zaragoza.
- Platalina genovensium*: NMNH 268766. Peru, Carivelli.
- SUBFAMILY Brachyphyllinae (=Phyllonycterinae)
- Brachyphylla cavernarum*: Personal collection, T. Griffiths (TAG) 2, and UMA 3086. Both from Puerto Rico.
- Erophylla sezekorni*: AMNH 164255, 164281. From Bahamas, New Providence, Hunt's Cave.
- Phyllonycteris poeyi*: AMNH 176023. From Cuba, Habana, 3 mi. E Tapaste, Cueva del Indio. TAG 1, 3. Haiti?
- Subfamily Phyllostominae
- Macrotus waterhousii*: TTU 12484, 12485, 12486, 12487, 12488. All from Arizona, Pinal Co., 25 mi. S Casa Grande-Old Mammon Mine. University of Vermont (UVM) 2372, 2374. From Haiti, Dept. du Sud, 1 mi. SE Duchity, 2400'. UVM 2939, 2410. Haiti, Dept. du Sud. AMNH 120972, 120977. From Dominican Rep., Chavon, E of La Romana, caves near the river.
- Phyllostomus hastatus*: AMNH 202308. Trinidad.
- Micronycteris nicefori*: UMA 2819. From Panama.
- Subfamily Stenodermatinae
- Artibeus jamaicensis*: UVM 1651, 1656. From Haiti, Dept. du Sud. UVM 3501, 3503. From Haiti, Dept. du Sud, 6 km. SW Miragoâne, 580 m.
- Phyllops haitiensis*: UVM 2750. Haiti, Dept. du Sud.
- Uroderma bilobatum*: UMA 3034. Panama, Colon Prov., Santa Rosa.
- Vampyressa pusilla*: UMA 3334. Panama Canal Zone, Bohio Point Ridge.
- Vampyrops helleri*: UMA 2695. Trinidad, St. George Co., Simla, 5 mi. N Arima.
- Subfamily Carollinae
- Carollia perspicillata*: UMA 3060. Panama Canal Zone, 2 km. N Frijoles.
- Subfamily Desmodontinae
- Desmodus rotundus*: AMNH 208895, 208899, 208902. All from Mexico, Oaxaca, S Felipe del Agua (Cerro S. Felipe).

Additionally, the basicranial region and teeth of the following specimens were examined:

- Glossophaga soricina*: AMNH 92234, 92235, 92236, 92237, 92238, 92239, 92240, 92241, 92242, 92631, 92700.
- G. longirostris*: AMNH 130665.
- Monophyllus redmani*: AMNH 19106, 19107, 23782, 23783, 41157.
- Lichonycteris obscura*: NMNH 331258, 335187, 362595, 364348, 483374.
- Leptonycteris nivalis*: NMNH 88017, 88018, 88019, 88026.
- Leptonycteris curasoae*: NMNH 101850, 105130 (alcoholic with skull removed), 434424.
- Anoura geoffroyi*: NMNH 88022, 88023, 92260, 92263, 92420, 319248, 319250, 319251, 323182.
- Anoura caudifer*: NMNH 483371, 499308, 499309, 499310.
- Hylonycteris underwoodi*: NMNH 331260, 337984.
- Scleronycteris ega*: NMNH 407889.
- Lonchophylla thomasi*: AMNH 209358. NMNH 361570, 361571, 393013, 460097.
- Lonchophylla hesperia*: NMNH 498827, 498828, 498829, 498830, 498831.
- Lonchophylla handleyi*: NMNH 507172.
- Lionycteris spurrelli*: AMNH 97220, 97221, 97222, 97224, 97260, 97261, 97264. NMNH 499303, 499304, 499305, 499306.
- Platalina genovensium*: NMNH 268765 (alcoholic with skull removed).

Because of small size, muscles of many specimens were exceedingly fragile. Formalin-preserved specimens were less prone to muscle breakage than those specimens which had been stored in isopropyl alcohol for a long period. A binocular dissecting microscope was used for all dissections. Complete drawings of all dissections and other anatomical preparations were made at a scale of either 10× or 5× the natural size. From these, selected drawings showing specific anatomical differences were inked for presentation.

Tongue sectioning for all species examined followed classic histological technique as described in Humason (1972). Tongues were excised just anterior to the hyoid bone (ba-

sihyal), as close to the bone as possible. Each tongue was then re-fixed in buffered formalin solution, embedded in paraffin, and sectioned. Staining was done with Mallory Triple Connective Tissue Stain, and/or with hematoxylin and eosin. All measurements given to identify particular tongue segments are in microns from the tip of the tongue.

In the descriptive sections of this paper, the morphology of *Glossophaga soricina* is described in great detail. All other glossophagines, and then all other bats dissected are described in less detail in separate sections under each muscle. At the end of each muscle description is a section entitled "Comments." This section is designed to emphasize the functional and systematic highlights of each muscle, points to be especially remembered when reading the Systematic Conclusions.

ACKNOWLEDGMENTS

This work was part of the author's doctoral dissertation at the University of Massachusetts. I am indebted to the members of my doctoral committee, Drs. David Klingener, Margery Coombs, Karl Koopman, Charles Pitrat, Dana Snyder, and Donald Kroodsma, for their thoughtful guidance during the course of this study and for their careful reading of the manuscript. I am grateful to Dr. James Dale Smith for his rigorous review of the manuscript. I thank my fellow graduate students from the University of Massachusetts Museum of Zoology for their friendship and encouragement while this study was in progress, particularly Jeanne Bertoni, Carroll Schloyer, Doug Smith, and William Wall. I am grateful to my wife, Cara-Sue, and my daughters Jennifer and Anne for their support, and for putting up with me during the tough moments of preparing this work.

I thank the following individuals and institutions for providing me with specimens: Dr. Karl F. Koopman, American Museum of Natural History; Dr. Charles O. Handley, National Museum of Natural History, Smithsonian Institution; Dr. Robert J. Baker, The Museum, Texas Tech University; Dr. Philip Myers, University of Michigan Museum of Zoology; Dr. David J. Klingener, University

of Massachusetts Museum of Zoology; and Dr. Charles A. Woods, University of Vermont Museum of Zoology.

This work was supported in part by University Fellowship #87015 from the University of Massachusetts. Illinois Wesleyan University generously provided logistical support in the preparation of the manuscript, plus technical support from Pat Meyers and the Media Center in mounting the illustrations. Special thanks to Judith Switzer for assistance.

Finally, I will always be grateful to the late Dr. Herbert Potswald for his friendship, support, and interest in my work.

DESCRIPTION OF THE MUSCLES

BRANCHIOMERIC MUSCULATURE

MYLOHYOID GROUP

The muscles of this group are innervated by the mylohyoid nerve, a branch of N. mandibularis, which is a branch of N. trigeminus (V). The mandibular nerve enters both of the muscles described on their deep surfaces.

M. MYLOHYOIDEUS

Figures 3, 6, 9, 11, 14, 16, 18

ORIGIN: In *Glossophaga soricina*, from the medial surface of the mandible. The origin extends for much of the length of the mandibular ramus, from a point about 1 mm. posterior to the symphysis to the angle of the jaw.

INSERTION: Into its antimere, forming a raphe along the ventral midline of the jaw region.

OTHER GLOSSOPHAGINES: The muscle is the same in all glossophagines dissected. In some individuals, the mylohyoid is quite thin anteriorly, to the point of revealing the geniohyoid beneath. This anterior thinness is variable within a species; however, in all cases the mylohyoid consists of a solid sheet of muscle.

OTHER BATS: In the three genera of brachyphyllines, the origin and insertion of the mylohyoid are the same, but there is a slight break in the muscle anteriorly. This has the effect of dividing the mylohyoid into thick

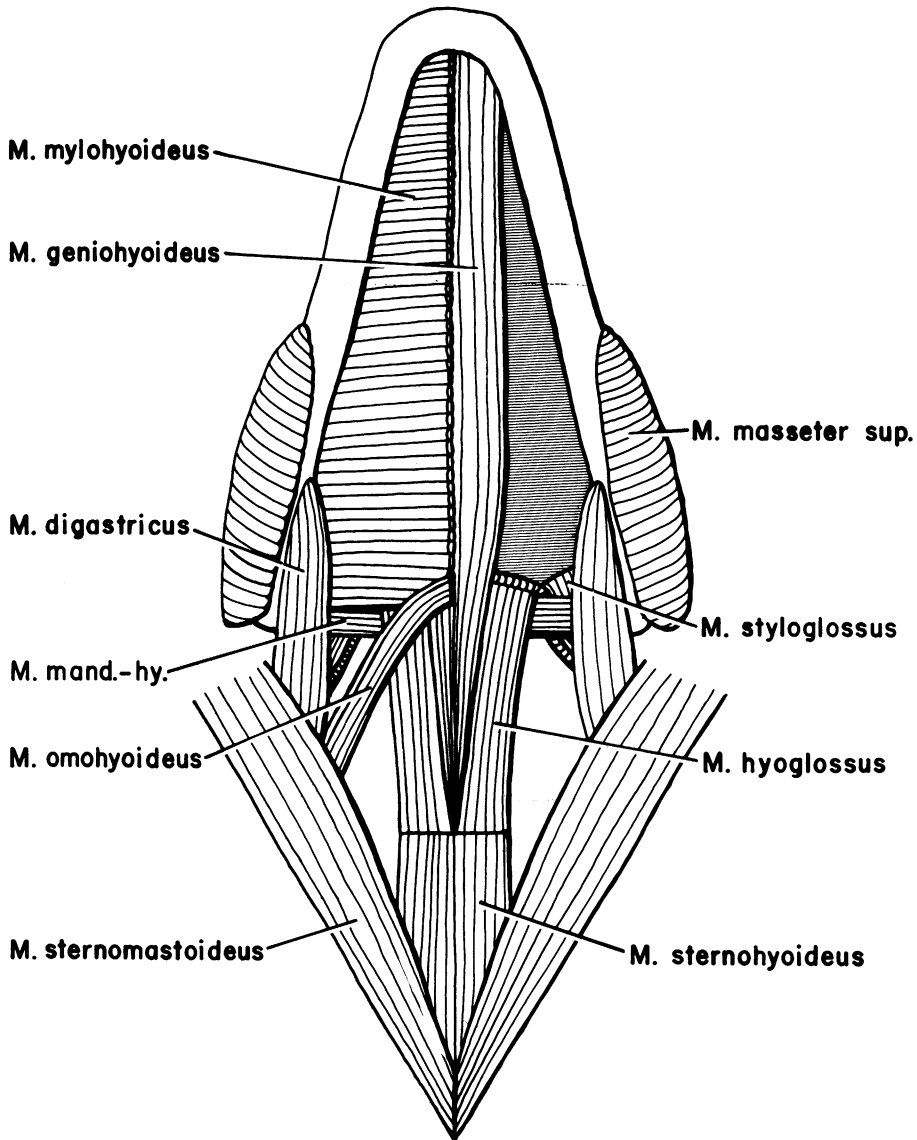


FIG. 3. Ventral view of the superficial hyoid musculature of *Glossophaga soricina*. Bar = 1 mm.

anterior and posterior parts, separated by a fleshy aponeurosis. In all three phyllostomines, there is a pronounced break, which results in the mylohyoid having a distinct anterior and a distinct posterior part. This is also the case in all five stenodermatine genera dissected. In *Carollia* and *Desmodus*, the mylohyoid is a single sheet. This is particularly true in *Carollia*; the specimen I dis-

sected had the most robust mylohyoid muscle I have ever observed on a bat.

COMMENTS: Obviously, there are two quite different conditions for this muscle in the Phyllostomidae: (1) a single, non-divided mylohyoid found in all glossophagines, *Carollia*, and *Desmodus*; and (2) a divided mylohyoid found in all phyllostomines and stenodermatines. In the Brachyphyllinae,

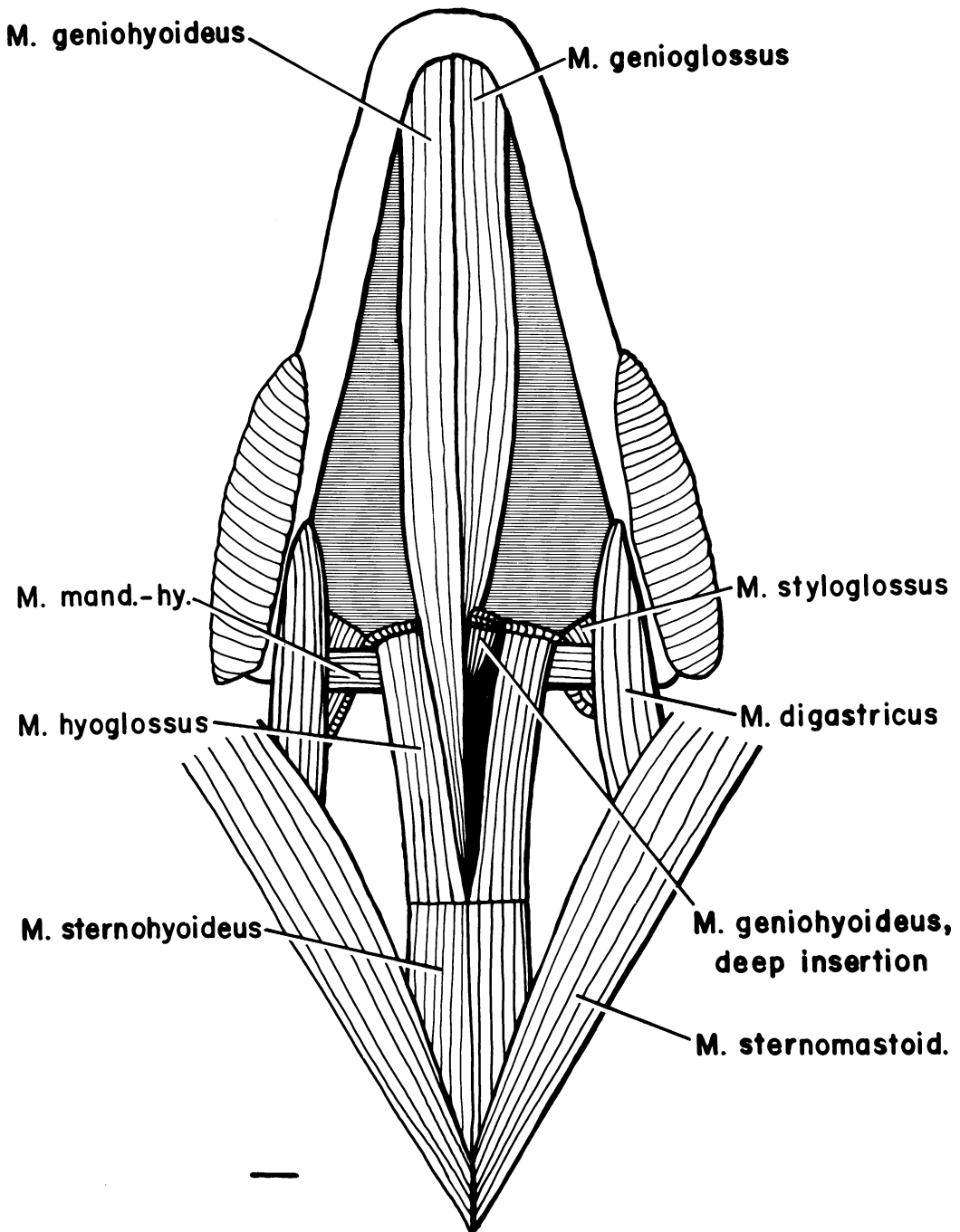


FIG. 4. Ventral view of the deep hyoid musculature of *Glossophaga soricina*. Bar = 1 mm.

there is an aponeurosis anteriorly where the muscle becomes quite thin, but the muscle is essentially unbroken as in the glossopha-

gines. The primitive condition is obviously the undivided one, found in most bats (see Sprague, 1943; Griffiths, 1978a, 1978b, and

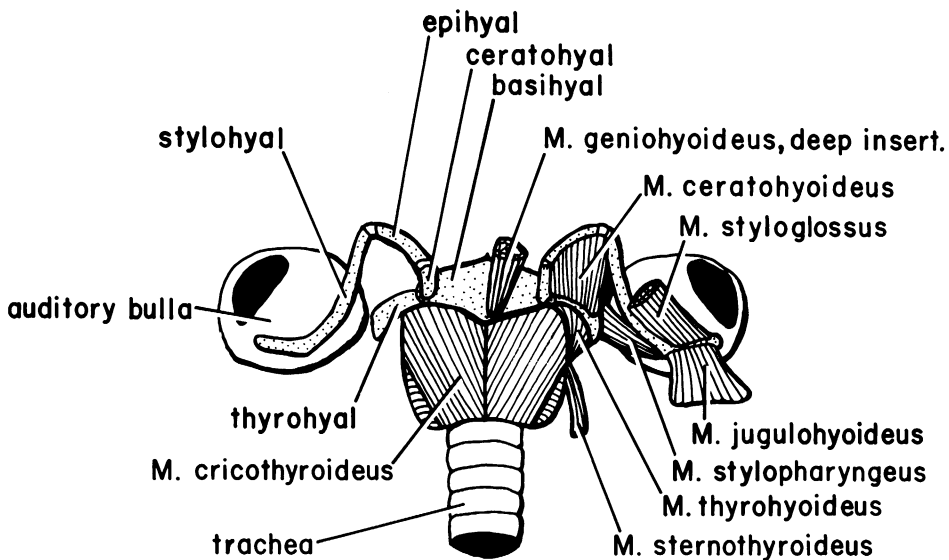


FIG. 5. Ventral view of the hyoid apparatus and larynx of *Glossophaga soricina*. Bar = 1 mm.

in press). The divided condition could very well be a synapomorphy shared by the Phyllostominae and Sternodermatinae.

M. MANDIBULO-HYOIDEUS

Figures 3, 4, 6, 7, 9, 10–12, 14, 16, 18, 19

M. mylohyoideus profundus (Griffiths, 1978a).

ORIGIN: In *Glossophaga soricina*, from the medial surface of the mandible, just dorsal and slightly posterior to the origin of the posterior edge of the mylohyoid.

INSERTION: This muscle passes deep to the anterior digastric and hyoglossus muscles, to insert on the ventrolateral surface of the basihyal bone, and into the lateral and dorsal fibers of the sternohyoid.

OTHER GLOSSOPHAGINES: The muscle is the same in all glossophagines dissected. In some individuals, the insertion into the fibers of the sternohyoid is reduced or absent, but this is variable within genera.

OTHER BATS: This muscle is the same in all bats dissected.

COMMENTS: The mandibulo-hyoid muscle obviously developed in the phyllostomid bats in response to the freeing of the sternohyoid-hyoglossus complex from the basihyal. Since the mylohyoid proper could no

longer directly act on the hyoid apparatus, its function of lateral pull was assumed by this small muscle that I suggest may have originally been part of the posterior mylohyoid. The mandibulo-hyoid is found in all phyllostomids, and thus is of no value for the taxonomic problem at hand.

HYOID CONSTRICTOR GROUP

The muscles of this group are innervated by branches of N. facialis (VII), some of which are extremely small and difficult to trace completely.

M. STYLOHYOIDEUS

ORIGIN: In *Glossophaga soricina*, from the medial surface of the anterior $\frac{1}{2}$ –1 mm. of the stylohyal bone. The origin of this muscle is very closely associated with the origin of the stylopharyngeus.

INSERTION: On the posterolateral tip of the thyrohyal and on the lateral basihyal.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus* and *Lichonycteris*. In *Leptonycteris* this muscle is variable. In about half the specimens dissected it was absent. In the other half, it was reduced to a few fibers embedded in fascia. In *Lonchophylla*,

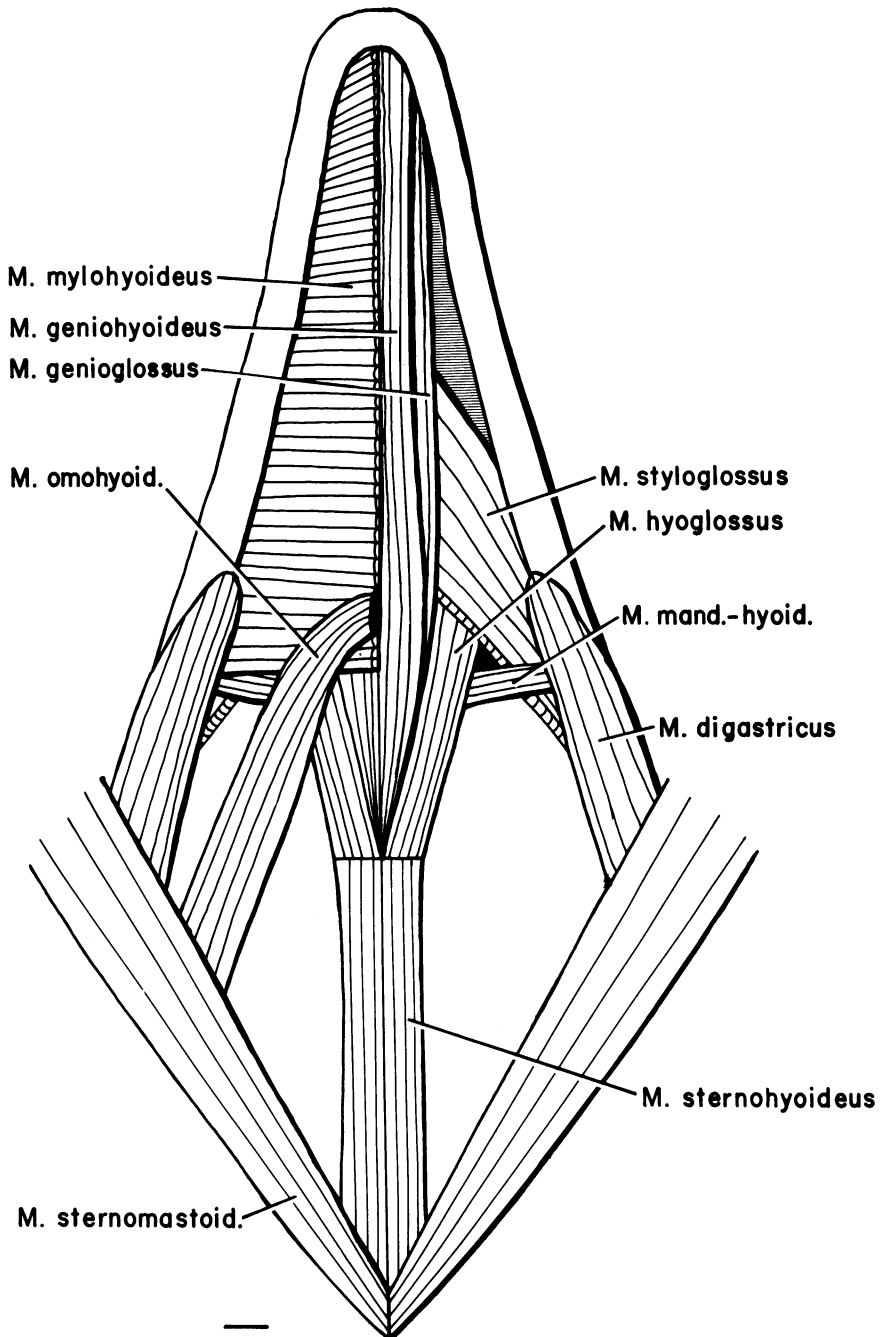


FIG. 6. Ventral view of the superficial hyoid musculature of *Lonchophylla robusta*. Bar = 1 mm.

Lionycteris, *Platalina*, *Anoura*, *Hylonycteris*, *Choeroniscus*, and *Choeronycteris*, this muscle was absent in all specimens dissected.

OTHER BATS: This muscle is present in *Phyllonycteris* and *Erophylla*, but completely absent in *Brachyphylla*. In *Phyllonycteris*,

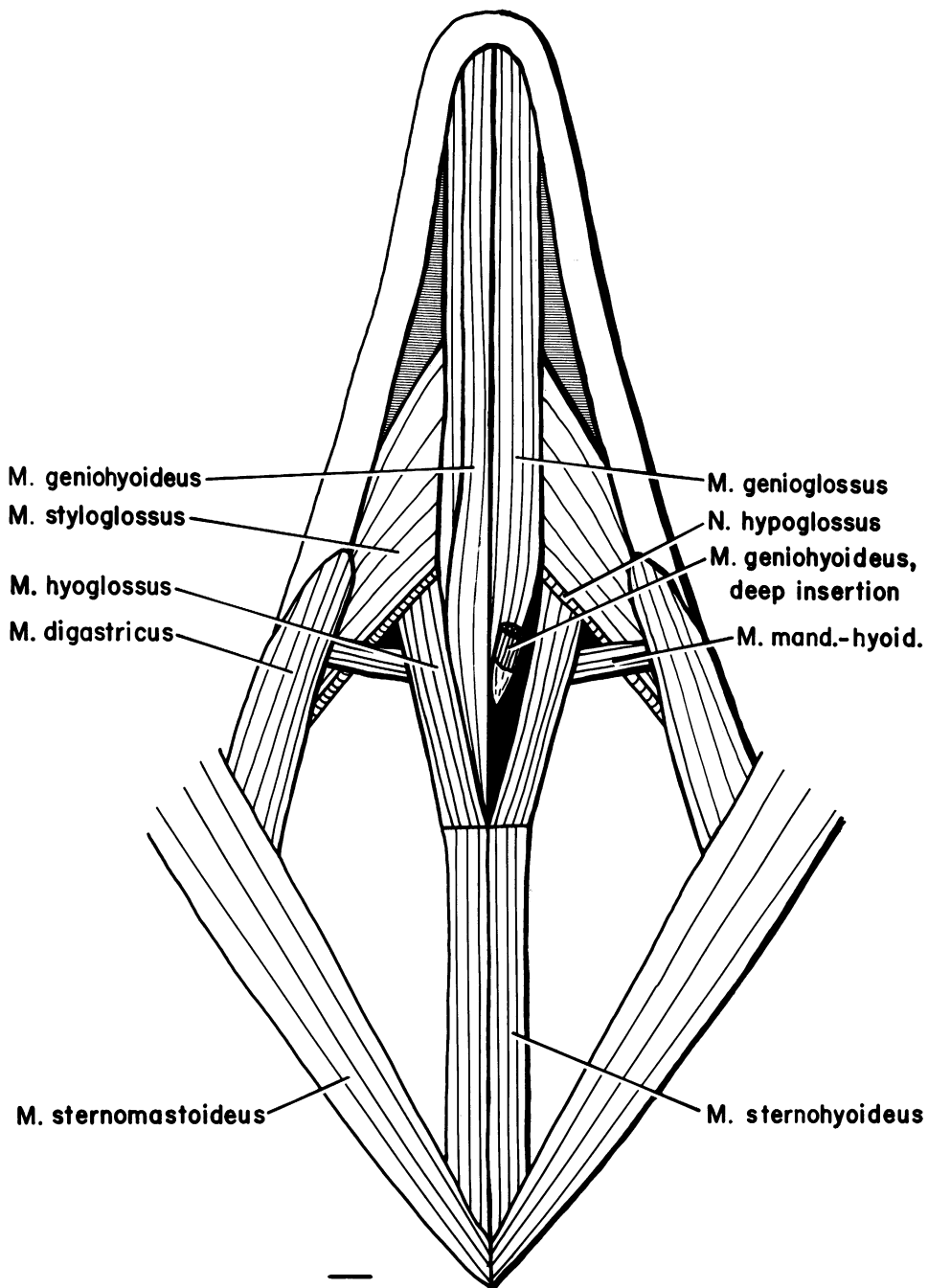


FIG. 7. Ventral view of the deep hyoid musculature of *Lonchophylla robusta*. Bar = 1 mm.

this is a well-defined muscle that originates from the medial stylohyal and passes medially and anteriorly to insert by tendon on the hyoid bone at the ceratohyal/epihyal joint.

In *Erophylla* this muscle is very reduced; it inserts on the ceratohyal only. In all phyllostomines and stenodermatines dissected, this muscle is absent. The muscle is absent in

Desmodus, but present (though reduced) in the specimen of *Carollia* dissected. In *Carollia*, the insertion is on the tip of the thyrohyal.

COMMENTS: Sprague (1943) reported that this muscle was absent in most Microchiroptera he dissected, including all phyllostomids. Obviously, the presence or absence of this muscle is somewhat variable. Nevertheless, *Phyllonycteris*, *Erophylla*, *Glossophaga*, *Monophyllus*, *Lichonycteris*, *Carollia* and some specimens of *Leptonycteris* share the plesiomorphic condition of retaining the stylohyoid. All other phyllostomids are apomorphic in that they have lost the stylohyoid.

M. JUGULOHYOIDEUS

Figures 5, 8, 13, 15, 17, 20

ORIGIN: In *Glossophaga soricina*, from the basioccipital shelf, about 1 mm. posterior to the auditory bulla.

INSERTION: This muscle passes ventrally and anteriorly, curving around the posterior surface of the auditory bulla to insert on the expanded lateral tip of the stylohyal bone.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus*, *Lichonycteris*, *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, *Lonchophylla*, *Lionycteris*, and *Platalina*.

OTHER BATS: This muscle is similar in all phyllostomids dissected.

COMMENTS: This muscle is comparatively more robust in all "glossophagine" genera dissected. Functionally, this is to be expected, because the jugulohyoid muscle must anchor the distal end of the anterior hyoid cornu against the pull of the styloglossus muscle (see *M. styloglossus*).

M. SPHINCTER COLLI PROFUNDUS

This muscle is nominally a skin muscle, but it is included here because it takes origin from the basihyal region and is innervated by *N. facialis*. Sprague (1943) also included this muscle in his work on the hyoid region of bats.

ORIGIN: In *Glossophaga soricina*, this muscle originates from the fascia of the posterior mylohyoid region.

INSERTION: This muscle is extremely reduced in all specimens examined, consisting

at most of a few fibers that pass laterally in fascia, to insert weakly on the inner skin surface of the cervical region.

OTHER GLOSSOPHAGINES: This muscle is similar in form in *Monophyllus*, *Lichonycteris*, *Leptonycteris*, *Anoura*. In *Hylonycteris* reduction is almost complete, and in *Choeroniscus* and *Choeronycteris* no trace of this muscle could be observed. In *Lonchophylla*, *Lionycteris*, and *Platalina* this muscle was very different in form. It consisted of two distinct parts, both originating from the fascia of the posterior mylohyoid region as in *Glossophaga*. One part passed laterally to insert on the inner surface of the cervical skin. The other part passed anterolaterally to insert on the inner surface of the cervical skin at a 45-degree angle just lateral to the mandible.

OTHER BATS: In *Brachyphylla*, the sphincter colli profundus is very similar to the same muscle in *Lonchophylla*. This muscle is absent in *Erophylla* and *Phyllonycteris*, except for fascial tracts that pass laterally where the muscle used to be. In the phyllostomines dissected, this muscle is quite variable. In *Micronycteris* there are three distinct slips, all originating from the basihyal raphe region. One slip passes anterolaterally, one passes laterally, and one passes posterolaterally. *Macrotus* and *Phyllostomus* both lack the slip that passes posterolaterally, and thus have only two slips. All five genera of stenodermatines have a sphincter colli profundus that is similar: it consists of two bellies that pass anteriorly, one anterior to the other. The anterior slip is very similar to the anterior slip in the phyllostomines. The posterior slip is similar to the slip in the phyllostomines that passes laterally, except that in the stenodermatines it passes anteriorly as well as laterally. In *Carollia* this muscle is similar to the condition observed in *Macrotus* and *Phyllostomus*. In *Desmodus*, this muscle consists only of a single slip that passes anterolaterally from the basihyal region.

COMMENTS: The plesiomorphic condition is obviously having three distinct heads, passing anterolaterally, laterally, and posterolaterally (see Sprague, 1943). This is found only in *Micronycteris* of all the bats dissected here. In *Macrotus*, *Phyllostomus*, all the stenodermatines, *Carollia*, *Brachyphylla*, *Lonchophylla*, *Lionycteris*, and *Pla-*

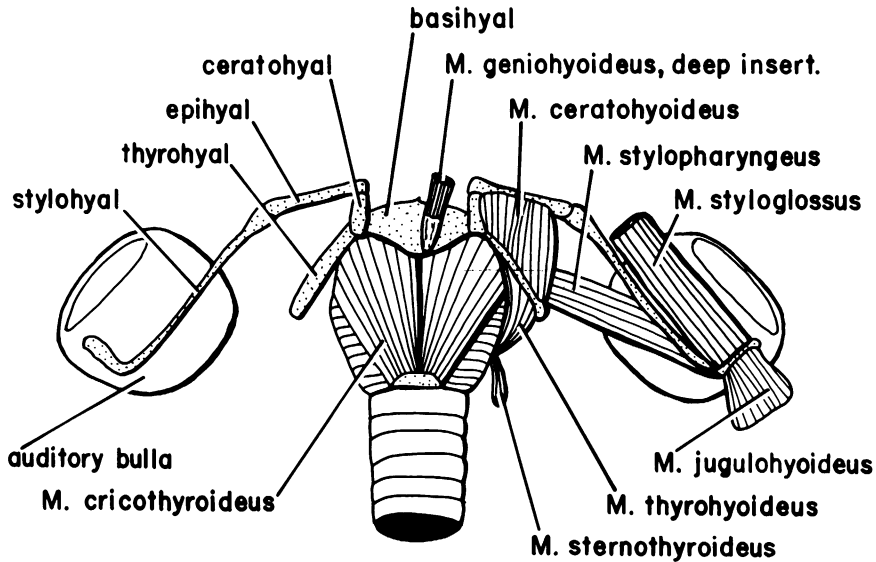


FIG. 8. Ventral view of the hyoid apparatus and larynx of *Lonchophylla robusta*. Bar = 1 mm.

talina the posterior slip of this muscle shows a progression of loss, from only a single weak lateral slip to complete loss. In *Erophylla* and *Phyllonycteris*, this muscle is absent. Other than the distinctive "both bellies passing anteriorly" found in all the Stenodermatinae, this muscle is so variable it seems to be of minimal use in a systematic study. In the glossophagines, it is interesting that more "advanced" nectar-feeders have lost this muscle, whereas *Lonchophylla*, *Lionycteris*, and *Platalina* have one of the more primitive conditions observed. This argues against the placement of these three genera with the more "advanced" glossophagines, as has been done in the past (see Systematic Conclusions).

GLOSSOPHARYNGEAL GROUP

The muscles of this group are innervated by branches of N. glossopharyngeus (IX).

M. STYLOPHARYNGEUS Figures 5, 8, 13, 15, 17, 20

ORIGIN: In *Glossophaga soricina*, from the posteromedial border of the stylohyal bone, at a point about 2 mm. from the lateral tip.

INSERTION: This muscle passes medially to insert in the fibers of the pharyngeal wall,

between the hyopharyngeus and thyropharyngeus muscles.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus*, *Lichonycteris*, *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, *Lonchophylla*, *Lionycteris*, and *Platalina*.

OTHER BATS: This muscle is similar in all bats dissected.

M. CERATOHYOIDEUS Figures 5, 8, 13, 15, 17, 20

ORIGIN: In *Glossophaga soricina*, from the anterior edge of the thyrohyal bone (lesser hyoid cornu), and from the fibers of the thyrohyoid muscle.

INSERTION: This muscle passes anteriorly to insert on the medial tip of the stylohyal, on the epihyal, and on the lateral tip of the ceratohyal bones.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus*, *Leptonycteris*, and *Anoura*. In *Lichonycteris*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, *Lonchophylla*, *Lionycteris*, and *Platalina* it inserts on the entire posterior surface of the epihyal and the lateral tip of the ceratohyal (not on the medial stylohyal at all).

OTHER BATS: In all three brachyphylline

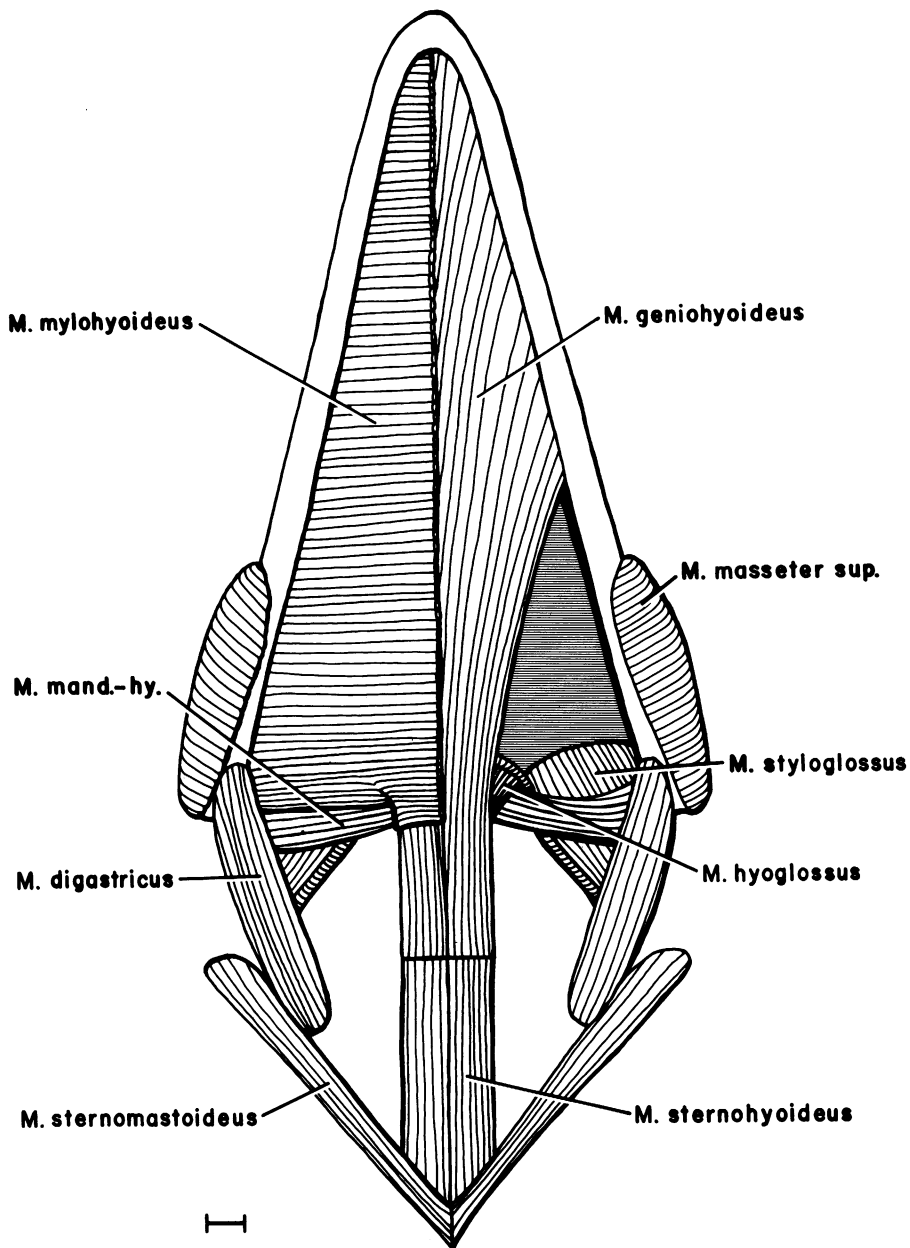


FIG. 9. Ventral view of the superficial hyoid musculature of *Choeronycteris mexicana*. Bar = 1 mm.

genera, this muscle inserts on the ceratohyal and epihyal only. In the Phyllostominae and Stenodermatinae the muscle insertion varies considerably among genera, with what appears to be great taxonomic significance. In *Micronycteris*, the insertion is on the ceratohyal, epihyal, and medial stylohyal (as in

Glossophaga). In *Macrotus* and *Phyllostomus*, the insertion is only on the epihyal and stylohyal, with the reduced ceratohyal playing no part. In the Stenodermatinae, three different conditions are seen. In *Vampyressa pusilla* and *Vampyrops helleri*, insertion is on all three anterior cornu elements, as in *Glos-*

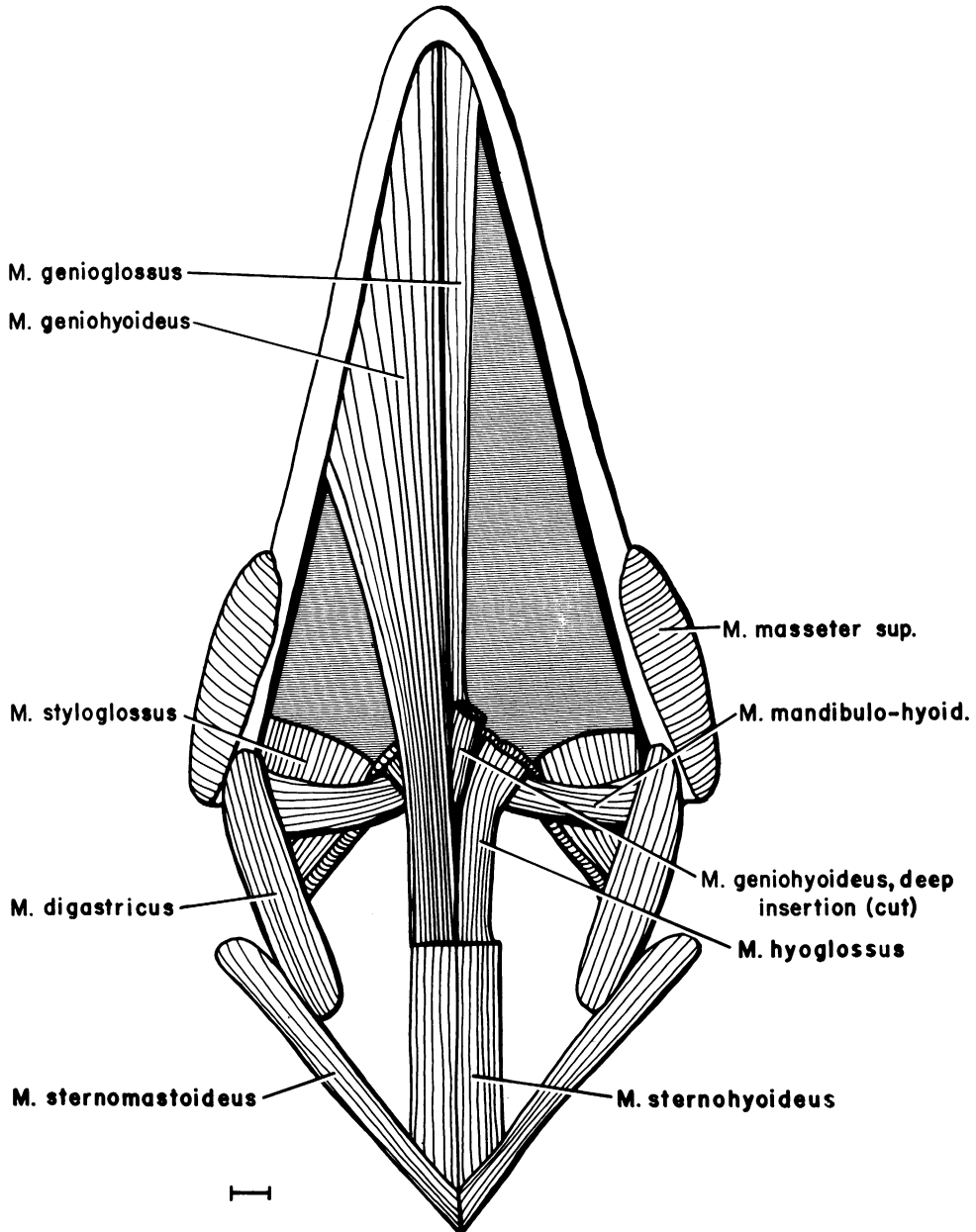


FIG. 10. Ventral view of the deep hyoid musculature of *Choeronycteris mexicana*. Bar = 1 mm.

sophaga. In *Artibeus* and *Phyllops*, insertion is on the ceratohyal and epihyal only. In *Uroderma*, insertion is on the ceratohyal and lateral basihyal. In *Carollia*, the insertion is as in *Artibeus*, and in *Desmodus* the insertion is as in *Macrotus*.

COMMENTS: The plesiomorphic condition

is difficult to ascertain with certainty here due to the wide variability of this muscle. It is interesting to note that the three distinct conditions observed in the stenodermatines dissected correspond very well to the branches of the stenodermatine phyletic tree presented by Baker (1973).

PHARYNGEAL CONSTRICTOR GROUP

The muscles of this group are innervated by branches of the N. vagus (X) as follows: N. laryngeus cranialis innervates M. cricothyroideus; N. recurrens innervates Mm. hyopharyngeus, thyropharyngeus, and cricothyroideus.

M. CRICOTHYROIDEUS
 Figures 5, 8, 13, 15, 17, 20

ORIGIN: In *Glossophaga soricina*, from the entire ventral surface of the cricoid cartilage, medial to the origin of the cricopharyngeus.

INSERTION: This muscle passes anteriorly and laterally fanning out to insert on the ventral and ventrolateral thyroid cartilage walls, and on the ventral edge of the short posterior thyroid cornu.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus*, *Lichonycteris*, *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, *Lonchophylla*, *Lionycteris*, and *Platalina*.

OTHER BATS: This muscle is similar in all bats dissected.

COMMENTS: In all phyllostomids, this muscle is very simple structurally (unlike moroopids and vespertilionids, see Griffiths, 1978b, in press). This is associated, no doubt, with the diminished role played by echolocation in food gathering.

M. HYOPHARYNGEUS

M. constrictor pharyngeus superior, Sprague, 1943; superior constrictor, Novick and Griffin, 1961

This muscle is almost completely absent in *Glossophaga soricina*; only a few muscle fibers of what may be the remnants of this muscle were found attached to the dorsal buccopharyngeal fascia. This is also the case in *Monophyllus redmani*, *Lichonycteris obscura*, *Leptonycteris sanborni*, *Anoura geoffroyi*, *Hylonycteris underwoodi*, *Choeroniscus godmani*, *Choeronycteris mexicana*, *Lonchophylla robusta*, *Lionycteris spurrelli*, and *Platalina genovensium*.

OTHER BATS: This muscle is similar (almost completely absent) in all brachyphyllines dissected, and in all other phyllostomids dissected.

M. THYROPHARYNGEUS

M. constrictor pharyngeus medius, Sprague, 1943; middle constrictor, Novick and Griffin, 1961

ORIGIN: In *Glossophaga soricina*, from the dorsal surface of the tip of the thyrohyal bone (posterior hyoid cornu).

INSERTION: This muscle passes dorsally, then medially to insert into the dorsal pharyngeal midline and into its antimerere.

OTHER GLOSSOPHAGINES: This muscle is similar in all glossophagines dissected.

OTHER BATS: This muscle is similar in all bats dissected.

M. CRICOPHARYNGEUS

M. constrictor pharyngeus inferior, Sprague, 1943; inferior constrictor, Novick and Griffin, 1961

ORIGIN: In *Glossophaga soricina*, the muscle originates in several slips from the lateral border of the cricoid cartilage and from the posterior thyroid cornu.

INSERTION: The posterior slips pass dorsally to insert on the pharyngeal midline, and in their antimerere. The anterior slips pass dorsally and anteriorly to also insert on the pharyngeal midline and their antimereres.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus*, *Lichonycteris*, *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, and *Choeronycteris*. In *Lonchophylla*, *Lionycteris*, and *Platalina* there were only two slips.

OTHER BATS: In the Brachyphyllines the muscle is similar, though there are only two slips present. In all the phyllostomines and stenodermines dissected, there are three slips present in this muscle, as is the case in *Carollia*. In *Desmodus*, this muscle consists of a single large slip.

COMMENTS: Note that all "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina* are similar.

MYOTOMIC MUSCULATURE

LINGUAL GROUP

The muscles of this group are innervated by the N. hypoglossus (XII).

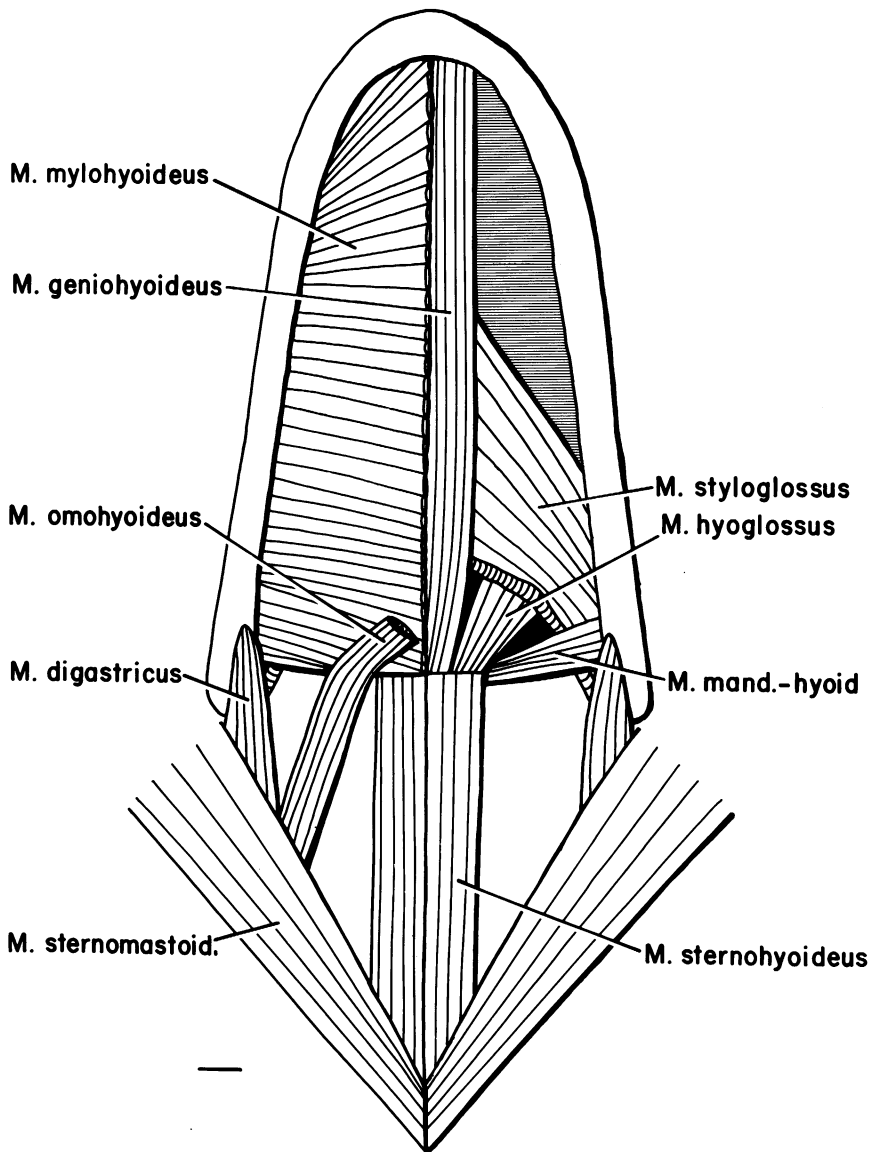


FIG. 11. Ventral view of the superficial hyoid musculature of *Brachyphylla cavernarum*. Bar = 1 mm.

M. GENIOGLOSSUS

Figures 4, 6, 7, 10, 12

ORIGIN: In *Glossophaga soricina*, from the medial surface of the anterior 1 mm. of the mandible, deep to the origin of the geniohyoid.

INSERTION: This muscle passes posteriorly to insert into the ventral surface of the tongue just lateral to the tongue midline. In *G. sor-*

icina this muscle curves laterally as it approaches the basihyal bone. It inserts on the posterior 3 mm. of the venter of the tongue, and does not insert on the basihyal.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus*, *Lichonycteris*, *Lep-tonycteris*, *Anoura*, *Hylonycteris*, *Choeronis-cus*, and *Choeronycteris*. In *Lonchophylla* and *Lionycteris* this muscle begins inserting

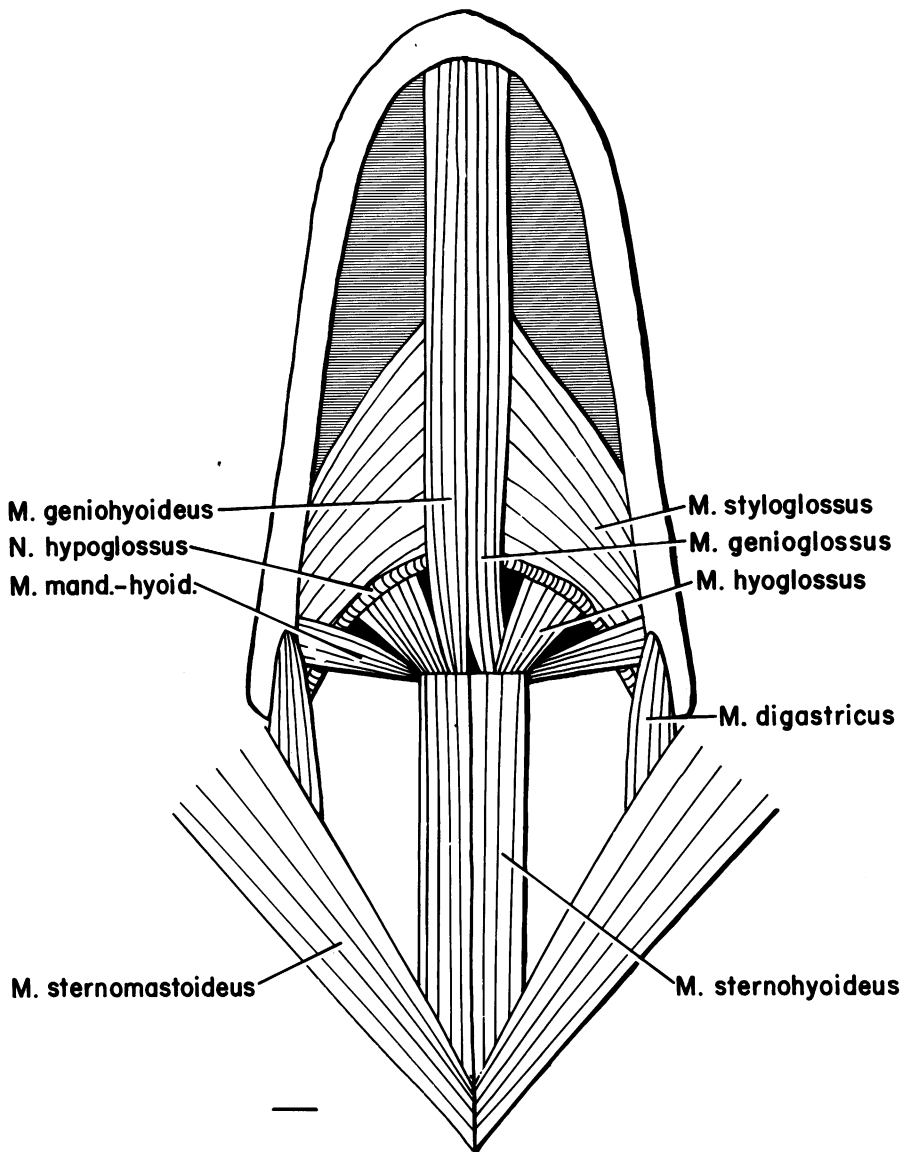


FIG. 12. Ventral view of the deep hyoid musculature of *Brachyphylla cavernarum*. Bar = 1 mm.

much farther anteriorly on the venter of the tongue. Instead of inserting in only the posterior 3 mm., this muscle inserts into the posterior half of the ventral tongue surface, just lateral to the midline. In *Platalina*, the genioglossus inserts about halfway between these two extremes, inserting into the posterior 7 mm. of the tongue.

OTHER BATS: In the Brachyphyllinae, this muscle inserts into much of the length of the

ventral tongue surface. It is interesting to note that in all three brachyphyllines, this muscle seems to be in several parts, or slips, that are easily separable. In all other phyllostomids, this muscle inserts over much of the ventral tongue surface.

COMMENTS: Once more, all the "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina* are united by a synapomorphic character. In this case, the

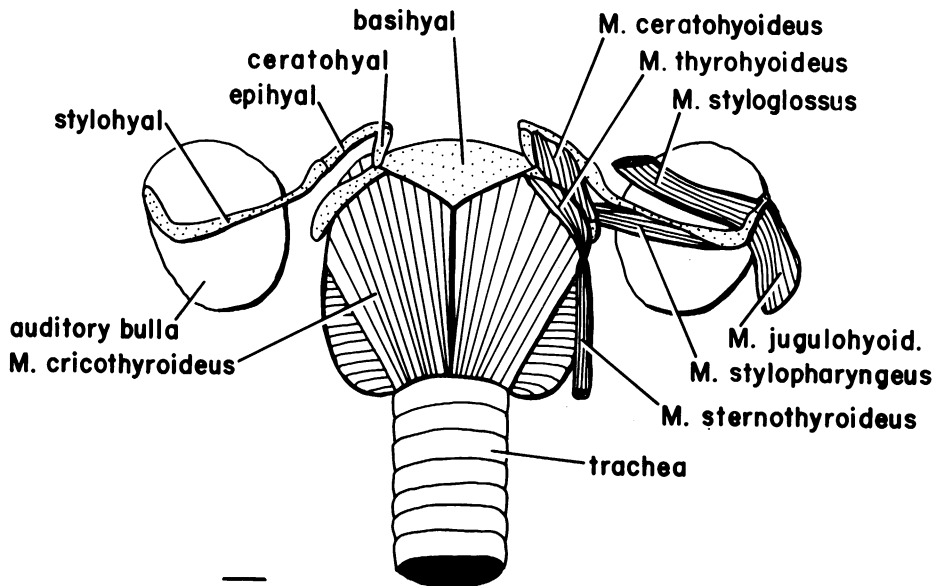


FIG. 13. Ventral view of the hyoid apparatus and larynx of *Brachyphylla cavernarum*. Bar = 1 mm.

condition seen in *Lonchophylla/Lionycteris* could be “ancestral” to the condition in the other glossophagines, or it could be independently derived. The genioglossus of *Platalina* is most easily derived from the *Lonchophylla/Lionycteris* condition. There seems to be an interesting synapomorphous condition uniting the three brachyphyllines, too: the separability of this muscle into slips.

M. HYOGLOSSUS

Figures 3, 4, 6, 7, 9, 10–12, 14, 16, 18, 19

ORIGIN: In *Glossophaga soricina*, from the former basihyal raphe (now disconnected from the basihyal bone); or more accurately, from the insertion of the sternohyoideus. The hyoglossus and sternohyoideus have fused to form a single muscle that passes unbroken from the sternum to the tongue.

INSERTION: This muscle passes anteriorly to insert in the posterior tongue surface, medial to the insertion of the styloglossus.

OTHER GLOSSOPHAGINES: The hyoglossus is similar in *Monophyllus*, *Lichonycteris*, *Lonchophylla*, *Lionycteris*, and *Platalina*. In *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeronycteris*, and *Choeronycteris* the origin and insertion are the same. The hyoglossi of these

bats, however, are covered completely by the expanded insertion of the geniohyoideus, which forms a “tunnel” that encompasses the hyoglossus (see *M. geniohyoideus*). The basihyal raphe has almost completely disappeared, and the former break between the hyoglossi and sternohyoidei is not visible in any of these six genera, except as the point at which the geniohyoideus inserts.

OTHER BATS: In the Brachyphyllinae, this muscle originates by tendon from the basihyal bone. In all other phyllostomids dissected, this muscle originates by a very short tendon from the basihyal bone.

COMMENTS: See *M. geniohyoideus* Comments.

M. STYLOGLOSSUS

Figures 3–20

ORIGIN: In *Glossophaga soricina*, from the expanded distal tip of the stylohyal, and from the posterior 4 mm. of the lateral surface of the stylohyal bone.

INSERTION: This muscle passes anteriorly and somewhat medially, to insert in the posterolateral “corner” of the tongue. The fibers of this muscle intermingle (at right angles) with those of the hyoglossus.

OTHER GLOSSOPHAGINES: This muscle is

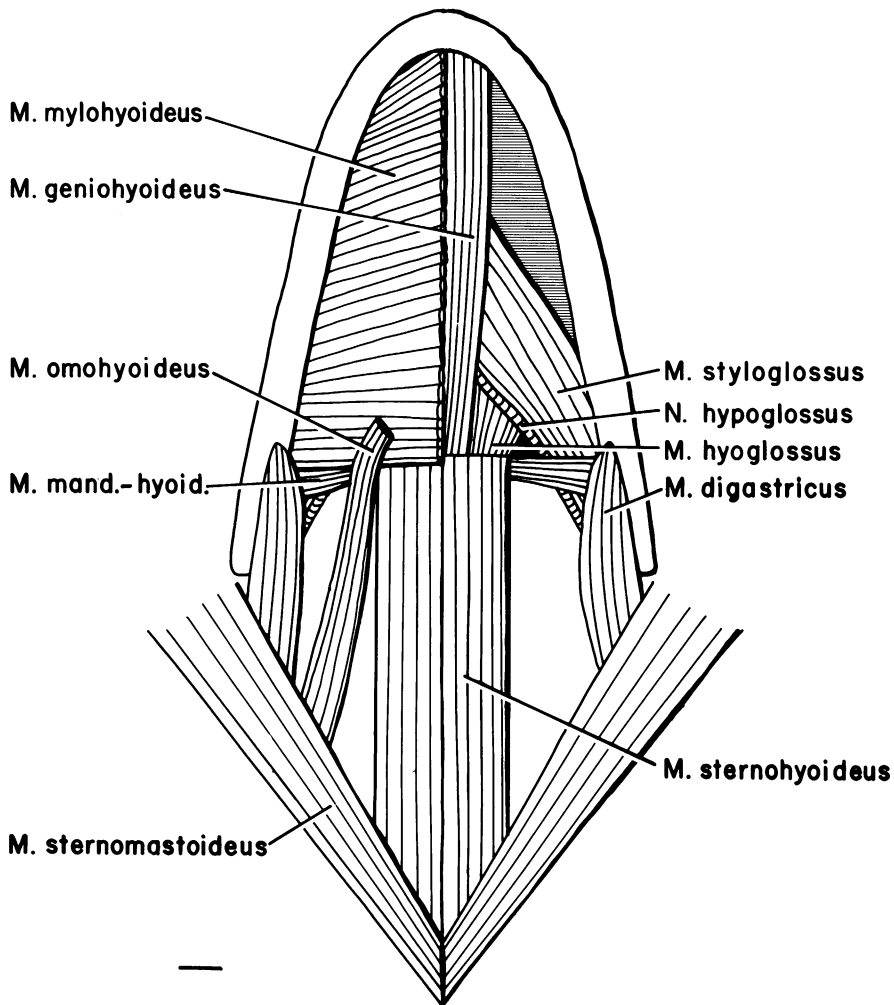


FIG. 14. Ventral view of the hyoid musculature of *Phyllonycteris poeyi*. Bar = 1 mm.

similar in *Monophyllus*, *Lichonycteris*, *Leptoncycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, and *Choeronycteris*. In *Lonchophylla*, *Lionycteris* and *Platalina* the insertion of this muscle is not in the posterior "corner" of the tongue, but rather into the lateral tongue surface, as in the bats below.

OTHER BATS: In the Brachyphyllinae, the origin of this muscle is similar to that of the Glossophaginae. The insertion is into the lateral surface of the tongue for much of the tongue length. This is true of all phyllostomids dissected.

COMMENTS: Occasionally, this muscle is very reduced (*Leptoncycteris* AMNH 122936),

or is composed of two distinct heads (*Desmodus* AMNH 208902). These seem to be peculiarities of individual specimens, however, and not entire species. The apomorphic condition observed here (the posterior insertion of this muscle) is once again found in all "glossophaginae" other than *Lonchophylla*, *Lionycteris*, and *Platalina*.

MEDIAL VENTRAL CERVICAL GROUP

The muscles of this group are innervated by an anastomosis of nerves made up of the anterior cervical nerves, except for *M. geniohyoideus* which is apparently innervated

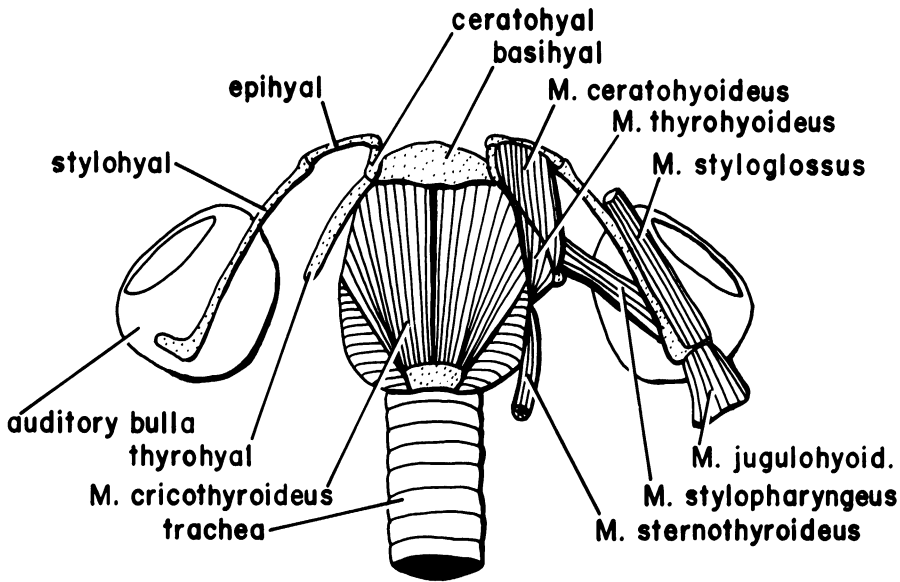


FIG. 15. Ventral view of the hyoid apparatus and larynx of *Phyllonycteris poeyi*.

by *N. hypoglossus* (XII). Despite the apparent differing innervations, these muscles are treated as a group on the basis of similar embryonic differentiation (Edgeworth, 1916).

M. GENIOHYOIDEUS

Figures 3-12, 14, 16, 18, 19

ORIGIN: In *Glossophaga soricina*, by tendon from the medial surface of the mandible at a point approximately 2 mm. lateral to the symphysis.

INSERTION: There are actually two separate insertions for this muscle: a superficial insertion and a deep insertion. As this muscle passes posteriorly, it splits. The superficial fibers pass ventral to the basihyal and continue posteriorly to insert in the fibers of the hyoglossus, and in the fibers of the sternothyroideus via the former basihyal raphe. This insertion is relatively weak. The deep fibers of this muscle insert directly on the anterior surface of the basihyal bone; this insertion is relatively strong.

OTHER GLOSSOPHAGINES: The geniohyoideus is similar in *Monophyllus*, *Lichonycteris*, *Lonchophylla*, *Lionycteris* and *Platalina*. In *Leptonycteris*, *Anoura*, *Hylonycteris*,

Choeronycteris, and *Choeroniscus* the geniohyoideus is very different. The origin is essentially the same, though it is expanded laterally on the medial mandible. The muscle passes posteriorly in the same fashion as in *Glossophaga*, and splits into a superficial and a deep insertion. The deep insertion is on the anterior face of the basihyal, as in *Glossophaga*. However, the superficial insertion is not relatively weak, as in *Glossophaga*. Rather it is very well developed and strong, inserting in a loop around the ventral and dorsal surfaces of the intersection of the hyoglossus and sternothyroideus muscles. To do this, the geniohyoideus literally forms a "tunnel" around the hyoglossus, enclosing it almost completely (see figs. 9 and 10).

OTHER BATS: In the Brachyphyllinae, this muscle inserts by tendon to the basihyal. In all other phyllostomids, this muscle inserts via short tendon to the basihyal.

COMMENTS: There seem to be two apomorphic states in the glossophagine bats: (1) where the geniohyoid has a strong, deep basihyal bone insertion, and a weak, superficial basihyal raphe insertion; and (2) where the geniohyoid has a strong insertion in both places. In no. 2, the geniohyoid accomplishes

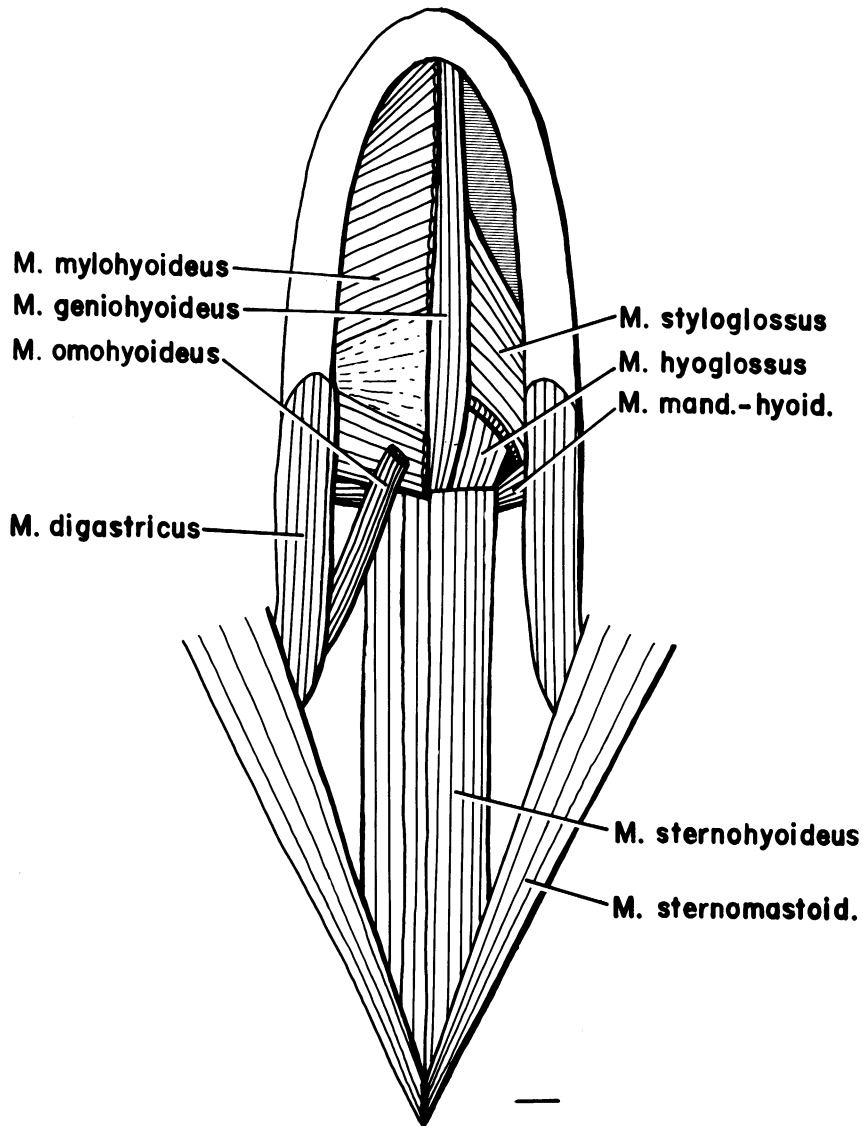


FIG. 16. The hyoid musculature of a phyllostomine bat, *Macrotus waterhousii*. Bar = 1 mm.

this strong insertion by forming a tunnel which envelops the hyoglossus. Condition no. 2 could be derived from condition no. 1, or the two could have independently evolved. In any event, the tunnel insertion (condition no. 2) is definitely an apomorphous condition that has never been reported for any other mammal group. It therefore most strongly links the genera that share this trait: *Lepto-*

nycteris, *Anoura*, *Hylonycteris*, *Choeronycteris*, and *Choeronycteris*.

M. STERNOHYOIDEUS

Figures 3, 4, 6, 7, 9-12, 14, 16, 18

ORIGIN: In *Glossophaga soricina*, from the dorsal surface of the xiphoid process of the sternum.

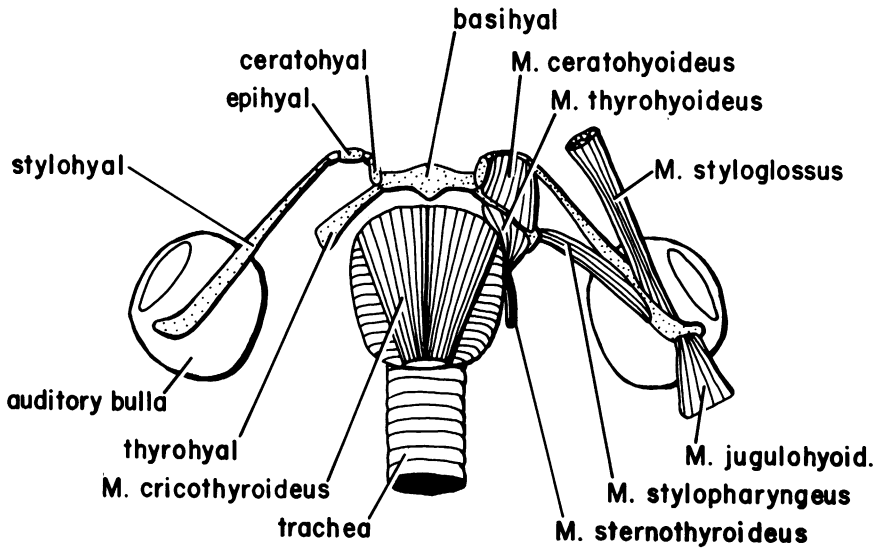


FIG. 17. Ventral view of the hyoid apparatus and larynx of a phyllostomine bat, *Macrotus waterhousii*. Bar = 1 mm.

INSERTION: This muscle passes anteriorly to insert by raphe in the fibers of the hyoglossus and in the superficial fibers of the geniohyoideus muscle. There is no connection to the hyoid apparatus.

OTHER GLOSSOPHAGINES: The sternohyoideus is similar in *Monophyllus*, *Lichonycteris*, *Lonchophylla*, *Lionycteris*, and *Platylina*. In *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, and *Choeronycteris* the origin of the sternohyoideus is similar to that in *Glossophaga*. The insertion is in the fibers of the hyoglossus, and in the highly modified circular insertion of the geniohyoideus (see *M. geniohyoideus*). In one individual of *Lonchophylla robusta* and *Lionycteris spurrellii* there was a remnant of the basihyal tendon present.

OTHER BATS: In the Brachyphyllinae, this muscle originates from a point slightly posterior to the "normal" origin, although not shifted as far posteriorly as in the glossophagines. In *Erophylla*, medial fibers of this muscle originate from the anterior body of the sternum (not the manubrium), whereas more lateral fibers of this muscle originate

from the lateral manubrium and proximal head of the clavicle. In *Erophylla*, the medial fibers alone have a shifted origin. In both *Brachyphylla* and *Phyllonycteris*, the medial fibers take origin from the anterior body of the sternum as well, but also the more lateral fibers have a shifted origin too. They take origin from the proximal head of the first rib, instead of from the lateral manubrium. In both *Brachyphylla* and *Phyllonycteris*, there are extremely weak, lateralmost fibers that retain the origin from the medial head of the clavicle. In all three genera, the insertion of the sternohyoideus is via tendon to the basihyal bone.

In all other phyllostomids except *Desmodus*, this muscle originates from the dorsal surface of the manubrium of the sternum, and from the medial head of the clavicle and sterno-clavicular articulation. In *Desmodus*, the origin is similar to that of *Phyllonycteris*.

COMMENTS: Obviously, the posterior shift of the origin of the sternohyoideus muscle is an apomorphic condition, as in the insertion into the fibers of the hyoglossus, rather than the basihyal bone. All three brachyphyllines,

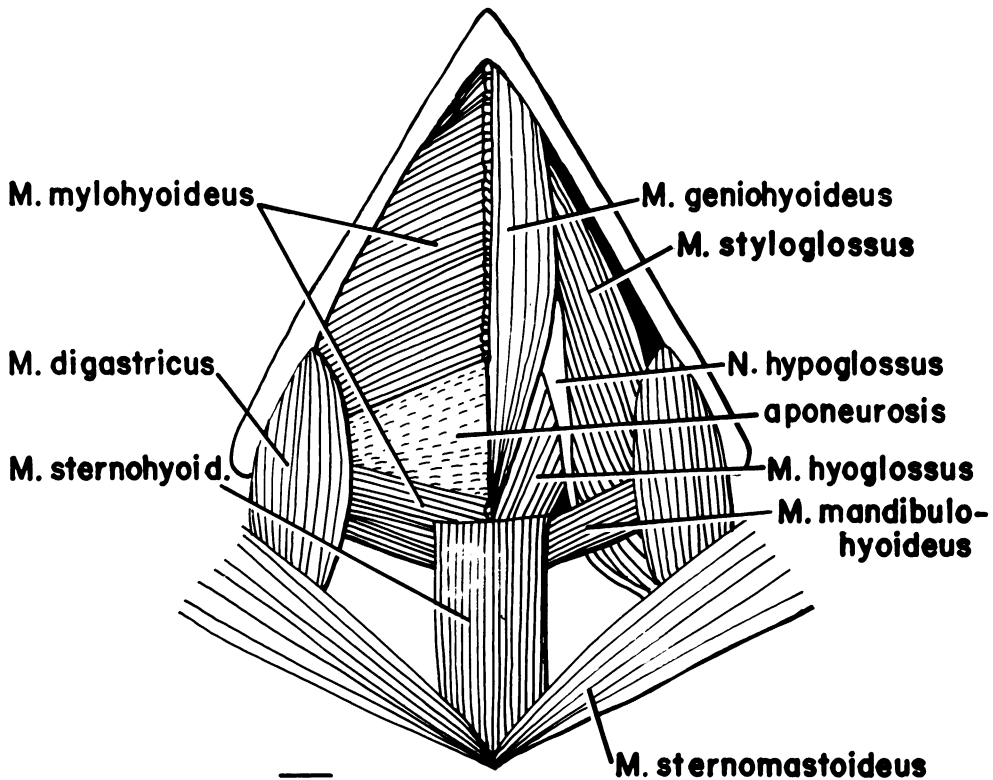


FIG. 18. The superficial hyoid musculature of a stenodermatine bat, *Vampyressa pusilla*. Bar = 1 mm.

including *Brachyphylla*, share a slightly posterad shifted origin of this muscle. The question of whether the shifts in the glossophagines are synapomorphies or due to convergence is discussed below.

M. STERNOTHYROIDEUS

Figures 5, 8, 13, 15, 17

ORIGIN: In *Glossophaga soricina*, from the dorsal surface of the medial clavicle, just lateral to the sterno-clavicular articulation.

INSERTION: This muscle runs anteriorly to insert on the lateral surface of the thyroid cartilage, just posterior to the origin of the thyrohyoideus muscle.

OTHER GLOSSOPHAGINES: The sternothyroideus is similar in *Monophyllus*, *Lichonycteris*, *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, *Lonchophylla*, *Lionycteris*, and *Platalina*.

OTHER BATS: The origin and insertion of

this muscle is the same in the Brachyphyllinae and in all phyllostomids dissected.

M. OMOHYOIDEUS

Figures 3, 6, 11, 14, 16

This muscle is reduced in all glossophagines and absent in many specimens.

ORIGIN: In *Glossophaga soricina*, from the deep surface of the bone of the scapula immediately surrounding the scapular notch.

INSERTION: This muscle passes ventrally and medially, curving around the cervical area deep to both the sternomastoid and cleidomastoid muscles. It inserts weakly in the fibers of the hyoglossus and mylohyoid muscles.

OTHER GLOSSOPHAGINES: This muscle is similar in *Monophyllus* (though slightly more robust), *Lichonycteris*, *Leptonycteris*, *Anoura* (more reduced), *Hylonycteris* (more reduced), *Choeroniscus*, and *Choeronycteris*

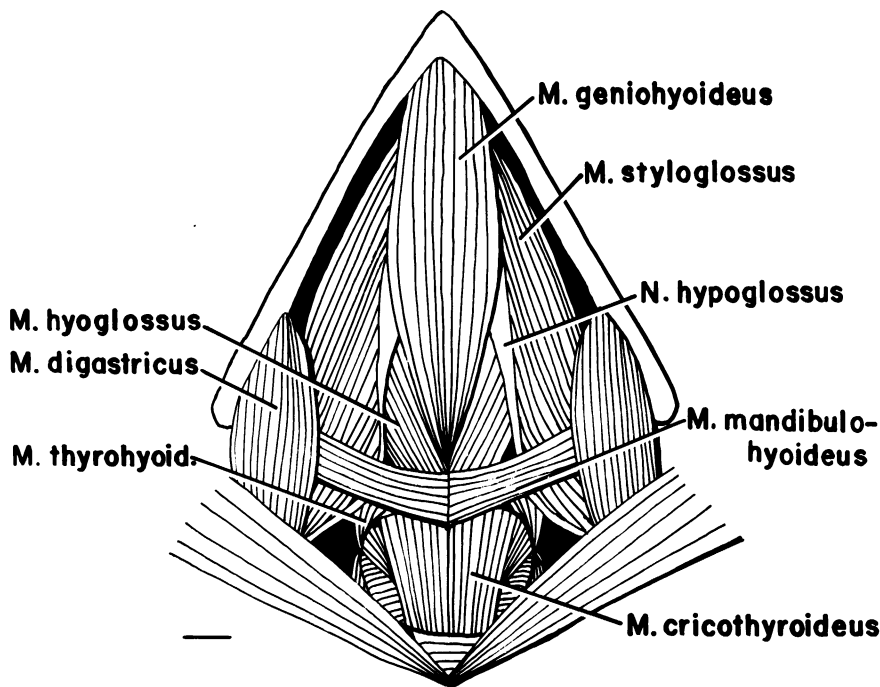


FIG. 19. The deep hyoid musculature of a stenodermatine bat, *Vampyressa pusilla*. Bar = 1 mm.

(extremely reduced). In *Lonchophylla* and *Platalina* this muscle is much more robust. This muscle was not observed in the single specimen of *Lionycteris* dissected, but this was probably due more to the poor state of preservation of the hyoid region.

OTHER BATS: In the Brachyphyllinae, the origin and insertion of this muscle are into the sternohyoid and mylohyoid muscles, though this muscle appeared to be absent in one specimen of *Erophylla* (AMNH 164281). In the remaining phyllostomids this muscle was variable within species. When present, the origin and insertion were the same as in *Brachyphylla*.

COMMENTS: Because of the extreme variation observed, this muscle is unreliable as a taxonomic indicator.

M. THYROHYOIDEUS Figures 5, 8, 13, 15, 17

ORIGIN: In *Glossophaga soricina*, from the lateral surface of the thyroid cartilage, just anterior to the insertion of the sternothyroideus muscle.

INSERTION: This muscle passes anteriorly, fanning out as it does so, to insert on the thyrohyal bone (posterior hyoid cornu) and partially in the fibers of the ceratohyoideus muscle.

OTHER GLOSSOPHAGINES: The thyrohyoideus is similar in all glossophagine bats dissected.

OTHER BATS: The thyrohyoideus is similar in all bats dissected.

TONGUE MORPHOLOGY AND HISTOLOGY

EXTERNAL MORPHOLOGY

GLOSSOPHAGINAE: To avoid confusion and facilitate comparison, I follow the terminology used by Greenbaum and Phillips (1974) in their work on the tongues of *Leptonycteris sanborni* and *L. nivalis*. The tongues of all "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina* are similar (see figs. 21, 27, 28, and 29). Greenbaum and Phillips (1974) identified seven types of papillae on the tongues of *Leptonycteris*: hair-

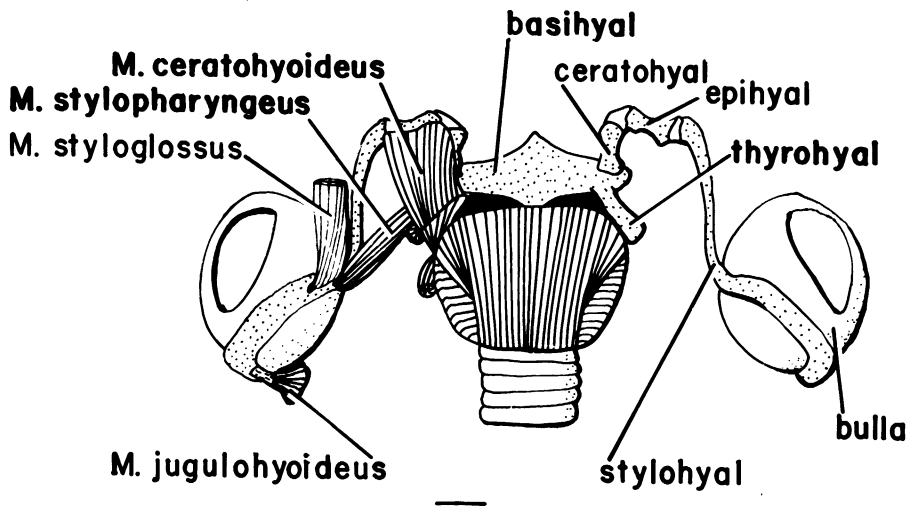


FIG. 20. Ventral view of the hyoid apparatus and larynx of a stenodermatine bat, *Vampyressa pusilla*. Bar = 1 mm.

like papillae, horny papillae, bifid papillae, singly-pointed papillae (two types, fleshy and hooklike), fungiform papillae, and circumvallate papillae. I agree completely with the classification of papilla types as proposed by Greenbaum and Phillips (1974). See figure 21 for relative placement of the various papilla types on the tongue.

The hairlike papillae are distributed over the anterolateral surface of the tongue in all "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina*. These papillae form an anterior "brush," presumed by Greenbaum and Phillips (1974) and Howell and Hodgkin (1976) to be used in nectar-feeding (see fig. 21). The horny papillae are found in all "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina* on either side of the dorsal midline of the tongue. Their arrangement, shown in figure 22, is of some interest. Generally, they consist of two or more large, posteriorly-directed papillae, surrounded by several smaller papillae. The shape and number of horny papillae seems constant within a genus, but varies between genera except in the cases of *Monophyllus*/*Glossophaga* and *Hylonycteris*/*Choeroniscus*/*Choeronycteris*. The bifid papillae, singly-pointed papillae, and fungiform papillae are distributed as shown in figure 21, and are common to all "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina* (see be-

low). The circumvallate papillae are present in all "glossophagines" except *Lonchophylla*, *Lionycteris*, and *Platalina*, where they are absent. In *Glossophaga*, *Monophyllus*, *Lichonycteris*, and usually *Leptonycteris*, there are four circumvallate papillae: two lateral and two medial. In every specimen dissected, the lateral papillae were larger than the medial ones. In one specimen of *Leptonycteris sanborni*, one medial circumvallate papilla was missing. In every specimen of *Anoura*, *Hylonycteris*, *Choeroniscus*, and *Choeronycteris* dissected only the two large lateral circumvallate papillae were present.

In *Lonchophylla*, *Lionycteris*, and *Platalina* the external tongue morphology is completely different. There are only two papilla types present: short hairlike papillae and fleshy monofid papillae. Additionally, there is a deep, longitudinal groove in the lateral surface of the tongue from a point just posterior to the tip to the base of the tongue. The short hairlike papillae do not form a brush tip, but rather form a line just dorsal to and just ventral to the longitudinal groove. The fleshy monofid papillae coat the dorsal tongue surface. All other papilla types are absent.

BRACHYPHYLLINAE: The tongues of *Erophylla* and *Phyllonycteris* are similar to one another, and to the tongues of the *Glossophaga*-type glossophagines. The tongue of

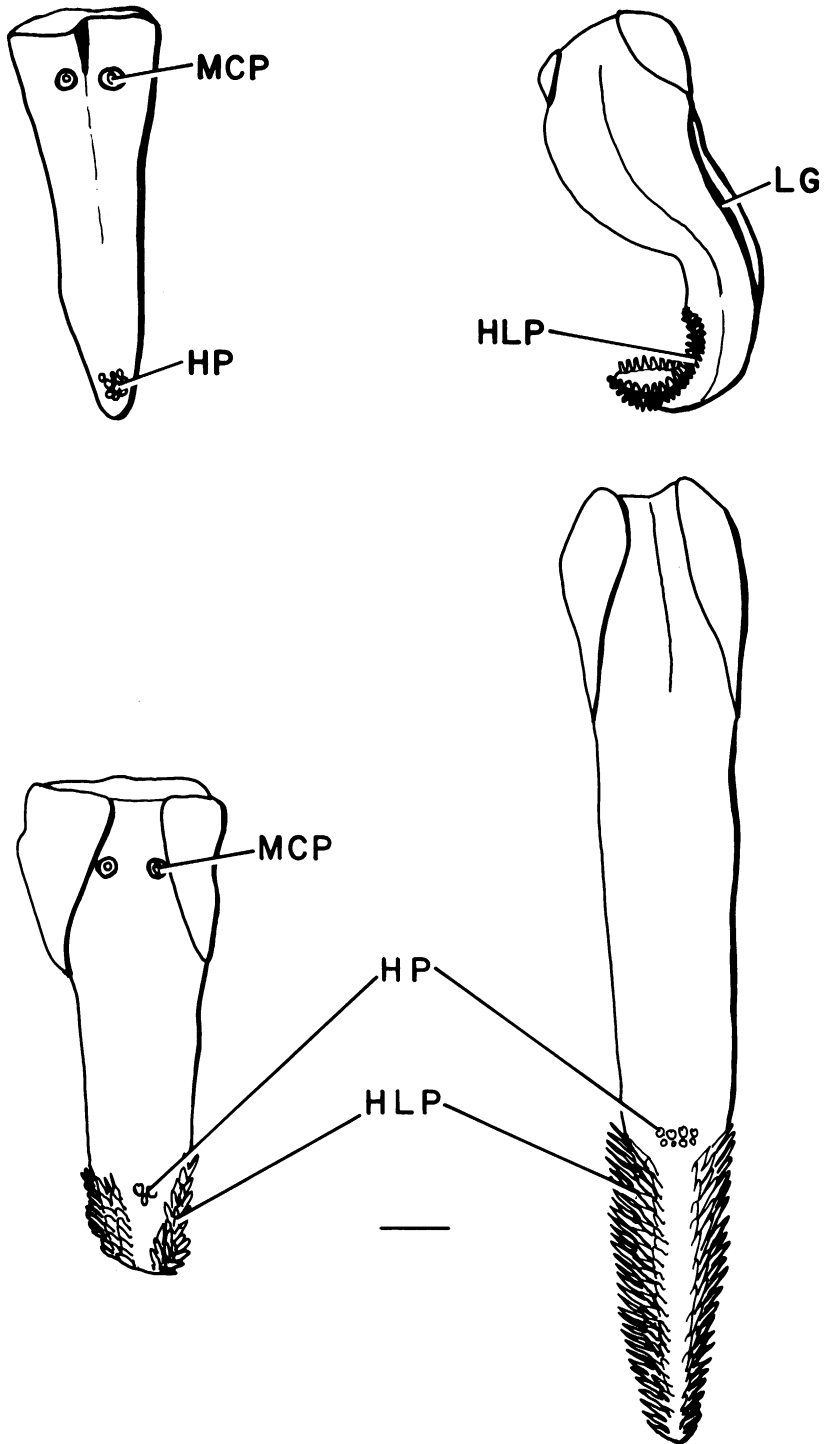


FIG. 21. Upper left: the tongue of *Macrotus waterhousii*, dorsal surface. Upper right: the tongue of *Lionycteris spurrelli*, dorsal surface. Lower left: the tongue of *Glossophaga soricina*, dorsal surface. Lower right: the tongue of *Choeronycteris mexicana*, dorsal surface. Bar = 1 mm. MCP = median circumvallate papilla, LG = longitudinal groove, HP = horny papillae, HLP = hairlike papillae.

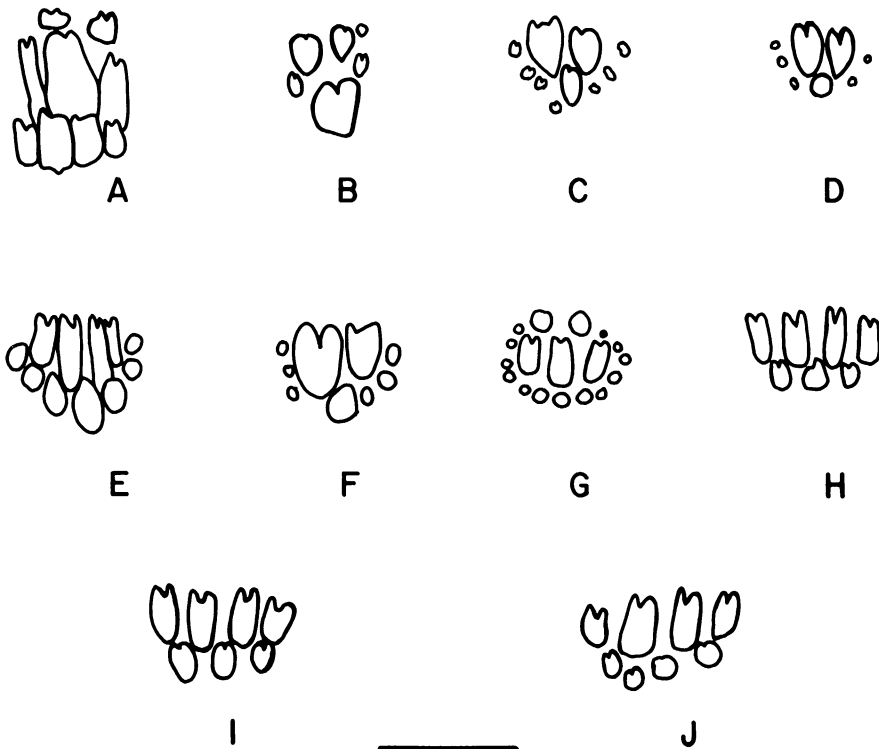


FIG. 22. The horny papillae of the bats examined in this paper. A. *Brachyphylla*, B. *Phyllostomeris*, C. *Glossophaga*, D. *Monophyllus*, E. *Lichonycteris*, F. *Leptonycteris*, G. *Anoura*, H. *Hylonycteris*, I. *Choeroniscus*, J. *Choeronycteris*. Bar = 1 mm.

Brachyphylla is morphologically different. The *Brachyphylla* tongue has horny papillae, singly-pointed papillae (mostly fleshy), fungiform papillae, and circumvallate papillae. It does not have hairlike papillae at the tip, and no bifid papillae were observed. Figure 23 shows the arrangement of papillae on the tongue of *Brachyphylla*. There are only two medial (and no lateral) circumvallate papillae present.

In *Erophylla* and *Phyllostomeris*, the tongues are similar to that of *Brachyphylla* in some respects, and to those of the *Glossophaga*-type "glossophagines" in others (see fig. 23). No bifid papillae are present, but there are hairlike papillae forming a brush tip similar to that of *Glossophaga*. Four circumvallate papillae are present in all specimens dissected, though the medial two are always larger. In all other respects, the tongues of *Erophylla* and *Phyllostomeris* are similar to that of *Brachyphylla*.

OTHER BATS: The three phyllostomine genera are similar. All three have horny papillae, singly-pointed (mostly fleshy monofid) papillae, fungiform papillae, and circumvallate papillae (two lateral and two medial). Figure 21 shows the placement of these papillae on the tongue surface. The horny papillae and the circumvallate papillae are virtually identical in *Phyllostomus* and *Micronycteris*. The horny papillae in these two genera form a distinctive 3/4 row (three anterior and four posterior, see fig. 24A) and the circumvallate papillae are all large and well developed. In *Macrotus*, the horny papillae show a less orderly appearance (fig. 24B), and the two lateral circumvallate papillae are very reduced.

All five stenodermatine genera have a generally similar tongue morphology. All have horny papillae, singly-pointed (mostly fleshy) papillae, fungiform papillae, and four circumvallate papillae. They also all share a distinctive cluster of bifid papillae located in

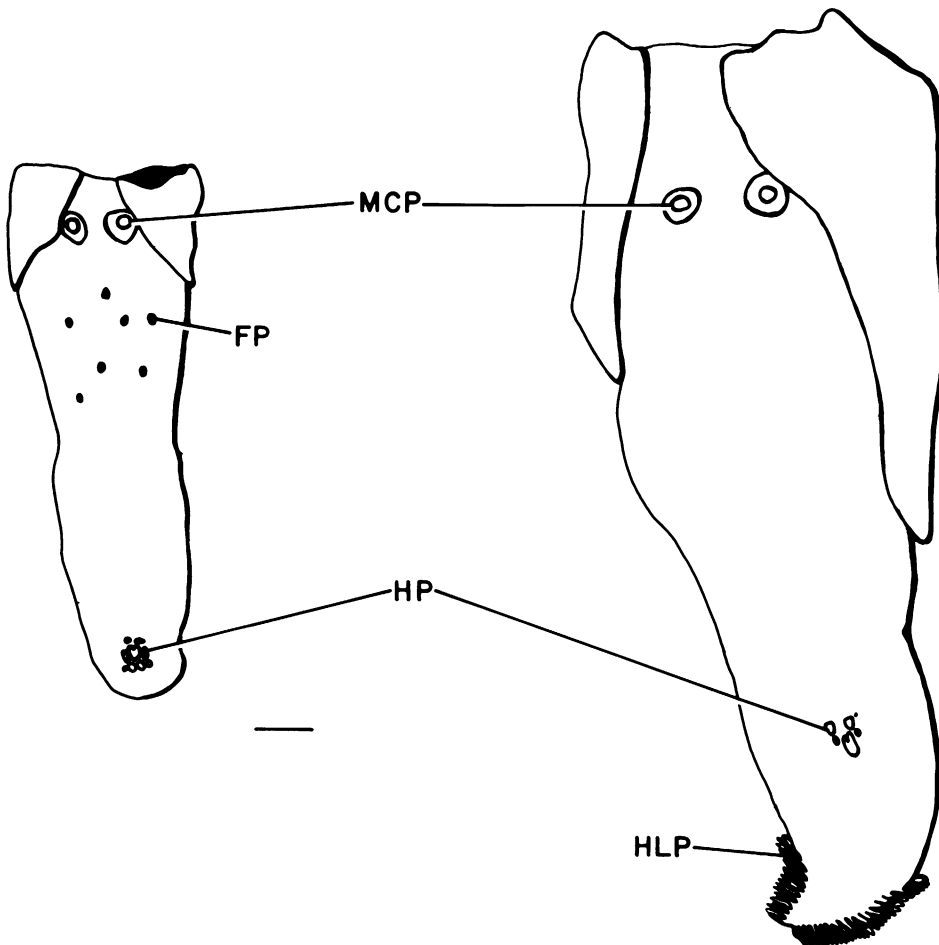


FIG. 23. Dorsal surfaces of the tongues of *Brachyphylla cavernarum* (left) and *Phyllonycteris poeyi* (right). Bar = 1 mm. MCP = median circumvallate papilla, FP = fungiform papilla, HP = horny papilla, HLP = hairlike papillae.

the posteromedian region of the dorsal tongue surface (though this cluster is reduced in *Vampyressa*). The horny papillae of *Uroderma* resemble those of *Phyllostomus/Micronycteris* in having the 3/4 pattern (fig. 24); all other stenodermatines have a "less orderly" *Macrotus*-type appearance (see fig. 25). Interestingly, the three tongue types observed in the Stenodermatinae correspond well to the three divisions of the Stenodermatinae proposed by Gardner (1977).

The tongue of *Carollia* is most similar to the *Glossophaga*-type tongue in some characters. There are no hairlike papillae, but the horny papillae consist of two large, poste-

riorly directed papillae, surrounded by several smaller papillae (fig. 26). There are no bifid papillae, but the remaining papilla types of *Glossophaga* are present. There are four circumvallate papillae.

The tongue of *Desmodus* is, in some respects, most similar to the tongues of *Lonchophylla*, *Lionycteris*, and *Platalina*. There are very few papilla types on the tongue surface: essentially there are only fleshy monofid papillae and perhaps a few fungiform papillae. No other type is present. Additionally, there is a longitudinal groove along the lateral tongue surface, though this groove is not nearly as deep as the one in the *Lonchophylla*

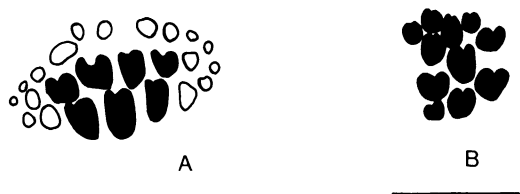


FIG. 24. The horny papillae of *Phyllostomus hastatus* (left) and *Macrotus waterhousii* (right). The major papillae are filled in to distinguish them from the minor papillae (ones that do not open posteriorly, see text). Bar = 1 mm.

group of bats. There are no hairlike papillae lining the groove in *Desmodus*, as there are in the *Lonchophylla* group.

INTERNAL HISTOLOGY

GLOSSOPHAGINAE: All glossophagines examined except *Lonchophylla*, *Lionycteris*, and *Platalina* have a similar internal tongue morphology (see figs. 27 and 28). Anteriorly in the tongue, there is a single, midline lingual artery, rather than left and right lingual ar-

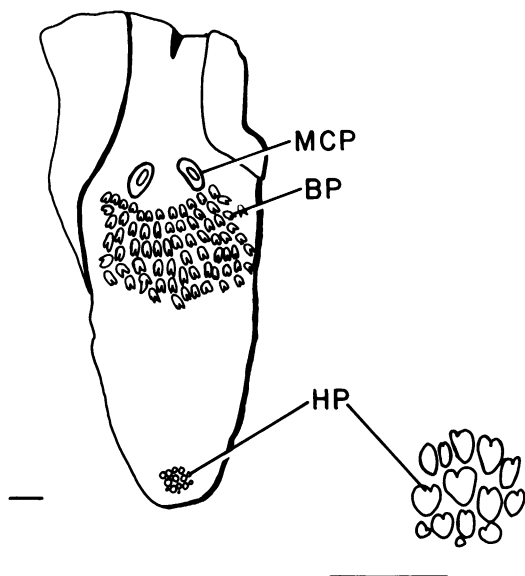


FIG. 25. Dorsal surface of the tongue of the stenodermatine bat, *Artibeus jamaicensis*, with an inset of the horny papillae. Bars = 1 mm. MCP = median circumvallate papilla, BP = bifid papillae, HP = horny papilla.

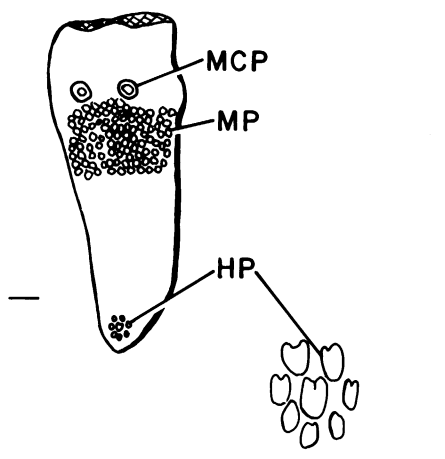


FIG. 26. Dorsal surface of the tongue of *Carollia perspicillata* and an inset of the horny papillae. Bars = 1 mm. MCP = median circumvallate papilla, MP = monofid papillae, HP = horny papilla.

teries as in most mammals. To either side of the artery are two large lingual veins, connected to the artery by artero-venous shunts. The horizontal lingual musculature passes around each of these lingual veins (fig. 27), enclosing them. Toward the tip of the tongue, branches of the lingual veins pass laterally and dorsally into the interior of each hairlike papilla.

The intrinsic tongue structure of the remaining three genera is shown in figure 29. Most prominent are the deep longitudinal grooves on each side of the tongue. Undoubtedly, the shape of these grooves is controlled by the complex bundles of skeletal muscle that pass in all directions within the tongue. There are left and right lingual arteries and veins, plus accessory arteries and veins in the dorsal part of the tongue.

BRACHYPHYLLINAE: The intrinsic tongue structure of *Phyllostomus* and *Erophylla* is very similar to that of the *Glossophaga*-like glossophagines. There is a single, midline lingual artery connected by shunts to two slightly enlarged lingual veins (fig. 31). The intrinsic muscle bundles are also similar. In *Brachyphylla*, however, the tongue structure is more similar to the non-nectar-feeder tongues described below (fig. 30). There are two lingual arteries and veins, with no sign

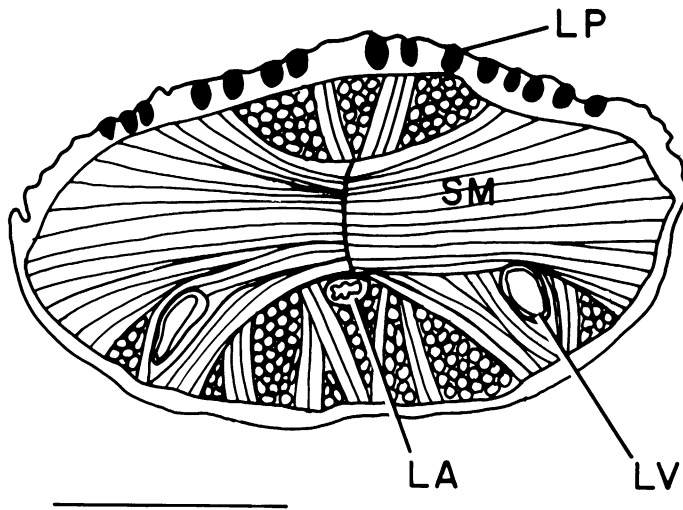


FIG. 27. Cross section of the tongue of *Glossophaga soricina*. Bar = 1 mm. LP = lingual papilla, LA = lingual artery, LV = lingual vein, SM = skeletal muscle.

of the large shunts found in most glossophagines. There is not a single, midline lingual artery present.

OTHER BATS: In all phyllostomines and stenodermatines studied, the intrinsic lingual structure is the same. There are two lingual arteries and veins, with predominantly horizontal skeletal muscle bundles passing around them (fig. 32). In *Carollia*, these horizontal muscle bundles are extraordinarily well developed. In *Desmodus*, the tongue has predominantly horizontal muscle bundles. There is a groove in the lateral tongue surface, quite dissimilar to the groove of *Lonchophylla*, *Lionycteris*, and *Platalina* in that it is not so deep, and there are no complex muscle bundles inserting on it.

SYSTEMATIC CONCLUSIONS

The systematic relationships of the 16 genera studied are presented in the cladogram, figure 33. Tongue and hyoid apomorphies are summarized in table 1. The traditional subfamily "Glossophaginae" is clearly a diphyletic group, and the new subfamily "Brachyphyllinae" (proposed by Baker, 1979) may not be a valid group. The three genera *Lonchophylla*, *Lionycteris*, and *Platalina*, heretofore regarded as glossophagines, have morphologically distinctive tongue and hyoid

regions. Although they share certain hyoid characters with the "other glossophagines" (posterior shift of the sternohyoid origin and development of a sternoglossus complex by loss of the connection to the basihyal), I regard these characters as convergent characters rather than as synapomorphies. The same two character states have occurred independently in at least three other groups within the Mammalia (see Doran and Baggett, 1971, or Griffiths, 1978a) in animals that must hyperextend the tongue to feed. The strongest arguments for *Lonchophylla*, *Lionycteris*, and *Platalina* having become independently nectivorous can be seen in the tongue morphology (see figs. 21, 27, and 29). The tongues of these three genera have lost most of the papilla types found on the tongues of other phyllostomids, most notably the horny and circumvallate types. Although there are hairlike papillae present, they are very differently arranged than in the *Glossophaga*-like glossophagines. Rather than being concentrated on the anterodorsal surface to form a brush tip, the hairlike papillae are arranged in two lines, one line just dorsal and one line just ventral to a deep longitudinal groove (see fig. 21) that runs the length of the tongue in all three genera. The internal tongue structure is also very different (compare figs. 27 and 29). In *Lonchophylla*, *Lio-*

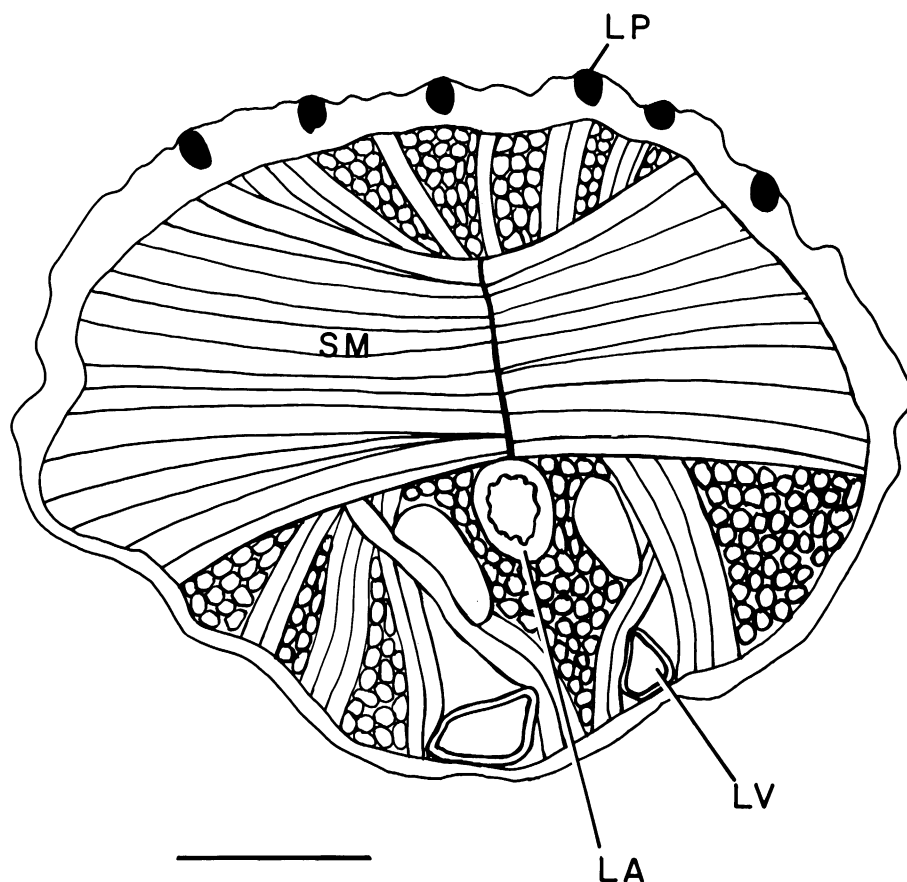


FIG. 28. Cross section of the tongue of *Hylonycteris underwoodi*. Bar = 0.5 mm. LP = lingual papilla, LA = lingual artery, LV = lingual vein, SM = skeletal muscle.

nycteris, and *Platalina*, there are complex bundles of muscle running in many directions within the tongue, probably to control the shape of the groove during nectar-feeding. These complex bundles are not present in other phyllostomids.

It is most unlikely that a bat line that had developed this morphologically complex tongue would lose these adaptations, and then develop the equally complex tongue found in *Phyllonycteris*, *Erophylla*, and the remaining glossophagines. It is therefore likely that the common ancestor shared by *Lonchophylla*/*Lionycteris*/*Platalina* and the other glossophagines was not a nectar-feeder, and that the two lines developed nectar-feeding independently. I thus propose that the genera *Lonchophylla*, *Lionycteris*, and *Platalina* are an independently derived line, united by the synapomorphies of the tongue

(already described), and by: (1) *M. cricopharyngeus* reduced to two, rather than three slips; and (2) the posterior shift of the origin of the sternohyoid and formation of a "sternoglossus" complex. Note that certain other muscle modifications such as posterior shift of the insertion of the styloglossus, are present in the other nectar-feeding line, but not in this one. None of the characters I have examined distinguish *Lonchophylla* from *Lionycteris*, but *Platalina* has a slightly shifted insertion of the genioglossus, and thus I show it as distinct on the cladogram. Two final points should be made about this line. First, because I have demonstrated that there are non-glossophagines that are more closely related to the *Glossophaga-Choeronycteris* group than are *Lonchophylla*, *Lionycteris*, and *Platalina* the last three genera must be placed in a separate taxon of equal status to

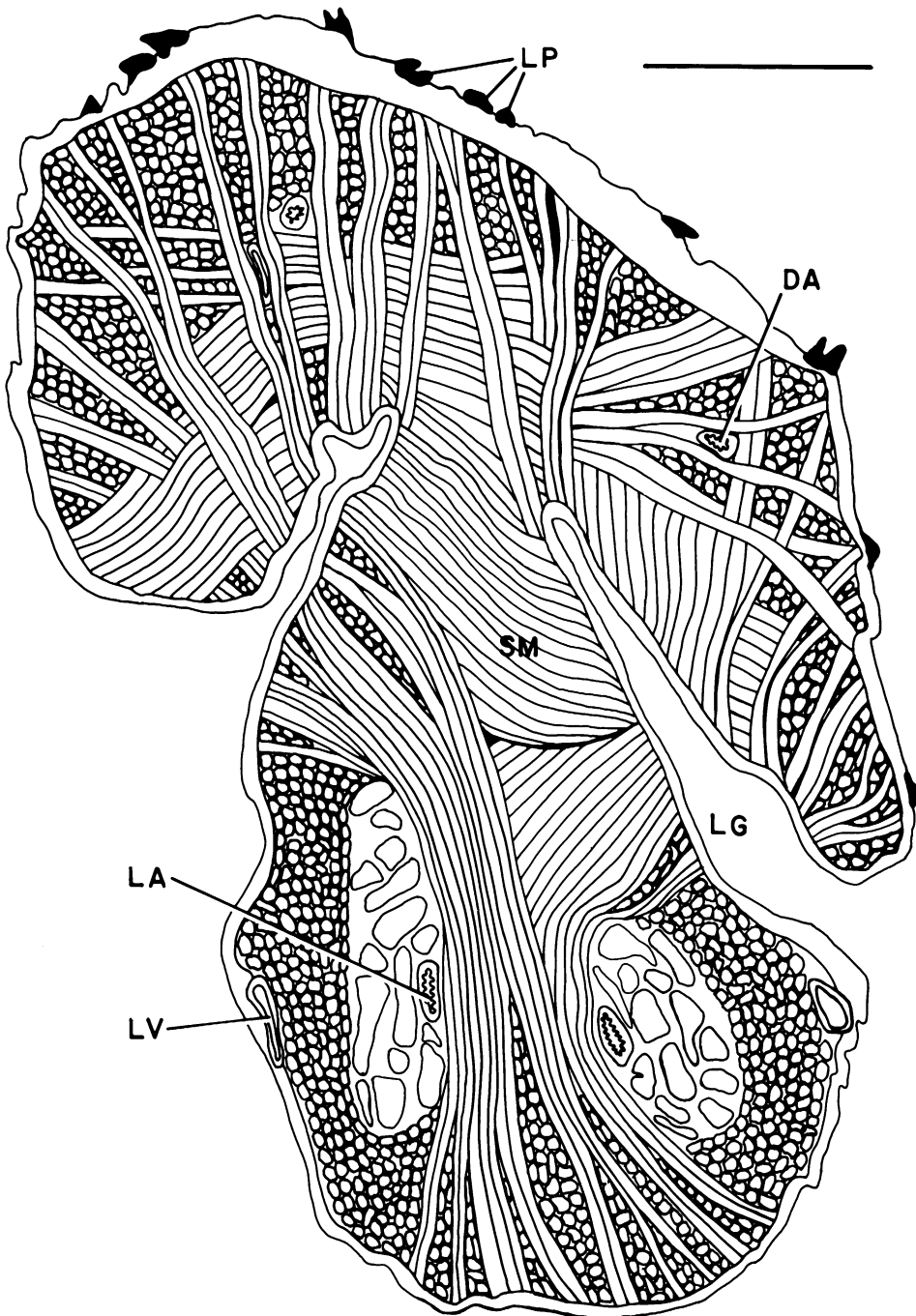


FIG. 29. Cross section of the tongue of *Lonchophylla robusta*. Bar = 1 mm. DA = dorsal artery, LA = lingual artery, LP = lingual papillae, LV = lingual vein, LG = longitudinal groove, SM = skeletal muscle.

the *Glossophaga-Choeronycteris* group. I thus must raise a new subfamily (see formal

classification below). Second, there may be other phyllostomids besides *Brachyphylla*,

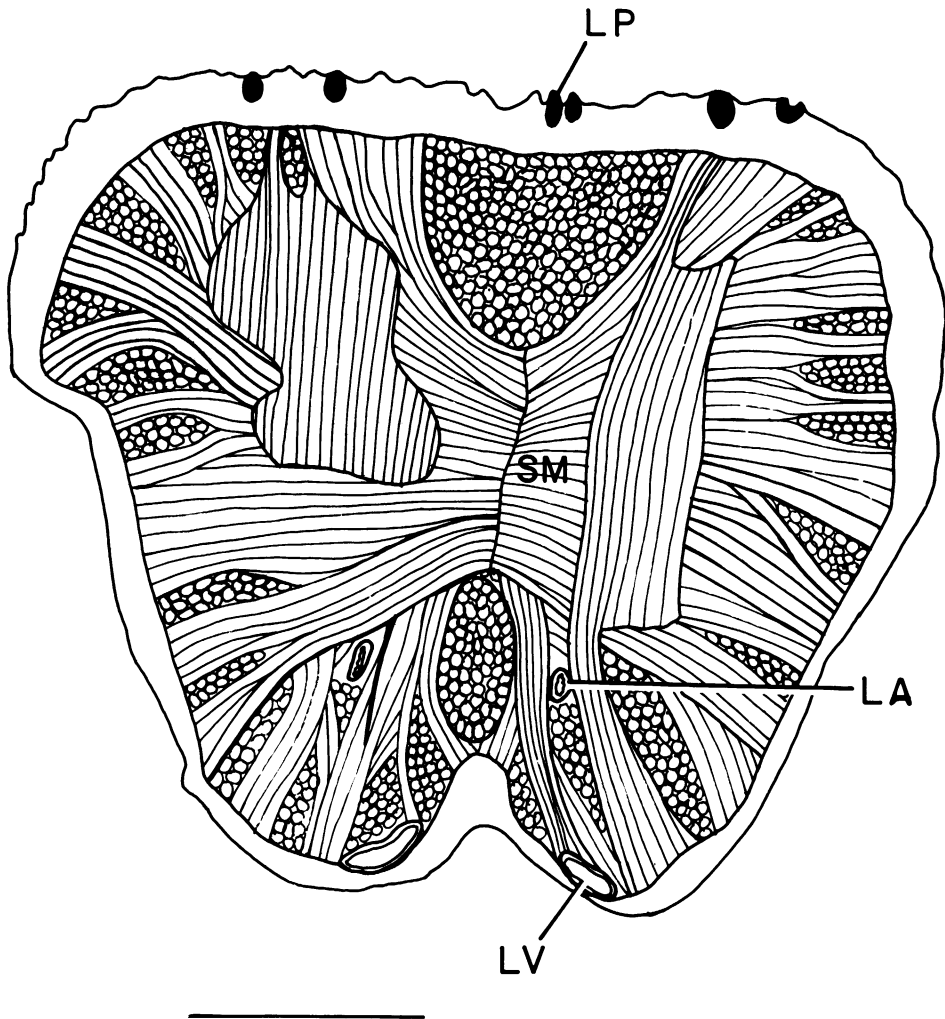


FIG. 30. Cross section of the tongue of *Brachyphylla cavernarum*. Bar = 1 mm. LA = lingual artery, LP = lingual papilla, LV = lingual vein, SM = skeletal muscle.

Phyllonycteris, and *Erophylla* that are also more closely related either to my new subfamily, or the subfamily Glossophaginae (*sensu stricto*). I have left the base of the cladogram open to signify this very likely possibility.

The remaining 13 genera form what appears to be a monophyletic group. The genus *Brachyphylla* is the only possible exception to this statement. Other than the small posterior shift of the origin of the sternohyoid, there is no synapomorphy clearly uniting *Brachyphylla* with the *Phyllonycteris-Choe-*

ronycteris group. *Brachyphylla* does not possess any of the complex internal or external tongue modifications observed in the other 12 genera. However, of all the bats examined in this study, *Brachyphylla* is the most similar to what the primitive, non-nectivorous ancestor of the other 12 might have looked like (for example, it has the proper hyoid bone morphology). For this reason, and because Nagorsen and Peterson (1975), Silva Taboada and Pine (1969), and Baker and Bass (1979) have all suggested that there may be a close relationship between *Brachyphylla*

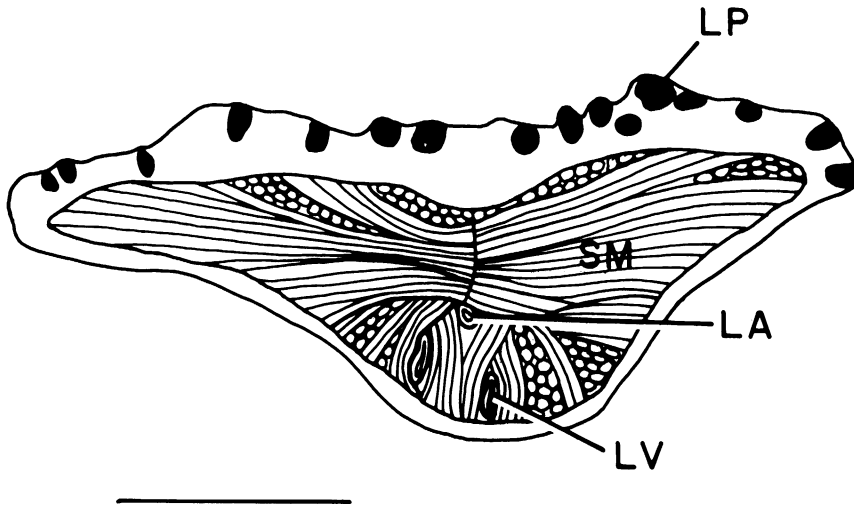


FIG. 31. Cross section of the tongue of *Erophylla sezekorni*. Bar = 1 mm. LA = lingual artery, LP = lingual papilla, LV = lingual vein, SM = skeletal muscle.

and *Phyllonycteris/Erophylla*, I tentatively place *Brachyphylla* at the base of the cladogram. The only other possible placement would be on the same line with *Phyllonycteris/Erophylla* (it could be a non-nectivore derived from a nectivorous ancestor), but I have no evidence to support this view. I must conclude that *Brachyphylla* is on a monogeneric line that is a sister-group to the *Phyllonycteris-Choeronycteris* group. *Brachyphylla* cannot be placed in the same subfamily as *Phyllonycteris/Erophylla*, as proposed by Baker (1979). For my arrangement, see my formal classification below, and see figure 33.

After Branching Point 1 on the cladogram, the remaining 12 genera are united by a strong set of synapomorphies. These are: (1) development of a single, midline lingual artery, large lingual veins, and shunts connecting the two; (2) development of hairlike papillae in a particular pattern on the anterodorsal tongue surface (a "brush-tip," see figs. 21 and 23); and (3) a peculiar 2/1 pattern of the major horny papillae (two papillae anterior and one posterior) shared by *Phyllonycteris*, *Erophylla*, and the more primitive *Glossophaginae* (*sensu stricto*).

After Branching Point 2, there is a very strong set of synapomorphies uniting *Glossophaga-Choeronycteris*. There is the posterior origin of the sternohyoideus from the

xiphisternum, and there is the elongation of the hyoglossus with the freeing of the sternohyoid-hyoglossus from the basihyal, forming a new "sternoglossus" complex. Both of these adaptations have been paralleled in the *Lonchophylla* line of nectar-feeders. However, the following derived character states have no parallels: (1) the styloglossus has an insertion far posterior, on the posterior corner of the tongue; and (2) the genioglossus inserts only into the posterior few mm. of the tongue venter, rather than over the entire ventral surface.

After Branching Point 3, there is a single character uniting the group *Leptonycteris-Choeronycteris*. Despite it being only a single character, it is a good synapomorphy that clearly unites *Leptonycteris-Choeronycteris* as a holophyletic group. This character is the tunnel insertion of *M. geniohyoideus*, where the geniohyoidei completely envelop the hyoglossi (fig. 9). This derived condition could easily have developed from the geniohyoid found in *Glossophaga/Monophyllus/Lichonycteris* (or for that matter, from the geniohyoideus arrangement found in *Lonchophylla/Lionycteris/Platalina*, though the tongue morphology is very different). I suggest that the expanded tunnel insertion of the geniohyoid in the *Leptonycteris-Choeronycteris* group would facilitate elongation of the

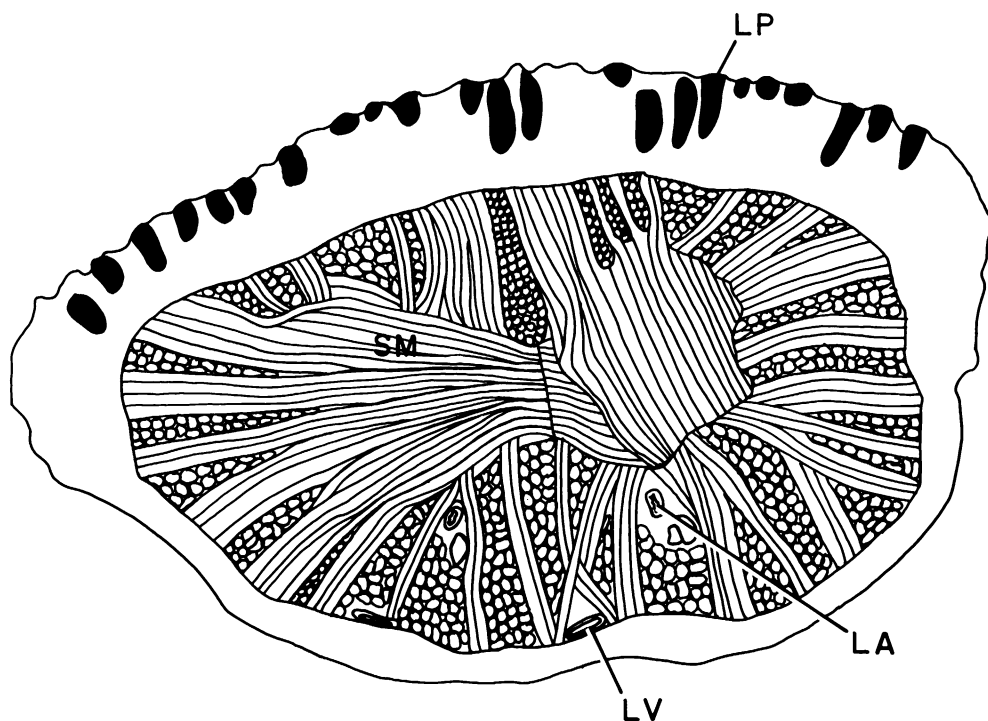


FIG. 32. Cross section of the tongue of *Micronycteris nicefori*. Bar = 0.5 mm. LA = lingual artery, LP = lingual papilla, LV = lingual vein, SM = skeletal muscle.

contracted sternohyoid, thus aiding in extending the tongue maximally (see fig. 10). Regardless of the functional reason for developing the tunnel insertion, the condition is apparently unique to this group; it has not even been reported in the various other mammal groups that hyperextend the tongue (Doran and Baggett, 1971).

The other line to the left at Branching Point 3 must also be justified since there is more than one genus on the line. All three genera, *Glossophaga*, *Monophyllus*, and *Lichonycteris* possess the apomorphies at Branching Point 2, but do not have the tunnel insertion synapomorphy of Branching Point 3. It is clear that all three genera are placed at the proper grade of glossophagine evolution, but unfortunately, the character states of the hyoid and tongue regions do not help here to sort out the genera cladistically. *Glossophaga* and *Monophyllus* are very similar in every

respect and possibly should be combined in the genus *Glossophaga* (Varona, 1974, does this). It is not surprising that the characters of the hyoid and tongue regions fail to separate them. The placement of *Lichonycteris* is more of a problem. *Lichonycteris* has been placed with *Platalina/Hylonycteris/Scleronycteris* (Gardner, 1977; and see Smith, 1976); and with *Hylonycteris* alone (Phillips, 1971). Additionally, there are certain dental similarities to *Leptonycteris*, and Thomas (1895) suggested in the original generic description that *Lichonycteris* resembled both *Glossophaga* and *Choeronycteris*, especially the latter. The characters I have used in this study suggest that *Lichonycteris* should not be placed after *Leptonycteris* or before *Phylonycteris/Erophylla*. I have placed it as an early offshoot of the *Glossophaga/Monophyllus* line, rather than choosing the other option of placing it on its own monogeneric

TABLE 1

Summary of the Apomorphies Used in Constructing the Nectar-Feeding Bat Cladogram (fig. 33)

+ = presence of the character; 0 = absence of the character; +/- = variable.

Derived Character State	Br	Ph	Er	Gl	Mo	Li	Le	An	Hy	Ch	Cht	Lo	Lio	Pl
1) post. shift of sternohyoid origin	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2) xiphoid origin of sternohyoid	0	0	0	+	+	+	+	+	+	+	+	+	+	+
3) loss of sternohyoid's connection to hyoid bone	0	0	0	+	+	+	+	+	+	+	+	+/0	+/0	+
4) hyoglossus elongated and loses connection to hyoid bone	0	0	0	+	+	+	+	+	+	+	+	+	+	+
5) double insertion of geniohyoid	0	0	0	+	+	+	+	+	+	+	+	+	+	+
6) tunnel insertion of geniohyoid	0	0	0	0	0	0	+	+	+	+	+	0	0	0
7) post. shift of styloglossus insertion	0	0	0	+	+	+	+	+	+	+	+	0	0	0
8) post. shift of genioglossus insertion	0	0	0	+	+	+	+	+	+	+	+	+	+	see text
9) loss of the stylohyoid	+	0	0	0	0	0	+/0	+	+	+	+	+	+	+
10) reduction of sphc. col. prof.	0	0	0	0	0	0	0	0	+	+	+	0	0	0
11) cricopharynx reduced to two bellies	0	0	0	0	0	0	0	0	0	0	0	+	+	+
12) groove in tongue lined w/ hairlike papillae	0	0	0	0	0	0	0	0	0	0	0	+	+	+
13) almost complete loss of ling. papillae	0	0	0	0	0	0	0	0	0	0	0	+	+	+
14) brush tip formed by hairlike papillae	0	+	+	+	+	+	+	+	+	+	+	0	0	0
15) two medial CV papillae absent	0	0	0	0	0	0	+/0	+	+	+	+			see text
16) horny papillae in 3/4 pattern	0	0	0	0	0	0	0	0	+	+	+	0	0	0
17) single midline ling. art.	0	+	+	+	+	+	+	+	+	+	+	0	0	0
18) enlarged ling. veins	0	+	+	+	+	+	+	+	+	+	+	0	0	0

line either after or before the *Glossophaga/Monophyllus* line. This decision is based not on lingual morphology, but rather for karyotypic and dental reasons discussed in the next section.

After Branching Point 6, there are only minor characters uniting the *Anoura-Choronycteris* group (and there are some dental characters discussed in the next section that

suggest that the placement of *Anoura* in this position should be regarded as tentative). The synapomorphies after Branching Point 6 are: (1) complete loss of the two medial circumvallate papillae; and (2) complete loss of *M. stylohyoideus*. Ashlock (1974) quite correctly pointed out that generally one should be suspicious of "loss" characters on a cladogram. There is little question that *Anoura* belongs

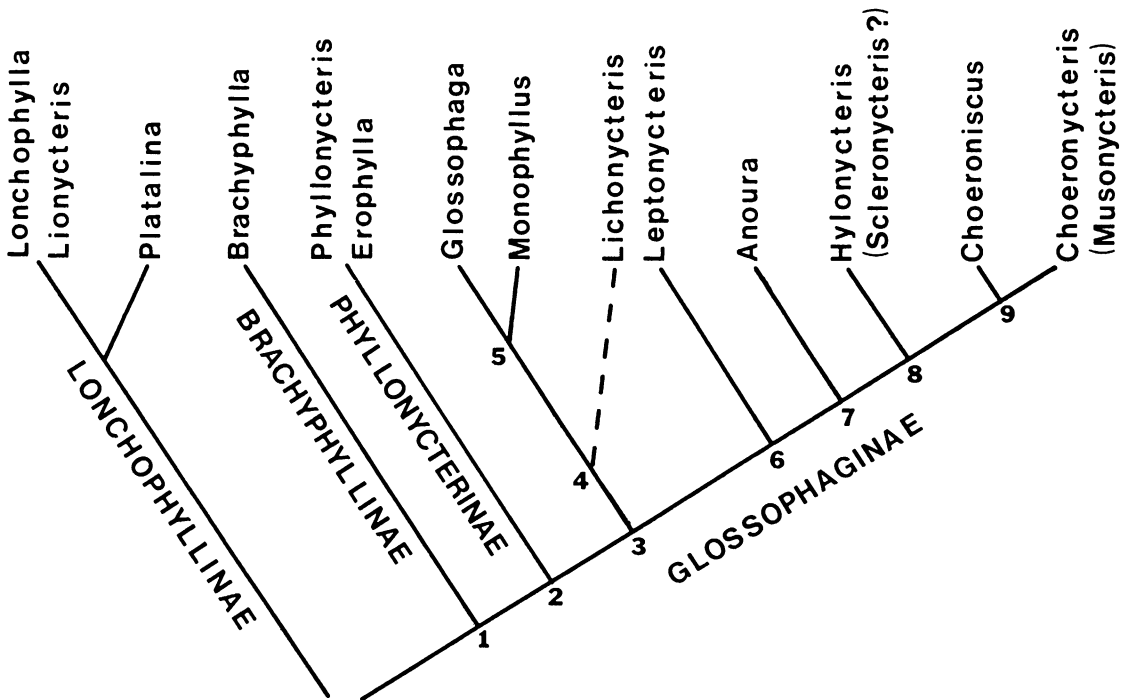


FIG. 33. Cladogram showing the relationships of the nectar-feeding genera discussed herein. See text for characters used.

with *Leptonycteris*, *Hylonycteris*, *Choeroniscus*, and *Choeronycteris* but its placement on the cladogram merely shows the point it seems to fit best and, as with *Lichonycteris*, should be regarded as tentative.

After Branching Point 7, there are once again several strong synapomorphies that indicate that the *Hylonycteris-Choeronycteris* group is monophyletic. *Scleronycteris* and *Musonycteris* exist only as study skins in collections, so obviously I have not dissected them. I place them near what I believe are their closest relatives, based on my examination of their teeth and basicranial regions. Synapomorphies of the entire group include: (1) a strong reduction of the sphincter colli profundus muscle, and (2) the development of a complex 4/3 pattern of the horny papillae (see fig. 22) that is unique to this group of glossophagines. Additionally, Phillips (1971) reported, and I confirm here, that the genera of the *Hylonycteris-Choeronycteris* group share an unusual and highly derived basicranial morphology, where the pterygoid processes are strongly inflected and contact the

auditory bullae posteriorly. There are other dental and karyotypic data uniting this group, discussed below.

The remaining three genera are all closely related, probably having become generically distinct comparatively recently. The characters of the hyoid and lingual regions are insufficient to distinguish between them, and so I must rely on dental and karyotypic observations, discussed below.

SUPPORTING EVIDENCE FROM OTHER DISCIPLINES

The analyses of the karyotypic and dental data have produced apparently conflicting phylogenies for the subfamily Glossophaginae (see figs. 1 and 2). The purpose of this section is to reexamine these data, and show that they support the cladogram presented here as well as they support the phylogenies constructed by Phillips (1971) and Gardner (1977).

Upper Incisors: Evidence from the examination of the glossophagine upper incisors

(Winkelmann, 1971; Phillips, 1971) and my own personal observations support the cladogram I present here. The incisors of *Lonchophylla*, *Lionycteris*, *Platalina*, and *Glossophaga* are the least reduced, or most primitive. They resemble the upper incisors of *Brachyphylla*, *Phyllonycteris*, and *Erophylla* in that the inner incisors are notably larger than the outer ones, and have broad cutting edges (Phillips, 1971), whereas the outer incisors are more pointed. *Monophyllus* and *Leptonycteris* also have "relatively unreduced" upper incisors (Phillips, 1971), though the inner pair is reduced to the same size as the outer pair. Apparently because of this reduction, a small gap has developed between the two inner incisors of these two genera (see Winkelmann, 1971). The trend for reduction of the incisors continues through *Anoura* and *Hylonycteris* to *Choeroniscus*, *Choeronycteris*, and *Musonycteris* where the inner incisors are small, peglike teeth separated by a wide gap, and the outer incisors are reduced as well. Interestingly, the upper incisor configuration of *Lichonycteris* is an additional strong argument against placing this genus with *Hylonycteris*, *Choeroniscus*, or *Choeronycteris*. The upper incisors of *Lichonycteris* are reduced, but in a different manner. The inner incisors are broad and the outer incisors are pointed, as in *Glossophaga*. There is almost no gap between the inner incisors (though they are very reduced), as there is in all the more advanced glossophagines. The incisors of *Lichonycteris* could be most easily derived from those of *Phyllonycteris*, *Erophylla*, or *Glossophaga* though, of course, the condition in these bats is primitive for the subfamily as a whole. The differently reduced incisors in *Lichonycteris* can only be used to emphasize the lack of relationship to the *Hylonycteris-Choeronycteris* group. Unfortunately, there is no good incisor synapomorphy uniting the *Glossophaga/Monophyllus* line and *Lichonycteris*.

Upper Canines: In *Lonchophylla*, *Lionycteris*, *Brachyphylla*, *Phyllonycteris*, *Erophylla*, *Glossophaga*, *Monophyllus*, *Leptonycteris*, and *Anoura*, the canines are unreduced, with a prominent cingular style (Phillips, 1971, and personal observ.). The canines are reduced in *Platalina*, *Lichonycteris*,

and the *Hylonycteris-Choeronycteris* group. If my cladogram is correct, the upper canines would have had to become reduced independently three times: once in *Platalina*, once in *Lichonycteris*, and once in the *Hylonycteris-Choeronycteris* group. There is no evidence for or against this view.

Upper Premolars: The upper premolars are all simple, primitive teeth in *Lonchophylla*, *Lionycteris*, *Glossophaga*, *Monophyllus*, and *Leptonycteris* (Phillips, 1971). *Anoura* has similar upper premolars, but possesses a permanent P2, which is probably a duplicated P3 (Koopman, personal commun.), and thus not of great taxonomic significance. The remaining genera (*Platalina*, *Lichonycteris*, *Hylonycteris*, *Scleronycteris*, and the *Choeronycteris/Choeroniscus* group) all have specialized upper premolars (Phillips, 1971). The *Choeronycteris/Choeroniscus* line has become extremely specialized, with the premolars reduced to long, thin teeth. *Hylonycteris* and *Lichonycteris* show similar reductions, with the loss of various shelves and styler elements, which caused Phillips (1971) to group the two genera together (see fig. 2). This would not be permitted in a cladistic analysis, however, because as Phillips (1971) himself pointed out, the second upper premolar in *Lichonycteris* retains the primitive "postero-lingual shelf" and the "small anterior and posterior styles" as in the less derived, *Glossophaga*-like teeth. I believe that the more primitive tooth morphology of *Lichonycteris* argues against including *Lichonycteris* with the more advanced glossophagines.

Upper Molars: Phillips (1971) used differences he observed in the configuration of the upper molars as a primary means of classification of the glossophagines. I suggest that the upper molar configurations support my cladogram (fig. 33) at least as well as they support his phylogenetic tree (fig. 2). *Platalina*, *Hylonycteris*, *Scleronycteris*, *Choeroniscus*, and *Choeronycteris* all share the derived character of obliteration of the anterior half of the W-shaped ectoloph (found in the more "primitive" glossophagine genera). Removal of *Platalina* from the group (which I have shown elsewhere to be not closely related to the others) allows the use of this character as a synapomorphy uniting the genera

after Branching Point 7 on my cladogram. The primitive W-shaped ectoloph is prominent in *Glossophaga*, *Monophyllus*, and *Anoura* but in *Leptonycteris* the anterior half is considerably straighter than in the *Glossophaga* ectoloph. This straightening could be considered a precursor to the condition in the *Hylonycteris-Choeronycteris* group, though *Anoura*, which retains the prominent W-shaped ectoloph, would have to be moved out of the *Leptonycteris-Choeronycteris* group if this character were found to be significant. Once again, *Lichonycteris* retains the primitive state of a character, which suggests that it does not belong among the more advanced genera.

Lower Incisors: The lower incisors are completely absent in *Lichonycteris*, *Anoura*, *Hylonycteris*, *Scleronycteris*, *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (Phillips, 1971, and personal observ.). In *Lonchophylla*, *Lionycteris*, and *Platalina*, the lower incisors are very large, flat teeth (Phillips, 1971; Winkelmann, 1971) with distinctive "trifid" crowns (Phillips, 1971). These distinctive incisors can be used as a synapomorphy uniting the above three genera. The lower incisors are present (primitive condition) in *Glossophaga*, *Monophyllus*, and *Leptonycteris*. Except for the condition in *Lichonycteris* (which would have to be the result of convergence), these data could be interpreted as a synapomorphous character (loss of lower incisors) uniting the genera after Branching Point 6 on my cladogram.

Lower Canines: The lower canines of every genus to the right of Branching Point 7, plus *Lichonycteris*, are reduced. This reduction could be considered a synapomorphy uniting the *Hylonycteris-Choeronycteris* group. Again, *Lichonycteris* would have had to develop the condition independently.

Lower Premolars: There is considerable variation in premolar morphology among the various genera (Phillips, 1971). In my opinion, the only good synapomorphy uniting a group is the character of long, thin premolars found in *Choeroniscus*, *Choeronycteris*, and *Musonycteris* (see Phillips, 1971); this would unite the group above Branching Point 8.

Lower Molars: The lower molars of all glossophagine genera are remarkably similar (Phillips, 1971). In *Musonycteris* and *Choeronycteris*

the molars are long and thin, with a "flange" on the postcristid (Phillips, 1971) which is present, though underdeveloped in *Choeroniscus*. This character can be used to unite *Choeronycteris* and *Musonycteris* above Branching Point 9 on the cladogram.

Basicranial Region: Phillips (1971) correctly reported that the pterygoid processes of *Choeroniscus*, *Choeronycteris*, and *Musonycteris* have an inflected tip that comes in contact with the auditory bullae. Additionally, *Hylonycteris* has a slightly inflected region that could be considered a precursor to that above. Phillips (1971) used the pterygoid character (and several upper molar characters) to divide the glossophagines into a "*Choeronycteris* group" and a "*Glossophaga* group." The condition noted in the *Choeronycteris* group is clearly a synapomorphy that unites *Choeroniscus-Musonycteris*, and *Hylonycteris-Musonycteris* (if the condition in *Hylonycteris* is a valid precursor). Phillips's "*Glossophaga* group" is not a valid group because the pterygoids of all these bats are primitive (except for *Anoura*, which in a few cases shows some pterygoid inflection). Phillips (1971) was thus using a symplesiomorphic condition to unite a group.

Karyology: Unfortunately, because of the rarity of many of the species of the Glossophaginae, some genera have not been karyotypically examined. Additionally, only a few have been examined with the G and C banding techniques now available (see Baker and Bass, 1979). The karyotypic data available can be interpreted to support the cladogram presented here.

Baker (1967, 1973, 1979) proposed that the primitive karyotype for phyllostomid bats is: diploid number ($2n$) = 30–32, fundamental number (FN) = 56–60. If this be the case, then *Brachyphylla*, *Phyllonycteris*, *Erophylla*, *Glossophaga*, *Monophyllus*, and *Leptonycteris* would share the least derived (32/60) karyotype within the nectar-feeder complex. The *Lichonycteris* karyotype (either 28/50 or 24/44, Baker, 1979) is most similar to, and most easily derivable from, the karyotype of one of the above bats (I have suggested from the *Monophyllus/Glossophaga* line), as Gardner (1977) illustrated. The remaining genera (*Anoura-Choeronycteris*), with successively decreasing $2n$ and FN's (see Baker,

1979) can be derived from this *Glossophaga*-like karyotype (Baker, personal commun.). The arrangement I present (fig. 33) also explains why the karyotypes of *Lonchophylla* and *Lionycteris* are so different from those of the "other glossophagines" (*Platalina* has not yet been karyotyped), as Gardner (1977) showed. Baker (personal commun.) has stated that it would take a large number of chromosomal rearrangements to derive the karyotypes of *Lonchophylla* and *Lionycteris* from the "other glossophagines"; this is easily explained by my suggestion that the "lonchophylline" bats are not closely related to the glossophagines (*sensu stricto*).

Summary and Formal Classification: Except for some problems in the dentition of *Lichonycteris*, the karyotypic, dental, and hyoid/lingual data can be interpreted to support the cladogram presented here (fig. 33). I stress that although there may be problems with the exact placement of *Lichonycteris* and possibly *Anoura*, the available evidence strongly supports the monophyly of the Glossophaginae (minus *Lonchophylla*, *Lionycteris*, and *Platalina*), the distinctiveness and monophyly of the three lonchophylline genera, the monophyly of the *Phyllonycteris-Choeronycteris* group, the monophyly of the *Leptonycteris-Choeronycteris* group, and the monophyly of the *Hylonycteris-Choeronycteris* group. The overall form of the cladogram is probably correct, though *Lichonycteris* and *Anoura* may be slightly misplaced.

I am opposed to the hierarchical classification presented by many cladists, where each branch of the cladogram must be designated as a higher taxonomic group. Using this method, making the slightest change on any level disturbs the stability of the classification. I am also in favor of the principle of disturbing the current classification the least when making changes. The simplest method of following both precepts is presented below.

- Family Phyllostomidae
 - Subfamily Phyllostominae
 - Subfamily Stenodermatinae
 - Subfamily Carollinae
 - Subfamily Desmodontinae
 - Subfamily Brachyphyllinae
 - Brachphylla*

Subfamily Phyllonycterinae

Phyllonycteris

Erophylla

Subfamily Glossophaginae

Glossophaga

Monophyllus

Lichonycteris

Leptonycteris

Anoura

Hylonycteris

Scleronycteris

Choeroniscus

Choeronycteris

Musonycteris

NEW SUBFAMILY

Subfamily Lonchophyllinae

Lonchophylla

Lionycteris

Platalina

Because of the distinct differences in tooth morphology between the phyllonycterines and glossophagines, I am not now in favor of including *Brachyphylla*, *Phyllonycteris*, and *Erophylla* in the subfamily Glossophaginae, though this may eventually be done (perhaps at the Tribe level). For now, I have applied the traditional classification system to my results recognizing that *Brachyphylla* cannot be considered a member of the Phyllonycterinae under the rules of cladistic classification. The only option available until such time as it might be included in the Glossophaginae is to relegate it to its own monogeneric subfamily Brachyphyllinae (name proposed by Baker, 1979).

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