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**Neotropical Nectar-feeding Bats (Family Phyllostomidae) Revisited: Lingual
Data Support a Recently-proposed Molecular Phylogeny.**

A Senior Research Honors Paper Presented
By

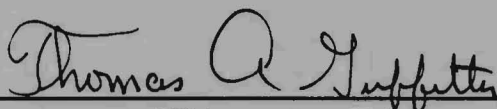
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April 25, 2001

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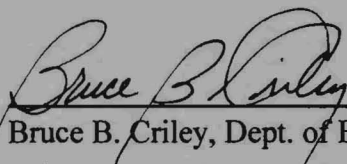
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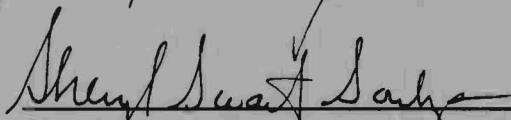
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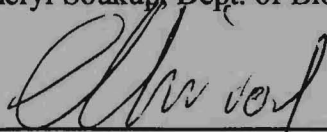
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ABSTRACT

From the early 1900s to the 1970s, all New World nectar-feeding bats were classified under the subfamily Glossophaginae. During the last few decades of the 20th century, however, several analyses supported the hypothesis that this taxon was an unnatural grouping. T. A. Griffiths (1982) proposed creating a new subfamily, the Lonchophyllinae, which would include *Lonchophylla*, *Lionycteris*, and *Platalina*, three genera formerly included in the Glossophaginae. This proposal raised significant controversy. A recent molecular study by R. J. Baker and colleagues (2000) examined the *RAG2* gene DNA sequence in a large number of bats in the family Phyllostomidae, including *Lonchophylla*, *Lionycteris*, and *Lonchorhina*. The evidence suggested that *Lonchophylla* and *Lionycteris* are more closely related to *Lonchorhina* (a non-nectarivorous genus) than to the Glossophaginae *sensu* Griffiths (*Platalina* was not available for examination). In this study, I present observations on the lingual morphology of *Lonchorhina* that support Baker et al.'s placement of *Lonchorhina* with *Lonchophylla* and *Lionycteris*. While *Lonchorhina* does not exhibit the extreme adaptations for nectar-feeding found in the lonchophylline genera, it does share several derived lingual character states with the lonchophyllines. These character states are not found in *Macrotus*, *Micronycteris*, or *Phyllostomus*, other members of the subfamily Phyllostominae (in which *Lonchorhina* has traditionally been placed). While this is clearly a work-in-progress, data collected to date provide some support for Baker et al.'s hypothesis, and thus for Griffiths' (1982) original creation of the subfamily Lonchophyllinae.

INTRODUCTION

In 1878, Dobson presented descriptions of 401 species of New World bats in his Catalogue of the Chiroptera. At that time, this record was the only systematic classification of the Order Chiroptera, all other works being compilations. He categorized bats based on descriptions of several morphological characters including skeletal characters, dentition, and pinna (ear) morphology. Dobson classified bats into two suborders, six families, and eight subfamilies. The family Phyllostomidae was divided into two subfamilies: the Lobostominae and the Phyllostominae. The Phyllostominae were further divided into the groups Vampyri, Glossophagae, Stenodermata, and Desmodontes. The seven genera and ten species that Dobson placed in the Glossophagae were distinguished from other groups by:

- Moderately long muzzle
- Well-developed erect portion of the nose-leaf
- Long filiform papillae located laterally on the tongue
- Large interfemoral membrane
- Distinct calcaneum and tail

The genus *Lonchorhina* was placed in the group Vampyri along with *Carollia*, *Macrotus*, and *Phyllostoma*. The group Glossophagae included *Glossophaga* and *Choeronycteris*. The genera *Lonchophylla*, *Lionycteris*, and *Platalina* were not included in his work.

With few exceptions, Dobson's classification of Glossophagae, based on species known at the time, remained valid. In fact, it served as the basis for other classifications until Miller (1907) revisited Dobson's work and added to it. Miller presented a new classification based on the structure of the wing, shoulder girdle, sternum, and cusps of the teeth. He distinguished two suborders, 17 families, and 19 subfamilies. The family Phyllostomidae was divided into seven

subfamilies and, like Dobson, Miller placed *Glossophaga* and *Choeronycteris* together, along with *Lonchophylla* and *Anoura*, in the subfamily Glossophaginae. In addition, *Lonchorhina* and *Phyllostomus* were included in the subfamily Phyllostominae.

Later, the genera *Lionycteris* (Thomas, 1913), *Choeroniscus* (Thomas, 1928), and *Platalina* (Thomas, 1928) were added, along with two other genera, to the Glossophaginae. Other than these additions, Miller's classification of the Glossophaginae has been used as the basis for all subsequent work, including the very important classification by Simpson (1945), and until recently, was undisputed. Thus, the traditional taxonomy includes *Lonchorhina*, *Macrotus*, *Micronycteris*, and *Phyllostomus* in the subfamily Phyllostominae. The genera *Lonchophylla*, *Lionycteris*, *Platalina*, *Glossophaga*, *Choeroniscus*, *Choernycteris*, *Leptonycteris*, *Monophyllus*, and *Anoura* are traditionally included in the subfamily Glossophaginae.

Beginning in the 1960s, evidence began to accumulate that suggested that the Glossophaginae was not a monophyletic group; in other words, new data suggested that perhaps nectar-feeding had evolved independently at least twice in Neotropical bats. Baker (1967) was the first to suggest that the Glossophaginae was an unnatural group. His analysis of karyotypic data supported the separation of the family Phyllostomidae into seven groups. However, not all of these groups corresponded to the seven traditional subfamilies. Although his work was preliminary, it suggested that *Leptonycteris* and *Glossophaga*, glossophagines, are more closely related to *Phyllostomus*, *Trachops*, and *Macrotus*, phyllostomines, than to other glossophagines examined. He also found that the karyotypes of *Choeroniscus* and *Choeronycteris*, the other glossophagines studied, were more similar to that of *Carollia*, of the subfamily Carollinae, than to the *Leptonycteris*-*Glossophaga* group. Further evidence showed that *Anoura*, another glossophagine, had a karyotype that was distinct from both glossophagine groups examined.

Baker concluded that the subfamily Glossophaginae was derived from two or more different lines of non-nectar-feeders (Baker, 1967, 1970). Later, the genus *Monophyllus*, traditionally a glossophagine, was included in the *Leptonycteris-Glossophaga* group (Baker and Lopez, 1970). Baker and Bass (1979) published a study suggesting that the karyotypes of several glossophagine genera, including *Glossophaga* and *Monophyllus*, are derived from that of *Macrotus*, a phyllostomine, thus supporting a polyphyletic origin in the Glossophaginae. Slaughter (1970) noted a similarity between the primitive teeth found in *Glossophaga* and *Macrotus*, suggesting that these genera shared a recent common ancestor. Furthermore, Slaughter confirmed the relationship between *Choeroniscus* (an “advanced” glossophagine) teeth and the teeth found in the carolline line. Winkelmann (1971) provided further evidence for the polyphyletic origin of the glossophagines in his investigation of lingual and hyoid anatomy. He reported distinctly different intrinsic and extrinsic lingual morphology between the groups of glossophagines.

Phillips (1971) divided the subfamily Glossophaginae into two groups: a *Glossophaga* group and a *Choeronycteris* group (Figure 1). He proposed that either the glossophagines had two separate evolutionary origins or the two groups arose from an early branch in a single ancestor. Gardner (1977) also separated the glossophagines into a *Choeronycteris* group and a *Glossophaga* group, with *Anoura* separate from both, reflecting Baker’s (1967, 1970) findings (see Figure 2). While both studies proposed different relationships between the two groups, both support Baker’s (1967, 1970) hypothesis.

Immunological studies by Gerber and Leone (1971) also supported the division of the glossophagines into the two previously mentioned groups. The evidence suggested, however, that the *Glossophaga* group is more closely related to *Carollia* than to *Choeronycteris*, and that *Choeronycteris* is closer to the phyllostomines than to other glossophagines. This is the exact

opposite of Baker's (1967, 1970) proposal. Baker et al. (1981) presented electrophoretic and immunological evidence that also contradicted earlier karyotypic studies (Baker 1967, 1970) that supported a polyphyletic origin in the Glossophaginae. Baker et al. (1981) reported data suggesting that *Glossophaga*, *Monophyllus*, *Anoura*, *Leptonycteris*, *Choeroniscus*, and *Hylonycteris* are closely related. This close relation would not support a polyphyletic origin for the glossophagines. Chromosome banding pattern studies by Stock (1975) also did not support Baker's (1967, 1970) conclusion that *Choeroniscus* and *Carollia* were closely related. Stock proposed that the karyotypes of these two genera were only similar in terms of gross morphology.

Griffiths (1978) noted that nectar-feeders of the Glossophaginae have unique lingual and hyoid modifications, including special sinuses and muscles for extending the tongue that are not found in non-nectar-feeders. In a later study, Griffiths (1982) noted that certain lingual and hyoid characters are found in all Glossophaginae except *Lonchophylla*, *Lionycteris*, and *Platalina*. These three genera, in contrast, demonstrated unique morphological modifications, including a deep lateral lingual groove. These modifications led Griffiths to propose a new subfamily, Lonchophyllinae, which would include these three genera (Figure 3). He divided the remaining glossophagines into two clades. One included *Glossophaga*, *Monophyllus*, and *Lichonycteris*, while the other contained *Leptonycteris*, *Anoura*, *Hylonycteris*, *Choeroniscus*, *Choeronycteris*, and possibly *Scleronycteris* and *Musconycteris*. Griffiths concluded that either nectarivory arose once and the lonchophyllines lost the sinuses and developed the grooves (or the glossophagines lost the grooves and developed sinuses) or it arose twice, leading to two lines of nectarivorous bats. Although this distinction of *Lonchophylla* and *Lionycteris* from the rest of the glossophagines was supported by Gardner's (1977) karyotypic studies (*Platalina* was not

examined), Griffiths' proposal raised significant controversy (Griffiths, 1983; Warner, 1983; Haiduk and Baker, 1984; Smith and Hood, 1984).

Griffiths and Criley (1989) compared the groove found in the lonchophyllines (Griffiths, 1982) (see Figure 10) to the groove found in *Desmodus*, a vampire bat. The vampire bats are the only other group of bats possessing a groove. They concluded that the grooves of lonchophyllines and vampire bats were not homologous; rather, the grooves had evolved independently.

In a recent study, Baker et al. (2000) examined the RAG2 gene (Recombination-Activating-Genes-2), which produces a protein involved in the assembly of immunoglobulins. It is a slowly evolving gene that does not affect morphology and is thus ideal for use in studying phylogenies. Baker et al. (2000) found evidence confirming the separation of *Lonchophylla* and *Lionycteris* from the rest of the glossophagines (Figure 4). Furthermore, these genera were shown to be very closely related to the genus *Lonchorhina*.

The purpose of this study is to use lingual morphology to examine Baker et al.'s (2000) hypothesis. Specifically, I am looking for adaptations or pre-adaptations for nectar-feeding in *Lonchorhina* that are similar to those that Griffiths (1982) and Griffiths and Criley (1989) observed in the tongues of lonchophylline bats.

MATERIALS AND METHODS

The tongue of one museum specimen of *Lonchorhina aurita* (American Museum of Natural History 149218) was excised and sectioned using standard histological sectioning techniques. Sections were stained using Gill's II stain and Eosin as a counter stain. Histological morphology of the tongue was examined using a Nikon binocular compound microscope. The tongue

appeared to have four distinct morphological regions from tip to base. Written descriptions of the four quarters were made. Typical sections were projected using a Bausch and Lomb optical slide projector, and drawings were made of each of these sections. Selected drawings were inked for inclusion in this paper. Data are summarized in Table 1, which also includes data from Griffiths (1982), Griffiths and Criley (1989), and Winkelmann (1971) for outgroup comparison purposes. Data were analyzed using PAUP (Swofford, 2000) and MacClade (Maddison and Maddison, 1992) phylogenetic analysis programs.

OBSERVATIONS

The tongue is described from tip to base.

FIRST QUARTER (Figure 5)

The anterior-most portion of the tongue is triangular-shaped, with three major divisions of skeletal muscle present. A large horizontal band of transverse muscle meets in the center of the tongue and extends to the lateral edge. The fibers are packed solid in the medial portion of the tongue, but become more sparse laterally. There are also dorsal-ventral bands of muscle on either side of the central meeting of the transverse muscle. The peripheral areas around these two muscle groups are filled with longitudinal muscles. There are several small bifid papillae on the dorsal surface and a few extending around the dorsolateral edge of the tongue. Taste buds are also visible throughout the tongue, oriented vertically. The epithelium extends all the way around the tongue, but is approximately four times thicker on the dorsal surface than on the ventral surface. A single lingual nerve appears in each half (right and left) of the tongue in the anterior-most portion of the tongue, but within the first quarter of the tongue splits into several bundles (the bundles can be seen in Figures 6, 7, and 8). There are two main groups of nerve bundles, one

in each of the lower quadrants of the tongue. The nerves are found medially in each quadrant. Each group is associated with a single blood vessel, and the bundles are mostly found medial to the vessel. Later in this portion of the tongue, there is occasionally a second vessel located dorsal to the first one but still in the lower quadrants. Towards the end of this first quarter of the tongue, the overall shape of the tongue becomes much more circular and the diameter increases. The transverse bands of muscle no longer appear strictly horizontal and vertical, but somewhat oblique. The nerve bundles continue to increase in number.

SECOND QUARTER (Figure 6)

At this point the tongue is nearly circular. There are several large nerve bundles on each side in a more or less vertical linear arrangement. They are still found in the lower quadrants, typically medial to the blood vessel. A few small nerve bundles are migrating laterally, staying in the ventral half of the tongue. At least 19 separate nerve bundles are visible throughout the section of the tongue. Occasionally, a second smaller blood vessel is visible dorsal to each original vessel throughout this quarter of the tongue. Small filiform papillae are found in the first portion of this quarter; while they are still located mostly on the dorsal surface, they are also on the dorsolateral surface. Throughout the second quarter, however, larger filiform papillae appear and the smaller ones fade away. Occasionally, two vertically-oriented taste buds appear immediately next to each other. There are also occasional fungiform papillae, some with taste buds, found towards the lateral edge of the dorsal surface. At the end of this quarter of the tongue, an unusual group of salivary glands appears in the ventral half of the tongue. These glands are found near the center of the ventral left quadrant. In a few sections there is a duct leading from the glands to the lateral ventral surface. These glands contain neutrophilic, possibly

mucous-secreting cells. It was also noted that at the end of this quarter of the tongue, a few bundles from the linear group of nerve bundles begin to move closer to the center of the tongue in each of the ventral quadrants, then begin to move ventrally. Another group of nerve bundles remains in the original position, dorsal and medial to the blood vessel.

THIRD QUARTER (Figure 7)

The unusual salivary glands are found in both ventral quadrants now, located towards the center of each quadrant, lateral to the blood vessels and nerves. These glands seem to proliferate in the ventral half of the tongue throughout this quarter. Midway through this quarter, Von Ebner's glands appear in the dorsal half of the tongue and quickly proliferate, displacing much of the longitudinal muscle. The glands of Von Ebner do, however, remain in the dorsal half of the tongue.

Occasionally, fungiform papillae appear on the lateral edge of the dorsal surface, along with the large filiform papillae. At the end of this quarter, a single circumvallate papilla appears on each side of the midline on the dorsal surface. In addition, a second large blood vessel appears above the original vessel in each quadrant.

FOURTH QUARTER (Figures 8 and 9)

An indentation in the epithelium in the shape of a half-circle appears on the left side of the tongue (Figure 9). It is located on the lateral surface, but on the dorsal half of the tongue. In subsequent sections, tissue fills in this half circle such that a thin groove is formed in the epithelium. This groove opens at the lateral wall and runs ventrally and medially into the tongue. The epithelium definitely follows the groove in, indicating that this is a true groove and not an

artifact. The groove gradually shortens, becomes a slight indentation, and disappears. When the left groove is barely visible, the same half-circle indentation appears on the right side, and goes through the same process. One group of nerves is now located on the ventral surface of each ventral quadrant. The second group of nerves is still found near the vessels. Throughout this quarter of the tongue, the unusual salivary glands begin to move dorsally and invade the space in the dorsal half of the tongue that contains Von Ebner's glands. The unusual glands fill in most of the dorsal half and Von Ebner's are now only found in the ventral portion of the dorsal half of the tongue. The unusual glands are also still located in the ventral half of the tongue in the center of each quadrant as they were before. Eventually, the unusual glands completely fill in the dorsal half of the tongue and Von Ebner's disappear. The unusual glands remaining in the ventral half also disappear eventually. In this last quarter of the tongue, the overall shape is flatter and more rectangular. The tonsils also become visible. There are four blood vessels in each of the ventral quadrants, near the center of each quadrant. A few small vessels appear in the very center of the ventral half of the tongue. The papillae are still of the large filiform type and are concentrated on the lateral edges of the dorsal surface. The transverse muscle is very sparse, and the space around it is filled in with longitudinal muscles and the unusual salivary glands.

DISCUSSION

The phylogenetic origin of neotropical nectar-feeding bats has been debated heavily in the last several decades. Baker (1967) was the first to suggest that the subfamily Glossophaginae was not monophyletic, i.e. did not share a single common ancestor. He proposed that nectar-feeding may have arisen at least twice in the New World. Other researchers have supported this hypothesis (Baker, 1970; Baker and Lopez, 1970; Gerber and Leone, 1971; Phillips, 1971; Stock,

1975; Gardner, 1977; Baker and Bass, 1979). However, there has been no general consensus as to precisely how the glossophagines should be divided. Griffiths (1982) proposed the creation of a new subfamily, the Lonchophyllinae, into which he placed the genera *Lonchophylla*, *Lionycteris*, and *Platania* (Figure 3). This was not accepted without criticism at the time (Griffiths, 1983; Warner, 1983; Haiduk and Baker, 1984; Smith and Hood, 1984). Nearly 20 years later, however, Baker et al. (2000) confirmed Griffiths' hypothesis using genetic data; their results suggest that *Lonchophylla* and *Lionycteris* were, in fact, more closely related to *Lonchorhina*, a non-nectar-feeding genus than to other glossophagines *sensu* Griffiths (Figure 4).

The lingual data described in this study support Baker et al.'s (2000) conclusion that *Lonchophylla* and *Lionycteris* are most closely related to *Lonchorhina* (Figure 4) than to glossophagines. Lingual data observed are summarized in Table 1. Lateral tongue grooves, a diffuse lingual nerve, unusual salivary glands, circular tongue shape, and obliquely arranged intrinsic horizontal musculature are found in all three lonchophylline genera *sensu* Griffiths (1982) as well as in *Lonchorhina*. These character states have not been observed in any other known bats. The two most unusual characters seen in the *Lonchorhina* tongue are the incipient lateral groove (see Figures 9 and 10) and the unique salivary glands (see Figures 7 and 8). The function of either structure is presently unknown. The grooves seen in the lonchophyllines function in nectar-feeding, but *Lonchorhina* is primarily considered to be an insect-feeder (Gardner 1977). Gardner (1977) does, however, cite anecdotal evidence from Panama that *Lonchorhina* may also feed on nectar. It is thus possible that the incipient lingual groove represents an adaptation that evolved into the deep grooves seen in the Lonchophyllinae.

Cladograms that result from of analysis of data summarized in Table 1 are shown in Figures 11 (Maddison and Maddison, 1992), 12 (Swofford, 2000), and 13 (Swofford, 2000).

Although there is variation in the branching patterns in the three cladograms, all depict a single common ancestor leading to *Lonchorhina* and the lonchophyllines. All three most parsimonious trees are highly supported by statistical analyses, with a calculated retention index of 1.0 and a consistency index of 1.0, which is as high as these values can be in PAUP (Swofford, 2000) and in MacClade (Maddison and Maddison, 1992). The lingual data presented here strongly support the work of Baker et al. (2000), and thus confirm Griffiths' (1982) placement of these genera into a separate subfamily, Lonchophyllinae.

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TABLE 1

Summary of the characters used in constructing the cladograms in Figures 11, 12, and 13. Data from *Macrotus*, *Phyllostomus*, *Lonchophylla*, *Lionycteris*, *Platalina*, and the Glossophaginae are from Griffiths (1982), Griffiths and Criley (1989), and Winkelmann (1971).

	distal tongue shape	groove	nerve morphology	unusual salivary gland	lingual groove papillae	mid- tongue bifid papillae	intrinsic horizontal musculature	lingual arteries	lingual vein	arteriovenous shunts	lingual papillae of tip
Lonchorhina	circular	present and shallow	diffuse grouping	present	absent	present	obliquely arranged	two	normal	absent	absent
Macrotus	spatulate	absent	tight grouping	absent	absent	absent	straight across	two	normal	absent	absent
Phyllostomus	spatulate	absent	tight grouping	absent	absent	absent	straight across	two	normal	absent	absent
Micronycteris	spatulate	absent	tight grouping	absent	absent	absent	straight across	two	normal	absent	absent
Lonchophylla	circular	present and deep	diffuse grouping	present	present	present	obliquely arranged	two	normal	absent	absent
Lionycteris	circular	present and deep	diffuse grouping	present	present	present	obliquely arranged	two	normal	absent	absent
Platalina	circular	present and deep	diffuse grouping	present	present	present	obliquely arranged	two	normal	absent	absent
Glossophaginae	oval	absent	tight grouping	absent	absent	absent	straight across	one single midline	enlarged	present	paint- brush tip

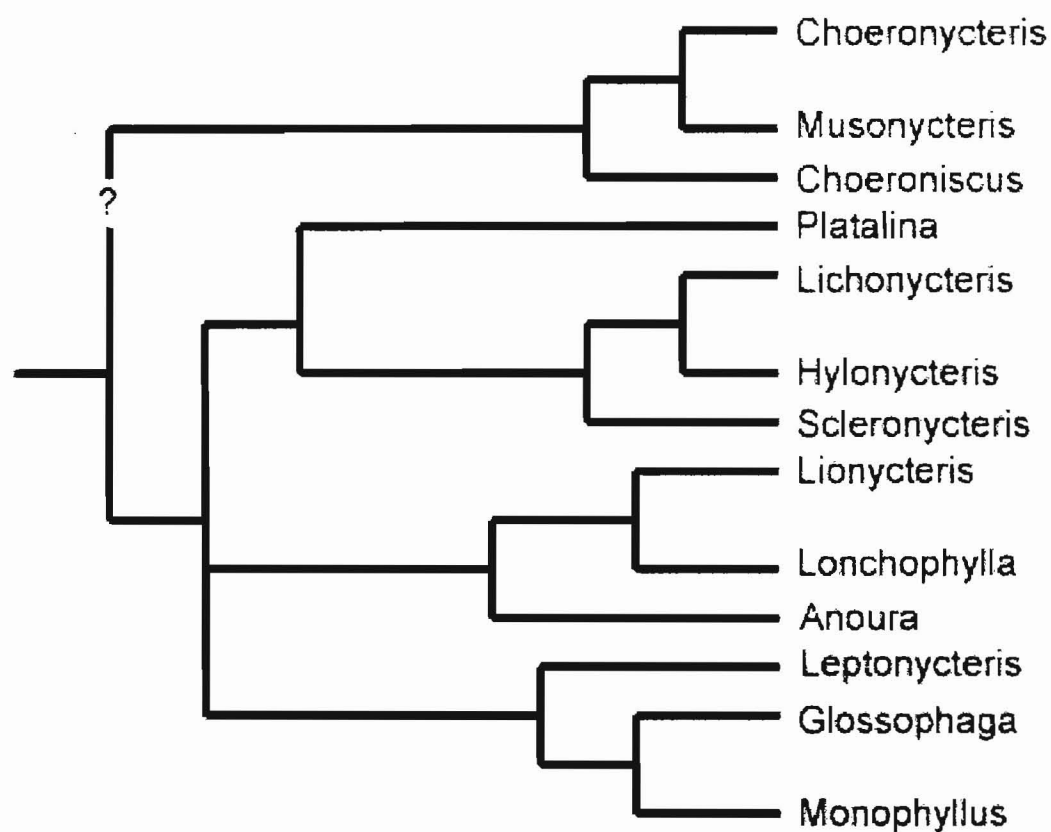


Figure 1. Possible evolutionary relationships among the genera of the Glossophaginae. Redrawn from Phillips (1971).

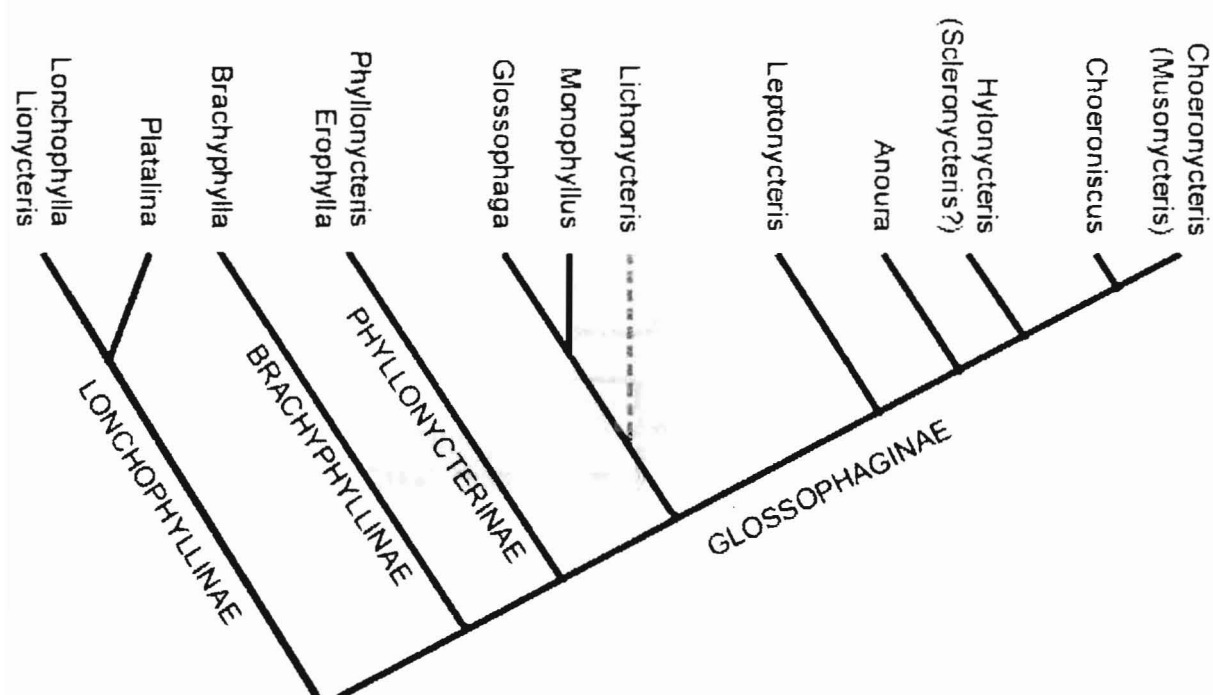


Figure 3. Proposed cladogram of the relationships of nectar-feeding genera of the Phyllostomidae. Redrawn from Griffiths (1982).

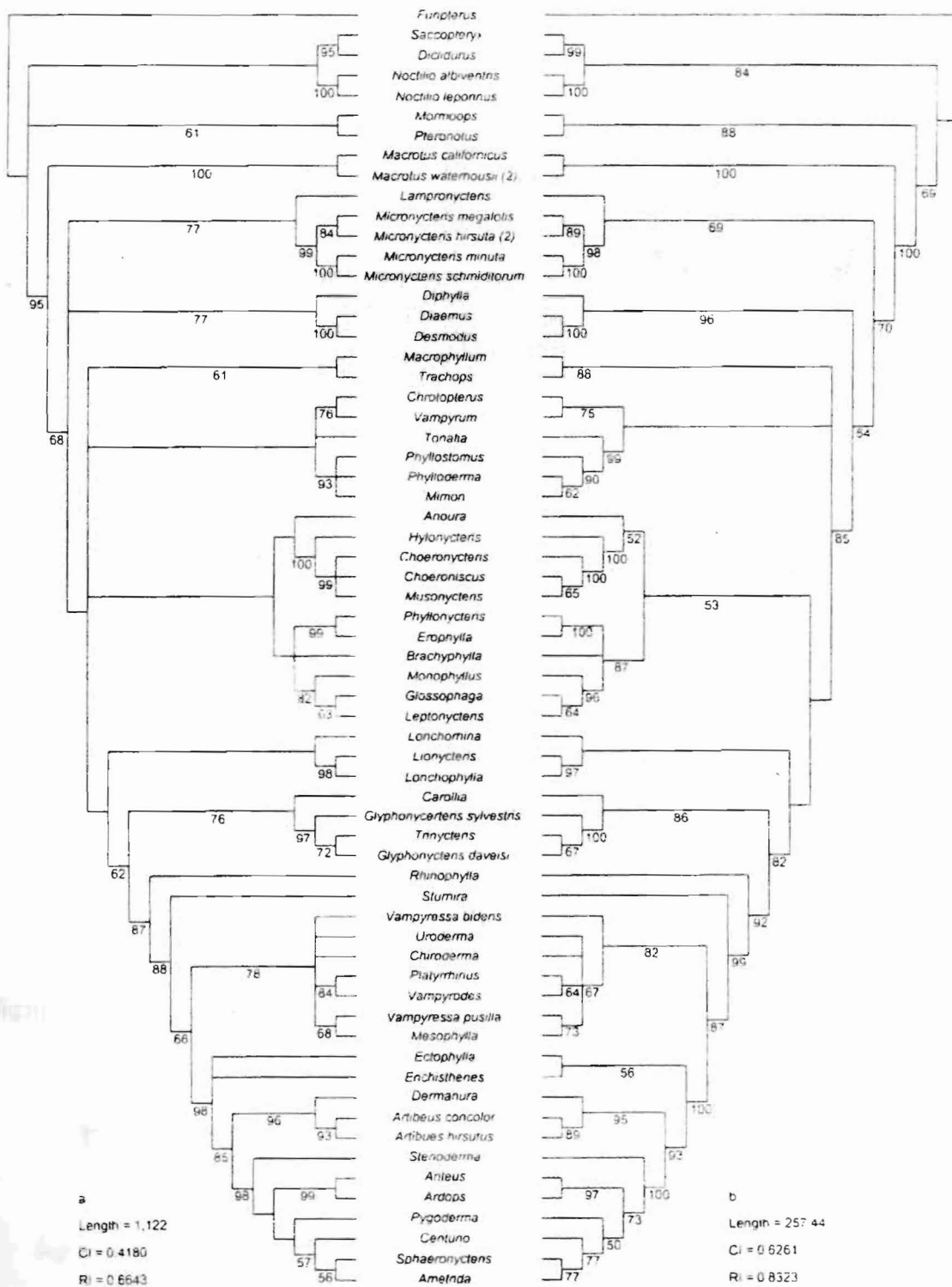


Figure 4. Two cladograms showing possible relationships in the Phyllostomidae. From Baker et al. (2000).

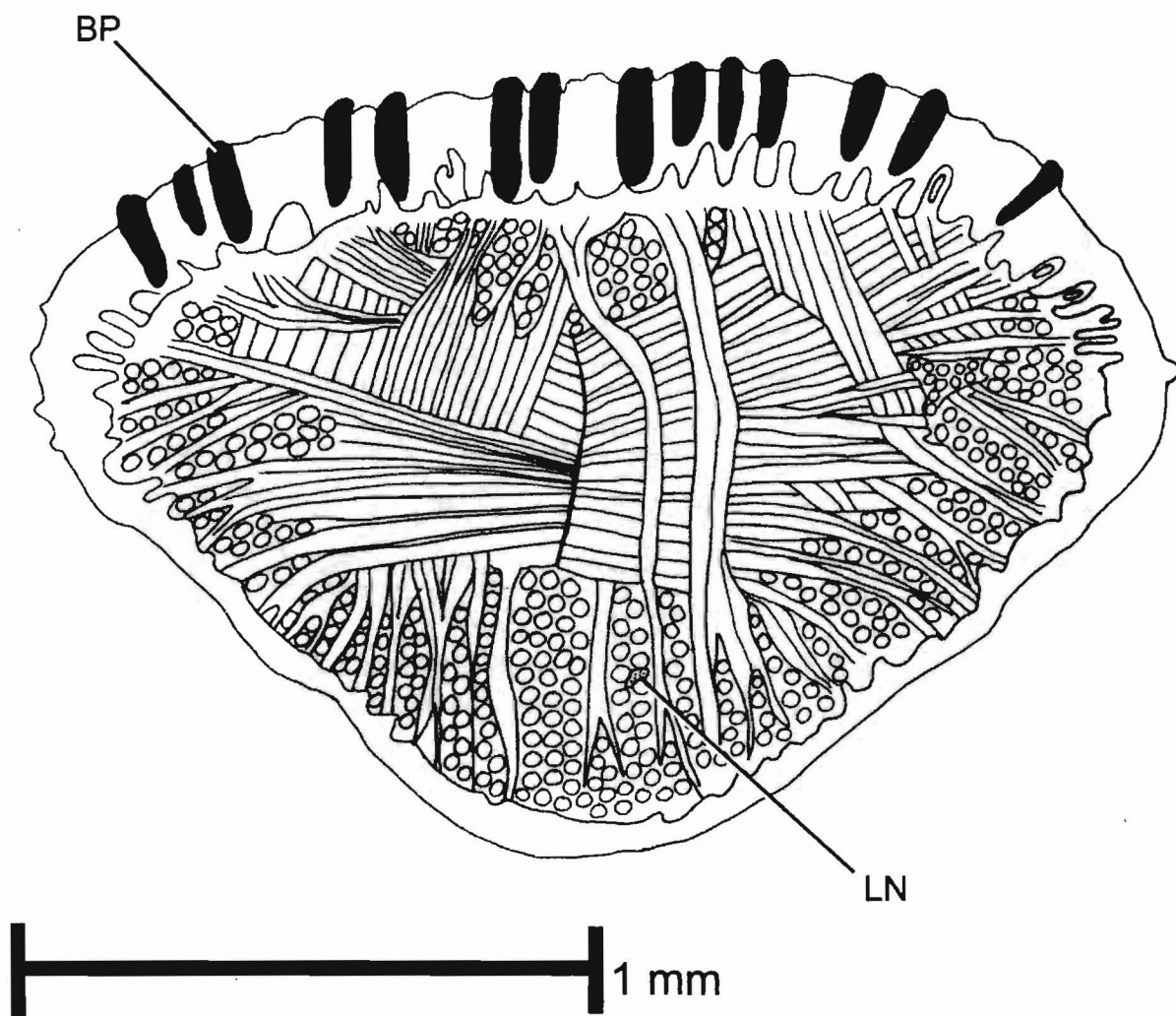


Figure 5. Cross-section from the first quarter of the tongue of *Lonchorhina*. BP = bifid papilla,
LN = lingual nerve.

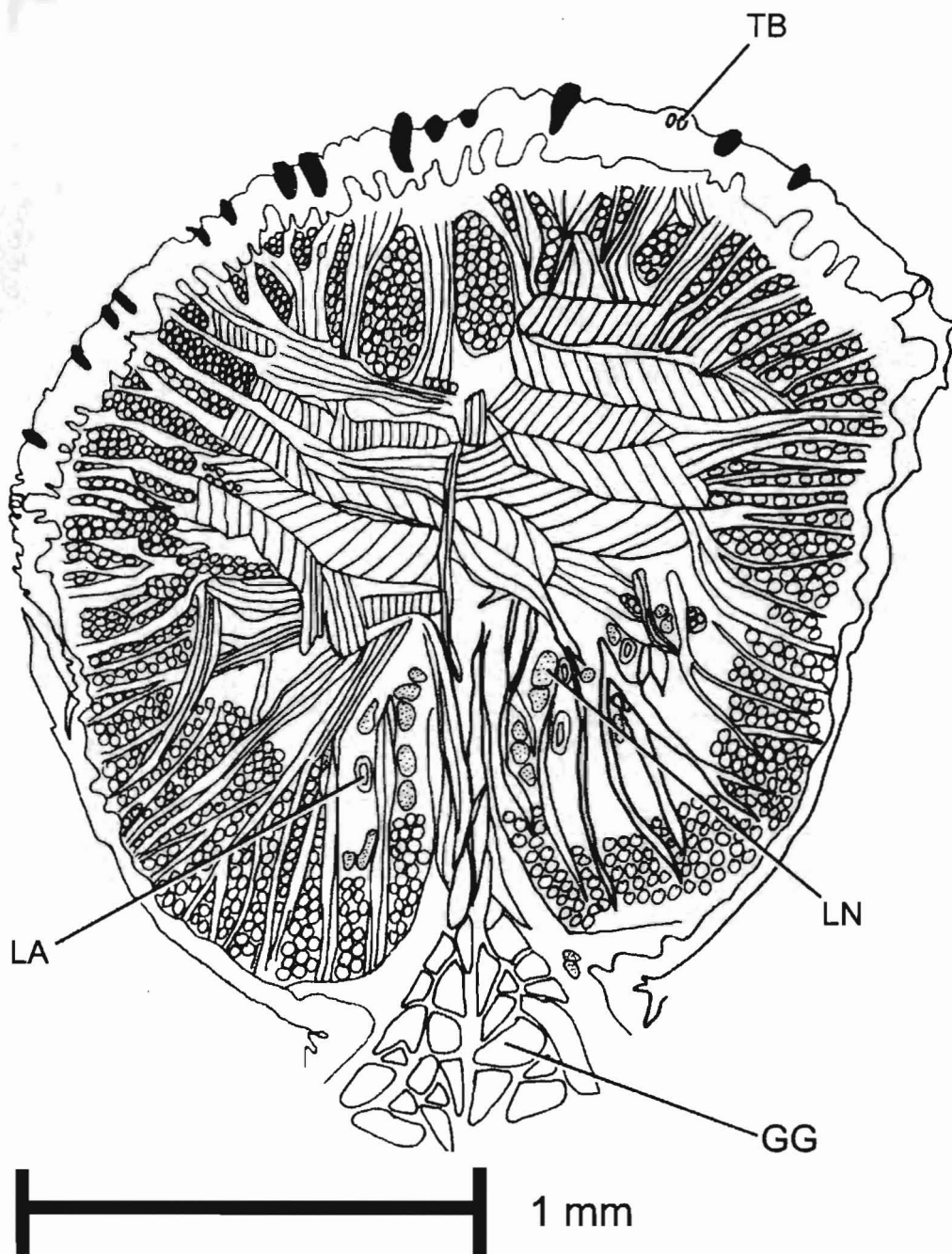


Figure 6. . Cross-section from the second quarter of the tongue of *Lonchorhina*. GG = genioglossus, LA = lingual artery, LN = lingual nerve, TB = taste bud.

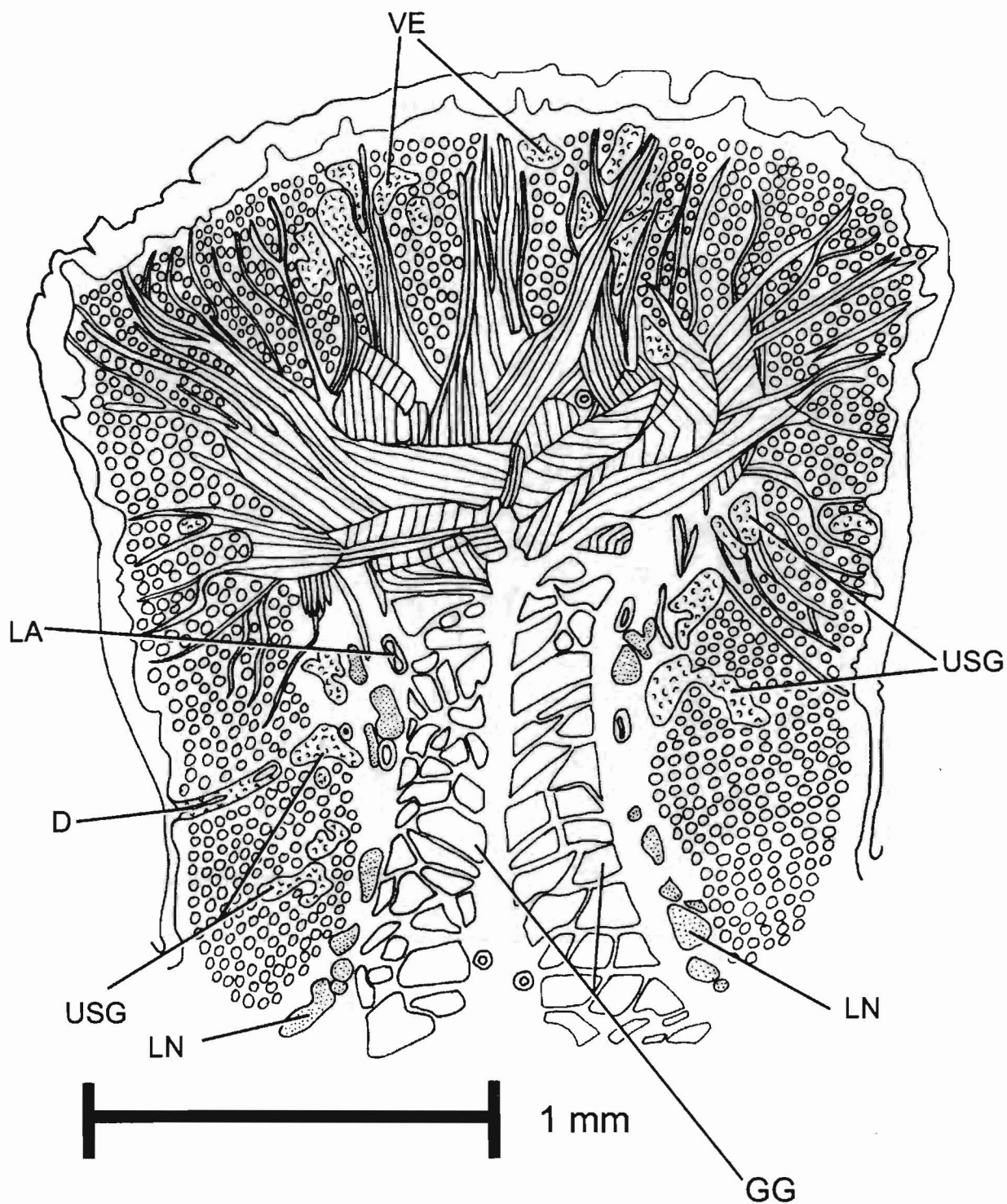


Figure 7. Cross-section from the third quarter of the tongue of *Lonchorhina*. D = duct from unusual salivary gland, GG = genioglossus, LA = lingual artery, LN = lingual nerve, USG = unusual salivary gland, VE = glands of Von Ebner.

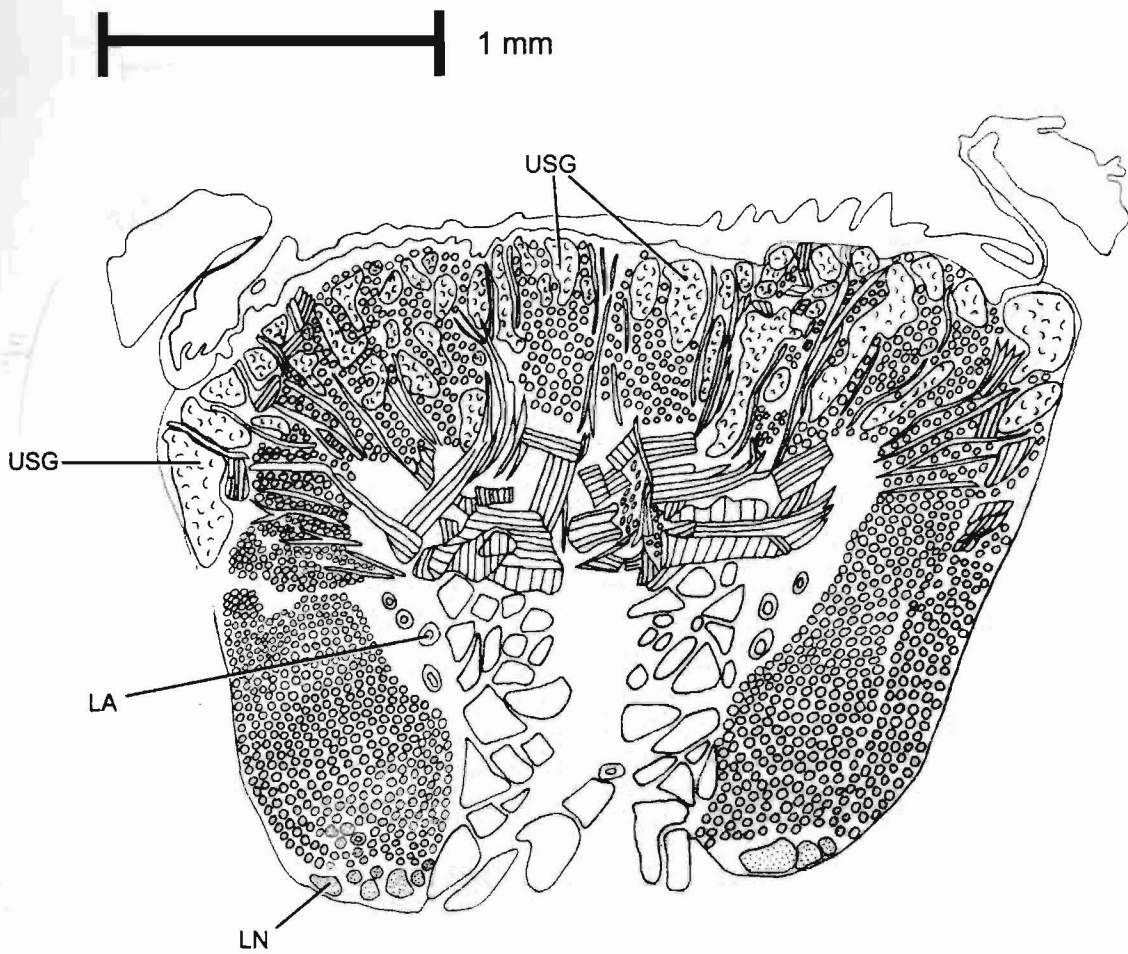


Figure 8. Cross-section from the fourth quarter of the tongue of *Lonchorhina*. LA = lingual artery, LN = lingual nerve, USG = unusual salivary glands.

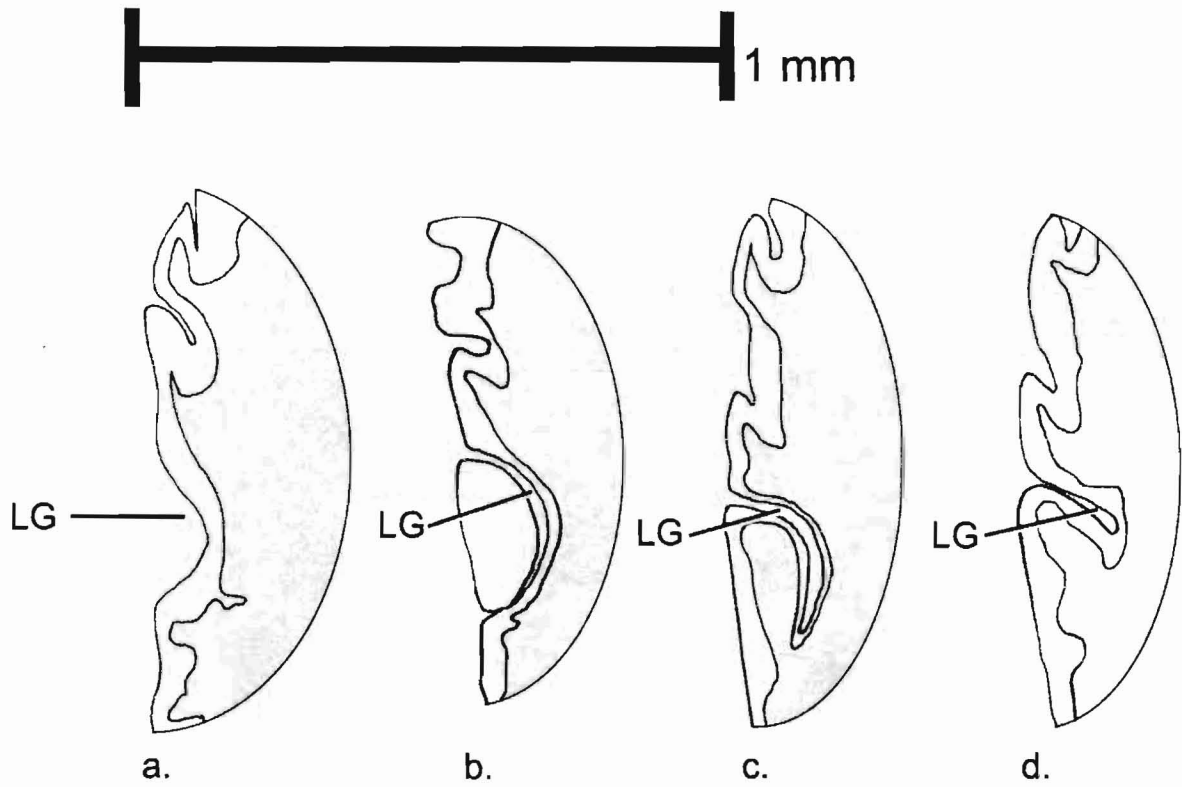


Figure 9. Cross-sectional view of lateral tongue, focusing on the progression of the groove in the last quarter of the tongue. Figures a, b, c, d are serial sections extending anterior to posterior, respectively. LG = lingual groove.

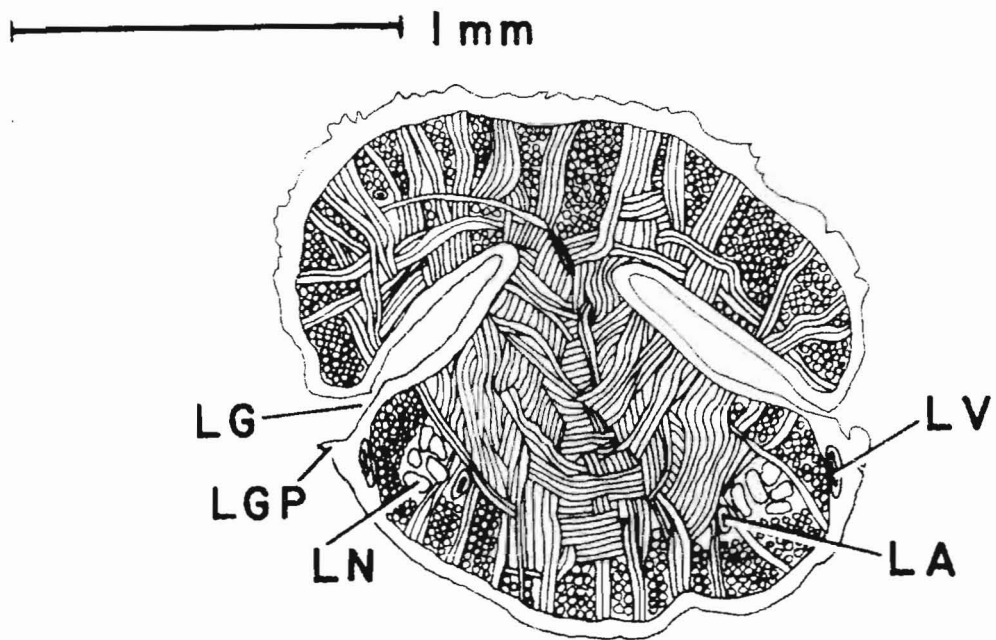


Figure 10. Cross-section of the tongue of *Lonchophylla robusta*. LA = lingual artery, LG = lingual groove, LGP = lingual groove papilla, LN = lingual nerve, LV = lingual vein. From Griffiths and Criley (1989).

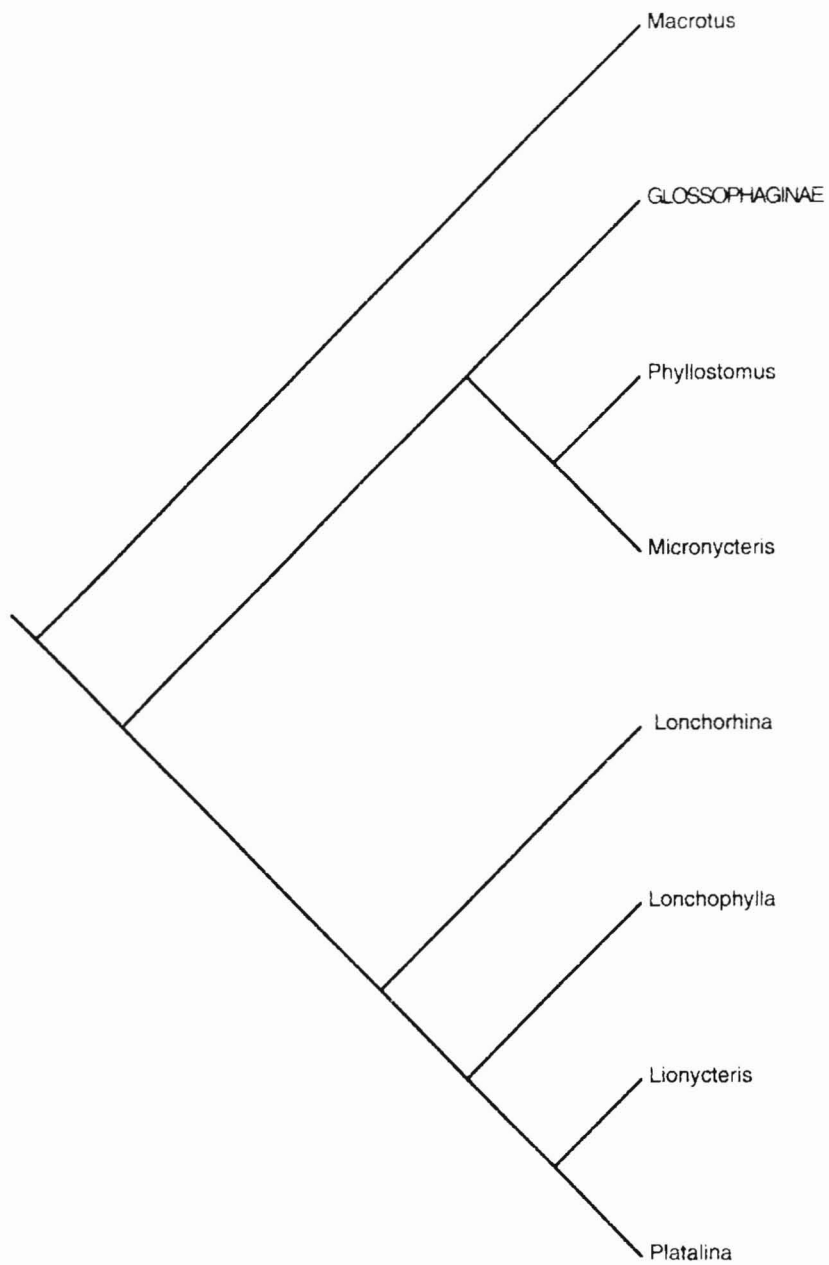


Figure 11. Cladogram showing the relationships of several genera of New World bats. Created using MacClade (Maddison and Maddison, 1992).

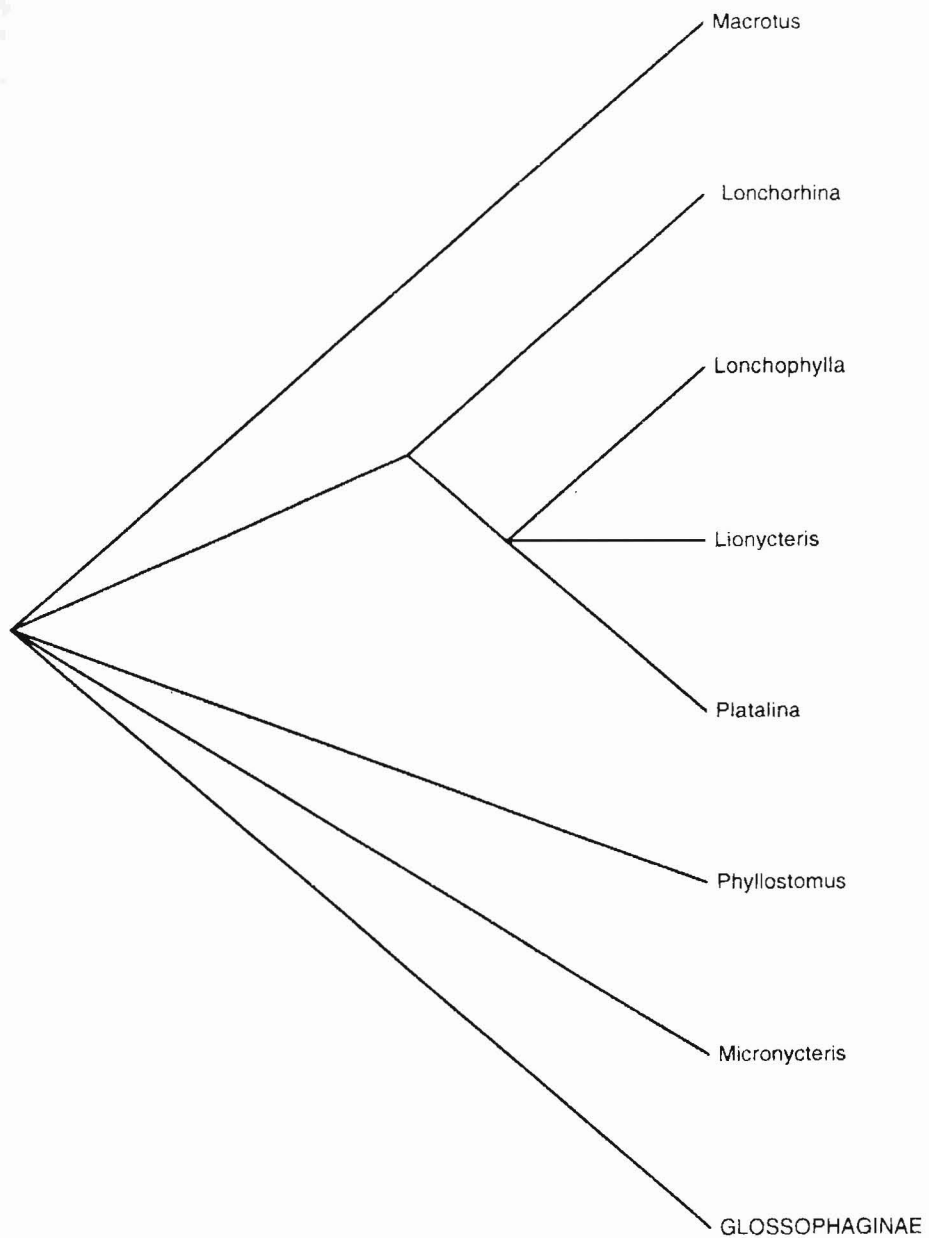


Figure 12. Cladogram showing the relationships of several genera of New World bats. Created using PAUP (Swofford, 2000).

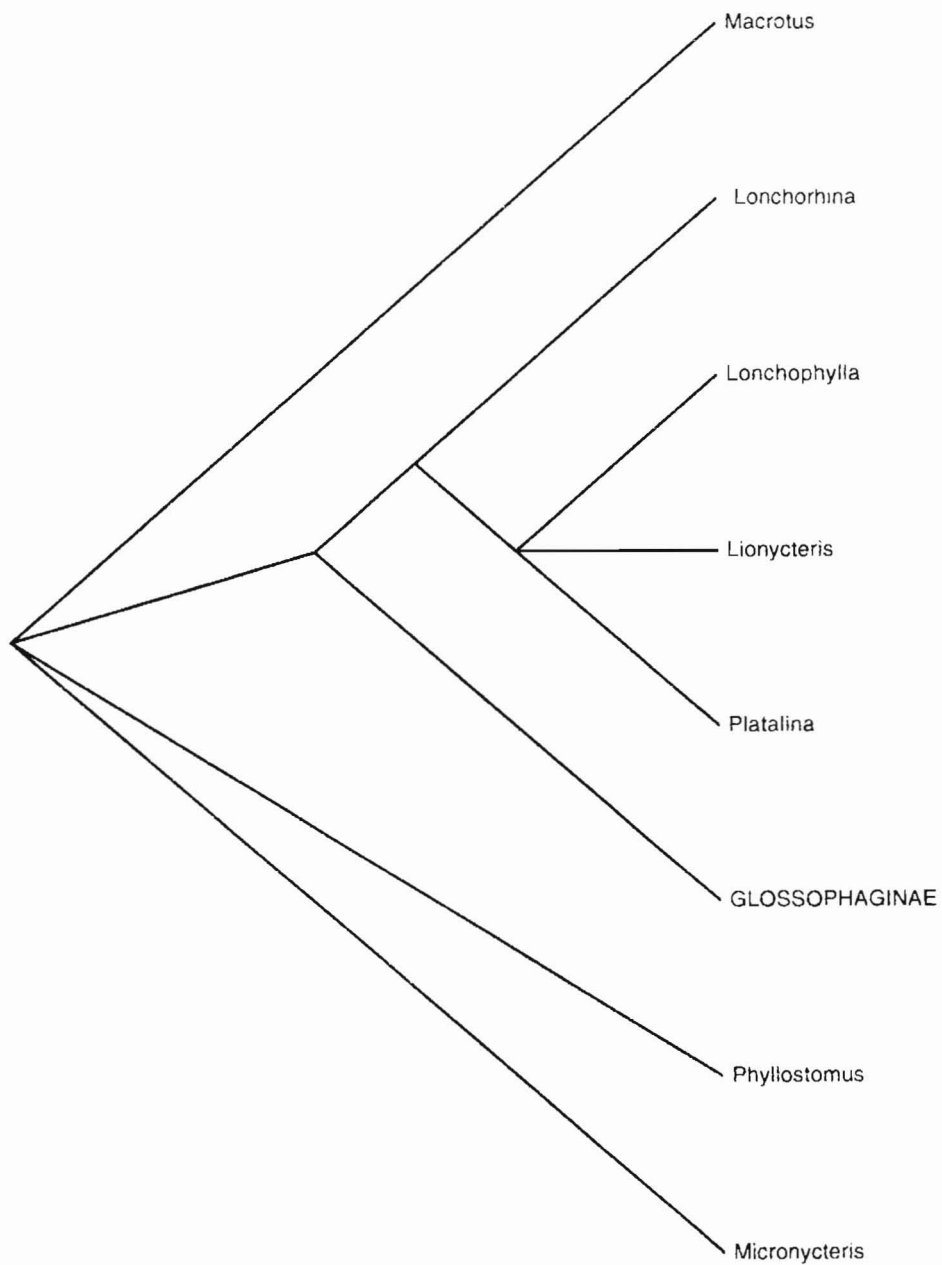


Figure 13. Cladogram showing the relationships of several genera of New World bats. Created using PAUP (Swofford, 2000).