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Systematic Relationships of Natalid and Furipterid Bats, Based on Hyoid Morphology (Chiroptera: Natalidae and Furipteridae)

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A Senior Research Honors Paper Presented
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ABSTRACT

The musculature of the hyoid regions of two species of bats (Order Chiroptera) from two separate families, Natalidae and Furipteridae, were examined using standard microscopic dissection techniques. Morphological variation was described and characters were scored and entered into the computer program PAUP, Phylogenetic Analysis Using Parsimony, along with characters of families previously examined by Griffiths. Cladistic analysis revealed support for the placement of Natalidae and Furipteridae together within the Superfamily Nataloidea, along with the families Thyropteridae and Myzopodidae, as recently proposed by Simmons (1998). The inclusion of Myzopodidae is surprising from a geographical standpoint. Myzopodids are endemic to Madagascar, while thyropterids, natalids and furipterids are found in Central America and northern South America. Thus, the placement of the Myzopodidae with the other three sympatric families implies that all four of these families share an unknown common ancestor in Africa, perhaps an unknown fossil species of bats.

INTRODUCTION

The evolutionary relationships between extant bats have been controversial for as long as bats have been identified. The relationship between the four families of bats in this study, the Natalidae, Furipteridae, Thyropteridae, and Myzopodidae, has been the subject of much investigation. These families have generally been grouped in close association with each other by many past investigators, but their placements in with respect to each other are different in different studies. Two cladograms of bat phylogeny were proposed by James Dale Smith that attempted to present the "generally accepted view" of bat evolution at the time. (Smith, 1976) Smith suggested that the Thyropteridae and Furipteridae as the most closely related, with the Natalidae as the next closest relative, all three of which made a monophyletic group. Myzopodidae, according to Smith, belonged with the Vespertilionidae in a different group. Smith's study was criticized for the fact that his cladograms were derived from his own perceptions of character polarities based on his own research and on character he used from past research of others (Winge 1892, Miller 1907, Simpson 1945, Davis 1970, Koopman and Jones 1970 and Hill 1974) rather than from actual character analysis. Van Valen (1979) proposed a bat phylogeny that was greatly different than that proposed by Smith three years earlier. Regarding the four families in question, Van Valen brought the Furipteridae down to the level of subfamily within the family Natalidae. Furipteridae were previously considered a separate family, but Van Valen presented a phylogeny that showed the Furipteridae belonged in the family Natalidae, while the Natalidae, Thyropteridae and Myzopodidae, were still considered separate families. These three families were considered by Van Valen to belong to a monophyletic group.

Novacek (1980) studied the auditory region of extant bats and Luckett (1980) studied their fetal membrane morphology and development. Novacek proposed a cladogram that was significantly different than any previous study. Novacek placed the Furipteridae with the Thyropteridae, and kept the Natalidae as the next branch. Myzopodidae were omitted from Novacek's cladograms. Alternatively, Luckett seemed unable to come up with any substantial evidence to support any old relationships or propose any new ones. He did find some evidence for the close relationships of the Vespertilionidae and Thyropteridae, but his cladogram did not include the Furipteridae, Natalidae or Myzopodidae.

Eisenberg (1981) proposed a cladogram that showed many similarities to Smith's studies in 1976, suggesting that studies done on single organ systems, such as those of Novacek and Luckett, were not best suited for reclassification of phylogenetic relationships. Like Smith, Eisenberg placed Thyropteridae and Furipteridae closest together, with Natalidae in the same group. However, the Myzopodidae was placed as a separate branch with the Vespertilionidae. All five of these families, along with the Mystacinidae and Molossidae, were placed in one superfamily, the Vespertilionoidea.

Pierson (1986) studied the transferrin immunological distance data of extant bats and proposed a set of phylogenetic hypotheses based on these studies. Her cladograms were significantly different than those proposed by Smith (1976) or Eisenberg (1981). Pierson's cladogram placed the Natalidae and Furipteridae together as a monophyletic branch at the base of the entire tree. However, the Thyropteridae was placed as a separate branch, not grouped with the Natalidae or Furipteridae, but rather most closely related to the Vespertilionidae. The family Myzopodidae was omitted from the study.

Novacek (1991) proposed two phylogenies that differed substantially from those of his contemporaries and those he had himself proposed eleven years earlier. These two cladograms were created not by analysis of explicit characters, but by considering studies done by Koopman

(1987), Novacek (1987) and Pierson (1986). Both of Novacek's new hypotheses were unable to resolve the relationships between the four families of bats in question, and are represented on the cladograms as unresolved polytomies. However, it is worth noting that although the relationships among these four families are unresolved, they are still grouped together on the cladogram as being closely related. Fenton (1992) proposed a phylogeny that did not reflect any new analyses, but focused more on consideration of other previously done studies. The four families discussed his study were again placed with the Vespertilionidae and Molossidae in the Superfamily Vespertilionoidea. Fenton was not able to resolve the relationships among the Natalidae, Furipteridae and Thyropteridae, and these three families are represented on his cladogram as an unresolved polytomy. Fenton proposed that the Myzopodidae were more closely related to the Molossidae than the Natalidae, Furipteridae and Thyropteridae.

Simmons (1998) proposed a new phylogeny, basing her results on morphology and rRNA restriction sites. Her study concluded the close relationship between the Thyropteridae, Myzopodidae, Furipteridae, and Natalidae. Her cladogram suggested that the closest relationship among these four families was between the Furipteridae and Natalidae. Her cladogram also was unable to resolve the relationships between that the Myzopodidae, Thyropteridae and the branch leading to the Natalidae and Furipteridae, and these are represented by an unresolved polytomy. Simmons took these four families out of the superfamily Vespertilionoidea and placed them in their own, newly created Superfamily Nataloidea.

The purpose of this study is to use the hyoid region data to test which of the above hypotheses is best supported. In particular, this study will use the data to see if there is a support for a close relationship of the Thyropteridae, Myzopodidae, Furipteridae and Natalidae, to the exclusion of all other families, as proposed by Simmons in 1998.

MATERIALS AND METHODS

Specimens fixed in formalin and preserved in 70% ethyl alcohol of two species of bats, *Natalus stramineus* and *Furipterus horrens,* were dissected for examination using standard microdissection techniques. One specimen of each species was dissected (American Museum of Natural History 185046 and 69162, respectively.) Observations and several pencil drawings were made of all muscles of and related to the hyoid region. These drawings were made on a scale of 10X. Pencils drawings were also made for the hyoid apparatus and larynx. Selected pencil drawings were then inked for inclusion in this work. The morphological characters that were revealed from these two specimens were then entered into the computer program PAUP, Phylogenetic Analysis Using Parsimony (Swofford, 2000), along with the previously collected data of the other families within Chiroptera by Griffiths.

RESULTS

Mylohyoid Group-

This group of muscles is innervated by the mylohyoid nerve, a branch of the N. mandibularis, which in turn is a branch of the N. trigeminus (V).

M. mylohyoid (Figures 2,4)

Origin: In *Natalus*, from the posterior medial one third of the body of the mandible. In *Furipterus,* the origin is also from the medial surface of the mandible and is from a sheet of fascia.

Insertion: In *Natalus*, onto its antimere along the ventral midline, as well as onto the ventral tip of the basihyal and onto the ventral surface of the thyrohyal. Insertion in *Furipterus* is into its antimere along the ventral midline.

Comments: The muscle is quite thin in *Natalus*

M. mylohyoid profundus (Not figured)

This muscle is absent in both *Natalus stramineus* and *Furipterus horrens.*

M. mandibulo-hyoid (Figures 2,4)

Origin: From the medial surface of the mandible from a point one-millimeter posterior to the mandibular symphysis in *Natalus.* In *Furipterus,* the origin is by deep tendon from the medial mandible on the deep side (dorsal surface) of the digastrics.

Insertion: In *Natalus*, onto its antimere along the ventral midline. The posterior-most fibers insert into the anterior mylohyoid. Modified mandibulo-hyoid attaches strongly to the ventral surface of the geniohyoid. In *Furipterus*, this muscle passes medially to insert onto its antimere on the ventral midline superficial to the mylohyoid.

Comments: In *Natalus*, the muscle is quite thing. Also, there is no trace of a mandibulo-hyoid tendon. In *Furipterus*, the sphinctor colli profundus seems to originate from the anterior half of the mandibulo-hyoid at its insertion on the ventral midline.

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. stylohyoid

This muscle is completely absent in both *Natalus* and *Furipterus.*

M. jugulohyoid (Figures 3,5)

Origin: In both bats, from the paracoccipital region of the skull immediately posterior to the auditory bulla in both species.

Insertion: In *Natalus*, this muscle passes ventrally, then curves around the posterior surface of the auditory bulla to insert on the medial "blade" of the hatchet-shaped lateral tip of the stylohyal. In *Furipterus*, the muscle inserts on the lateral tip of the stylohyal.

M. sphinctor colli profundus (Not figured)

Origin: In *Furipterus*, from the anterior fibers of the mandibulo-hyoid.

Insertion: In *Furipterus*, this muscle passes anteriorly and laterally to insert on the deep surface of the skin approximately at the level of the base of the ear.

Comments: This muscle is completely absent in *Natalus*.

Glossopharyngeal Group-

This group of muscles is innervated by branches of the N. glossopharyngeus (IX).

M. stylopharyngeus (Figures 3,5)

Origin: From the medial surface of the midpoint of the stylohyal in both species.

Insertion: Onto the lateral pharyngeal wall just anterior to the thyropharyngeus in both species.

M. ceratohyoideus (Figures 3,5)

Origin: From the anterior face of the thyrohyal in both *Furipterus* and *Natalus*.

Insertion: Onto the posterior surfaces of the ceratohyal, the entire epihyal and medial tip of the stylohyal in both species.

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 cricopharyngeus.

M. hyopharyngeus (Not figured)

Origin: From the buccopharyngeal fascia in the region of the basihyal in both species.

Insertion: This muscle passes dorsally and medially to insert onto its antimere on the dorsal midline of the esophagus in *Natalus*. In *Furipterus*, the muscle inserts weakly into its antimere.

Comments: This muscle is extremely reduced in *Natalus*.

M. thyropharyngeus (Not figured)

Origin: In both species, from the dorsal surface of the thyrohyal.

Insertion: This muscle passes dorsally and then medially to insert onto its antimere on the dorsal midline of the esophagus just posterior to the stylopharyngeus in *Natalus*. In *Furipterus*, the muscle inserts onto its antimere along the dorsal midline of the pharynx.

M. cricopharyngeus (Not figured)

Origin: From the dorsal surface of the cricoid cartilage and the posterior thyroid cartilage in both species.

Insertion: This muscle passes dorsally and then medially to insert onto its antimere on the dorsal midline of the pharynx *Natalus*. In *Furipterus*, the muscle inserts into its antimere along the dorsal midline of the pharynx.

Lingual Group-

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

M. genioglossus (Figures 2,4)

Origin: From the posterior surface of the mandible just lateral to the mandibular symphysis in *Natalus*. In *Furipterus*, the muscle originates from the medial surface of the anterior half of the mandible.

Insertion: Onto the anterior surface of the basihyal and into the ventral midline of the posterior half of the tongue in *Natalus*. The entire muscle inserts onto the ventral midline of the tongue in *Furipterus*.

Comments: This muscle is fused to the geniohyoid, which lies ventral to it in *Natalus*. In *Furipterus*, the anterior one-third bulges out and the muscle is rather large as well.

M. hyoglossus

Origin: From the lateral surface of the basihyal and the anterior surface of the thyrohyal in *Natalus*. In *Furipterus*, the origin is from the anterior lateral surface of the basihyal.

Insertion: Onto the posterior tongue deep to the hypoglossal nerve and the styloglossus in *Natalus*. In *Furipterus*, the muscle passes laterally to run under the hypoglossal nerve to insert deep to it onto the ventral surface of the tongue.

Comments: This muscle is very broad and is a single, unbroken sheet of muscle in Natalus. In both species, this muscle splits the styloglossus into two distinct bellies.

M. styloglossus (Figures 2,3,4,5)

Origin: From the midpoint of the ventral surface of the stylohyal in *Natalus* and from the ventral surface of the stylohyal in *Furipterus*.

Insertion: Onto the lateral surface of the tongue for much of its length in both species.

Comments: This muscle is split into two bellies by the hyoglossus. The deep belly of the styloglossus is not very well developed in *Natalus* and is not very large in *Furipterus*.

Medial Ventral Cervical Group-

This group of muscles is innervated by a network of nerves made up of anterior cervical nerves, except for M. geniohyoid, which is apparently innervated by N. hypoglossus. Despite the seemingly differing innervations, these muscles are treated as a group on the basis of similar embryonic differentiation.

M. geniohyoid (Figures 2,4)

Origin: By tendon, from the posterior surface of the mandible just lateral to the mandibular symphysis in both species.

Insertion: Onto the anterior surface of the basihyal in both species.

Comments: In *Natalus* and *Furipterus*, this muscle is not very well developed. The anterior half of the geniohyoid is fused strongly to the genioglossus, which lies dorsal to it. In *Furipterus*, the tendon is fused with the fascia that is anterior to the mylohyoid. The muscle is also rather thin.

M. sternohyoid (Figures 2,4)

Origin: In *Natalus*, from the medial-most part of the anterior manubrium of the sternum. In *Furipterus*, the muscle originates from the dorsal surface of the medial manubrium and does not come from the lateral wing of the manubrium at all.

Insertion: Onto the posterior surface of the basihyal in *Natalus*. In *Furipterus*, the muscle passes anteriorly lateral to the trachea, separated from its antimere. It travels medially as it approaches the basihyal anteriorly and inserts into the posterior surface of the ventral basihyal.

M. sternothyroid (Figure 2,3,4,5)

Origin: In *Natalus*, from the medial-most part of the anterior manubrium of the sternum, immediately dorsal (deep) to the origin of the sternohyoid. In *Furipterus*, the muscle originates from the anterior and dorsal surface of the medial manubrium lateral to the origin of the sternohyoid.

Insertion: Onto the lateral surface of the thyroid cartilage in both species. In *Furipterus*, the muscle inserts posterior to the origin of the thyrohyoid.

Comments: In *Furipterus*, the posterior-most portion of the muscle travels laterally to the sternohyoid. The muscle passes under the omohyoid to the larynx.

M. omohyoid (Figure 3)

Origin: In *Furipterus*, from the anterior edge of the scapula, just proximal to the scapular notch.

Insertion: In *Furipterus*, onto the lateral basihyal, just lateral to the insertion of the sternohyoid.

Comments: This muscle is rather thin and weakly developed in *Furipterus*. The omohyoid is completely absent in *Natalus*.

M. thyrohyoid (Figures 2,3,4,5)

Origin: From the lateral surface of the thyroid cartilage of the larynx in both species.

Insertion: Onto the posterior surface of the basihyal as well as onto the medial thyrohyal in *Natalus*. In *Furipterus*, the muscle passes anteriorly to insert onto the posterior surface if the thyrohyal.

Comments: The muscle is extremely robust in *Natalus*.

Hyoid Apparatus

In *Natalus*, the basihyal is roughly triangular with a prominent, ventrally-projecting entoglossal process. The thyrohyal is fused to the lateral edge of the basihyal and is relatively short. The ceratohyal and the epihyal are roughly the same length and are not fused. The stylohyal is rather long and has hatchet-shaped lateral tips. There are synovial joints between the basihyal and the elements of the anterior cornu. In *Furipterus*, the basihyal is relatively small and thin withy a ventrally-projecting entoglossal process. The thyrohyal is not fused to the basihyal. The ceratohyal is approximately twice the length of the small epihyal. The ceratohyal and epihyal are also not fused. The stylohyal is rather long and does not have the hatchet-shaped lateral tips that the stylohyal of *Natalus* has.

CONCLUSIONS

Simmons (1998) proposed some changes to the traditional classification of the Order Chiroptera. Conventionally, the families Natalidae, Furipteridae, Myzopodidae and Thyropteridae had been placed in the Superfamily Vespertilionoidea, along with three other families of bats, the Mystacinidae, Vespertilionidae and the Molossidae. Simmons proposed a cladogram that set these four families apart from the rest of the tree significantly enough to place them in their own Superfamily Nataloidea (Figure 1). To test this hypothesis, hyoid and laryngeal character were entered into two phylogenies analysis programs: PAUP and MacClade. Two equally parsimonious cladograms were generated using PAUP. Further examination by MacClade revealed that there were no more parsimonious trees.

The first cladogram (Figure 6) places these four families as a monophyletic group, distinctly apart from the rest of the tree. Of this group, the Thyropteridae for the most basal line.

The Furipteridae are the next line off the tree. The Myzopodidae and the Natalidae are linked as the two most closely related families. However, this most parsimonious tree does place these four families apart from the other families, thus seeming to support the hypothesis that Simmons (1998) proposed. This is surprising because the Myzopodidae are endemic to Madagascar, and the Natalidae are found in Central and South America.

The second equally parsimonious cladogram that was generated (Figure 7) shows these four families being set off from he remainder of the cladogram. The Thyropteridae form the most basal line, but the Myzopodidae form the next line off the tree. In this cladogram, the Natalidae and Furipteridae are most closely related. The placement of the Natalidae as closely related to the Furipteridae is what was expected, since their distributions over almost completely. However, the placement of the Myzopodidae between the Natalidae/Furipteridae branch and the Thyropteridae branch is surprising because of the geographical separation of the Myzopodidae. If this cladogram is correct, the Myzopodidae would need to have migrated across Africa to colonize Madagascar, leaving the other three families behind.

Both cladograms are equally parsimonious with sixty-nine steps. Each supports the formation of the Superfamily Nataloidea, as separate from the Superfamily Vespertilionoidea, proposed by Simmons (1998). Although it is surprising that the Myzopodidae do not form the basal line in either cladogram, there is strong support for Simmons' classification, which took the families Natalidae, Furipteridae, Myzopodidae and Thyropteridae out of the Superfamily Vespertilionoidea and placed them in their own Superfamily Nataloidea. Not only did these four families in question consistently fall out together as a monophyletic group in this study, but also the placement of the Vespertilionidae was also consistent. Traditionally, the Vespertilionidae were placed in the Superfamily Vespertilionoidea, along with the Natalidae, Furipteridae, Thyropteridae, Myzopodidae, Molossidae and Mystacinidae. Simmons proposed that not only should the four families of this study be placed in their own Superfamily Nataloidea, but that the Vespertilionidae be placed in its own Superfamily Vespertilionoidea. In the cladograms proposed in this study, this hypothesis is strongly supported. In figure 6 and 7, the Vespertilionidae fall out as their branch, more closely related to the Mystacinidae, Phyllostomidae, Mormoopidae and Noctilionidae than to the Superfamily Nataloidea. In fact, what was traditionally though to be a monophyletic group (the Superfamily Vespertilionoidea) is seen here to be a paraphyletic group. Thus, this data strongly support Simmons proposed classification changes.

As mentioned previously, geographically, the Myzopodidae are endemic to Madagascar, while the other three families, Thyropteridae, Natalidae and Furipteridae are found thousands of miles away in parts of Central and South America, in most cases overlapping each other. The placement of these four families together as a monophyletic group implies that they share an unknown common ancestor, possibly an unknown fossil species of bat. It is likely that the ancestor occupied a region between the Americas and Madagascar, perhaps in Africa. If so, the Myzopodidae migrated east to Madagascar and the ancestor of the Thyropteridae, Furipteridae and Natalidae migrated west to Central and South America.

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Table 1:

Description of nineteen characters entered into the data matrix.

Characters for analysis:

Character 1: Midline hyoid muscles attached by muscle fibers (0) or tightly by tendon (1) or loosely by tendon (2) or unattached (3) to basihyal.
Character 2: Mylohyoid profundus absent (0) or present (1).
Character 3: Mylohyoid inserts on basihyal (0) or onto basihyal and thyrohyal (1) or onto basihyal via tendon (2).
Character 4: Stylohyoid with slip superficial to digastric (0) or superficial slip absent (1).
Character 5: Stylohyoid with deep slip to digastric (0) or deep slip absent (1).
Character 6: Mandibulo-hyoid present and hooked by tendon to digastric (0) or absent (1) or mandibulo-hyoid present and not hooked directly to digastric (2).
Character 7: Hyoglossus originates as a broad, unbroken sheet from the basihyal and thyrohyal (0) or from the basihyal and thyrohyal separated by a space (1) or from the basihyal alone (2).
Character 8: Styloglossus with one belly (0) or with two bellies separated by lateral hyoglossus (1).
Character 9: Styloglossus originates from expanded tip of stylohyal (0) or from midpoint of stylohyal (1).
Character 10: Ceratohyoid insertion on the ceratohyal, epihyal, and medial stylohyal (0) or on the ceratohyal and epihyal (1) or on the ceratohyal alone (2) or on the epihyal alone (3) or on the lateral half of the epihyal and the medial quarter of the stylohyal (4).
Character 11: Omohyoid originates from scapula (0) or from clavicle midpoint (1) or absent (2).
Character 12: Ceratohyal unreduced (0) or reduced to one-half the length of epihyal (1) or ceratohyal reduced to tiny element or absetn (2).
Character 13: Epihyal unreduced (0) or reduced to one-half the length of ceratohyal (1).
Character 14: Peculiar anterior fusion of geniohyoid and genioglossus absent (0) or present (1).
Character 15: Mylohyoid originates from entire mandible (0) or from posterior one-half of mandible only (1).
Character 16: Sphinctor colli profundus present (0) or absent (1).
Character 17: Thyrohyoid insertion onto thyrohyal (0) or insertion onto basihyal (1)
Character 18: Sternothyroid origin from clavicle (0) or from sterno-clavicular articulation (1) or from manubrium of sternum (2).
Character 19: Stylohyal with blunt pointed end (0) or stylohyal with hatchet-shaped ends (1).

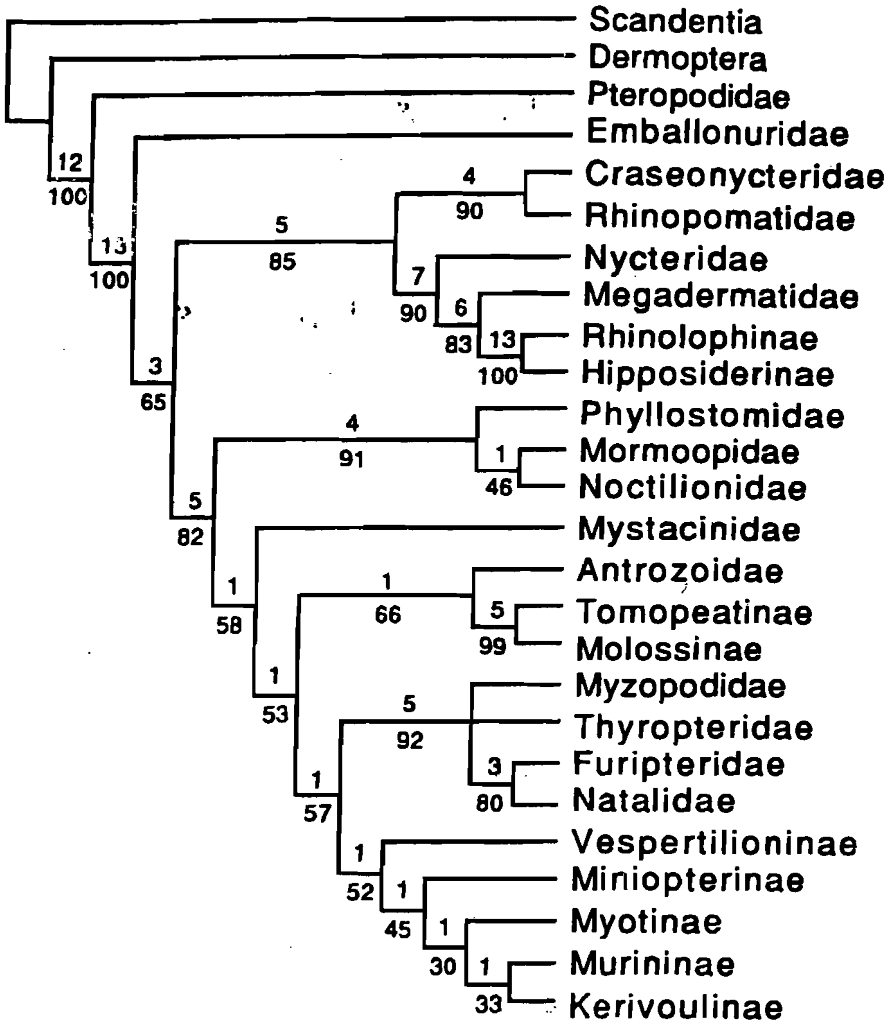
Table 2:

Data matrix for all nineteen families analyzed.

Good Data	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Scandentia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Dermoptera	0	0	0	1	1	1	0	0	0	3	2	0	0	0	0	0	0	0	0
3	Megachiropter	0	0	1	1	1	1	0	0	0	1	0	0	1	0	0&1	0	0	0	0
4	Emballonurida	0	0	1	0	1	1	0	0	1	1&2	1	1	0	0	0	0	0	1&2	0
5	Rhinopomatid	0	0	1	0	1	0	0	0	1	1	1	2	0	0	0	0	0	1	0
6	Craseonycteri	0	0	1	0	1	0	0	0	1	1	1	2	0	0	0	0	0	1	0
7	Nycteridae	0	0	0	0	1	1	2	0	1	2	1	0	0	0	0	0	0	0	0
8	Megadermatid	0	0	0	0	1	0	2	0	1	1	1	0	0	0	0	0	0	0	0
9	Rhinolophidae	0	0	0	1	0	0	2	0	1	4	1	1	0	0	0	0	0	0	0
10	Vespertilionid	0&1	1	1	0	1	0&1	1	1	1	1&3	0&2	1&2	0&1	0	0&1	0&1	1	0&2	0
11	Mystacinidae	2	1	2	1	1	0	1	1	1	3	2	1	0	0	0	0	0	0	0
12	Noctilionidae	2	1	2	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0
13	Mormoopidae	2	1	2	0	1	1	1	1	1	1	2	1	0	0	0	0&1	0	0	0
14	Phyllostomida	2&3	1	2	0	1	1	1	1	1	3	0&2	1	0	0	0&1	0&1	0	0	0
15	Hipposiderida	0	0	1	0	0	0	2	0	1	4	1	1	0	0	0	0	0	0	0
16	Natalidae	0	1	1	1	1	2	0	1	1	0	2	0	0	1	1	0&1	1	2	1
17	Furipteridae	0	1	0	1	1	0	2	1	1	0	0	0	1	1	1	1	1	2	0
18	Thyropteridae	0	1	1	1	1	0	0	1	1	1	2	0	0	1	1	0	0	2	0
19	Myzopodidae	0	1	1	1	1	0	0	1	1	1	2	0	0	1	1	0	1	2	1

Figure 1:

Cladogram proposed by Simmons (1998).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Pteropodidae
Emballonuridae
Craseonycteridae
Rhinopomatidae
Nycteridae
Megadermatidae
Rhinolophinae
Hipposiderinae
Phyllostomidae
Mormoopidae
Noctilionidae
Mystacinidae
Antrozoidae
Tomopeatinae
Molossinae
Myzopodidae
Thyropteridae
Furipteridae
Natalidae
Vespertilioninae
Miniopterinae
Myotinae
Murininae
Kerivoulinae
12
100
13
100
3
65
5
85
4
90
7
90
6
83
13
100
5
82
4
91
1
46
1
58
1
53
1
66
5
99
1
57
5
92
3
80
1
52
1
45
1
30
1
33

Figure 2:

Ventral view of the superficial (left) and deep (right) musculature of the hyoid region of *Natalus stramineus*.

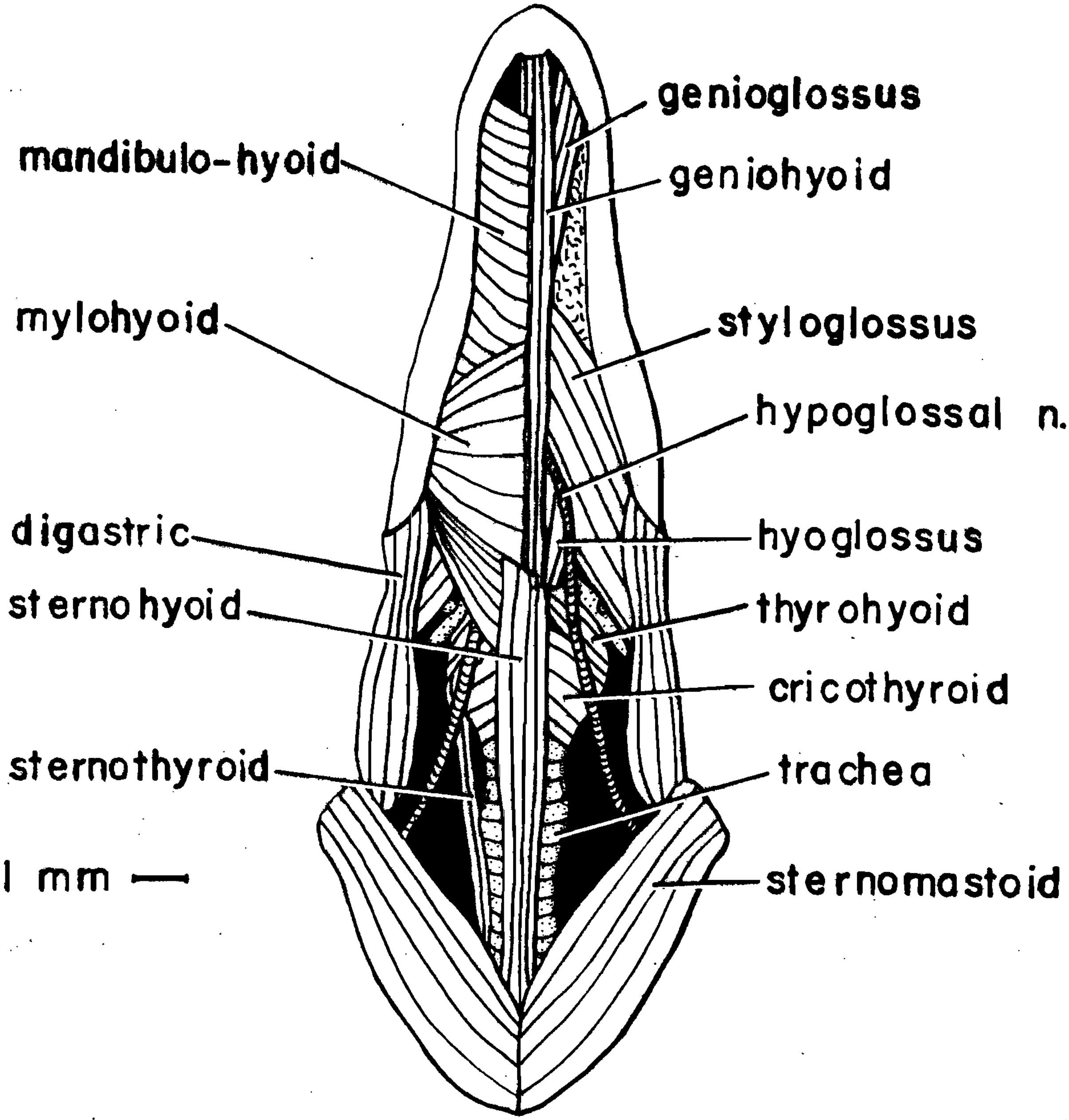
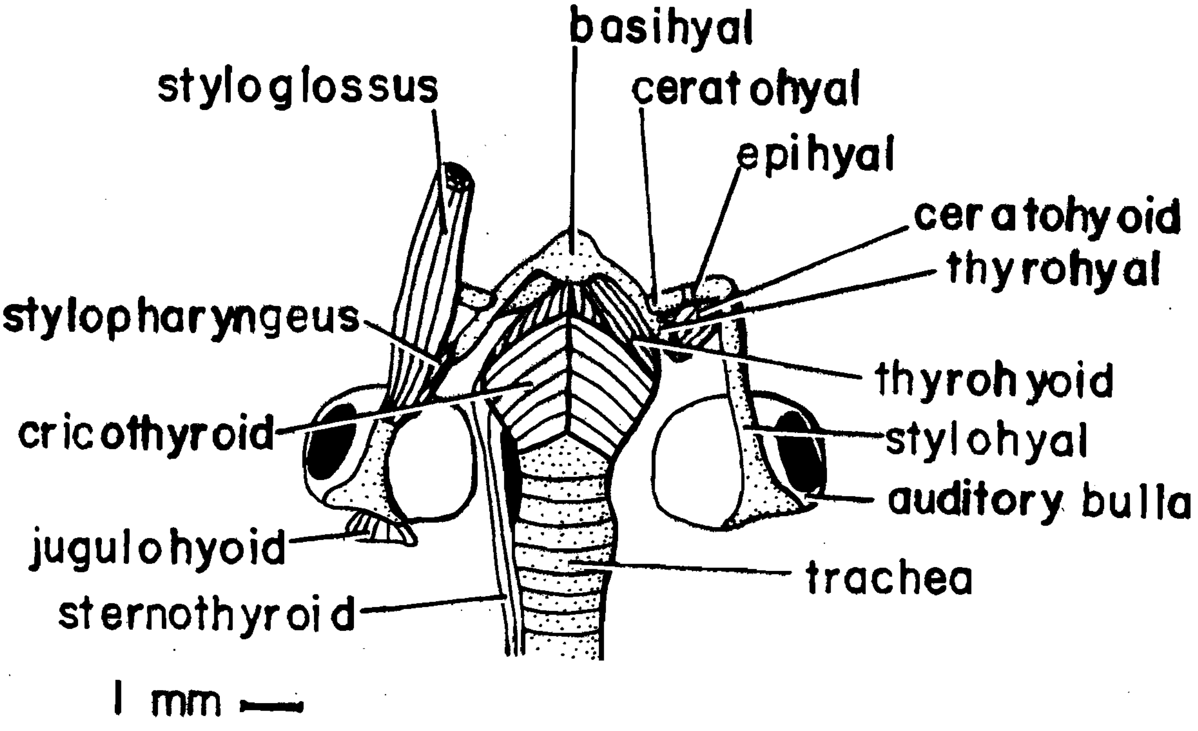

genioglossus
mandibulo-hyoid
geniohyoid
mylohyoid
styloglossus
hypoglossal n.
digastric
hyoglossus
sternohyoid
thyrohyoid
cricothyroid
sternothyroid
trachea
1 mm
sternomastoid

Figure 3:

Ventral view of the hyoid apparatus and larynx of *Natalus stramineus*.



basihyal
styloglossus
ceratohyal
epihyal
ceratohyoid
thyrohyal
stylopharyngeus
thyrohyoid
cricothyroid
stylohyal
auditory bulla
jugulohyoid
trachea
sternothyroid
1 mm

Figure 4:

Ventral view of the superficial (left) and deep (right) musculature

of the hyoid region of *Furipterus horrens*.

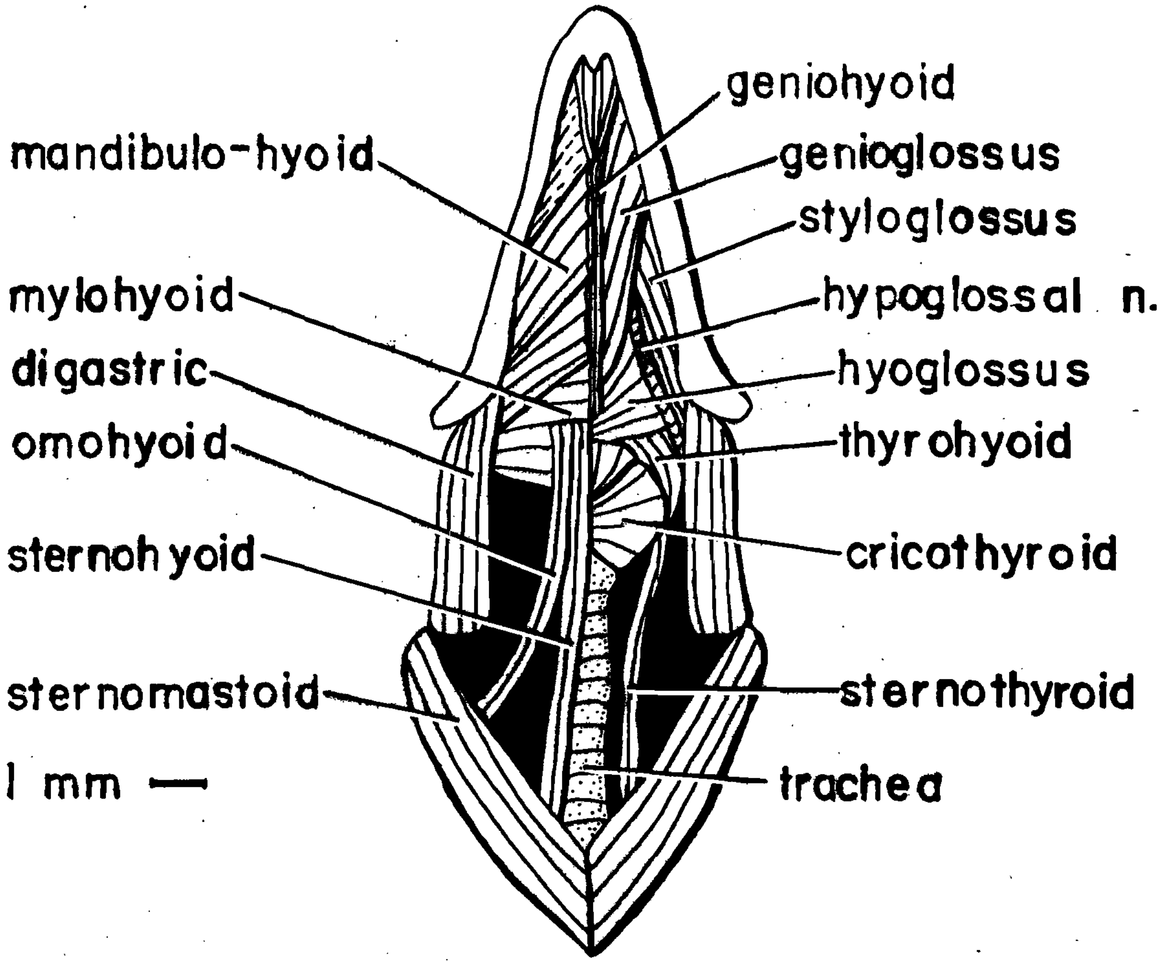

geniohyoid
mandibulo-hyoid
genioglossus
styloglossus
mylohyoid
hypoglossal n.
digastric
hyoglossus
omohyoid
thyrohyoid
sternohyoid
cricothyroid
sternomastoid
sternothyroid
1 mm
trachea

Figure 5:

Ventral view of the hyoid apparatus and larynx of *Furipterus horrens.*

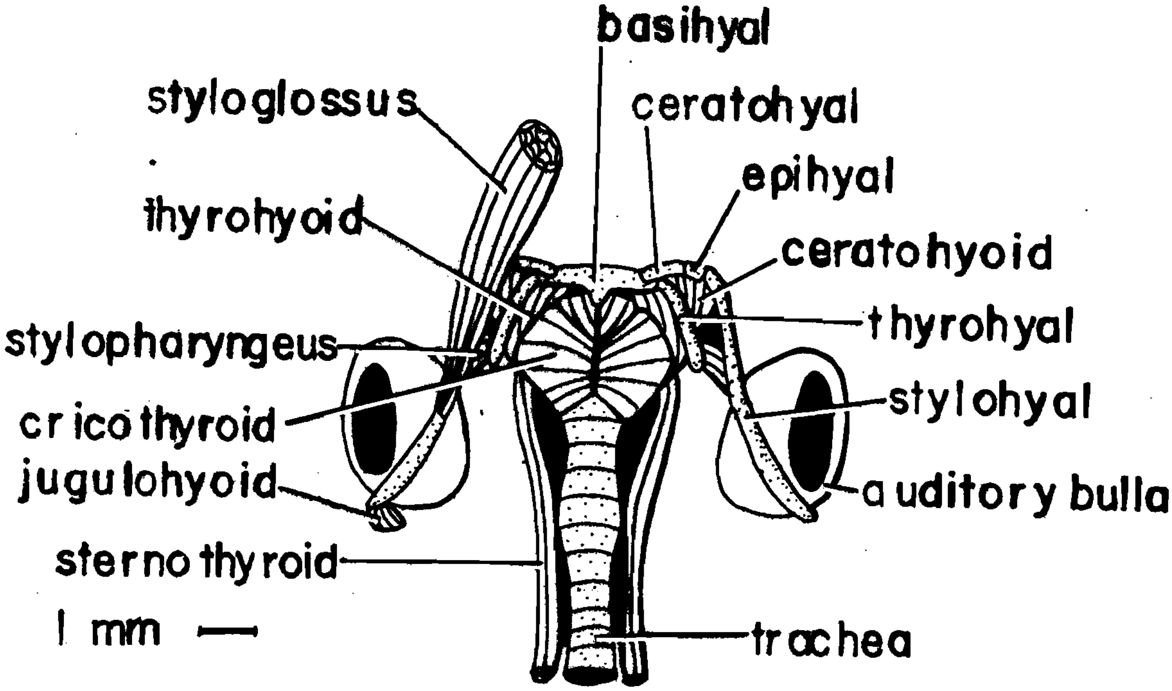

basihyal
styloglossus
ceratohyal
epihyal
thyrohyoid
ceratohyoid
thyrohyal
stylopharyngeus
cricothyroid
stylohyal
jugulohyoid
auditory bulla
sternothyroid
1 mm
trachea

Figure 6:

First cladogram of the Order Chiroptera which is based on hyoid musculature and hyoid apparatus morphology.

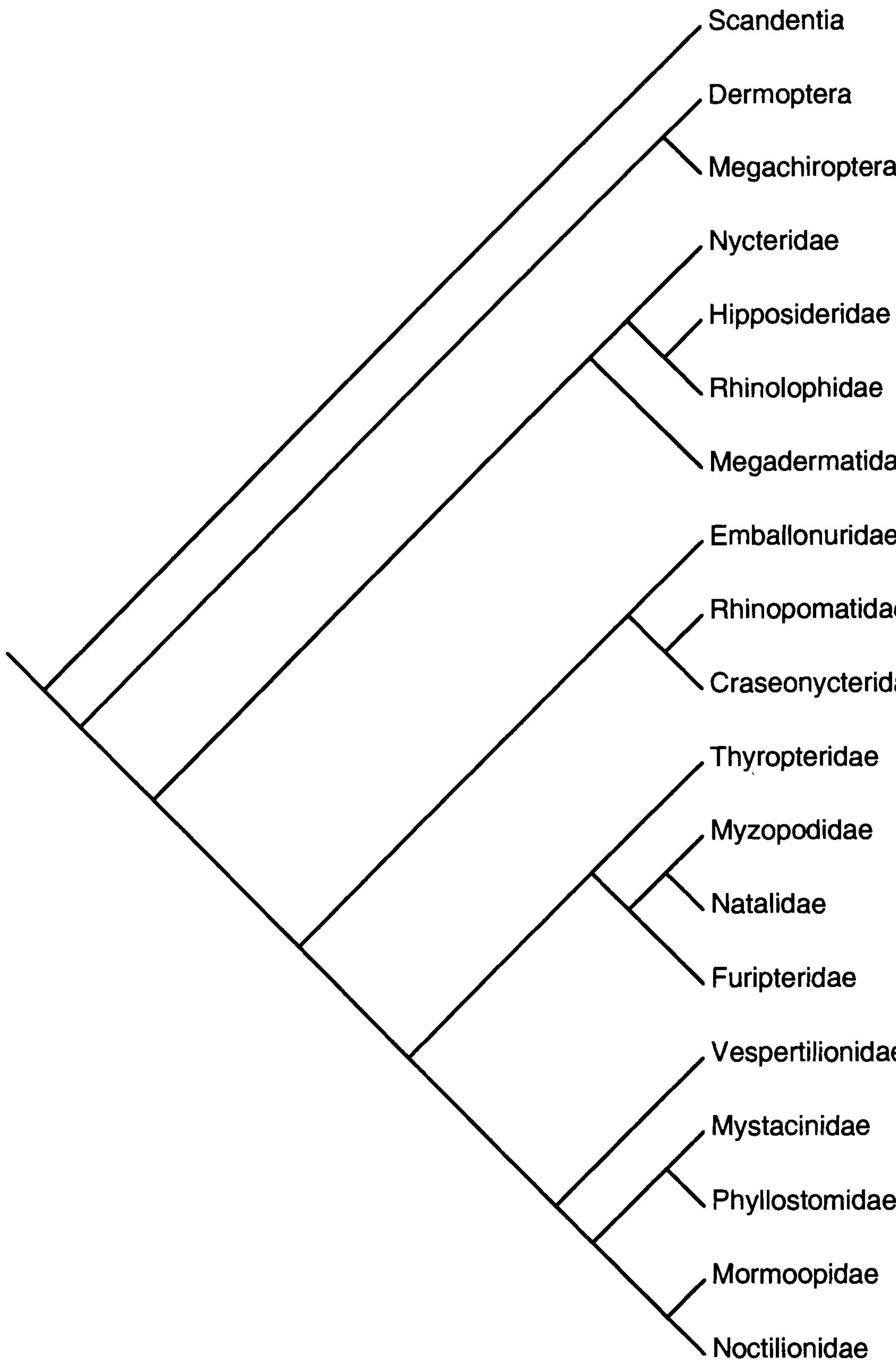
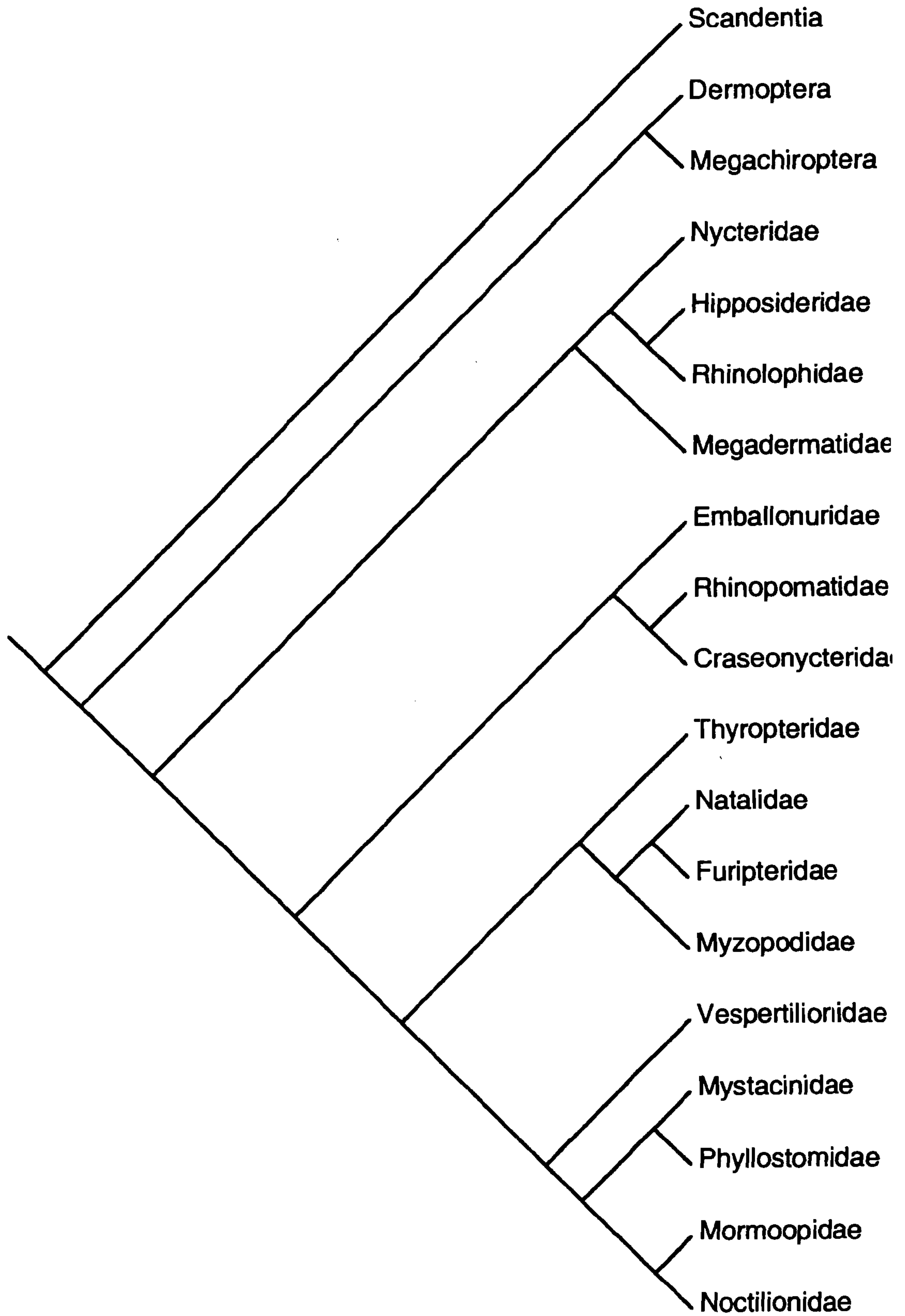

Scandentia
Dermoptera
Megachiroptera
Nycteridae
Hipposideridae
Rhinolophidae
Megadermatida
Emballonuridae
Rhinopomatida
Craseonycterid
Thyropteridae
Myzopodidae
Natalidae
Furipteridae
Vespertilionida
Mystacinidae
Phyllostomidae
Mormoopidae
Noctilionidae

Figure 7:

Second cladogram of the Order Chiroptera which is based on hyoid musculature and hyoid apparatus morphology.


Scandentia
Dermoptera
Megachiroptera
Nycteridae
Hipposideridae
Rhinolophidae
Megadermatidae
Emballonuridae
Rhinopomatidae
Craseonycterida
Thyropteridae
Natalidae
Furipteridae
Myzopodidae
Vespertilionidae
Mystacinidae
Phyllostomidae
Mormoopidae
Noctilionidae