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THE SYSTEMATIC RELATIONSHIP OF HIPPOSIDEROS COMMERSONI
MATUNGENSIS TO OTHER SPECIES OF RHINOLOPHIDAE (CHIROPTERA)

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ABSTRACT

The hyoid morphology of Hipposideros commersoni matungensis was dissected and compared to the morphology of other bats in the family Rhinolophidae. Several significant differences in morphology were found: a modified stylohyal, fused to the auditory bulla; loss of the stylohyoid; addition of a new muscle, possibly from the stylopharyngeus; a modified mylohyoid profundus; and insertion of the ceratohyoid onto only the stylohyal. Cladistic analysis suggests that of all bats examined, H. commersoni is most closely related to H. armiger, and Triaenops persicus is most closely related to Rhinonycteris aurantius. This result is unexpected because the ranges of the species are geographically distant: H. commersoni is an African bat, whereas H. armiger is from East Asia. Triaenops is also an African species, whereas Rhinonycteris is Australian.

INTRODUCTION

Bats of the families Rhinolophidae, Nycteridae and Megadermatidae compose the superfamily Rhinolophoidea, which is one of four superfamilies within the suborder Microchiroptera (Weber, 1928). The family Rhinolophidae contains 10 genera and 127 species; there are 47 species in the genus Hipposideros alone. The family is geographically widespread, ranging throughout the Old World. Of the bats studied herein, Hipposideros commersoni matungensis, Rhinolophus hildebrandti and Triaenops persicus are African species; H. armiger, H. diadema and R. affinis are Asian

species; Rhinonycteris aurantius is from Australia; and R. euryotis is found on New Guinea and surrounding small islands.

Earlier phylogenies and classifications have been based on skull and tooth morphology, but recently studies based on soft morphology have been published which suggest that the traditional classification of microchiropteran bats may be incorrect. In particular, studies of the hyoid region (Griffiths and Smith, 1991; Griffiths et al. 1992) suggest that the superfamily Rhinolophoidea might be polyphenetic; megadermatids may be more closely related to emballonurids, rhinopomatids and nycterids than to rhinolophids.

The purpose of this study is to dissect and describe the hyoid morphology of Hipposideros commersoni matungensis. The data obtained are compared with other rhinolophid data, as well as outgroup data for other families of bats described in previous studies (Griffiths and Smith, 1991; Griffiths et al., 1991, 1992), in order to construct a cladogram showing relationships within the family Rhinolophidae. This study is part of a continuing effort to describe the hyoid morphology of representatives of all microchiropteran genera and produce a cladogram for all microchiropteran bats.

MATERIALS AND METHODS

Fluid preserved museum specimens were dissected under a binocular dissecting microscope, and pencil drawings were made of all dissections. From the initial drawings, selected drawings were inked for inclusion in this paper. All of the specimens dissected

were from the American Museum of Natural History (AMNH) in New York. FAMILY RHINOLOPHIDAE: Hipposideros commersoni matungensis 237334; H. armiger 112767, H. diadema grisea 206744, Triaenops persicus 245398, Rhinolophus hildebrandti 216208, R. euryotis 158461 and Rhinonycteris aurantius 199980. All specimens except H. commersoni were dissected previously by Griffiths and Smith (1991) and Griffiths (unpublished). Sprague's (1943) description of R. affinis was also used. Additional specimens used for outgroup comparisons in this study from the families Emballonuridae, Nycteridae and Megadermatidae were described by Griffiths and Smith (1991) and Griffiths et al. (1992).

DESCRIPTION OF THE HYOID APPARATUS

Sprague (1943) and Griffiths and Smith (1991) provide the only previous detailed descriptions of the rhinolophid hyoid apparatus. In Hipposideros commersoni matungensis the basihyal is rectangularly-shaped with a prominent anterior process and two smaller posterior processes projecting from the ventral midpoint (Fig. 2). The thyrohyals are broad and strongly fused with the basihyal; the ends are blunt and bend dorsally. The epihyal, ceratohyal ("ceratohyal" and "hypohyal," respectively of Sprague, 1943) and stylohyal are thin and are joined by synchondral joints that show little separation between elements. The stylohyal is the longest, thinnest element of the anterior cornu; it bends dorsally and posteriorly towards the auditory bulla with which its expanded "foot" is fused.

OTHER BATS: The hyoid apparatus of Hipposideros armiger is similar to the above description, except that the basihyal is roughly butterfly-shaped, and the thyrohyals are pointed. Also, the ceratohyal articulates with the basihyal and epihyal by freely movable synchondral joints. The hyoid apparatus of H. diadema is similar to that of H. commersoni, except that there is no expanded stylohyal "foot" or fusion of synchondral joints between elements of the anterior cornu. In Rhinolophus spp. there is no fusion of synchondral joints or expansion of the stylohyal into a distal foot. The basihyal of R. affinis has an anterior and posterior process projecting from the ventral midpoint (Sprague, 1943). In both Rhinonycteris and Triaenops, the basihyal is more rectangular with a large depression in the ventral surface. The thyrohyals are reduced, but still fused to the basihyal. The reduced ceratohyal is behind the basihyal, and the rest of the anterior cornu is also very reduced and thin. However, the expanded "foot" of the stylohyal is fused to the auditory bulla (Griffiths and Smith, 1991).

Although the anatomy of the larynx is not the focus of this paper, a few morphological details of the larynx should be mentioned. All specimens studied have a complex cricothyroid muscle that originates from a large cricoid cartilage (Fig. 1 - 6). In H. commersoni, Triaenops and Rhinonycteris, there is a postlaryngeal chamber formed by expansion of tracheal rings. Both latter genera have two types of large post-laryngeal chambers: one being a "suppressor" and the other an "enhancer" of the vocal pulse

(Griffths, unpublished). Robin (1881) notes the presence of a median, dorsal pouch opening into the trachea in H. diadema and H. armiger, but this is not present in H. commersoni. The pouch is mostly cartilage with some fibrous tissue; Robin (1881) mentions similar structures found in Rhinopoma and Chilonycteris.

DESCRIPTION OF THE HYOID MUSCLES

Each muscle is described as it appears in dissected specimens of Hipposideros commersoni matungensis. Variation from the morphology of this species is described under "Other Rhinolophidae" (from Griffiths and Smith, 1991; Griffiths, unpublished). Descriptions of Megadermatidae, Nycteridae and Emballonuroidea specimens are included under "Other Yinochiroptera" (Griffiths and Smith, 1991; Griffiths et al., 1992).

BRANCHIOMERIC MUSCULATURE

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 posterior half of the mandibular body.

INSERTION: Anteriorly, into fibers of the mandibulo-hyoid and into its antimere along the ventral midline raphe; posteriorly onto

the lateral thyrohyal cartilage and onto the ventral tip of the basihyal.

OTHER RHINOLOPHIDAE: This muscle is similar in other rhinolophids; however, in R. euryotis the muscle inserts entirely on the basihyal and not on the thyrohyal at all (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: The hyoid morphology of megadermatids and emballonurids is similar to that of rhinolophids with some minor exceptions. In Rhinopoma, the mylohyoid does not extend as far anteriorly, and in Nycteris the muscle does not strongly insert onto the thyrohyal. Because Nycteris and all emballonurids have no mandibulo-hyoid, the mylohyoid continues to the mandibular symphysis (Griffiths and Smith, 1991).

COMMENTS: The modified insertion of the mylohyoid onto only the basihyal element is an autapomorphy of R. euryotis. This trait is coded as character state 3 in Table 1.

M. MYLOHYOIDEUS PROFUNDUS

The term "mylohoideus profundus" was coined by Griffiths (1978) to describe a deep, posterior piece of the mylohyoid which seemed to have become a separate muscle in phyllostomid bats. This deep mylohyoid apparently had remained attached to the basihyal as the remainder of the mylohyoid was displaced superficially by the development of a "free-floating" sterno-glossus complex (see Griffiths, 1978, 1982). In H. commersoni, fibers from the mylohyoid run deep dorsally and insert laterally to the sternohyoid-geniohyoid complex. In H. armiger, a few posterior-

most fibers are continuous with the rest of the muscle and insert deep on the basihyal, but these fibers do not constitute a separate muscle.

OTHER RHINOLOPHIDAE AND OTHER YINOCHEIROPTERA: No mylohyoid profundus was found in any of the specimens dissected by Griffiths and Smith (1991).

COMMENTS: The modified mylohyoid profundus is a synapomorphy of H. commersoni and H. armiger, coded as character state 4 in Table 1.

M. MANDIBULO-HYOIDEUS

Figures 1, 3, 5

ORIGIN: From the posterior and medial surfaces of the anterior half of the mandibular body.

INSERTION: Into its antimere and into the ventral midline raphe and thus indirectly (by connective tissue) into the fibers of the anterior mylohyoid.

OTHER RHINOLOPHIDAE: This muscle is the same in other rhinolophids. In both H. commersoni and H. armiger a large pad of connective tissue fills the space deep to the mandibulo-hyoid, lateral to the geniohyoid and anterior to the mylohyoid. In Triaenops and Rhinonycteris the muscle is similar but less robust, and there is no pad of connective tissue (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: This muscle is similar to the rhinolophid condition in megadermatids. In rhinopomatids the mandibulo-hyoid narrows as it passes posteriorly to insert onto the

basihyal; also it is attached to a tendon running laterally and posteriorly deep to the digastric which attaches to its deep surface. This muscle was absent in all other families studied by Griffiths and Smith (1991).

COMMENTS: The presence of a pad of connective tissue deep to this muscle is an apomorphy, coded as character state 5 in Table 1.

HYOID CONSTRICTOR GROUP

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

M. STYLOHYOIDEUS

This muscle seems to be absent in H. commersoni.

OTHER RHINOLOPHIDAE: This muscle is absent in other rhinolophids. Sprague (1943) says it is present in H. diadema and in R. affinis, but Griffiths and Smith (1991) do not agree. Sprague calls a small muscle running from the medial surface of the stylohyal to the lateral tip of the thyrohyal the stylohyoid. However, this muscle cannot be a true stylohyoid because it runs directly from its origin to the insertion, instead of curving medially around the ventral digastric (so it would have to pass through the digastric to arrive at its present position). Griffiths and Smith (1991) propose that the muscle described by Sprague is a piece of an adjacent muscle (probably the stylopharyngeus) that attached to the lateral thyrohyal before detaching from the original muscle. This new muscle was found in all rhinolophids examined, including H. commersoni (Fig 2, 4, 6);

however, it is not as robust in Triaenops.

OTHER YINOCHEIROPTERA: In emballonurids, the stylohyoid is typical of true stylohyoids (originating from the stylohyal element, passing ventrally to the digastric to insert on the thyrohyal), but is absent in some genera (Taphozous and Saccolaimus) and shifted medially to insert on the basihyal in other genera (Peropteryx and Peronymous). In megadermatids and nycterids, the muscle is similar to the non-specialized emballonurid condition (Griffiths and Smith, 1991).

COMMENTS: Loss of the stylohyoid and addition of the new muscle (coded as character states 6 and 7 in Table 1) are two synapomorphies of rhinolophids.

M. JUGULOHYOIDEUS

Figures 2, 4, 6

ORIGIN: From the ventral surface of the paraoccipital shelf of the skull.

INSERTION: Onto the expanded foot of the stylohyal.

OTHER RHINOLOPHIDAE: In other rhinolophids, the muscle inserts onto the lateral tip of the stylohyal element. This muscle is not as robust in Rhinonycteris (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: This muscle is present but very reduced in several genera of emballonurids, while being completely absent in other genera. In megadermatids the muscle is robust and similar to the muscle in other rhinolophids. Nycterids also have a similar origin and insertion, but the muscle is reduced (Griffiths and Smith, 1991).

COMMENTS: This muscle is very broad and inserts directly on the stylohyal (no tendonous connection) in both H. commersoni and H. armiger. Although Sprague (1943) found that this muscle in H. diadema inserts by a flat tendon, not fleshy fibers, Griffiths and Smith (1991) do not agree. The extended insertion of this muscle along the foot of the stylohyal is a synapomorphy, coded as character state 8 in Table 1.

M. SPHINCTER COLLI PROFUNDUS

This muscle is completely absent in H. commersoni.

OTHER RHINOLOPHIDAE: The muscle is absent in all species examined except H. armiger, which has a few vestigial fibers originating from the basihyal raphe and embedding in the fascia of the neck (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: This muscle is completely absent in all emballonuroids and nycterids. It is present in all megadermatids except Macroderma, as a very robust muscle which originates from the sternohyoid raphe and fans out laterally and anteriorly to insert on the deep surface of the skin ventral to the ear (Griffiths and Smith, 1991; Griffiths et al. 1992).

COMMENTS: The loss of this muscle is a synapomorphy shared by all rhinolophids examined, coded as character state 9 in Table 1.

GLOSSOPHARYNGEAL GROUP

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

M. STYLOPHARYNGEUS

Figures 2, 4, 6

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

INSERTION: Into the lateral pharyngeal wall anterior to the thyropharyngeus.

OTHER RHINOLOPHIDAE: This muscle is similar in other rhinolophids. In both H. diadema and R. hildebranti, because of the reduced stylohyal element, a number of fibers of this muscle originate from the ventral surface of the auditory bulla. This muscle is very reduced in Triaenops and only a few fibers originate from the auditory bulla. This muscle is completely absent in Rhinonycteris (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: In all other species the muscle is similar to the general rhinolophid condition (Griffiths and Smith, 1991).

COMMENTS: The reduction of this muscle is a synapomorphy of Triaenops and Rhinonycteris (character state 10 in Table 1).

M. CERATOHYOIDEUS

Figures 2, 4

ORIGIN: From the anterior surface of the lateral tip of the thyrohyal element.

INSERTION: Onto the ventral surface of the stylohyal element.

OTHER RHINOLOPHIDAE: The origin of this muscle is the same in other rhinolophids, but the insertion on both the lateral half of the epihyal and the medial quarter of the stylohyal is variable.

In Rhinonycteris and Triaenops the muscle is absent (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: In emballonurids, the muscle originates from the anterior surface of the thyrohyal element and inserts onto the posterior surfaces of the epihyal and ceratohyal. However, the insertion is quite variable between and within genera. In megadermatids, the origin is the same but the insertion is onto the ceratohyal and the medial tip of the epihyal. In nycterids, the origin is the same but the muscle only inserts on the ceratohyal (Griffiths and Smith, 1991).

COMMENTS: The variation in insertion of this muscle is coded as an autapomorphy (character state 11 in Table 1) of H. commersoni. The loss of this muscle is a synapomorphy of Triaenops and Rhinonycteris (coded as character state 12 in Table 1).

PHARYNGEAL CONSTRICTOR GROUP

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

M. HYOPHARYNGEUS

Not figured

ORIGIN: From the fascia in the area of the pterygoid processes.

INSERTION: Into the connective tissue of the pharyngeal midline, deep and anterior to the fibers of the thyropharyngeus.

OTHER RHINOLOPHIDS AND YINOCHEIROPTERA: This muscle is the same in all bats examined (Griffiths and Smith, 1991).

M. THYROPHARYNGEUS

Not figured

ORIGIN: From the dorsal surface of the thyrohyal element.

INSERTION: Into the dorsal pharyngeal midline.

OTHER RHINOLOPHIDS AND YINOCHIROPTERA: This muscle is the same in all bats examined (Griffiths and Smith, 1991).

M. CRICOPHARYNGEUS

Not figured

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

INSERTION: Into the dorsal pharyngeal midline.

OTHER RHINOLOPHIDS AND YINOCHIROPTERA: This muscle is the same in all bats examined (Griffiths and Smith, 1991).

MYOTOMIC MUSCULATURE

LINGUAL GROUP

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

M. GENIOGLOSSUS

Figures 1, 3, 5

ORIGIN: From the posterior surface of the mandible, just lateral to the symphysis and dorsal to the tendonous origin of the geniohyoid.

INSERTION: Into the ventral surface of the posterior half of the tongue, then passing deep to the geniohyoid and onto the anterior surface of the basihyal.

OTHER RHINOLOPHIDAE: This muscle does not connect to the hyoid apparatus in H. armiger, H. diadema, R. hildebranti or Triaenops. Additionally, Sprague (1943) found it was not connected in R. affinis. This muscle was not observed in Rhinonycteris (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: This muscle is similar to the general rhinolophoid condition in both nycterids and emballonurids, although it is more robust in the latter. In megadermatids, the muscle is similar but the posterior fibers do not run deep to the hyoglossus (Griffiths and Smith, 1991).

COMMENTS: The insertion of this muscle onto the basihyal in H. commersoni is an autapomorphy (coded as character state 13 in Table 1).

M. HYOGLOSSUS

Figures 1, 2, 3, 5

ORIGIN: From the anterior and lateral surfaces of the basihyal and thyrohyal, closely associated with fibers from the geniohyoid and sternohyoid.

INSERTION: Into the lateral posterior half of the tongue.

OTHER RHINOLOPHIDAE: This muscle is similar in other rhinolophids, but there is no close association with the geniohyoid and sternohyoid.

OTHER YINOCHEIROPTERA: In emballonurids, this muscle inserts into the ventrolateral part of the tongue, deep to the hypoglossal nerve and the styloglossus muscle. In nycterids, the origin of this muscle is similar to rhinolophids. In megadermatids, the

muscle has an indirect tendonous attachment to the basihyal and is closely associated with the sternohyoid and geniohyoid (Griffiths and Smith, 1991).

COMMENTS: Very large, robust muscle. The close association of the hyoglossus, genioglossus and sternohyoid (coded as character state 14 in Table 1) is an autapomorphy of H. commersoni.

M. STYLOGLOSSUS

Figures 2 - 6

ORIGIN: From the distal foot of the stylohyal bone, posterior to the point of origin of the stylopharyngeus.

INSERTION: Into the lateral surface of the tongue.

OTHER RHINOLOPHIDAE: There is some variation in origin among rhinolophids. In H. armiger the origin is from the midpoint of the stylohyal, and in H. diadema the origin is on the movable (ligamentous) part of the stylohyal. In R. hildebrandti some fibers originate from the auditory bulla. This muscle originates from the distal "foot" of the stylohyal in Triaenops and Rhinonycteris.

OTHER YINOCHEIROPTERA: In emballonurids and nycterids, this muscle originates from the ventral surface of the stylohyal at about the midpoint. In megadermatids, the muscle is similar but enters the tongue more posteriorly.

COMMENTS: The origin of this muscle from the distal foot of the stylohyal is a synapomorphy of Triaenops and Rhinonycteris and an autapomorphy of H. commersoni (coded as character state 15 in Table 1).

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: Medial fibers originate by tendon from the mandibular symphysis; more lateral fibers attach with fleshy fibers to the mandible.

INSERTION: Onto the basihyal with the hyoglossus and sternohyoid.

OTHER RHINOLOPHIDAE: This muscle is similar in other rhinolophids, although it is not associated with the hyoglossus and sternohyoid. In Triaenops and Rhinonycteris, the muscle originates entirely by fleshy fibers (Griffiths and Smith, 1991).

OTHER YINOCHEIROPTERA: In emballonurids and nycterids, this muscle is similar to the rhinolophid condition but variable in size. In Rhinopoma the geniohyoid originates entirely by tendon. In megadermatids, the origin is entirely fleshy and the antimeres are fused for most of the muscle. Additionally, it is in the "free-floating" condition (see Griffiths, 1982).

COMMENTS: The origin of this muscle entirely by fleshy fibers in Triaenops and Rhinonycteris is a synapomorphy, coded as character state 16 in Table 1.

M. STERNOHYOIDEUS

Figures 1, 3, 5

ORIGIN: From the anterior surface of the manubrium of the sternum.

INSERTION: Superficial fibers insert onto the raphe formed with the geniohyoid; deep fibers insert onto the basihyal along with fibers from the geniohyoid and hyoglossus.

OTHER RHINOLOPHIDAE: In other rhinolophids, the muscle is similar but not associated with the geniohyoid and hyoglossus. In R. hildebranti the sternohyoid is very thin. In Triaenops, there seem to be two origins from the manubrium (medial and lateral), but there was variation between specimens examined.

OTHER YINOCHEIROPTERA: In megadermatids, the origin is the same but the muscle inserts directly onto fibers of the geniohyoid and hyoglossus (with a tendonous connection to the basihyal). In nycterids, this muscle is the same as the rhinolophid condition. In emballonurids, the sternohyoid also originates from the proximal head of the clavicle. In most emballonurid genera (except Rhinopoma) this muscle is attached to the larynx by fibers, effectively creating two muscles: a "sterno-cricoid" and a "cricohyoid" (Griffiths and Smith, 1991). In Emballonura and Coleura this muscle is deflected by tracheal expansions, attaching posteriorly to the larynx and then anteriorly to the basihyal (see Griffiths et al., 1991).

M. STERNOTHYROIDEUS

Figures 1 - 4

ORIGIN: From the anterior surface of the medial head of the clavicle, this muscle is attached to the sternohyoid by connective tissue for about half the distance of the sternohyoid.

INSERTION: This muscle passes anteriorly and laterally at the midway point of the trachea to insert on the lateral thyroid cartilage, just posterior to the origin of the thyrohyoid.

OTHER RHINOLOPHIDAE: In H. armiger, the sternothyroid closely follows the sternohyoid, but is not physically attached. In R. hildebranti, H. diadema, Triaenops and Rhinonycteris the muscle is very reduced.

OTHER YINOCHEIROPTERA: This muscle is similar in megadermatids and nycterids to the general rhinolophid condition. In emballonurids, the muscle is also similar, although the origin in Rhinopoma is wider (from the lateral manubrium, sterno-clavicle articulation and medial surface of the clavicle head) (Griffiths and Smith, 1991).

COMMENTS: Robust muscle. The close association of the sternohyoid and sternothyroid is a synapomorphy of H. commersoni and H. armiger, coded as character state 17 in Table 1.

M. OMOHYOIDEUS

Figure 1

ORIGIN: From the anterior medial surface of the clavicle.

INSERTION: Attached by fascia onto the lateral edge of the sternohyoid, continuing to the raphe formed with the geniohyoid.

OTHER RHINOLOPHIDAE: This muscle is absent in all other rhinolophids examined except H. diadema, in which a thin omohyoid originates from the scapula (Griffiths and Smith, 1991; Sprague, 1943) and inserts on the basihyal, lateral to the sternohyoid insertion. In Rhinonycteris and Triaenops, no omohyoid is found as described by Sprague (1943), but a prominent split dividing each sternohyoid longitudinally is observed. This could be 1) a muscle breaking away and becoming "omohyoidous" in all other Yinochiroptera, 2) the omohyoid completing fusion with the sternohyoid, or most probably 3) just a weird-looking sternohyoid (Griffiths, personal communication).

OTHER YINOCHIROPTERA: In emballonurids, the origin is similar to that of H. commersoni, but the muscle inserts on the basihyal and is anteriorly fused with the sternohyoid. This same condition is observed in nycterids. In megadermatids, the muscle inserts onto the posterior surface of the thyrohyal (Griffiths and Smith, 1991).

COMMENTS: This muscle is probably of little phylogenetic value to this study because of the variability between and within species, so it is not included in Table 1.

M. THYROHYOIDEUS

Figures 2, 4, 5, 6

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

INSERTION: Onto the length of the posterior surface of the thyrohyal, continuing to the posterior projection of the basihyal.

OTHER RHINOLOPHIDAE: The origin of this muscle is similar in all rhinolophids examined; however, it inserts only onto the posterior tip of the thyrohyal element in most species. In Triaenops and Rhinonycteris, the muscle inserts onto the entire thyrohyal (Griffiths and Smith, 1991).

OTHER YINOCHIROPTERA: This muscle is similar in all Yinochiroptera to the general rhinolophid condition.

COMMENTS: The insertion of this muscle onto the entire thyrohyal (coded as character state 18 in Table 1) is a synapomorphy of Triaenops and Rhinonycteris and a autapomorphy of H. commersoni.

DISCUSSION

Apomorphic character states of the rhinolophid hyoid regions are listed in Table 1, and the cladogram derived from these data is shown in Figure 7. Within the basal clade, there is one secondary clade formed by character state 8: the expanded insertion of the jugulohyoid onto the "foot" of the stylohyal. This group bissects into a clade including Triaenops and Rhinonycteris and a clade containing H. commersoni and H. armiger. All of the rhinolophids dissected share several synapomorphies: fusion of the thyrohyals to the basihyal (1), loss of the stylohyoid (6), addition of a new muscle (7) and loss of the sphincter colli profundus (9). Rhinolophus euryotis has an autapomorphic trait: insertion of the mylohyoid onto only the basihyal element (3).

Hipposideros commersoni and H. armiger share several traits:

a modified mylohyoid profundus (4), a pad of connective tissue between the mandibulo-hyoid and anterior mandible (5), and close association of the sternothyroid and sternohyoid (17).

Additionally, H. commersoni has several autapomorphic traits: insertion of the ceratohyoid onto only the stylohyal (11), insertion of the genioglossus onto the basihyal (13) and close association of the hyoglossus, geniohyoid and sternohyoid on the basihyal (14). Further dissection of other species in the genus Hipposideros may indicate that these traits are actually synapomorphies with other species.

Triaenops and Rhinonycteris share six synapomorphies: expansion of post-laryngeal chambers (2), reduction of the stylopharyngeus (10), loss of the ceratohyoid (12), origination of the styloglossus from the foot of the stylohyal (15), origination of the geniohyoid by fleshy fibers only (16) and attachment of the thyrohyoid onto the entire posterior edge of the thyrohyal (18). Although characters 2, 15 and 18 were also observed in H. commersoni, it is hypothesized that these traits evolved independently because 1) the postlaryngeal chambers have a different morphology, 2) the fibers of the thyrohyoid are oriented in opposite directions and 3) the origin of the styloglossus is more lateral in H. commersoni. Sprague (1943) also describes postlaryngeal chambers in R. affinis. These could have evolved convergently or Sprague could be wrong (he also notes postlaryngeal chambers in H. diadema, but Griffiths and Smith (1991) do not agree).

H. commersoni seems to be most closely related to H. armiger, while Triaenops and Rhinonycteris also seem to be very closely related. The results are initially surprising from a zoogeographic point of view because H. commersoni is found in Africa, but H. armiger is found in East Asia. Additionally, Triaenops is an East African/South Asian genus, whereas Rhinonycteris is Australian. It is hypothesized that the base species of each group originally ranged across the forests which were continuous over the Old World during the Miocene. When the forests retreated due to the cooling climate, gene flow was restricted and allopatric speciation occurred. The close relationship between Triaenops and Rhinonycteris seems to be a more extreme case of the same situation.

These results are part of an emerging pattern found in other species of Chiroptera, including emballonurid (Griffiths and Smith, 1991) and megadermatid bats (Griffiths et al., 1992). For example, Emballonura, a genus found in New Guinea, South Asia and surrounding islands, seems to be more closely related to Coleura, an African genus, than to another New Guinea genus, Mosia (Griffiths and Smith, 1991). Lavia frons, an African species, seems to be more closely related to two Megaderma spp. from South Asia than to Cardioderma cor, another African species. Seen from this perspective, the results found in this study become less surprising, and instead add to the evidence for this trend.

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TABLE 1
 Summary of Apomorphies Used in Constructing Cladogram (Fig. 7)
 (+ = apomorphic character state; - = plesiomorphic character state)

Character States	Taxon							
	com	arm	dia	Tri	Rhi	hil	eur	aff
1. Fusion of thyrohyals to basihyal	+	+	+	+	+	+	+	+
2. Expansion of post-laryngeal chambers	+	-	-	+	+	-	-	+
3. Insertion of mylohyoid onto basihyal only	-	-	-	-	-	-	+	-
4. Modified mylohyoid profundus	+	+	-	-	-	-	-	-
5. Pad of connective tissue between mandibulo-hyoid and anterior mandible	+	+	-	-	-	-	-	-
6. Loss of stylohyoid	+	+	+	+	+	+	+	+
7. Formation of new muscle	+	+	+	+	+	+	+	+
8. Expanded insertion of jugulohyoid on stylohyal "foot"	+	+	-	+	+	-	-	-
9. Loss of sphincter colli profundus	+	+/- ^a	+	+	+	+	+	+
10. Reduction of stylopharyngeus	-	-	-	+	+	-	-	-
11. Insertion of ceratohyoid onto stylohyal only	+	-	-	-	-	-	-	-
12. Loss of ceratohyoid	-	-	-	+	+	-	-	-
13. Insertion of genioglossus onto basihyal	+	-	-	-	-	-	-	-
14. Close assoc. of hyoglossus, geniohyoid and sternohyoid	+	-	-	-	-	-	-	-
15. Origination of styloglossus from stylohyal "foot"	+	-	-	+	+	-	-	-
16. Geniohyoid originates entirely by fleshy fibers	-	-	-	+	+	-	-	-
17. Close assoc. between sternothyroid and sternohyoid	+	+	-	-	-	-	-	-
18. Insertion of thyrohyoid onto entire thyrohyal	+	-	-	+	+	-	-	-

com = Hipposideros commersoni, arm = H. armiger, dia = H. diadema, Tri = Triaenops persicus, Rhi = Rhinonycteris aurantius, hil = Rhinolophus hildebrandi, eur = R. suryotis, aff = R. affinis.

^aGriffiths and Smith (1991) found only a few fibers, possibly fascia.

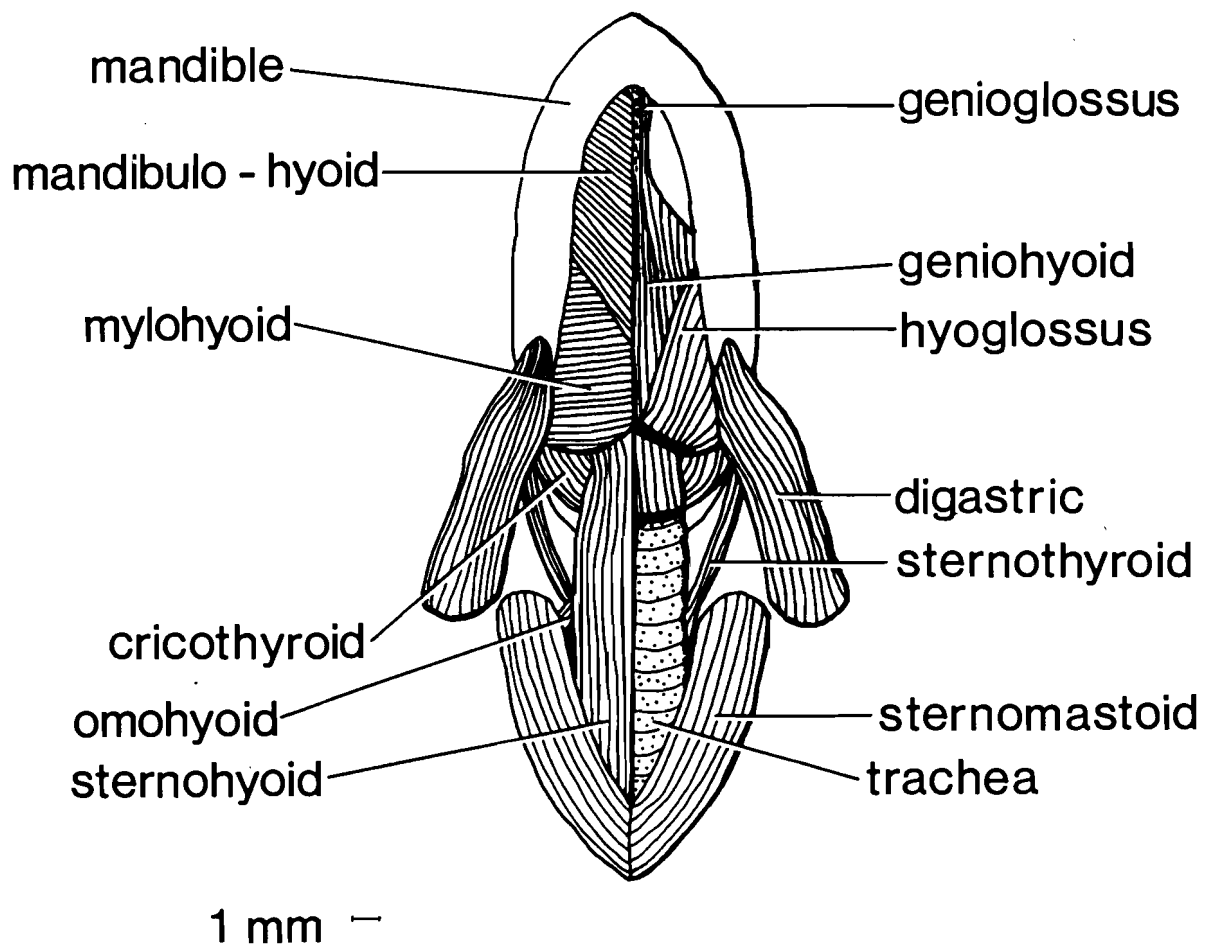


Fig. 1. Ventral view of the hyoid region of Hipposideros commersoni. Deeper structures are shown on the right (the specimen's left) side.

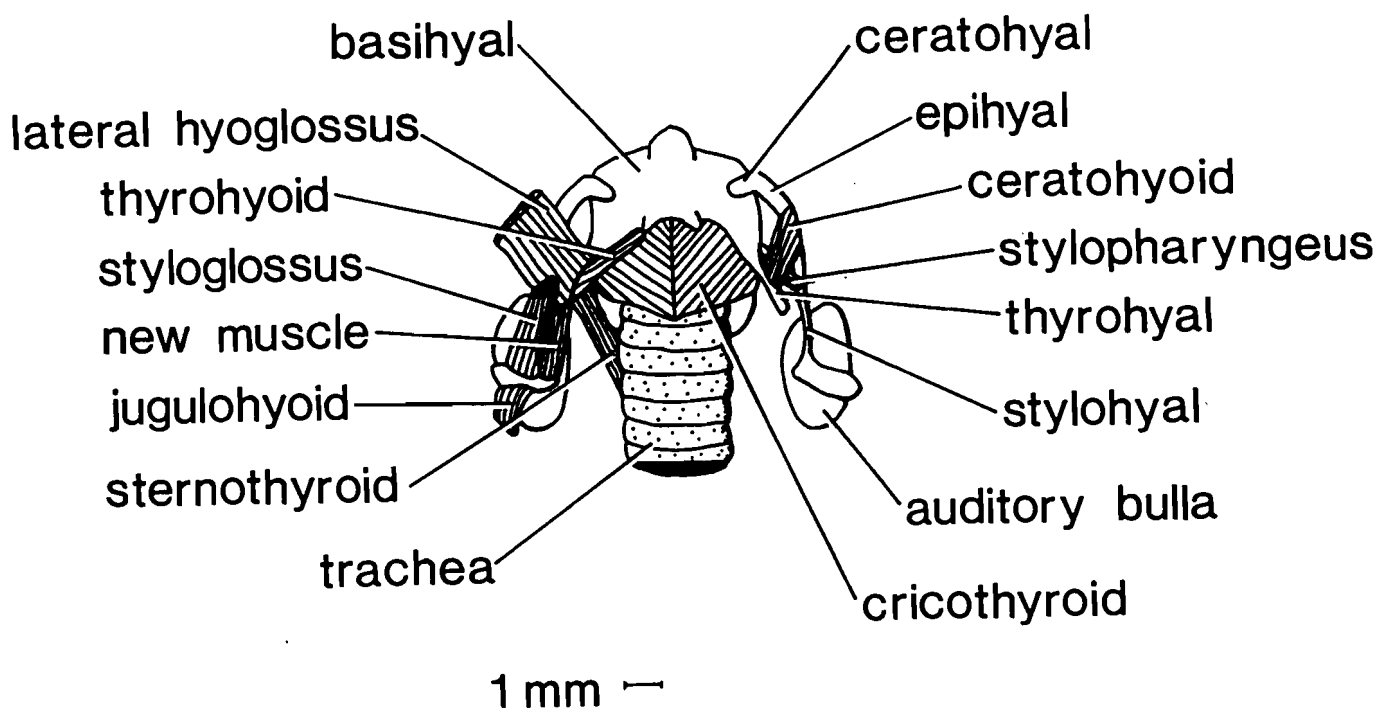


Fig. 2. Ventral view of the deep hyoid muscles, the hyoid apparatus and the larynx of Hipposideros commersoni.

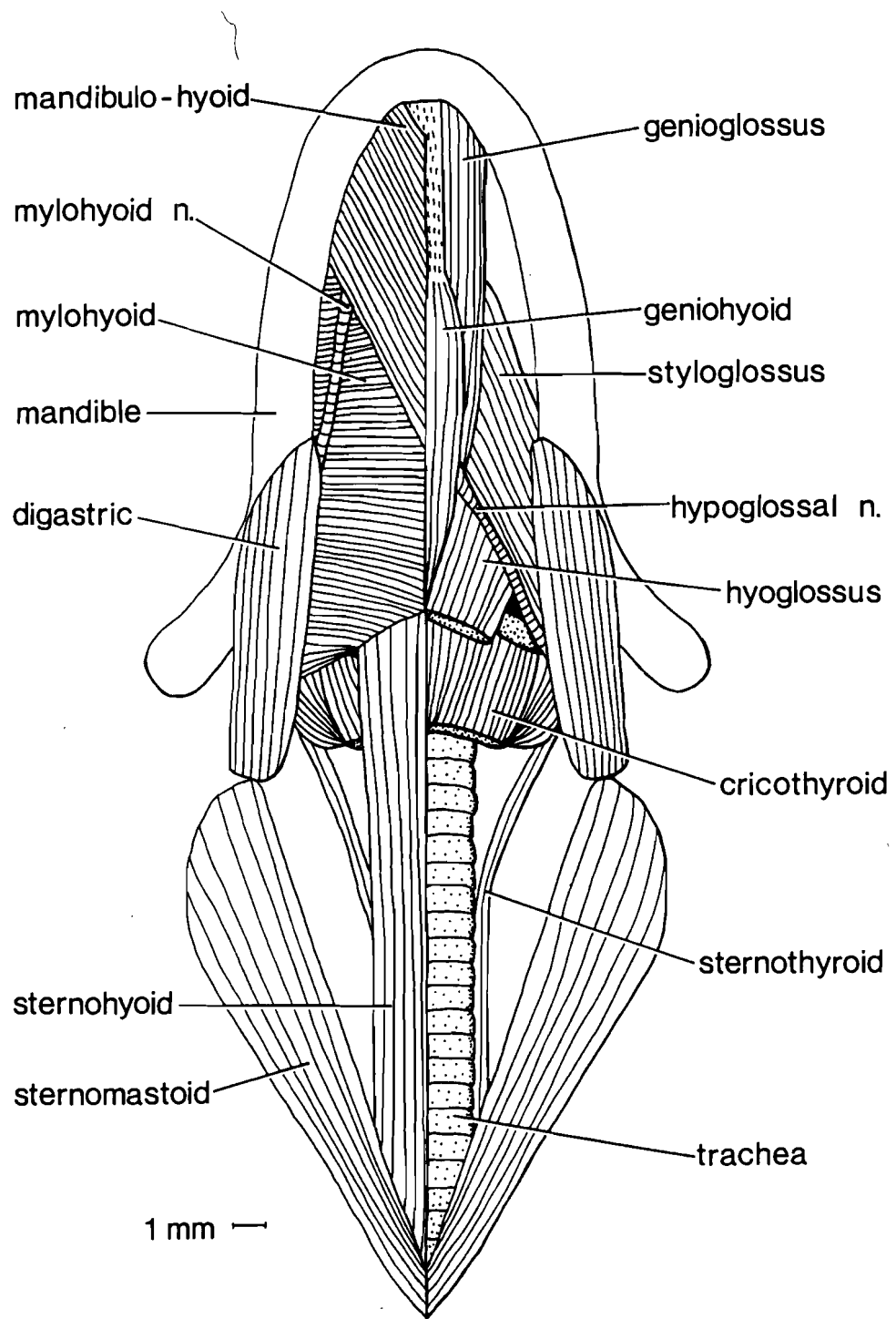


Fig. 3. Ventral view of the hyoid region of *Hipposideros armiger*. Deeper structures are shown on the right side of the illustration.

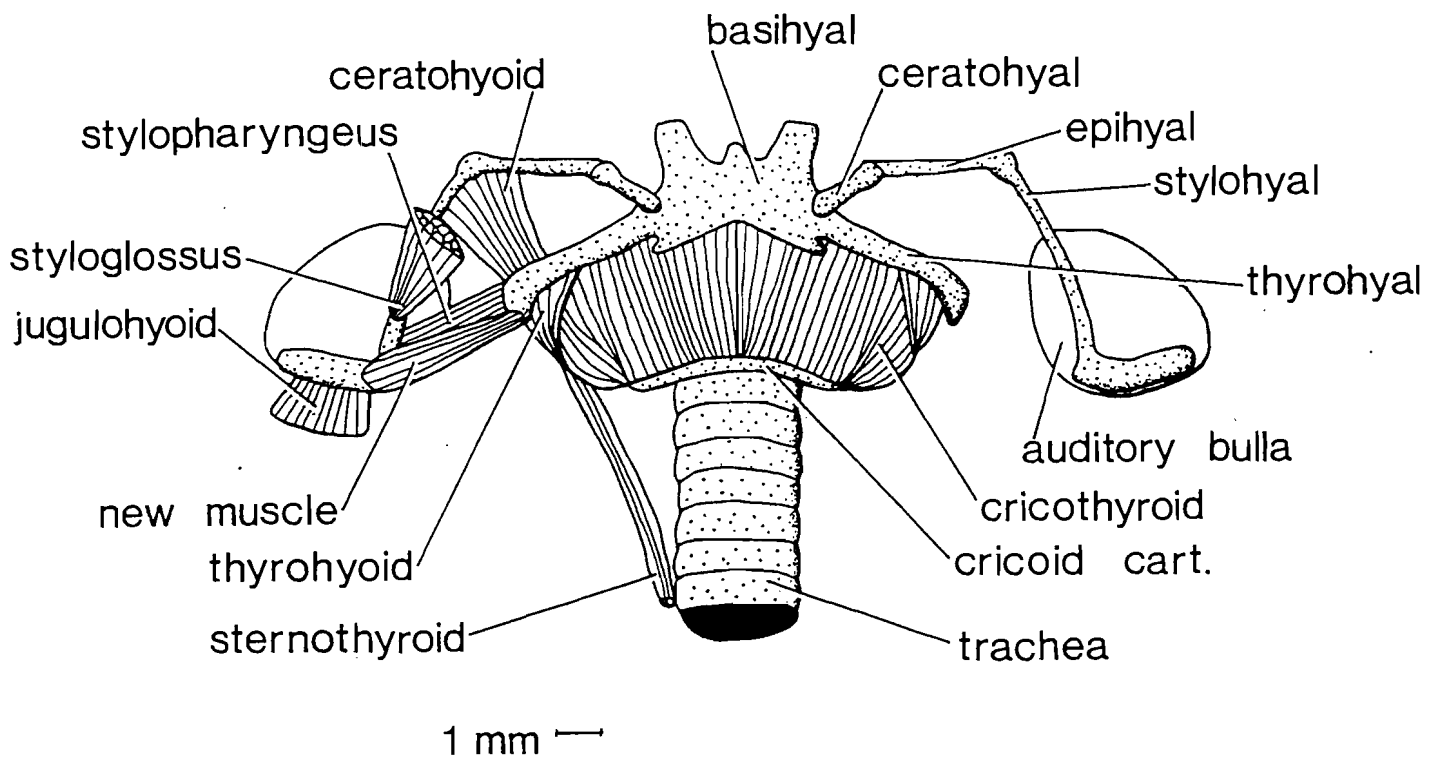


Fig. 4. Ventral view of the deep hyoid structures and the larynx of Hipposideros armiger.

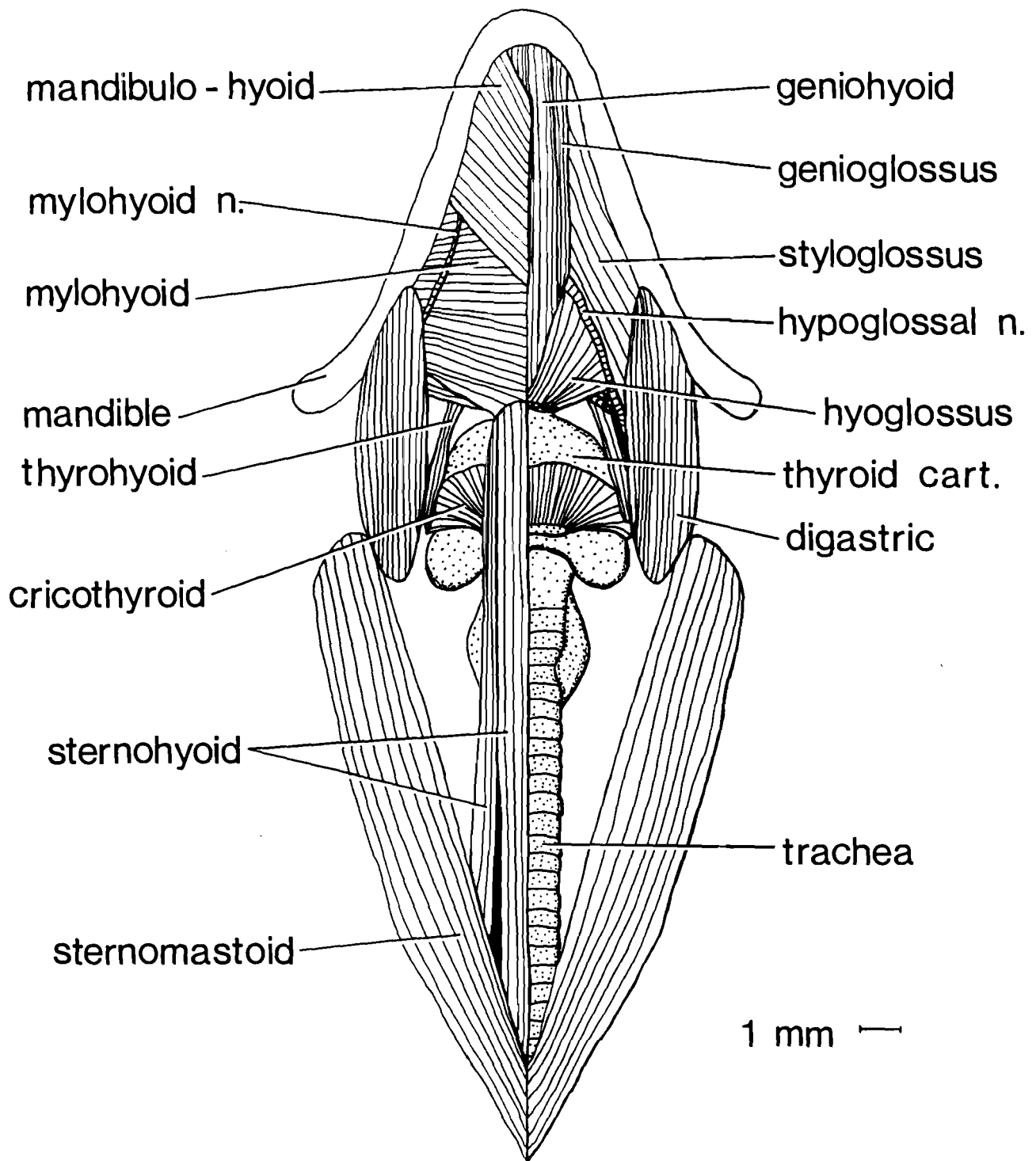


Fig. 5. Ventral view of the hyoid region of *Triaenops persicus*. Deeper structures are shown on the right side of the illustration.

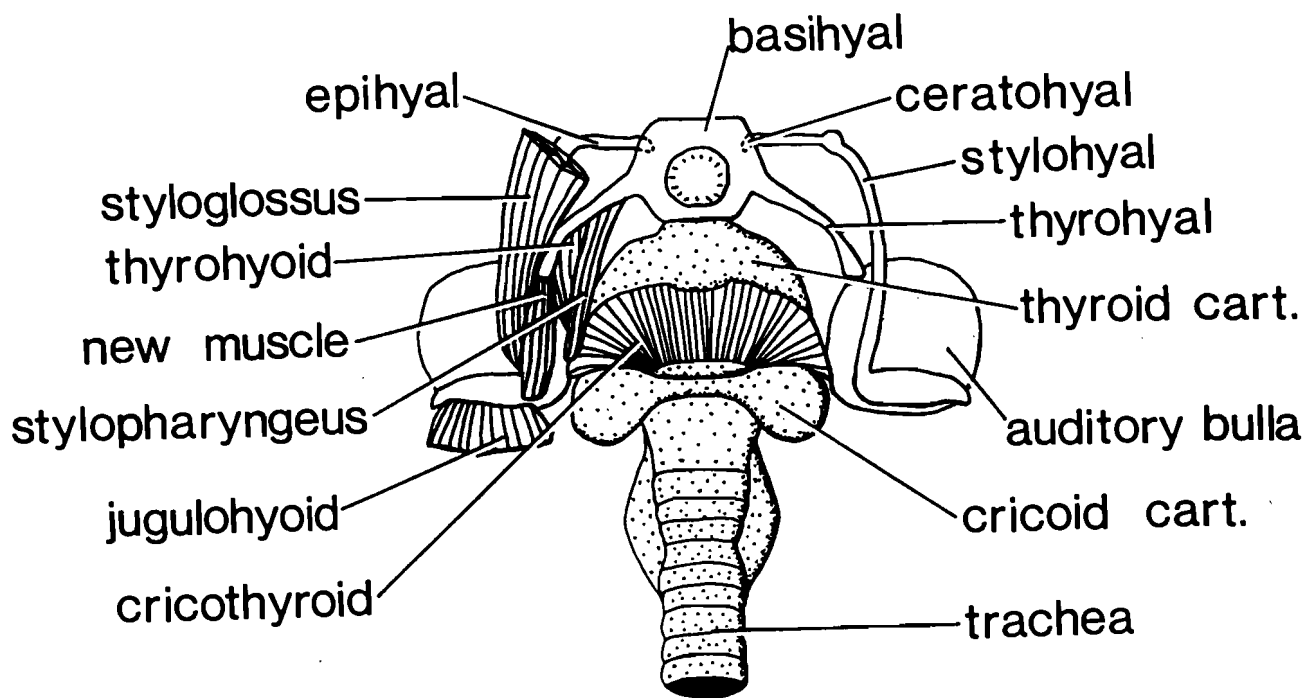


Fig. 6. Ventral view of the deep hyoid structures and the larynx of Triaenops persicus.

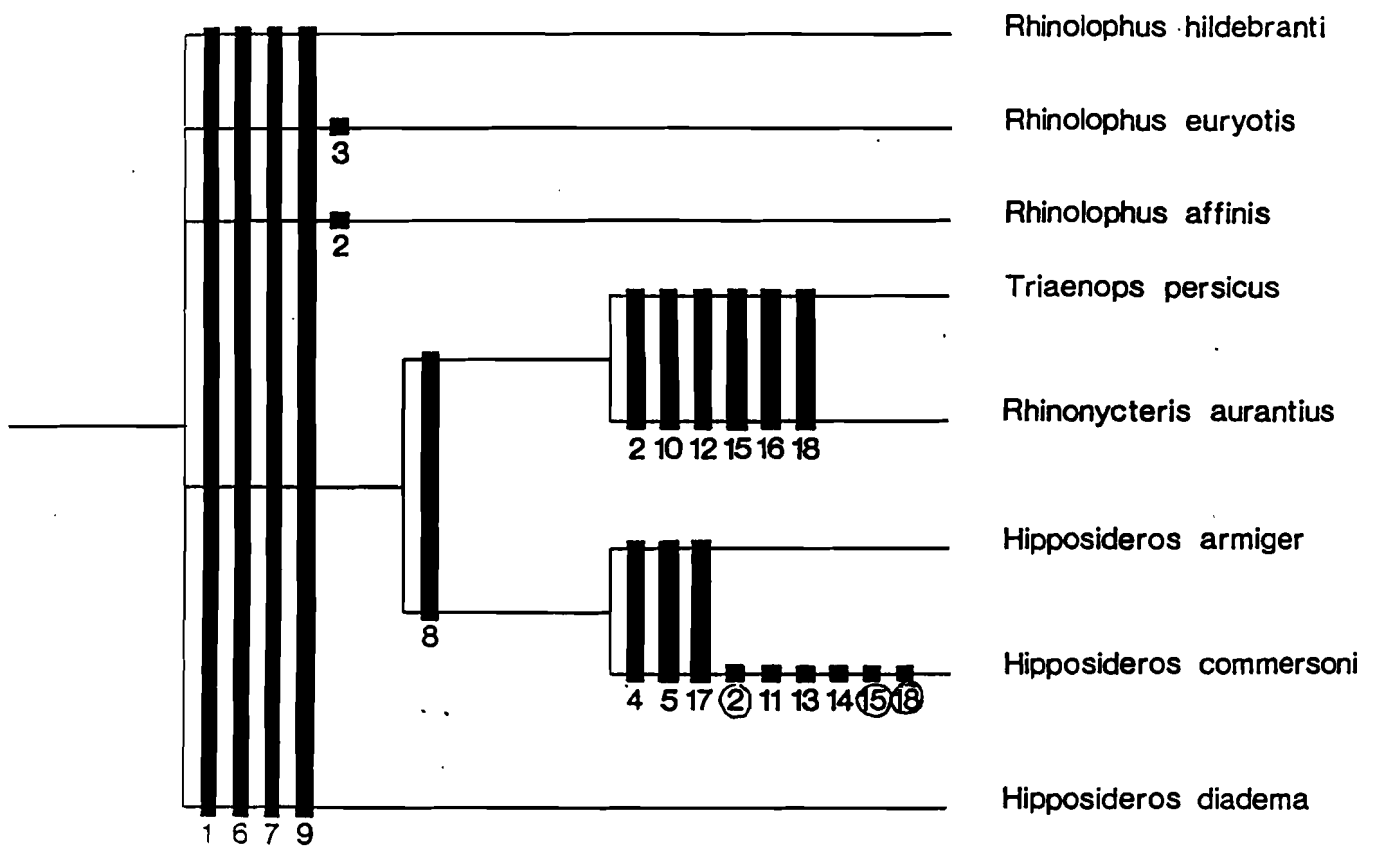


Fig. 7. Cladogram showing relationships among genera of rhinolophid bats described in this study. Numbers refer to character states listed in Table 1. There are three convergant events suggested (circled characters 2, 15 and 18 in Hipposideros commersoni).