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Systematic Relationships of Rhinolophid Bats: Based on Hyoid Morphology

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BASED ON HYOID MORPHOLOGY

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ABSTRACT

The hyoid regions of three species of bats within the family Rhinolophidae were dissected and compared with similar data of the hyoid region of other families obtained from Griffiths (personal communication). A cladistic analysis was performed using these data to analyze inter-generic relationships within the Rhinolophidae and inter-familial relationships between the families Rhinolophidae, Megadermatidae, Nycteridae, Rhinopomatidae and Emballonuridae. Two possible inter-generic cladograms are most parsimonious. Within the rhinolophids, either *Hipposideros diadema* or *Hipposideros armiger* is the most distantly related species depending on which of two characters, loss of the sphincter colli or loss of the omohyoid, has undergone convergent evolution. Both cladograms show a close association between *Triaenops persicus* and *Rhinonycteris aurantius*. At the inter-familial level, two most parsimonious cladograms were produced. Emballonurids, nycterids and rhinopomatids are closely united in both cladograms. A question of which of two characters, sternothyroid shift of origin or omohyoid shift of origin, has undergone convergent evolution leaves the relationship between rhinolophids and megadermatids unclear.

INTRODUCTION

Compared with New World bats little work has been done to try to establish systematic relationships within the bat family Rhinolophidae, or between the Rhinolophidae and other families. Based on skull, skeletal and epidermal characteristics, Weber (1928) placed the rhinolophid bat family into the superfamily Rhinolophoidea along with the families Megadermatidae and Nycteridae and placed the families Emballonuridae and Rhinopomatidae

into the superfamily Emballonuroidea. (Since the time of Weber's study one additional family, Craseonycteridae, has been discovered and placed into the superfamily Emballonuroidea). In 1984, Koopman grouped Rhinolophoidea with Emballonuroidea in the infraorder Yinochiroptera (Appendix I). Data collected in an immunological study by Pierson (1986) do not support the above classification of families. According to Pierson's data, rhinopomatids, megadermatids and rhinolophids are closely related, while emballonurids show no close association with any of the families. Within the family Rhinolophidae itself, almost nothing has been done to sort out the relationships among the eight genera containing a total of 124 species.

The purpose of this study is to provide another data base from which to analyze relationships at inter-familial and intra-familial levels. Griffiths (1982, 1983, and personal communication; Griffiths and Smith, in press) found the morphology of the hyoid region to be of significant value in elucidating systematic relationships among chiropterans. Using data collected from hyoid morphology of selected species of rhinolophids, megadermatids, nycterids, emballonurids and rhinopomatids (Griffiths and Smith, in press), I constructed an inter-familial cladogram to determine relationships between the families. From my data on the four selected genera of rhinolophids I also began to resolve systematic relationships within the family.

MATERIALS AND METHODS

A standard microscopic dissection of the hyoid region was performed on the following fluid preserved species:

Family Rhinolophidae

Hipposideros diadema grisea: American Museum of Natural History (AMNH) 206744.

Rhinolophus hildebrandti: AMNH 216208.

Triaenops persicus: AMNH 245393.

All dissections were performed using a binocular dissecting microscope. Using a scale of 10X the natural size, complete diagrams were made of the dissections at three levels: superficial ventral hyoid musculature, deep ventral hyoid musculature and ventral hyoid apparatus with associated musculature. The data obtained from the three species I examined were then compared to observations by Griffiths (personal communication) on the following two species of rhinolophids:

Hipposideros armiger: AMNH 112767.

Rhinonycteris aurantius: AMNH 199980.

A study of inter-familial relationships was done using my collective data on the family Rhinolophidae and data collected previously by Griffiths on the families Emballonuridae, Megadermatidae, Nycteridae and Rhinopomatidae. All references to the latter four families are taken directly from observations made by Griffiths.

DESCRIPTION OF HYOID APPARTUS

In Hipposideros diadema and Rhinolophus hildebrandti,the basihyal component of the hyoid apparatus is very large and triangular in shape (figs. 2, 4). The thyrohyal remains firmly attached to the basihyal throughout its length in R. hildebrandti and through most of its length in H. diadema. Articulating with the basihyal and epihyal in the anterior cornu, the ceratohyal in both species is freely moveable by synchondral joints. The epihyal itself is slightly longer than the ceratohyal,

articulating by synchondral joint with the stylohyal, a long, slender bone that curves posteriorly and laterally to the posterolateral rim of the auditory bulla. The stylohyal terminates in a flattened extension that is fairly strongly attached to the bulla. R. hildebrandti also has a very pronounced hyo-thyroid cartilage that attaches to the lateral tip of the basihyal and extends dorsally.

The hyoid apparatus of Triaenops persicus differs from H. diadema and R. hildebrandti in the several respects. The basihyal is more rectangular in shape with a central depression (fig. 6). Projecting outward from the basihyal, the thyrohyals are very much longer and narrower than found in the other two species. The ceratohyals are reduced to small nubs on the basihyal, whereas the epihyals are more elongated. Also, the stylohyal forms a more foot-like extension on the auditory bulla.

In Hipposideros armiger, the basihyal has a distinct butterfly shape with very large thyrohyals extending from it. Rhinonycteris aurantius and H. armiger, like Triaenops, have a stylohyal which terminates in a large foot that attaches to the bulla. With respect to other characteristics of the hyoid apparatus, H. armiger is very similiar to both H. diadema and R. hildebrandti while the apparatus of R. aurantius resembles T. persicus.

DESCRIPTION OF THE MUSCLES

For each muscle described below, the generalized rhinolophid condition is described first under "ORIGIN" and "INSERTION." If there is no generalized condition, the most pleisiomorphous (= primitive) condition is presented. Following this, variation from the generalized condition is described under "OTHER RHINOLOPHIDS."

MYLOHYOID GROUP

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

M. MYLOHYOIDEUS

Figures 1, 3, 5

ORIGIN: From the medial surface of the mandible for the posterior two-thirds of the mandibular body.

INSERTION: Anteriorly into the fibers of the mandibulohyoid, posteriorly onto the basihyal and medially into its antimere along the ventral midline raphe.

OTHER RHINOLOPHIDS: This muscle is the same in all bats examined.

M. MYLOHYOIDEUS PROFUNDUS

This muscle is completely absent in all rhinolophids dissected.

M. MANDIBULOHYOIDEUS

Figures 1, 3, 5

ORIGIN: From the medial surface of the anterior one-third of the mandible.

INSERTION: Into its antimere along the ventral midline raphe. Some fibers also insert into the mylohyoid.

OTHER RHINOLOPHIDS: This muscle is the same in all bats examined.

COMMENTS: In the superfamily Rhinolophoidea the mandibulohyoid is present in rhinolophids and megadermatids, but is entirely absent in

nycterids. In the Rhinopomatidae, the other family in which this muscle appears, the morphology differs. A tendon attaches to the large mandibulohyoid on each side and continues to the opposite side to attach to the posterior belly of the digastric muscle, possibly allowing the mandibulohyoid to aid in the opening of the jaws. This tendon is not present in either the rhinolophids or megadermatids, leaving the function of this muscle unknown in Rhinolophoidea. It is conceivable that the function has been lost and the mandibulohyoid is gradually disappearing -- accounting for its smaller size and characterizing the presence of this muscle as being a pleisiomorphic condition.

HYOID CONSTRICTOR GROUP

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

M. STYLOHYOIDEUS

Figures 2, 4, 6

The stylohyoid is absent in all specimens studied. However, there is a small muscle present that originates from the stylohyal (just posterior to the origin of the stylopharyngeus) and inserts onto the lateral tip of the thyrohyal. This muscle cannot be a true stylohyoid since it does not curve medially and ventrally around the ventral surface of the digastric. It instead lies underneath the digastric and has a short, straight run from its point of origin to its point of insertion. I tentatively call this the stylothyrohyoid.

OTHER RHINOLOPHIDS: This condition is the same in all rhinolophids examined.

M. JUGULOHYOIDEUS

Figures 2, 4, 6

ORIGIN: From the paroccipital region of the skull just posterior to the auditory bulla.

INSERTION: Onto the posterior surface of the expanded lateral tip of the stylohyal.

OTHER RHINOLOPHIDS: This muscle is the same in all bats examined.

M. SPHINCTER COLLI PROFUNDUS

This muscle is completely absent in all rhinolophids examined except *Hipposideros armiger*, in which Griffiths found a few muscle fibers embedded in fascia that appear to be vestigial remnants of the sphincter colli.

GLOSSOPHARYNGEAL GROUP

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

M. STYLOPHARYNGEUS

Figure 6

ORIGIN: From the ventral surface of the stylohyal element, slightly posterior to the origin of the styloglossus.

INSERTION: Into the lateral wall of the pharynx, anterior to the insertion of the thyropharyngeus.

OTHER RHINOLOPHIDS: This muscle is the same in *Hipposideros armiger*, but is completely absent in *Rhinonycteris aurantius*.

M. CERATOHYOIDEUS

Figures 2, 4

ORIGIN: This muscle is variable within rhinolophids. In *Hipposideros diadema* the ceratohyoid originates from the ventral surface of the thyrohyal, lateral to the insertion of the thyrohyoid. In *Rhinolophus hildebrandti* the ceratohyoid origin is still on the ventral surface of the thyrohyal, but it is medial to the thyrohyoid insertion. In *Triaenops persicus* the ceratohyoid is completely absent.

INSERTION: The ceratohyoid inserts onto the posterior surfaces of the ceratohyal and the medial quarter of the epihyal in both *H. diadema* and *R. hildebrandti*.

OTHER RHINOLOPHIDS: *Hipposideros armiger* is similar to *H. diadema* in that the ceratohyoid originates from the ventral surface of the lateral tip of the thyrohyal. However, the insertion is onto the posterior surfaces of the lateral half of the epihyal and the medial quarter of the stylohyal. As in *T. persicus*, the ceratohyoid in *Rhinonycteris aurantius* is completely absent.

PHARYNGEAL CONSTRICTOR GROUP

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

M. HYOPHARYNGEUS

Not figured

ORIGIN: From the dorsal basihyal.

INSERTION: Into the dorsal midline of the pharynx, deep to and anterior to the fibers of the thyropharyngeus.

OTHER RHINOLOPHIDS: This muscle is the same in all bats examined.

M. THYROPHARYNGEUS

Not figured

ORIGIN: From the dorsal surface of the thyrohyal bone.

INSERTION: Into the dorsal pharyngeal midline; superficial fibers into its antimere.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined.

M. CRICOPHARYNGEUS

Not figured

ORIGIN: From the lateral surface of the cricoid cartilage and from the dorsal surface of the posterior thyroid process.

INSERTION: Into the dorsal pharyngeal midline; superficial fibers into its antimere.

OTHER RHINOLOPHIDS: This muscle is the same in all bats examined.

MYOTOMIC MUSCULATURE

LINGUAL GROUP

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

M. GENIOGLOSSUS

Figures 1, 3, 5

ORIGIN: From the posterior surface of the mandibular midline, just dorsal to the tendonous origin of the geniohyoid.

INSERTION: Into the ventral midline of the tongue for much of the length of the tongue.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined. In *Hipposideros armiger*, however, the genioglossus is very robust.

M. HYOGLOSSUS

Figures 1, 3, 5

ORIGIN: From the ventral surface of the basihyal, extending from the middle to lateral edge of the basihyal. No fibers take origin from the thyrohyal.

INSERTION: Into the posterior ventrolateral surface of the tongue, just dorsal to the styloglossus.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined.

M. STYLOGLOSSUS

Figures 1, 2, 3, 4, 5, 6

ORIGIN: From the ventral surface of the midpoint of the stylohyal, just anterior to the origin of the stylopharyngeus.

INSERTION: Into the anterior ventrolateral surface of the tongue.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined.

COMMENTS: In *Rhinolophus hildebrandti* some fibers appear to be originating from the auditory bulla. The origin in *Triaenops* and *Rhinonycteris* is more posteriorly located on the "foot" of the stylohyal.

MEDIAL VENTRAL CERVICAL GROUP

The muscles of this group are innervated by a complex of nerves originating in the anterior cervical region, except for the geniohyoid which appears to be innervated primarily by N. hypoglossus (XII).

M. GENIOHYOIDEUS

Figures 1, 3, 5

ORIGIN: In Hipposideros diadema and Rhinolophus hildebrandti by a tendon (which extends for approximately one-third the total muscle length) from the posterior surface of the mandible, just lateral to the mandibular symphysis. INSERTION: Onto the anterior mid-ventral surface of the basihyal.

OTHER RHINOLOPHIDS: The geniohyoid of H. armiger is like that of H. diadema and R. hildebrandti in its tendinous origin. The insertions are the same for all bats examined.

COMMENTS: In Triaenops persicus and Rhinonycteris aurantius the geniohyoid also originates from the posterior surface of the mandible, just lateral to the mandibular symphysis, but by fleshy fibers.

M. STERNOHYOIDEUS

Figures 1, 3, 5

ORIGIN: Entirely from the manubrium of the sternum -- all fibers originate medial to the sterno-clavicular junction.

INSERTION: Onto the posterior edge of the basihyal. Some fibers insert, at least superficially, into the mylohyoid.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined.

COMMENTS: In R. hildebrandti the sternohyoid is very reduced, becoming thin near its origin, whereas the muscle is robust in all other bats examined. The sternohyoid is believed to have primitively had its origin from both the clavicle and the manubrium of the sternum with one belly coming from each and then fusing to form the single muscle (Sprague, 1943). The origin from the clavicle has not only been lost in rhinolophids, but also in both megadermatids and nycterids.

M. STERNOTHYROIDEUS

Figures 1, 2, 3, 4

ORIGIN: Entirely from the manubrium of the sternum -- all fibers originate medial to the sterno-clavicular junction.

INSERTION: Onto the lateral surface of the thyroid cartilage.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined.

COMMENTS: This muscle, being extremely thin and wispy, is very reduced in all specimens except H. armiger where it is fairly robust.

M. OMOHYOIDEUS

Figure 1

The omohyoid is completely absent in both Rhinolophus hildebrandti and Triaenops persicus. In Hipposideros diadema there is an omohyoid which has a tendonous origin from the anterior edge of the scapula and inserts onto the ventral surface of the posterior edge of the basihyal, lateral to the insertion of the sternohyoid.

OTHER RHINOLOPHIDS: This muscle is completely absent in both Hipposideros armiger and Rhinonycteris aurantius.

COMMENTS: In all other groups of mammals, the omohyoid has its origin from the anterior edge of the scapula. In most bats considered in this study, the origin has shifted medially to the clavicle. Sprague (1943) found an omohyoid of scapular origin in both Hipposideros diadema (which my observations confirm) and Rhinolophus affinus of the rhinolophids. The omohyoid of H. diadema, in its pleisiomorphic condition, is very thin -- almost transparent. Its function as a lateral pull on the hyoid apparatus is, therefore, much reduced. Considering the complete loss of the omohyoid in all of the other bats examined, in the family

Rhinolophidae as a whole, the need for this lateral pull on the hyoid has apparently been, or is in the process of being, lost.

M. THYROHYOIDEUS

Figures 1, 2, 3, 4, 5, 6

ORIGIN: From the lateral surface of the thyroid cartilage, just anterior to the insertion of the sternothyroid.

INSERTION: Onto the posterior surface of the tip of the thyrohyal.

OTHER RHINOLOPHIDS: This muscle is the same for all bats examined.

DISCUSSION

A study of relationships within the family Rhinolophidae has never before been conducted. My hypotheses about the relationships are, therefore, based solely on my data and the data that were previously collected by Griffiths (personal communication).

Of my data, seven apomorphies (derived characters) can be used to construct intra-familial cladograms (summarized in Table 1, figs. 7, 8). The presence of the stylothyrohyoid, the muscle that appears in rhinolophids instead of the stylohyoid, is one character state that strongly unites all five species: *Hipposideros diadema*, *H. armiger*, *Rhinolophus hildebrandti*, *Rhinonycteris aurantius* and *Triaenops persicus*. However, because of a question of which of two characters has converged (has evolved twice separately in evolutionary history), two intra-familial cladograms are proposed (figs. 7, 8). If loss of the sphincter colli, character 3, has occurred twice separately, then *Hipposideros diadema* would be the most distantly related species (fig. 7). If it was loss of the omohyoid (character 2) that underwent convergent evolution, then *H.*

armiger would be the most distantly related species (fig. 8). In either case, my data support a distant relationship (polyphyly) between members of the same genus -- Hipposideros armiger and Hipposideros diadema. It is possible that the genus Hipposideros is not monophyletic. Both cladograms show a close relationship between Triaenops persicus and Rhinonycteris aurantius supported by the collective losses of the ceratohyoid and sphincter colli and the shift in origin of the styloglossus onto the more distal "foot" of the stylohyal. Koopman and Jones (1970) placed Hipposideros, Rhinonycteris, and Triaenops in the subfamily Hipposiderinae and Rhinolophus in the subfamily Rhinolophinae. My data do not support Koopman and Jones' hypothesis, rather they support a closer relationship of Rhinolophus to Rhinonycteris and Triaenops.

I also examined inter-familial relationships between the families Rhinolophidae, Megadermatidae, Nycteridae, Rhinopomatidae and Emballonuridae based on my observations on the rhinolophids and on Griffiths' observations on the latter four families. The traditional classification of these families into superfamilies (Weber, 1928) does not concur with my data. My data support an association of the Nycteridae, a family within the traditional superfamily Rhinolophoidea, with two families traditionally placed in the superfamily Emballonuroidea: Rhinopomatidae and Emballonuridae (figs. 9, 10). Two inter-familial cladograms have been proposed because of a question of convergence. Shift of the sternothyroid origin onto the manubrium of the sternum is the shared-derived character uniting Rhinolphidae with Megadermatidae in figure 9 if character 1 (shift of omohyoid origin) has converged. However, if shift of the omohyoid origin only occurred once in the evolutionary history of these bats, then

Rhinolophidae is the most distantly related family and the character 5 has undergone convergent evolution (fig. 10).

My data do concur with an informal proposal by Klingener (personal communicaton) and by Pierson (1986). Klingener suggested there was a close relationship between Nycteris, a nycterid, and Taphozous, an emballonurid. He based his suggestion on some similarities in external morphology of the face in the two genera. An immunological study of blood proteins by Pierson (1986) supports a close association between rhinolophids, megadermatids and rhinopomatids and a more distant relationship with emballonurids. An immunological study such as Pierson's might be showing primitive conditions that have been retained in modern-day species (= homoplasy). In that case, Rhinolophidae, Megadermatidae and Rhinopomatidae may be retaining the primitive immunological condition while somewhere before the Nycteridae/Emballonuridae branch an evolutionary change occurred in the proteins studied, causing emballonurids to appear to be more distantly related. Thus, this interpretation of Pierson's data correlates with my cladograms (fig. 9, 10). Nevertheless, the original classification by Weber (1928) of the families into the superfamilies Emballonuroidea and Rhinolophoidea does not concur with the data I have collected based on morphology of the hyoid region.

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APPENDIX I

Classification of Yinochiropteran Bats

(Koopman, 1984)

Suborder Microchiroptera

- Infraorder Yinochiroptera
  - Superfamily Emballonuroidea
    - Family Emballonuridae (47)
    - Family Craseonycteridae (1)
    - Family Rhinopomatidae (3)
  - Superfamily Rhinolophoidea
    - Family Nycteridae (14)
    - Family Megadermatidae (5)
    - Family Rhinolophidae (124)

(Numbers in parentheses are numbers of species in each family)

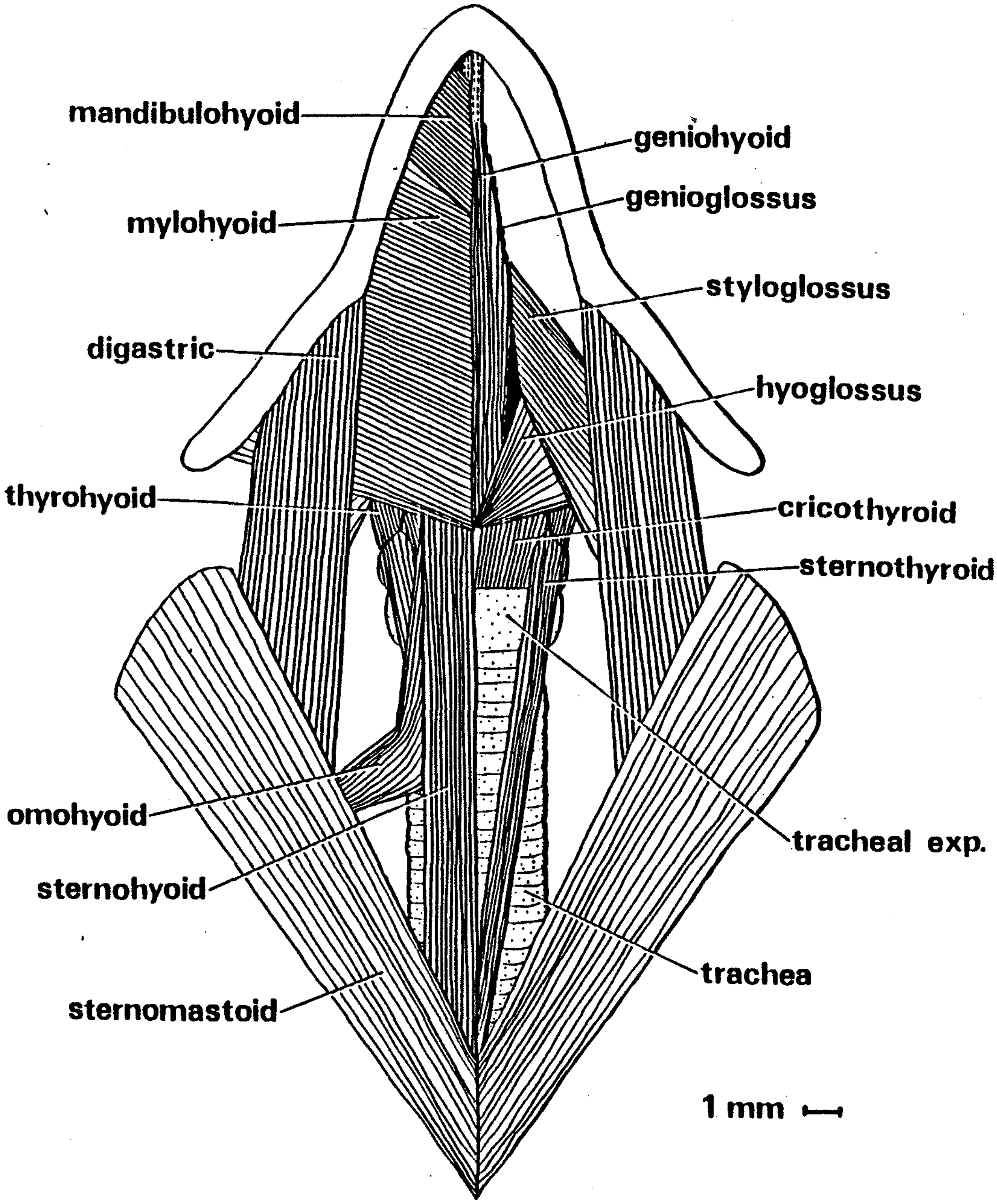

Fig. 1. Ventral view of hyoid musculature of Hipposideros diadema. Deeper structures are shown on the right of the illustration.

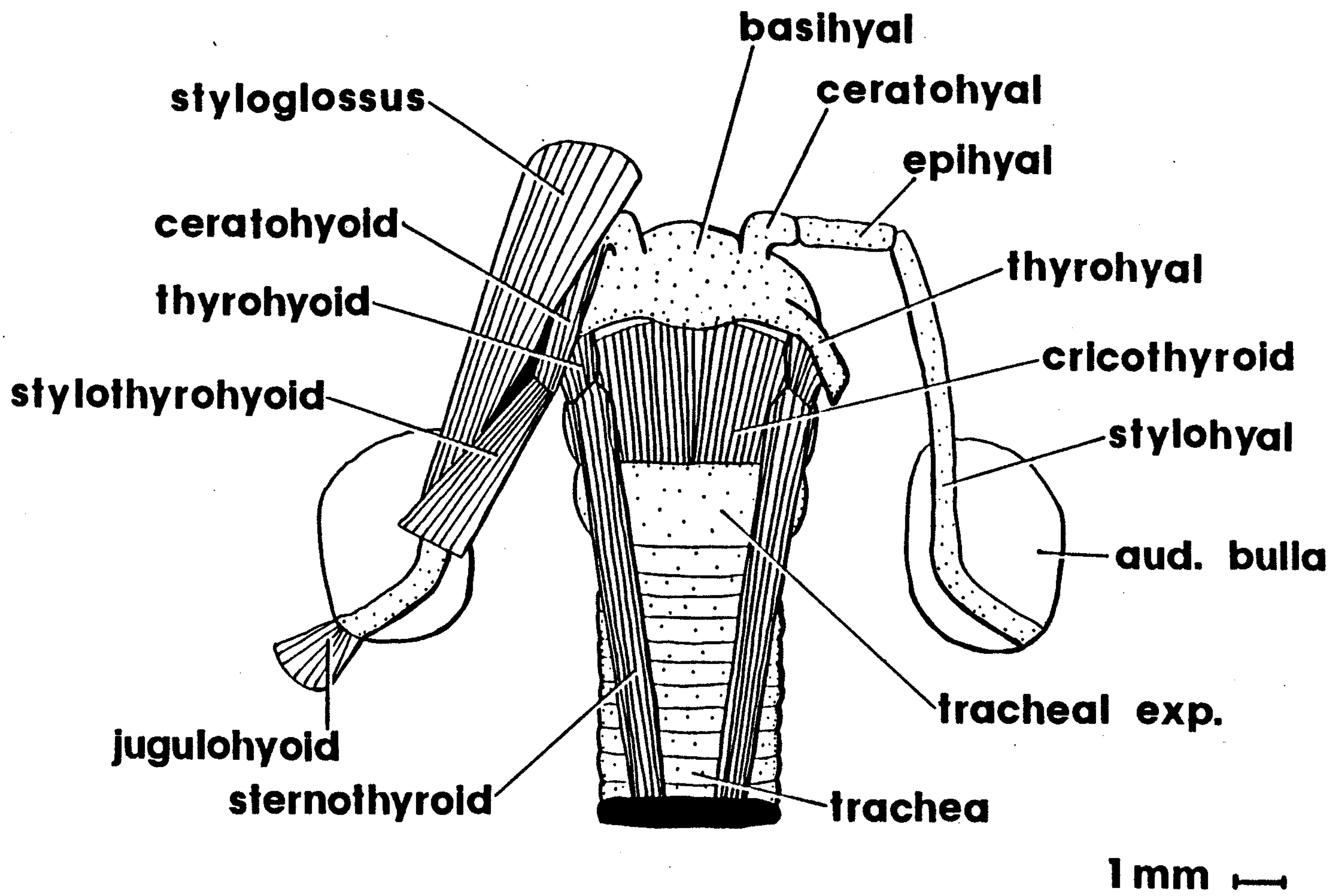

Fig. 2. Ventral view of the deep hyoid muscles, the hyoid apparatus and larynx of <u>Hipposideros diadema</u>.

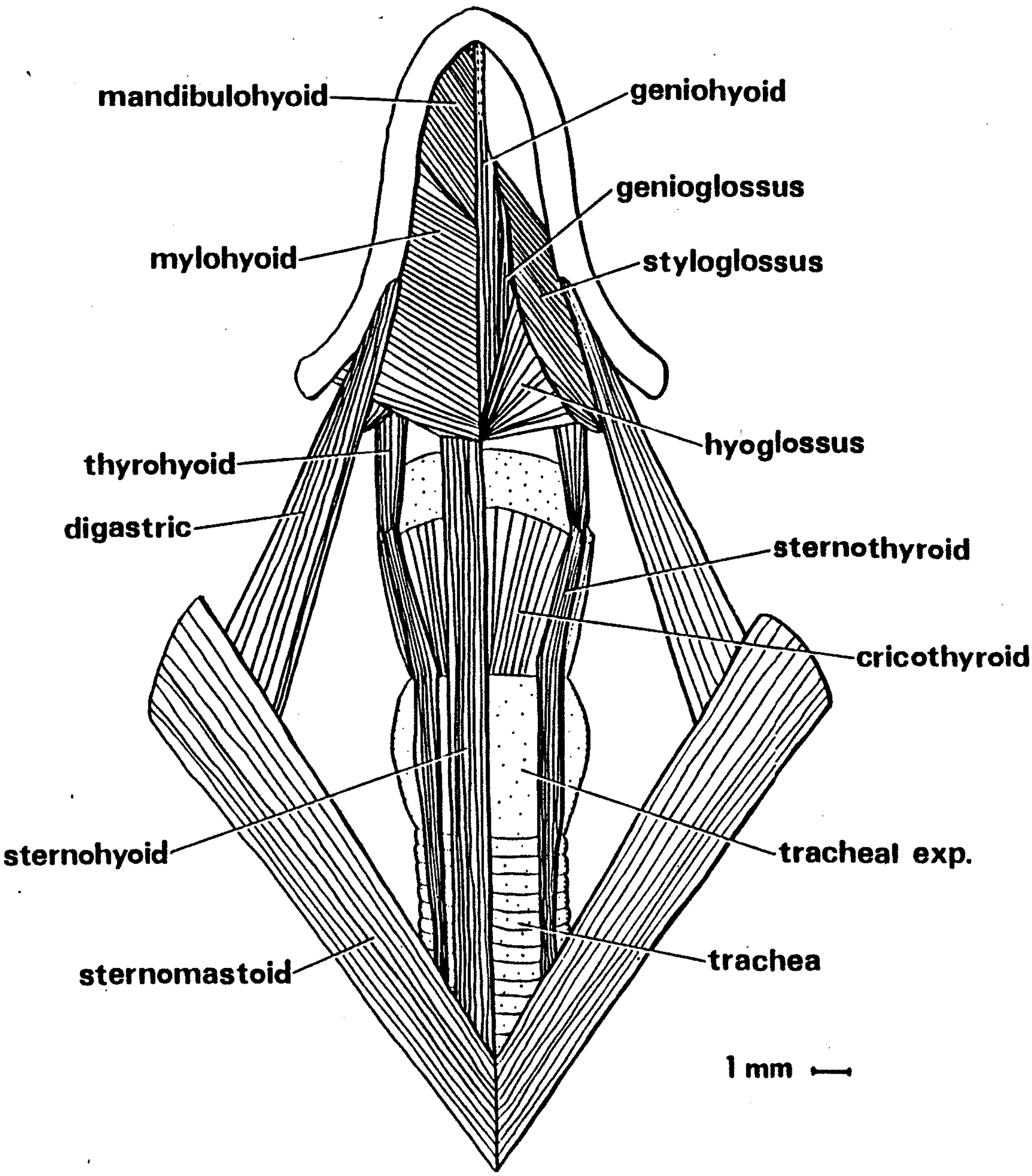

Fig. 3. Ventral view of hyoid musculature of _Rhinolophus hildebrandti_. Deeper structures are shown on the right of the illustration.

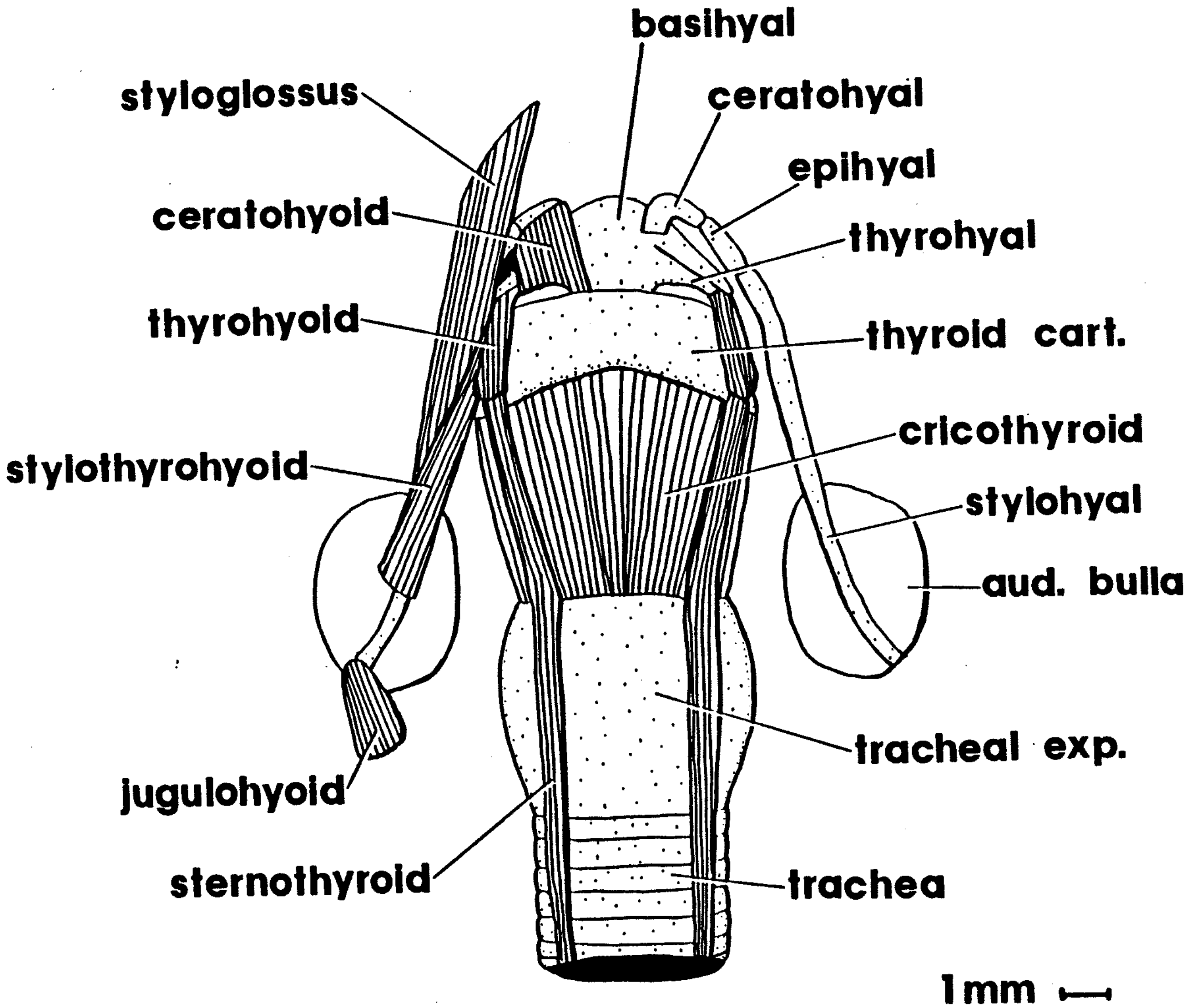

Fig. 4. Ventral view of the deep hyoid muscles, the hyoid apparatus and larynx of _Rhinolophus hildebrandti_.

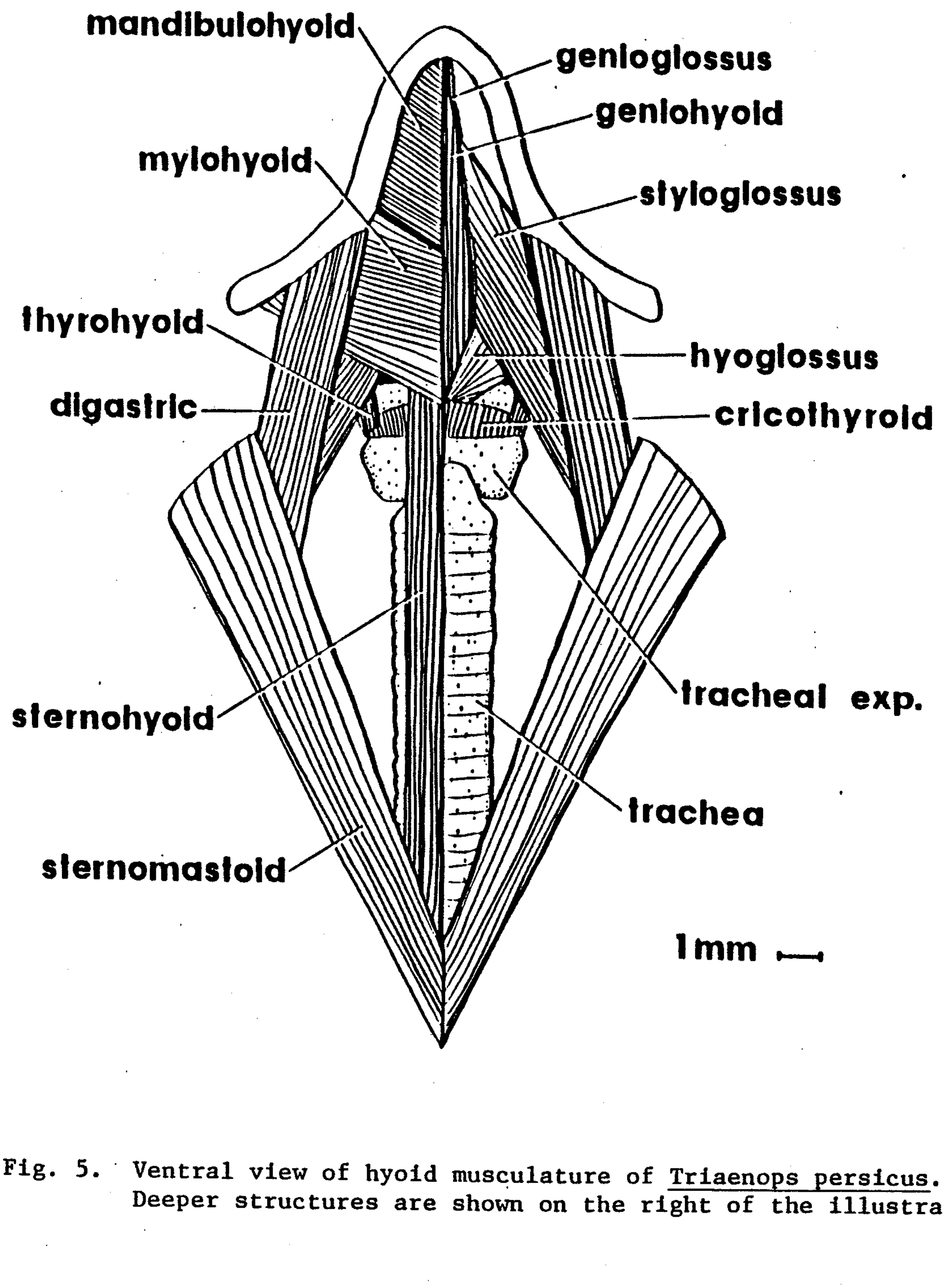

Fig. 5. Ventral view of hyoid musculature of Triaenops persicus. Deeper structures are shown on the right of the illustration.

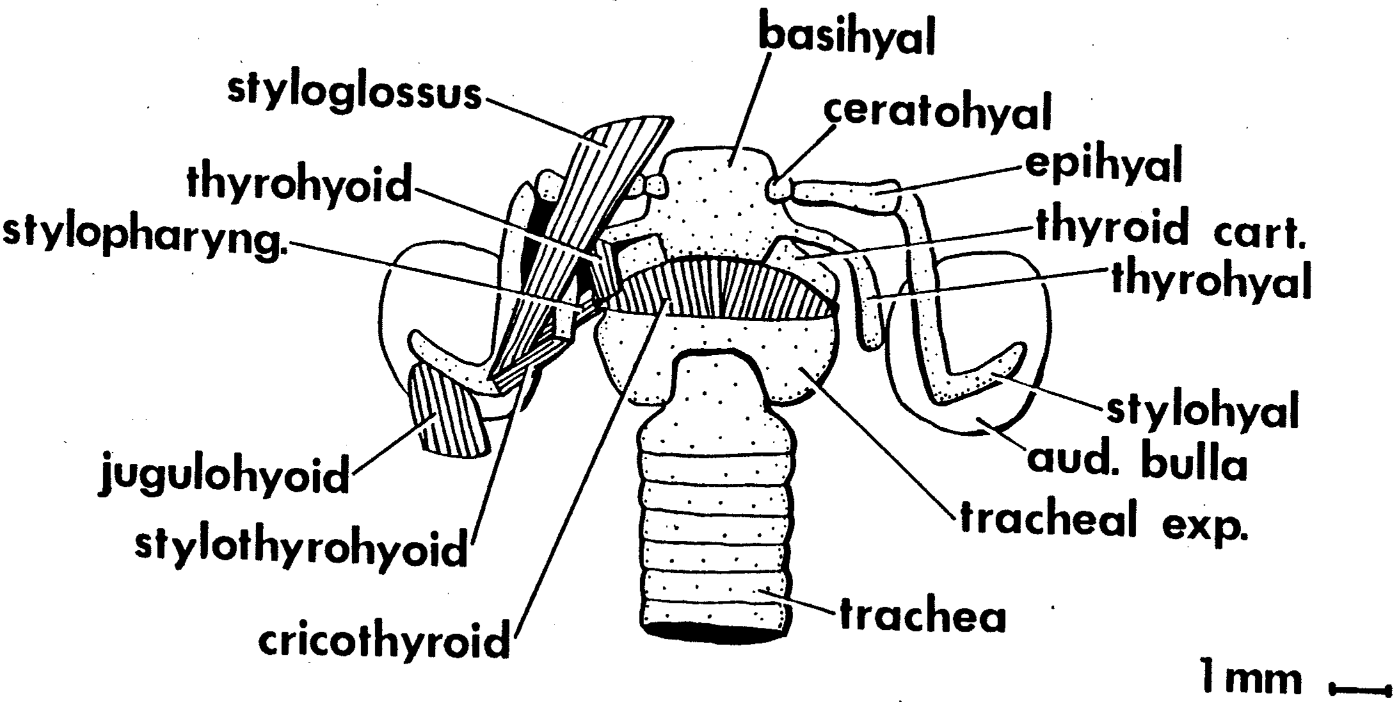

Fig. 6. Ventral view of the deep hyoid muscles, the hyoid apparatus and larynx of Triaenops persicus.

TABLE 1.

Summary of the Apomorphies Used in Constructing the Intra-familial Cladograms (figs. 7, 8). + = apomorphic character state; – = plesiomorphous character state.

CHARACTER STATE	SPECIES[a]				
	pers	hild	diad	aura	armi
1) "new" stylothyrohyoid	+	+	+	+	+
2) loss of omohyoid	+	+	–	+	+
3) loss of sphincter colli	+	+	+	+	–
4) loss of ceratohyoid	+	–	–	+	–
5) styloglossus origin shift onto foot of stylohyal	+	–	–	+	–
6) fleshy origin of geniohyoid	+	–	–	+	–
7) loss of stylopharyngeus	–	–	–	+	–

[a]Abbreviations of species: pers = Triaenops persicus, hild = Rhinolophus hildebrandti, diad = Hipposideros diadema, aura = Rhinonycteris aurantius, armi = Hipposideros armiger.

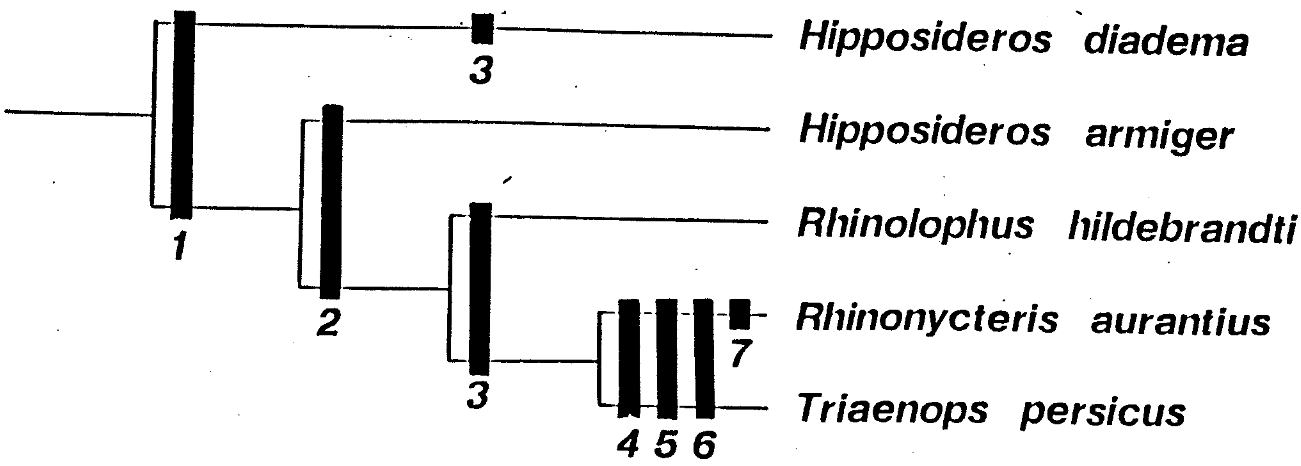

Fig. 7. Cladogram showing intra-familial relationships between genera examined in this study.

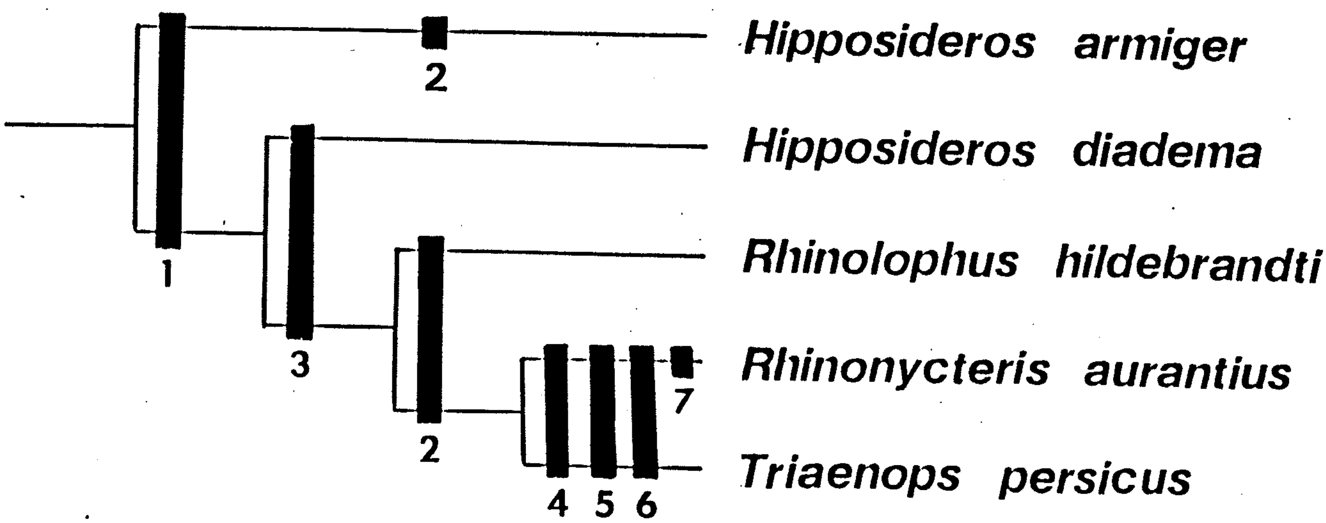

Fig. 8. Cladogram showing intra-familial relationships between genera examined in this study.

TABLE 2.

Summary of the Apomorphies Used in Constructing the Inter-familial Cladograms (figs. 9, 10). + = apomorphic character state; – = plesiomorphous character state.

CHARACTER STATE	FAMILIES[a] Rlop	Nyct	Mega	Rpom	Embl
1) omohyoid origin shift to clavicle	–	+	+	+	+
2) sternohyoid origin shift to manubrium only	+	+	+	+	–
3) loss of sphincter colli	–	+	–	+	+
4) loss of mandibulohyoid	–	+	–	–	+
5) sternothyroid origin shift to manubrium only	+	–	+	–	–

[a]Abbreviations of families: Rlop = Rhinolophidae, Nyct = Nycteridae, Mega = Megadermatidae, Rpom = Rhinopomatidae, Embl = Emballonuridae.

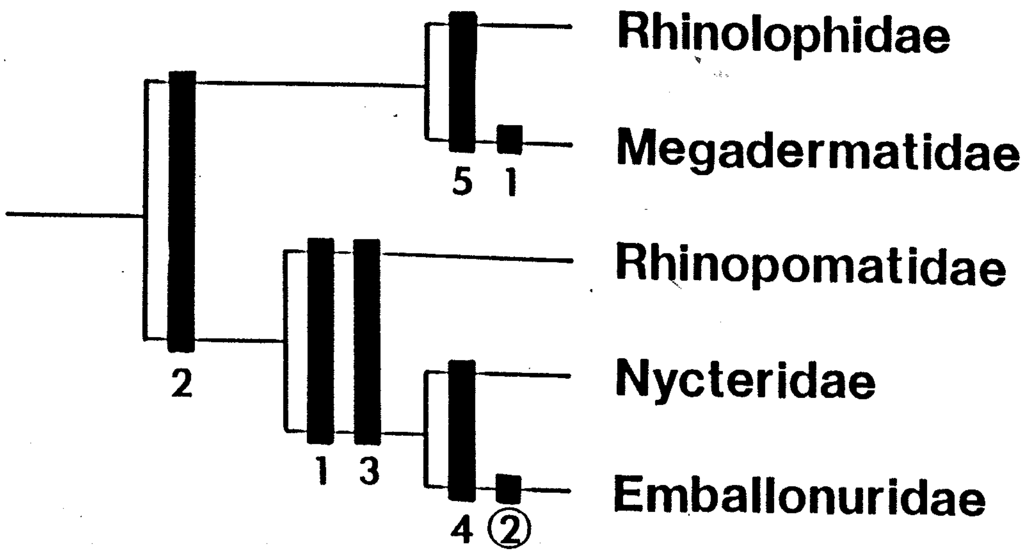

Fig. 9. Cladogram showing inter-familial relationships. Circled numbers indicate character reversals.

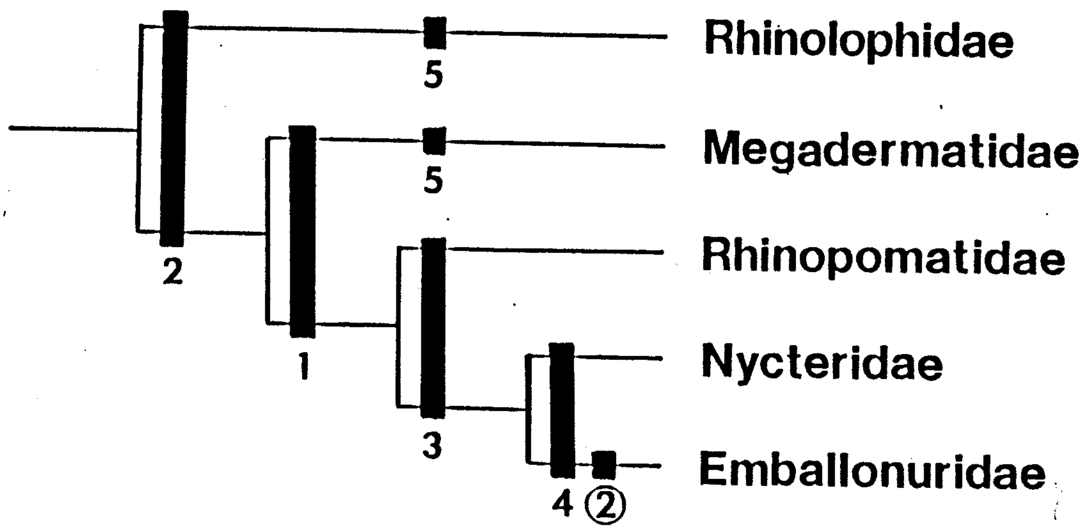

Fig. 10. Cladogram showing inter-familial relationships. Circled numbers indicate character reversals.