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The Anatomy of the Hyoid Region of Molossus Molossus and its Implication in Systematics

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ABSTRACT

The hyoid musculature and hyoid apparatus of a bat, *Molossus molossus* (Chiroptera: Molossidae) are dissected and described. A comparison is made with the hyoid structures of bats of the genera *Rhinopoma*, *Emballonura*, *Nycteris*, *Megaderma*, *Rhinolophus*, *Pteronotus*, *Phyllostomus*, and *Eptesicus*, which were previously described by my sponsor Griffiths and associates. In *Molossus*, the geniohyoid and sternohyoid insertions, as well as the hyoglossus origin, have lifted off the basihyal bone and jointly retain a direct attachment to the basihyal via a small tendon. The hyoglossus is split into three distinct bellies: the most superficial originates from the basihyal raphe, the second originates from the basihyal bone, and the third originates from a very reduced thyrohyal bone. A part of the mylohyoideus has broken away from the main muscle, retaining its insertion on the basihyal--it is termed the mylohyoid profundus. The jugulohyoid muscle is absent, as is the stylohyoideus. The styloglossus muscle is split into two distinct bellies by the hyoglossus muscle. A cladistic analysis of these data gives preliminary support to Koopman's proposal in 1984 for a separation of the superfamilies Emballonuroidea and Rhinolophoidea from the superfamilies Phyllostomoidea and Vespertilionoidea. These data provide the first compelling support for Koopman's taxonomic group Yangochiroptera, comprising the superfamilies Phyllostomoidea and Vespertilionoidea.

INTRODUCTION

Most major classifications of bats (Order Chiroptera) have followed the classification scheme of Linnaeus' "Systema Naturae" in 1758. Dobson (1875) identified all bats as belonging to two suborders: Megachiroptera (the "flying foxes" and the Old World nectar-feeders), and Microchiroptera (the remaining bats, mostly insectivorous). Within the suborder Microchiroptera, Weber (1928) first recognized four superfamilies (each of which he called "Tribus"): Rhinolophoidea, Phyllostomoidea, Emballonuroidea, and Vespertilionoidea. The fifteen families of microchiropteran bats known to Weber were placed in their four Superfamilies as follows:

Superfamily Emballonuroidea
- Family Rhinopomatidae
- Family Emballonuridae
- Family Noctilionidae

Superfamily Rhinolophoidea
- Family Nycteridae
- Family Megadermatidae
- Family Rhinolophidae

Superfamily Phyllostomoidea
- Family Mormoopidae
- Family Phyllostomidae

Superfamily Vespertilionoidea
- Family Natalidae
- Family Thyropteridae
- Family Furipteridae
- Family Myzopodidae
- Family Mystacinidae
- Family Vespertilionidae
- Family Molossidae

In his monumental work, *The Principles of Classification and A Classification of Mammals*, Simpson (1945) also follows Weber's system of superfamily classification. [It should be noted that the family Noctilionidae, ascribed in classifications by Weber (1928), Simpson (1945), and Koopman and Jones (1970) to the superfamily Emballonuroidea, has since been moved to the superfamily Phyllostomoidea

(Koopman, 1984).] Subsequent authors have also agreed with the classification outlined by Simpson (eg., Koopman and Jones, 1970; Smith, 1976; and Van Valen, 1979).

Koopman (1984) proposed an amended classification of Microchiropteran bats. Based on his study of premaxilla bone morphology, he proposed that the suborder Microchiroptera be divided into the Infraorder Yinochiroptera, comprising the superfamilies Emballonuroidea and Rhinolophoidea, and the Infraorder Yangochiroptera, comprising the superfamilies Phyllostomoidea and Vespertilionoidea. This proposal is highly controversial because there have been no other studies that support this subclassification, except for a study of hyoid morphology by Griffiths and Smith (in press), which shows a synapomorphy that unites all the families except Rhinolophidae within the Infraorder Yinochiroptera. This study of *Molossus molossus* hyoid morphology and comparisons to previously described hyoid morphologies of key genera within the four superfamilies --Emballonuroidea, Rhinolophoidea, Phyllostomoidea, and Vespertilionoidea (Sprague, 1943; Griffiths, 1982, 1983; Griffiths and Smith, in press) proposes to test whether there are derived characters of the hyoid region that support Koopman's proposal of the Infraorder Yangochiroptera.

MATERIALS AND METHODS

The hyoid region of an alcohol-preserved specimen (Texas Tech. 14363) of the species *Molossus molossus* was carefully dissected, described and drawn. Certain pencil drawings were selected for inking. The hyoid anatomy of the families Nycteridae, Megadermatidae, and Rhinolophidae (Superfamily Rhinolophoidea); Emballonuridae and Rhinopomatidae (Superfamily Emballonuroidea); Phyllostomidae (*Phyllostomus*) and Mormoopidae (*Pteronotus*) (Superfamily Phyllostomoidea); and Vespertilionidae (*Eptesicus*) (Superfamily Vespertilionoidea) were described

previously by Sprague, 1943; Griffiths, 1982, 1983; Griffiths and Criley, 1989; Griffiths et al, 1991; and Griffiths and Smith, in press. These data (Table 1) were used to perform a cladistic analysis of the Superfamilies Phyllostomoidea and Vespertilionoidea.

ACKNOWLEDGMENTS

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RESULTS

HYOID MUSCULATURE

MYLOHYOID GROUP

Muscles of this group are innervated by the N. mylohyoideus, a branch of N. trigeminus (V).

M. mylohyoideus [Figs. 1 and 2]

ORIGIN: This muscle originates from the medial surface of the mandibular body, for much of its length.

INSERTION: The anterior part of this muscle inserts on the mid-line raphe. The posterior part of this muscle runs laterally from one side of the medial surface of the mandibular body to the other side in one broad belly.

COMMENTS: This is a two-part muscle whose fibers run medially and laterally in its posterior portion. It then becomes a very thin, transparent triangular-shaped section, composed of transparent connective tissue sheet between the anterior and posterior parts of the muscle. The anterior slips of the muscle run medioanteriorly in thick slips to insert on the mid-line raphe.

M. mylohyoid profundus [Figs. 1 and 2]

ORIGIN: This muscle originates from the medial surface of the mandible, at about 6 mm anterior to where the mandible makes an angle as it turns dorsally.

INSERTION: Some superficial fibers insert weakly on the geniohyoideus and sternohyoideus muscles. Deeper fibers run medially deep to the basihyal raphe to insert directly on the basihyal bone.

COMMENTS: All the genera examined that belong to the Superfamilies Phyllostomoidea and Vespertilionoidea (ie. *Phyllostomus, Pteronotus, Eptesicus*, as well as *Molossus*) possess this derived character where part of the mylohyoid muscle has broken off and retained its insertion on the basihyal bone. The members examined of the Superfamilies Emballonuroidea and Rhinolophoidea possess the primitive trait. They do not have a mylohyoid profundus.

M. mandibulo-hyoideus

COMMENTS: This muscle was absent in this bat.

HYOID CONSTRICTOR GROUP

Muscles of this groups are innervated by N. facialis (VII).

M. stylohyoideus

COMMENTS: This muscle was absent in this bat. The absence of this muscle is a derived trait that is shared by all the members examined of the Superfamilies Phyllostomoidea and Vespertilionoidea. Of the members of the Yinochiroptera, Rhinolophids and some Emballonurids have also lost this muscle, probably by independent evolution of this derived trait.

M. jugulohyoideus

COMMENTS: This muscle was absent from this bat. None of the other members of the Superfamilies Vespertilionoidea or Phyllostomoidea have lost this muscle. However, Rhinopomatids and some Emballonurids share this derived trait. The jugulohyoideus is absent in these families. It is possible that *Molossus molossus* independently derived this character.

M. sphincter colli profundus [not illustrated]

ORIGIN: This muscle originates from the ventral surface of the sternohyoid muscle at the raphe which bissects the sternohyoid muscle where it emerges from under the pectoralis muscle.

INSERTION: This muscle inserts into the deep surface of the skin lateral to the mandible.

COMMENTS: This is a V-shaped muscle running anterolaterally out at about 45 degrees from its origin. The loss of the sphincter colli profundus is a derived character that groups all the families of the Superfamilies Emballonuroidea and Rhinolophoidea

except for Megadermatids, which still retain this muscle. Within the Superfamilies Phyllostomoidea and Vespertilionoidea, only the genus *Phyllostomus* possesses more than one belly of the muscle.

GLOSSOPHARYNGEAL GROUP

Muscles of this group are innervated by N. glossopharyngeus (IX).

M. stylopharyngeus [Fig. 3]

ORIGIN: This muscle originates from the medial edge of the stylohyal bone. It runs anteromedially in a rather broad belly.

INSERTION: This muscle inserts into the connective tissue on the lateral edge of the larynx. The insertion is just anterior and dorsal to where the sternothyroideus inserts and the thyrohyoideus originates.

COMMENTS: No comments.

M. ceratohyoideus [Fig. 3]

ORIGIN: This muscle originates from the posterior cornu (the thyrohyal bone, which in this bat is very reduced).

INSERTION: This muscle inserts on the ceratohyal bone alone.

COMMENTS: This is a very small muscle which runs almost directly anteriorly from its origin, so that in ventral view, the muscle is very difficult to see [Fig. 3]. The thyrohal bone is extremely reduced so that its position can be deduced best by observing the origin of the ceratohyoideus muscle. The ceratohyal bone is lost. The epihyal bone is more cartilagenous than calcified. It is elliptical in shape and seems loosely attached to the long lateral process of the basihyal bone.

The origins and insertions of the ceratohyoideus for the genera *Phyllostomus*, *Pteronotus*, *Eptesicus* and *Molossus* are included in Table 1 for reference. However,

the origins and insertions of the other genera vary so greatly that they were not included. These characters would not be very useful in cladistic analysis because it is not fully known which character is the primitive and which is the derived state.

PHARYNGEAL CONSTRICTOR GROUP

Muscles of this groups are innervated by N. vagus (X).

M. hyopharyngeus [not illustrated]

ORIGIN: From the fascia of the region of the lateral anterior pharynx.

INSERTION: Into the fascia of the anterodorsal pharynx, anterior to the insertion of the thyrohyoideus.

COMMENTS: All the muscles of the pharyngeal constrictor group are identical in origin and insertion to the corresponding muscles in all other families: Phyllostomidae, Mormoopidae, and Vespertilionidae.

M. thyropharyngeus [not illustrated]

ORIGIN: From the dorsal surface of the thyrohyal element (posterior cornu).

INSERTION: Into the dorsal pharyngeal midline, just anterior to the insertion of the cricopharyngeus.

COMMENTS: This muscle is remarkably similar in all bats.

M. cricopharyngeus [not illustrated]

ORIGIN: From the posterior cornu of the thyroid cartilage and the lateral cricoid cartilage.

INSERTION: Into the dorsal pharyngeal midline, just posterior to the insertion of the thyrohyoideus.

COMMENTS: There is only one slip to this muscle. In some phyllostomids there are two or three.

LINGUAL GROUP

Muscles of this group are innervated by N. hypoglossus (XII).

M. genioglossus [Fig. 2]

ORIGIN: This muscle originates from the medial surface of the anterior-most portion of the mandible, deep to the origin of the geniohyoid.

INSERTION: This muscle inserts into the muscles of the tongue .

COMMENTS: From its origin, this muscle passes posteriorly, directly deep to the geniohyoideus muscle, curves dorsally, and turns laterally to insert into the tongue just anterior to the basihyal bone.

In *Phyllostomus* and *Molossus*, the genioglossus turns laterally prior to inserting on the muscles of the tongue. No references as to whether the genioglossus turns laterally or not prior to its insertion also in *Pteronotus* and *Eptesicus* could be found (Sprague, 1943).

In *Pteronotus*, and in some species of Emballonurids, the genioglossus muscle's lateral edge is visible even without dissection of the superficial geniohyoideus. In these bats, the geniohyoideus is reduced in size compared to the genioglossus muscle.

M. hyoglossus [Figs. 1 and 2]

ORIGIN: This muscle originates from three bellies. The most superficial fibers originate from the basihyal raphe lateral to the insertion of the geniohyoid and sternohyoid muscles on the same raphe. A deeper belly of the hyoglossus, about .1 mm in diameter, originates from the ventrolateral portion of the basihyal bone and runs

anterolaterally at a sharp angle to disappear dorsal to the ventral belly of the styloglossus muscle after about 2 mm from its origin. The third belly of the hyoglossus muscle originates from the anterior cornu of the basihyal apparatus. It runs slightly dorsolateral to the second belly of hyoglossus to also disappear dorsal to the ventral belly of the styloglossus muscle.

INSERTION: This muscle inserts into the muscles of the tongue. The second and third bellies seem to insert between the two slips of styloglossus muscle (or seem to split the insertion of the styloglossus muscle into a dorsal part and a ventral part).

COMMENTS: This muscle originally seemed to be very small, until the second and third bellies were dissected. The separations between the three bellies of this muscle are very distinct.

The most superficial belly of the hyoglossus muscle, along with the geniohyoideus and the sternohyoideus, have lifted off their primitive connection to the basihyal bone. In the derived condition, they retain their attachment to the basihyal only through a small tendon. This "lifting off" of this band of muscles is shared by *Phyllostomus*, *Pternotus*, *Eptesicus*, and, of course, *Molossus molossus* -- representatives of the Superfamilies Phyllostomoidea and Vespertilionoidea. Among the other bats examined, only megadermatids possess this derived character, and it is independently acquired (Griffiths and Smith, in press).

M. styloglossus [Figs. 1 and 2]

ORIGIN: This muscle originates from two bellies, one posteroventral and the other anterodorsal on the stylohyal bone. Both run anteromedially to become a broad muscle. The two bellies are further split by the hyoglossus muscle's second and third bellies at about 5-6 mm from its origins.

INSERTION: This muscle inserts into the muscles of the tongue on the lateral tongue surface.

COMMENTS: There is a very distinct separation of bellies, even at their origins. Both bellies start to become a single belly at about where the hyoglossus muscle splits it, then the styloglossus muscle fibers merge into the tongue muscle.

The splitting of the styloglossus by the hyloglossus muscle is another derived character that groups the Superfamilies Vespertilionoidea and Phyllostomoidea together. *Phyllostoma*, *Pteronotus*, and *Eptesicus*, along with *Molossus molossus* possess this derived trait, while none of the examined members of the Superfamilies Emballonuroidea or Rhinolophoidea do.

MEDIAL VENTRAL CERVICAL GROUP

Muscles of this group are innervated by N. hypoglossus (XII).

M. geniohyoideus [Figs. 1 and 2]

ORIGIN: This muscle originates from the anteromedial part of the mandible.

INSERTION: Superficial fibers of this muscle inserts on the basihyal raphe. Deeper parts of this muscle attach to the middle of the basihyal bone via a small tendonous attachment.

COMMENTS: Ventral parts of the geniohyoideus muscle simply insert on the basihyal raphe, but a deep portion of the muscle inserts directly on the basihyal bone via a medially located tendonous attachment. As previously mentioned, in *Pteronotus* and some species of *Emballonura*, this muscle's size is reduced compared to that of the underlying genioglossus.

M. sternohyoideus [Fig. 1 and 2]

ORIGIN: This muscle originates as two slips on the anterior dorsal surface of the manubrium. It runs anteriorly to the raphe from which the sphincter colli profundus originates, before continuing anteriorly as one belly.

INSERTION: Superficial parts of this muscle inserts on the basihyal raphe. Deeper parts of the muscle are attached to the basihyal bone via a tendonous attachment.

COMMENTS: This muscle, along with the geniohyoid muscle and the most superficial belly of the hyoglossus muscle, have lifted off from the basihyal bone. They retain their attachment to the basihyal only through a small tendon. This "lifting off" of this group of muscles is also seen in *Phyllostomus*, *Pteronotus*, and *Eptesicus.*

M. sternothyroideus [Fig. 3]

ORIGIN: This muscle originates from just deep to the proximal head of the clavicle about 2.5 mm lateral to where the proximal head of the clavicle articulates with the sternum.

INSERTION: This muscle runs anteriorly and very slightly laterally from its origin to insert into the lateral edge of the larynx, at the origin of the thyrohyal muscle.

COMMENTS: No comments.

M. omohyoideus [Figs. 1 and 2]

ORIGIN: This muscle originates from the medial surface of the scapula bone.

INSERTION: This muscle inserts on the basihyal raphe lateral to the insertion of the sternohyoid muscle.

COMMENTS: The omohyoid muscle in this bat does not insert directly on the basihyal bone, merely on the basihyal raphe. This continues that significant distinction that the geniohyoideus, sternohyoideus, and one belly of the hyoglossus have merged into one another and, in a band, have lifted off their basihyal bone attachment. This derived character is found also in *Phyllostomus*. *Eptesicus* and *Pteronotus* have lost this muscle entirely. Among the other bats examined only Megadermatids have been

found to have an omohyoid muscle that originates from the scapula bone. Nycterids, rhinolophids, and emballonurids have the derived condition in which the omohyoideus orginates from the clavicle.

M. thyrohyoideus [Fig. 3]

ORIGIN: This muscle originates on the lateral edge of the larynx (thyroid cartilarge) where the sternothyroid muscle also inserts.

INSERTION: This muscle continues from its origin in a broad belly curving around the lateral edge of the larynx to insert on the very reduced thyrohyal bone.

COMMENTS: The thyrohyal bone is extremely reduced and therefore very difficult to dissect. It's position and orientation can be determined by the insertion of the thyrohyoid muscle on it, as well as the origin of the ceratohyoid muscle from it.

DISCUSSION AND CONCLUSIONS

Derived characters of the hyoid region and their occurrence in selected genera of all the bat superfamilies are depicted in Table 1 (data for *Molossus molossus* from this study, data for the remaining taxa from Sprague, 1943; Griffiths, 1982, 1983; Griffiths and Criley, 1989; Griffiths et al, 1991; and Griffiths and Smith, in press). Important derived characters used in my cladistic analysis include the presence of the mylohyoid profundus muscle, the mylohyoid muscle being split into two bellies, and the loss of the mandibulohyoideus. Other important synapomorphies are the loss of the stylohyoideus, the origin of the hyoglossus and the insertions of the sternohyoideus and geniohyoideus by a tendon instead of a direct attachment to the basihyal bone. Finally, the occurrence of two bellies of the styloglossus, split by the hyoglossus muscle, is another important derived character shared by members of the Superfamilies Phyllostomoidea and Vespertilionoidea.

From these data, the two most parsimonious cladograms (= evolutionary trees) for the families within Koopman's Yangochiroptera are shown in Figure 4. The second cladogram concurs most with the traditional viewpoint in that it groups the two vespertilionoid species together, although the two phyllostomoids appear as sister groups (= non-grouped lines) instead of the more accepted idea which would favor grouping of these phyllostomoids. Although it would appear in the second cladogram that *Phyllostomus* should be grouped along with *Eptesicus* and *Molossus* because all three genera share character 20 (Table 1), I have decided to exclude *Phyllostomus*, and show it as being on its own, monogeneric line. Character state 20 is found to be very variable within the family Phyllostomidae (Griffiths, personal communication); although certain species of *Phyllostomus* possess that derived character, many other phyllostomid genera possess the primitive character state. A within-group analysis of all phyllostomid bats makes it most probable that *Phyllostomus* evolved character state 20 independently (Griffiths, personal communication). Therefore, I treat the presence of character state 20 in *Phyllostomus* and *Eptesicus/Molossus* as an instance of homoplasy (=convergent evolution), and place *Phyllostomus* on its own line.

The first cladogram, although the most parsimonious one (ie. the simplest, assuming the least number of independently evolved derived characters), is controversial in that it completely disagrees with the accepted view. The grouping of *Pteronotus* with *Eptesicus* and *Molossus* with *Phyllostomus* breaks up the accepted superfamily grouping of these genera as proposed by Weber (1928) and Koopman (1984), among others.

Regardless of the groupings in their terminal branches, both of these cladograms provide the first strong supporting evidence for Koopman's Yangochiroptera (other than his own data on premaxilla anatomy, Koopman, 1984).

The hyoid anatomy data provide six synapomorphies (=shared derived characters) which support the grouping of the superfamilies Vespertilionoidea and Phyllostomoidea together.

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Table 1: Derived characteristics and their occurrence in selected taxa of the Microchiropteran bats.

Legend

- All data except those for *Molossus molossus* come from Sprague (1943), Griffiths (1982, 1983), Griffiths and Criley (1989), Griffiths et al (1991), and Griffiths and Smith (in press).
- "+" indicates presence of the derived character state
- "-" indicates presence of the primitive character state
- families Nycteridae, Megadermatidae, and Rhinolophidae belong to Superfamily Rhinolophoidea
- families Emballonuridae and Rhinopomatidae belong to Superfamily Emballonuroidea
- families Phyllostomidae (*Phyllostomus*) and Mormoopidae (*Pteronotus*) belong to Superfamily Phyllostomoidea
- families Vespertilionidae (*Eptesicus*) and Molossidae (*Molossus*) belong to the Superfamily Vespertilionoidea.

Characteristics \ Taxa	Nyct.	Moga.	Rhil.	Embal.	Rhin.	Phyll.	Ptero.	Eptes.	Molos.
1.presence of mylohyoid prof.	-	-	-	-	-	+	+	+	+
2.mylohyoid split into two bellies	-	-	-	-	-	+ / -	+	+	+
3.loss of mandibulohyoid	+	-	+	+	-	+	+	+	+
4.loss of stylohyoid	-	-	+	+ / -	-	+	+	+	+
5.reduction/loss of jugulohyoid	-	-	-	+ / -	+	-	-	-	+
6.loss of sphinc. col. prof.	+	-	+	+	+	-	-	-	-
7.origin of sphic. col. prof.		basihy raphe or sterno -hyal raphe				fascia of post. mylo-hyoid	lat. edge of basihy raphe	lat. edge of basihy raphe	ventral surface of sterno -hyoid raphe
8.insertion of sphinc. col. prof.						inner skin surface of cervical region	skin of throat	skin of throat	deep surface of skin lat. to mandible
9.two bellies of sphinc. col. prof.		-				2-3	-	-	-
10.insertion of ceratohyoid on epihyal only						-	+	-	+
11.insertion of ceratohyoid on ceratohyal and epihyal						-	-	+	-
12.insertion on ceratohyal, epihyal, and stylohyal						+	-	-	-
13.genioglossus insertion turns laterally						+	?	?	+
14.geniohyoid size reduced compared to genioglossus	-	-	-	+ / -	-	-	+	-	-
15.hyoglossus origin by tendon (shared as insertion of sternohyoid and geniohyoid)	-	+	-	-	-	+	+	+	+
16.loss of deeper belly of hyoglossus originating from lat. thyrohyal	-	+	-	-	-	+ / -	-	-	-
17.loss of third belly of hyoglossus originating from thyrohyal	+	-	+	-	-	-	-	-	-
18.styloglossus in two distinct bellies, split by hyoglossus	-	-	-	-	-	+ / -	+	+	+
19.styloglossus origin from expanded lat. stylohyal	-	-	+ / -	-	-	+	-	-	+
20.origin of sternohyoid from manubrium	+	+	+	-	+	+ / -	-	+	+
21.omohyoid originates from clavicle	+	+	-	+	+	-	lost	lost	-
22.loss of omohyoid	+ / -	-	-	-	-	-	+	+	-

Figure 1: Ventral view of the hyoid musculature of *Molossus molossus* (the musculature on the right side is removed to expose deeper structures). Bar equals 1 mm.

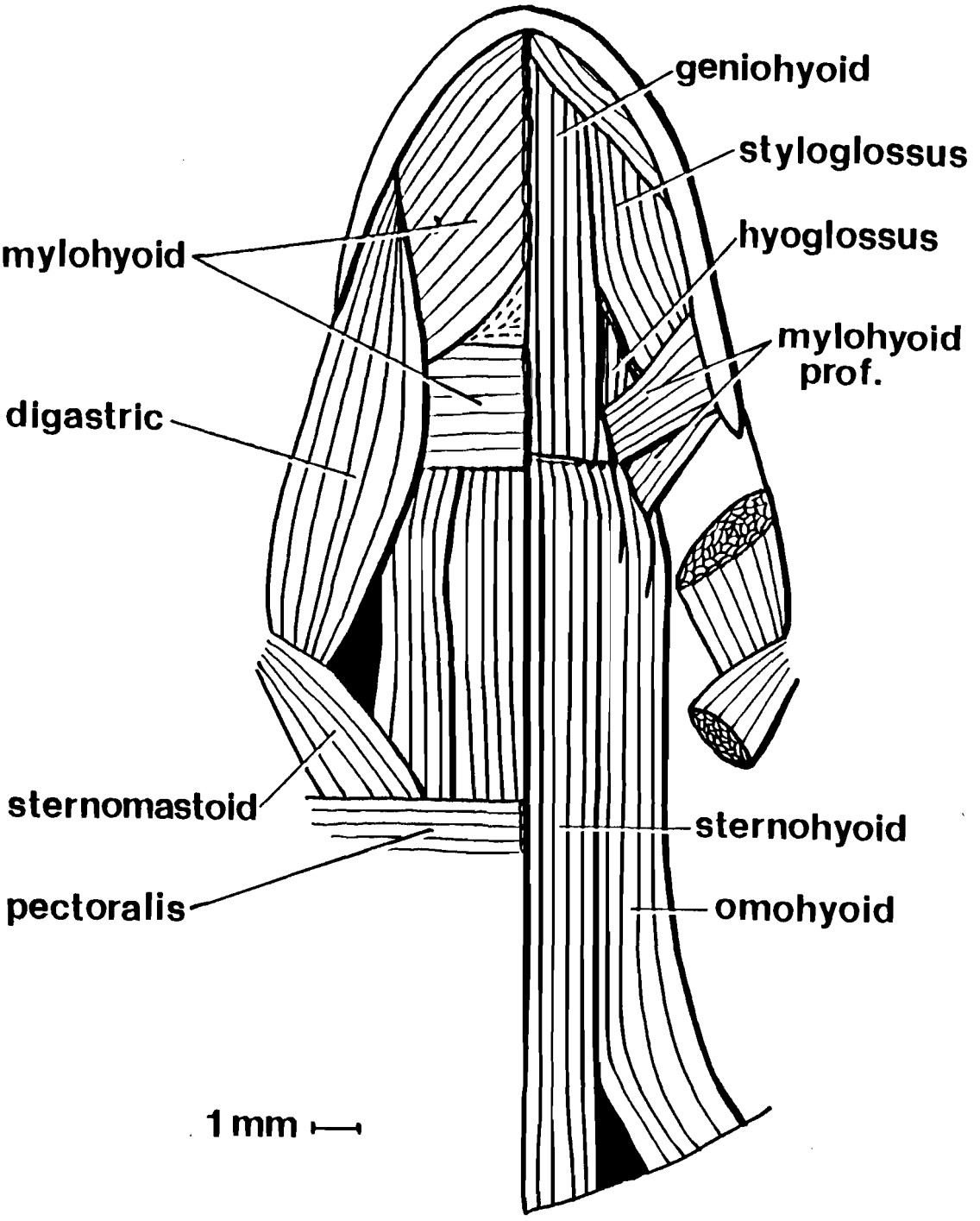

geniohyoid
styloglossus
hyoglossus
mylohyoid
mylohyoid prof.
digastric
sternomastoid
sternohyoid
pectoralis
omohyoid
1 mm

Figure 2: Ventral view of the hyoid musculature of *Molossus molossus* (the musculature on the right side is removed to expose deeper structures). Bar equals 1 mm.

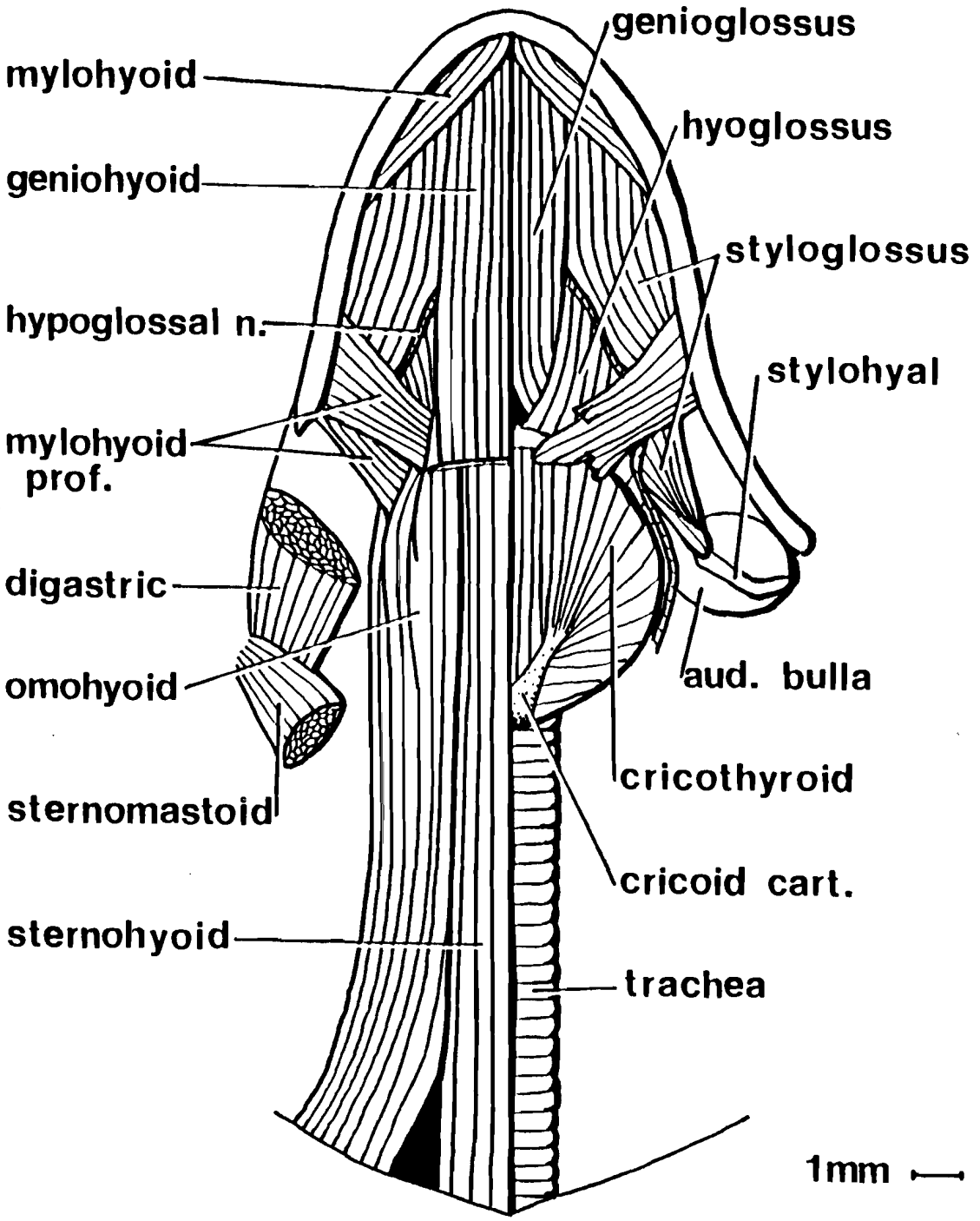

genioglossus
mylohyoid
hyoglossus
geniohyoid
styloglossus
hypoglossal n.
stylohyal
mylohyoid
prof.
digastric
omohyoid
aud. bulla
cricothyroid
sternomastoid
cricoid cart.
sternohyoid
trachea
1mm

Figure 3: Ventral view of the larynx and hyoid apparatus of *Molossus molossus* (the musculature on the right side is removed to expose deeper structures). Bar equals 1 mm.

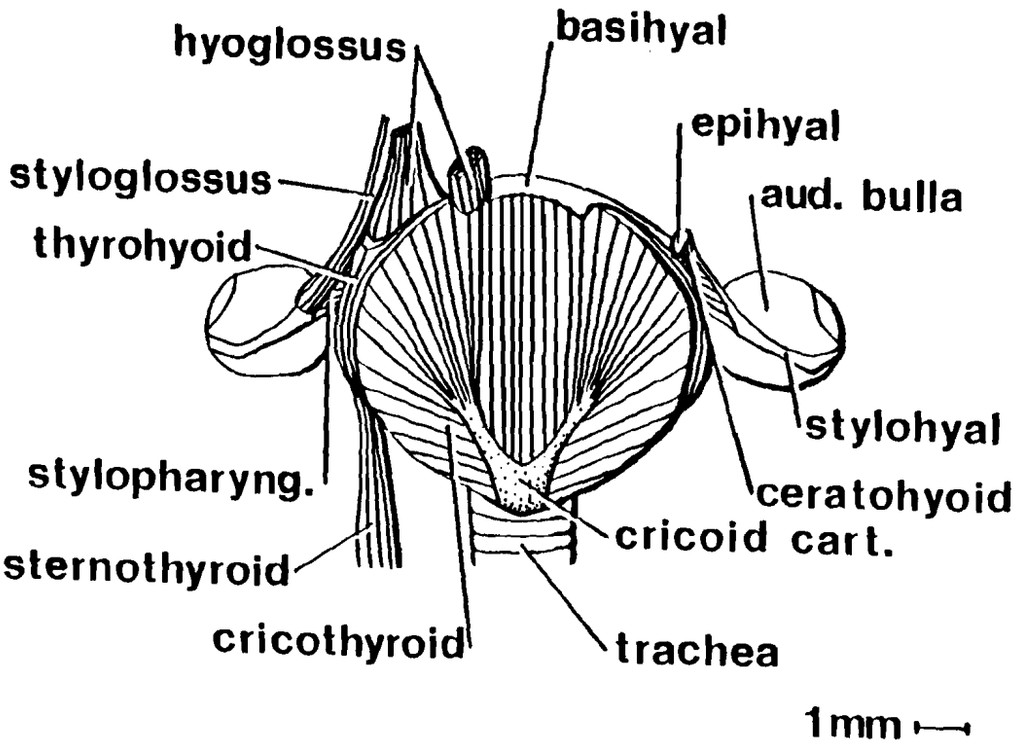
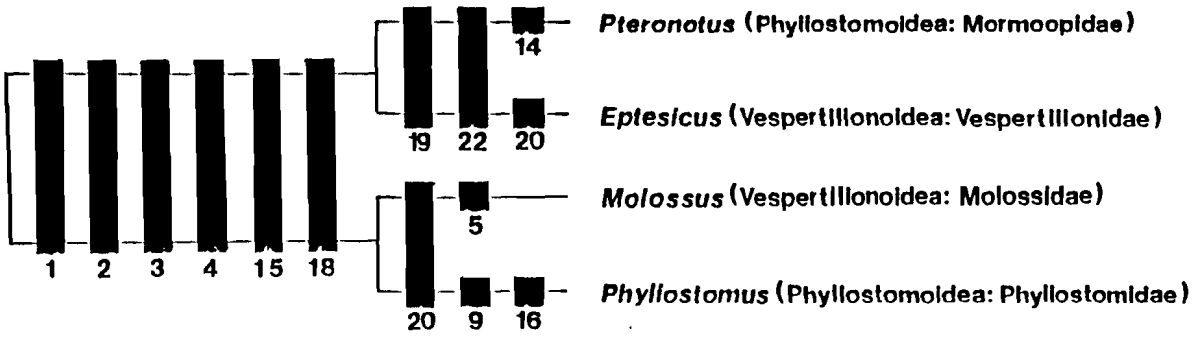
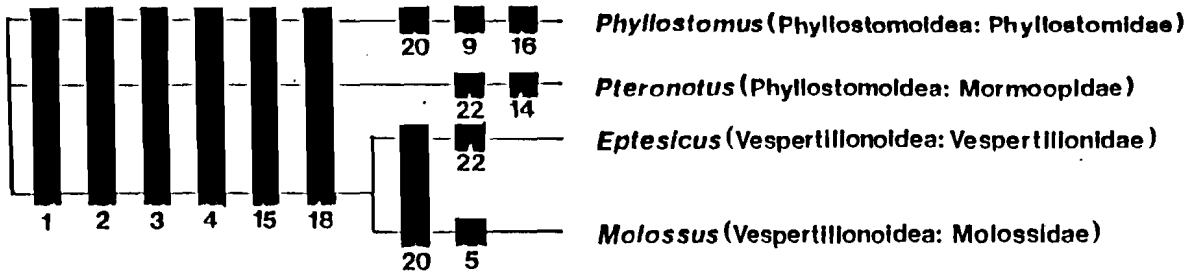

hyoglossus
basihyal
epihyal
styloglossus
aud. bulla
thyrohyoid
stylohyal
stylopharyng.
ceratohyoid
cricoid cart.
sternothyroid
cricothyroid
trachea
1mm

Figure 4: The two most parsimonious cladograms for the possible phylogenetic relationships between bats of the infraorder Yangochiroptera.


1 2 3 4 15 18
19 22 20
14
5
20 9 16
Pteronotus (Phyllostomoidea: Mormoopidae)
Eptesicus (Vespertilionoidea: Vespertilionidae)
Molossus (Vespertilionoidea: Molossidae)
Phyllostomus (Phyllostomoidea: Phyllostomidae)


1 2 3 4 15 18
20 9 16
22 14
22
20 5
Phyllostomus (Phyllostomoidea: Phyllostomidae)
Pteronotus (Phyllostomoidea: Mormoopidae)
Eptesicus (Vespertilionoidea: Vespertilionidae)
Molossus (Vespertilionoidea: Molossidae)