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Systematics of Megadermatid Bats (Chiroptera, Megadermatidae), Based on Hyoid Morphology

THOMAS A. GRIFFITHS,¹ ALLISON TRUCKENBROD,²
AND PAMELA J. SPONHOLTZ²

ABSTRACT

The hyoid musculature and hyoid apparatus of bats of the family Megadermatidae are described and compared with the hyoid morphology of bat families described elsewhere. Megadermatids share an apomorphic character state with nycterids, rhinopomatids, and emballonurids in that the omohyoid muscle has shifted its origin from the scapula to the mid-clavicle. We suggest that because of the omohyoid shift, megadermatids have been able to develop a morphological condition described previously only in New World phyllostomid bats. The sternohyoid, hyoglossus, and geniohyoid muscles have partially detached from the basihyal, retaining a connection only through a

tendon and a few deep fibers of the geniohyoid. The styloglossus muscle has a posteriorly shifted insertion, as in phyllostomids. Within the Megadermatidae, there is morphological variation in the origin of the sternohyoid, hyoglossus, and sphincter colli profundus muscles, in the morphology of the styloglossus, and in the insertion of the geniohyoid and ceratohyoid muscles. A cladistic analysis of the data suggests that *Lavia frons* is closely related to *Megaderma spasma* and *M. lyra*. *Cardioderma cor* is a sister species to the *Lavia-Megaderma* group. *Macroderma gigas* is the most distantly related of the four megadermatid genera.

INTRODUCTION

Megadermatid bats are a small family of insectivorous and carnivorous paleotropical

bats. There are four genera containing five extant species in the family. *Lavia frons* and

¹ Research Associate, Department of Mammalogy, American Museum of Natural History; Professor of Biology, Illinois Wesleyan University, Bloomington, IL 61702-2900.

² Student, Department of Biology, Illinois Wesleyan University.

Cardioderma cor are African species. *Macroderma gigas* is a large, carnivorous Australian species. *Megaderma lyra* and *Megaderma spasma* are sympatric in India, Sri Lanka, and through southeast Asia. *M. lyra* is also found as far west as Afghanistan, while *M. spasma* ranges farther east through the Philippines, Java, and various other small, western Pacific Islands. A number of fossil megadermatid genera are known from the Eocene, Oligocene, and Miocene strata of southern Europe and Africa, and from the Miocene of Australia (Hill and Smith, 1984; Hand, 1985).

Systematists have long associated megadermatids with bats of the families Nycteridae and Rhinolophidae.³ Miller (1907) provided a good summary of the classification schemes used in the 19th century. Although genera were shuffled back and forth between higher-level taxa in different classifications, the known megadermatids generally were placed with the nycterids, the rhinolophids, or both. Miller (1907) and other early 20th century taxonomists continued this association. Though most considered the megadermatids a distinct group meriting familial status, they continued to list them as being closely related to nycterids and/or rhinolophids. Miller (1907), for example, characterized the family as a "near ally of the Nycteridae," though he added that it is "well characterized as a family." After more than a century of informal recognition, Weber (1928) formally recognized the special relationship of nycterids, rhinolophids, and megadermatids by placing them in the superfamily Rhinolophoidea, one of four superfamilies he created within the suborder Microchiroptera. This arrangement has been followed with only minor modification in every subsequent formal classification of living bats, including those of Simpson (1945),

Koopman and Jones (1970), Smith (1976), Van Valen (1979), and Koopman (1984).

Traditional classifications have been based on skull and tooth morphology, and on external dermal characteristics. Studies based on soft morphology or on biochemical characters have appeared only recently, but a number of them have suggested that there may be problems with the traditional classification scheme. Novacek's (1980) analysis of the chiropteran auditory region suggested that megadermatids might be most closely related to furipterids, and to a group containing the phyllostomids, rhinopomatids, noctilionids, mormoopids, and mystacinids. Luckett's (1980) analysis of reproductive morphology suggested that megadermatids might be most closely related to vespertilionids and thyropterids. Pierson's (1986) analysis of transferrin immunological distance data suggested that megadermatids are in a clade with the rhinopomatids and rhinolophids. Most recently, Griffiths and Smith's (1991) analysis of hyoid morphological data suggested that megadermatids are more closely related to emballonurids, rhinopomatids, and nycterids than they are to rhinolophids (including hipposiderines). None of the above studies was conclusive enough to prompt a reclassification of microchiropteran bats, but each suggested that Weber's superfamily Rhinolophoidea might be problematic.

While there have been a number of studies of the relationship of the family Megadermatidae to other bat families, we are aware of only one study of relationships within the family, that of Hand (1985). Basing her conclusions on the tooth morphology of extinct and extant species of megadermatids, Hand (1985) concluded that *Macroderma gigas* and a fossil species of *Macroderma* are the two most derived members of the family. *Lyroderma lyra* (= *Megaderma lyra*) and a fossil species of *Lyroderma* compose the sister lineage to the two species of *Macroderma*. Successive sister groups then include a series of fossil forms; in order they consist of the "Dwornamor variant," *Megaderma mediterraneum*, *M. vireti*, and *M. brailloni*. The next sister lineage contains three species: the living *Megaderma spasma* and two fossil species of

³ Although we are well aware that some authorities, notably J. E. Hill, regard hipposiderine bats as a family in its own right, we herein follow K. F. Koopman in recognizing a single family, Rhinolophidae, containing two subfamilies: Rhinolophinae and Hipposiderinae. TAG hopes that dissections of the hyoid region of bats of both taxa will shed further light on this question, and he will address this issue in a subsequent paper on rhinolophids (sensu Koopman).

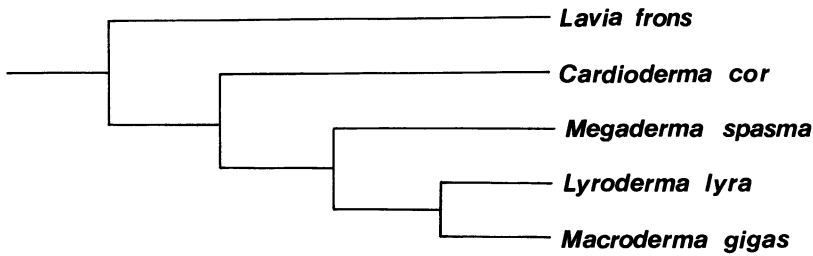


Fig. 1. Cladogram of living megadermatid bat species based on Hand's (1985) analysis of tooth and other cranial characters. Modified by us from Hand's figure 19 to include only living megadermatids; see Hand (1985) for justification of the branching pattern.

Megaderma. The sister group to this contains only the living African species *Cardioderma cor*. The African species *Lavia frons* is on its own line as the next sister group. Successive sister groups then contain the fossil *Necromantis adichaster*, the fossil known as the "Rusinga form," and various species of *Nycteris* which are used as outgroups. Hand's (1985) phylogeny of living megadermatids is shown in our figure 1 (modified by us from Hand's fig. 19). We have omitted all fossil forms studied by Hand for ease of comparison with our cladogram of living megadermatids based on hyoid morphology (fig. 10).

The purpose of the present work is to describe the hyoid morphology of representative specimens of all living genera and species of megadermatid bats. Data are compared with outgroup data for other families of bats described elsewhere (Griffiths, 1978a, 1978b, 1982, 1983; Griffiths and Smith, 1991; Griffiths et al., 1991), and are used to construct a cladogram showing relationships within the family. This paper is also the third in a series (Griffiths et al., 1991, and Griffiths and Smith, 1991, were the first and second) of which the ultimate aim is to describe the hyoid morphology of representatives of virtually all microchiropteran genera and produce a cladogram for the entire suborder Microchiroptera.

MATERIALS AND METHODS

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

mens dissected were from the collections of the American Museum of Natural History (AMNH) in New York. FAMILY MEGADERMATIDAE: *Cardioderma cor*: AMNH 184498, 205337, 219723; *Lavia frons*: AMNH 49383, 49384, 83390, 219725, 219726; *Macroderma gigas*: AMNH 197210, 236544, 236545; *Megaderma lyra*: AMNH 236215, 244941; and *Megaderma spasma*: AMNH 113773, 113774, 216804, 216805, 247252. Outgroup comparisons to determine character polarity within the Megadermatidae were made with genera of other bat families described in Griffiths (1978a, 1978b, 1982, 1983), Griffiths et al. (1991), and Griffiths and Smith (1991). Some information on genera not dissected by Griffiths or his associates was taken from Sprague (1943), though such information was used with caution because, in the experience of the senior author, data from sources other than personal observation are less reliable in phylogenetic analyses.

ACKNOWLEDGMENTS

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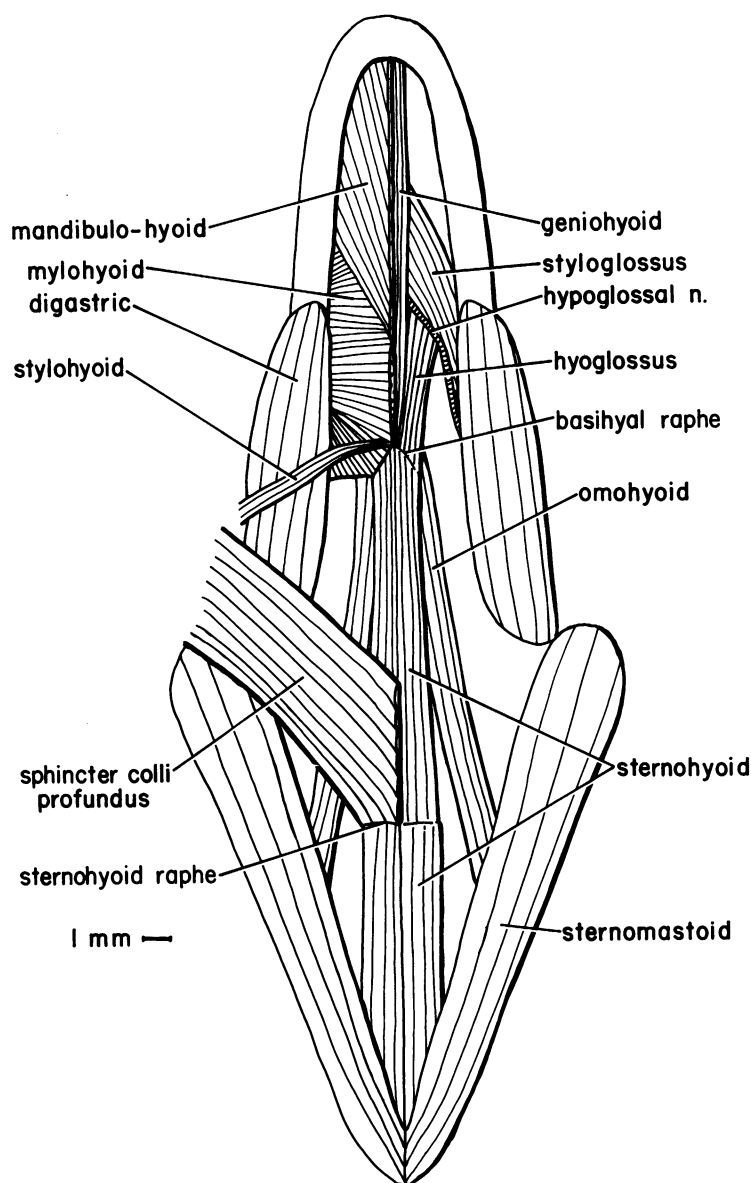


Fig. 2. Ventral view of the superficial hyoid muscles of *Megaderma lyra* (*M. spasma* is similar). Deeper structures are shown on the right (the bat's left side).

nied TAG during a research trip to the American Museum, providing invaluable support and assistance for this study and others. Portions of this work were supported by Faculty Development grants to TAG from Illinois Wesleyan University and by funding from the Department of Mammalogy at the American Museum.

RESULTS

HYOID APPARATUS (figs. 3, 5, 7, 9)

In megadermatid bats, the basihyal element of the hyoid apparatus is shaped like a bar, with a very well-developed entoglossal process projecting ventrally. From the lateral edge of each side of the basihyal, the thyrohy-

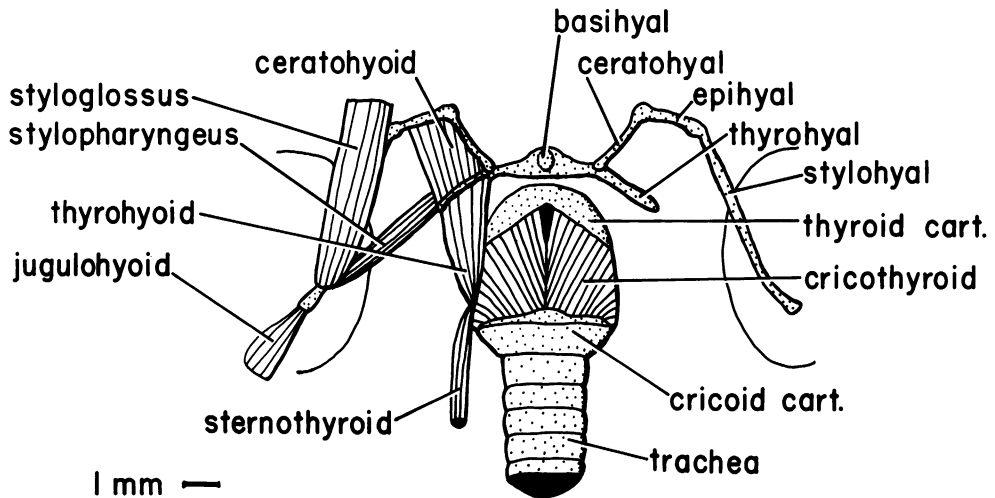


Fig. 3. Ventral view of the deep hyoid muscles and the hyoid apparatus of *Megaderma lyra* (*M. spasma* is similar, except for the ceratohyoid, see text).

al element extends laterally, posteriorly, and dorsally. The thyrohyals, which are fused to the basihyal, are well developed. In the anterior cornu of the hyoid apparatus there are three elements, separated from one another by synchondrosal joints. The ceratohyal and epihyal are straight rods, each about one-third the length of the stylohyal. The stylohyal is gently curved and, unlike the stylohyals of other families of bats (Griffiths, 1982; Griffiths and Smith, 1991), does not have a paddle-shaped "foot" at its lateral tip.

COMMENTS: Griffiths and Smith (1991) provided complete descriptions of the hyoid apparatus of rhinopomatid, emballonurid, nycterid, and selected rhinolophid genera. Compared with these other families, the megadermatid hyoid apparatus appears to have few, if any, apomorphies. The basihyal is primitive in all respects, with the possible exception of possessing a very large entoglossal process. If the character state "large entoglossal process" is an apomorphy, it is apparently an autapomorphy found only in megadermatids. The thyrohyals, ceratohyals, and epihyals are all simple, well-developed elements possessing no unusual or derived features. The stylohyals have no expansion (or at most a very slight expansion) at the lateral tip, but are otherwise not unusual. "Loss of a lateral stylohyal expanded tip"

might ultimately prove to be an interfamilial synapomorphy upon further dissection of other families of bats, but for now we consider it at most to be an autapomorphy of the family Megadermatidae. Of course, if they truly are apomorphies, both character states would be synapomorphies for all four genera, and would thus support the monophyly of the family Megadermatidae.

HYOID MUSCULATURE

For each muscle listed below, the anatomy of *Megaderma* (both species are virtually identical) is described first under Origin and Insertion. Variations from the condition found in *Megaderma* are described under Other Megadermatids. Unusual or noteworthy observations, or comparisons with genera described elsewhere are made in the Comments section sometimes found at the end of the muscle entry.

BRANCHIOMERIC MUSCULATURE

MYLOHYOID GROUP

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

M. mylohyoideus

Figures 2, 4, 6, 8

ORIGIN: From the medial surface of the posterior half of the body of the mandible.

INSERTION: Anteriormost fibers insert into the lateral geniohyoid muscle; the posterior fibers insert into the connective tissue of the midline raphe (and thus indirectly into the mylohyoid antimere, and indirectly into the mandibulo-hyoid, geniohyoid, sternohyoid, hyoglossus, and stylohyoid). A few of the most posterior fibers pass deep (dorsal) to the sternohyoid to insert onto the lateral surface of the entoglossal process of the basihyal.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: There are two notable features of the mylohyoid of megadermatid bats. First, the muscle does not extend very far anteriorly deep to the mandibulo-hyoid. It is confined to the posterior region of the intermandibular space, just as in the other families of bats that have a mandibulo-hyoid (the rhinopomatids and rhinolophids, Griffiths and Smith, 1991). In all other known families of bats (all of which lack the mandibulo-hyoid), the mylohyoid extends anteriorly almost to the mandibular symphysis (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991), though it may be apoeneurotic in its midregion in some phyllostomids (Griffiths, 1982). Second, the megadermatid mylohyoid inserts on the basihyal, but not on the thyrohyals. This condition is shared by megadermatids and all other known families of bats except rhinopomatids and emballonurids (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). Neither of these conditions is useful in analyzing intrafamilial relationships because there is no variation within the megadermatids. Griffiths and Smith (1991) discussed possible interfamilial synapomorphies, but a more thorough analysis of the variation in this muscle is postponed until the senior author has had a firsthand look at a larger number of families.

M. mylohyoideus profundus

Griffiths (1978a, 1982) described a deep portion of the mylohyoid that had broken away to become a separate muscle in phyllostomid bats. He termed this the "mylo-

hyoid profundus" in 1978, but then mistakenly called it the "mandibulo-hyoid" in 1982, because a misreading of Sprague (1943) convinced him that Sprague had discovered the muscle and named it "mandibulo-hyoideus." In phyllostomids, the deep mylohyoid apparently is functionally correlated with the development of the "free-floating" sternohyoid-hyoglossus-geniohyoid complex (Griffiths, 1982). It seems to be functionally important for a piece of the mylohyoid to retain its insertion on the basihyal, probably to provide lateral pull on the hyoid apparatus. Megadermatid bats have evolved a similar free-floating muscle complex, apparently by parallel evolution. Although there is a portion of the mylohyoid that passes deep to the free-floating complex in megadermatids, it has not separated from the main body of the mylohyoid as it has in advanced phyllostomids. We therefore report that a true mylohyoid profundus is lacking in megadermatids.

M. mandibulo-hyoideus

Figures 2, 4, 6, 8

ORIGIN: From the medial surface of the anterior mandibular body.

INSERTION: Anterior fibers insert on the midline raphe (and thus by connective tissue onto their antimere and onto the geniohyoid that lies beneath); posterior fibers insert on the common connective tissue shared by the sternohyoid, hyoglossus, geniohyoid, mylohyoid, and stylohyoid, and thus indirectly onto the basihyal which lies deeper.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: Sprague (1943) and Griffiths and Smith (1991) reported that a mandibulo-hyoideus is present in only three families of bats: megadermatids, rhinopomatids, and rhinolophids. Sprague (1943) suggested that the loss of this muscle was the evolved (derived) condition which, if true, would make the possession of the muscle a symplesiomorphy. Griffiths and Smith (1991) found that the mandibulo-hyoid of rhinopomatids is very different from that of rhinolophids and megadermatids in that it possesses a peculiar tendinous connection to the digastric raphe (Griffiths and Smith, 1991: figs. 1 and 2). If

the presence of this muscle is considered a synapomorphy, this might be interpreted as supporting Pierson's (1986) hypothesis that megadermatids are in a clade with rhinopomatids and rhinolophids (fig. 11). We cannot rule out this possibility, though we suggest that the peculiar morphology found in *Rhinopoma* makes the possibility of it being a synapomorphy tenuous. No other family of bats, including the known megachiropterans, has any trace of a mandibulo-hyoid (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). TAG will ultimately complete his dissections of rhinolophid genera, which might shed additional light on character polarity of this muscle's two character states. Although we are unsure whether to treat the presence of the mandibulo-hyoid as a synapomorphy or a symplesiomorphy, we present one possible interpretation of it as a symplesiomorphy (fig. 10) and one interpretation of it as a synapomorphy (fig. 11). Until dissections of rhinolophids are complete, we are unwilling to commit ourselves further.

HYOID CONSTRICTOR GROUP

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

M. stylohyoideus

Figures 2, 4, 6, 8

ORIGIN: From the lateral tip of the stylohyal element.

INSERTION: Into the midline connective tissue shared by the mylohyoid, mandibulo-hyoid, geniohyoid, sternohyoid, and hyoglossus. Indirectly via this connective tissue onto the entoglossal process of the basihyal.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: Sprague (1943) reported that this muscle was absent in megadermatids. We found it in all specimens examined, though it was reduced to a narrow strip of muscle in most. The condition of this muscle in most bats is the same as described here, except that the insertion is on the lateral tip of the thyrohyal (see Sprague, 1943; Griffiths, 1982; and Griffiths and Smith, 1991 for specifics). The muscle is absent in *Taphozous* and *Saccolaimus*, in the known rhinolophids (Griffiths and Smith, 1991), and in most phyllos-

tomids (see Griffiths, 1982). Interestingly, in the highly derived emballonurid genera *Peropteryx* and *Peronymus*, the insertion is on the basihyal, as in megadermatids (Griffiths and Smith, 1991). Undoubtedly this similarity is due to homoplasy. Although "shift of the insertion to the basihyal" probably is a synapomorphy uniting all four megadermatid genera, we have chosen not to use this character in our analysis because we believe that the shift was a necessary and integral part of the "freeing up" of the hyoid strap musculature from the basihyal (see below). To count the stylohyoid character and the strap muscle characters separately would falsely give too much weight to events that happened at the base of the megadermatid tree, because we believe that the shift in the stylohyoid insertion was the inevitable result of shifts in the strap musculature. If "shift of insertion of stylohyoid" was counted, it would be only one more character supporting the monophyly of the megadermatids.

M. jugulohyoideus

Figures 3, 7, 9

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

INSERTION: Onto the lateral tip of the stylohyal element.

OTHER MEGADERMATIDS: The muscle is absent in *Cardioderma* (fig. 5 and table 1, character 3), apparently having been replaced by connective tissue fibers that anchor the lateral tip of the stylohyal.

COMMENTS: In all other bats, when present, the origin and insertion are the same as in megadermatids. It is absent in the more derived genera of emballonurids (Griffiths and Smith, 1991), almost certainly due to homoplasy.

M. sphincter colli profundus

Figures 2, 4, 6, 8

ORIGIN: From the ventral surface of the raphe bisecting the sternohyoid (not the basihyal raphe, as in most other bat families).

INSERTION: This muscle passes anteriorly and laterally, fanning out as it does so to insert on the deep surface of the cervical skin at about the level of the ear (but ventral to it).

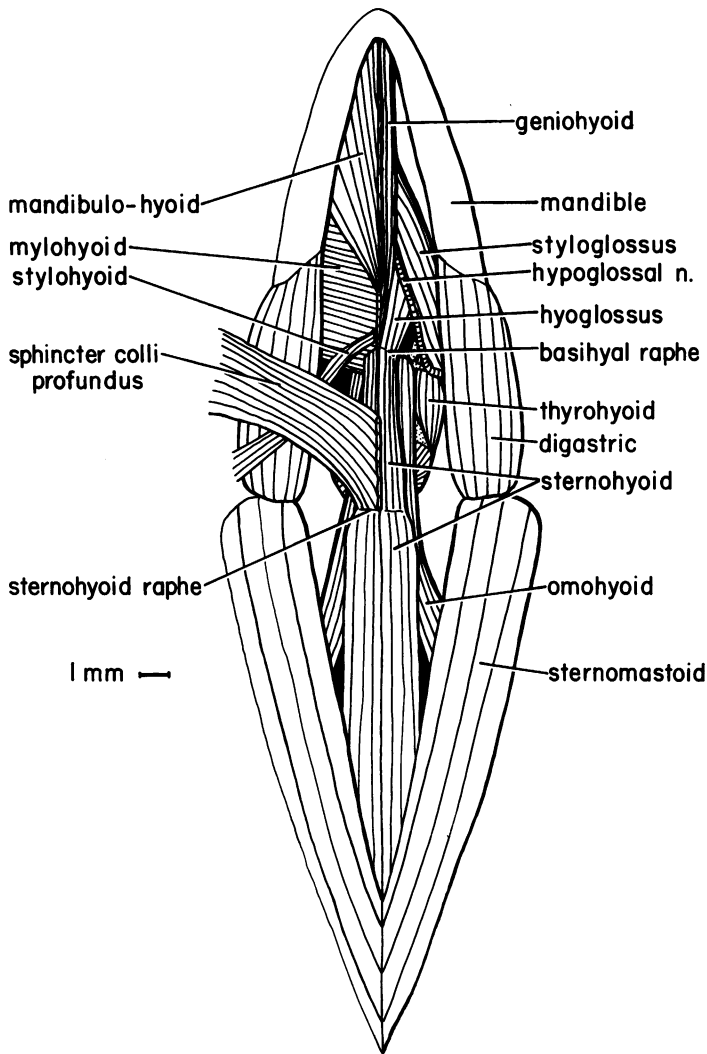


Fig. 4. Ventral view of the superficial hyoid muscles of *Cardioderma cor*. Deeper muscles are shown on the right (the bat's left side).

OTHER MEGADERMATIDS: The muscle is essentially the same in *Cardioderma* and *Lavia*. In all three genera, it is a well-developed muscle that is so powerful, it apparently has modified the morphology of the sternohyoid from which it takes origin. (Posterior to the origin of the sphincter colli, the sternohyoid is more robust, which suggests that the posterior sternohyoid and the sphincter colli act in concert to pull the cervical skin posteriorly.) In *Macroderma*, the muscle is very different. It originates more anteriorly, from the basihyal raphe instead of the sternohyoid raphe. From

this origin, it fans out anteriorly and laterally, inserting in the same manner as in other megadermatids.

COMMENTS: This muscle is heavy and extremely robust in megadermatids, perhaps the heaviest sphincter colli profundus muscle that TAG has ever observed in the Chiroptera. From its size, it is logical to conclude that it plays an important functional role in the ecology of megadermatids, perhaps in feeding, social signaling, moving the ears, or in some obscure action.

In most bats that possess a sphincter colli

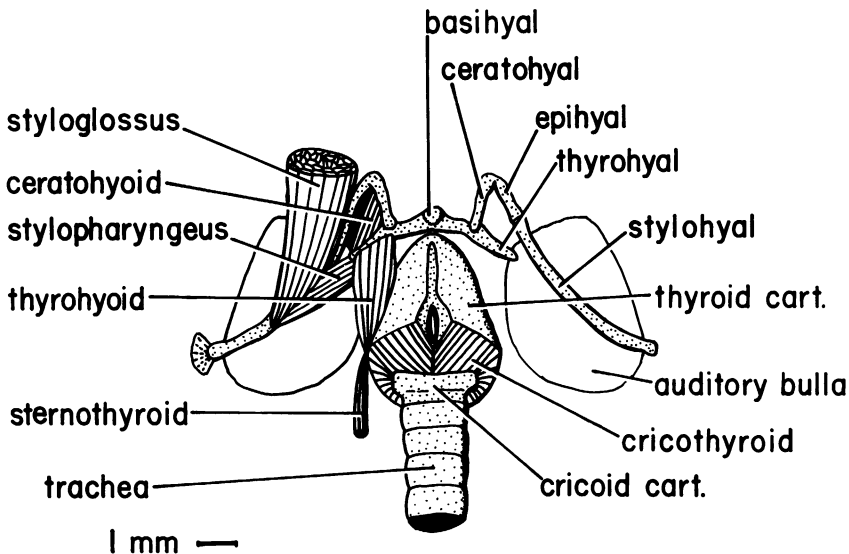


Fig. 5. Ventral view of the deep hyoid muscles and the hyoid apparatus of *Cardioderma cor*.

profundus, the muscle originates anteriorly, from the basihyal raphe (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991). Other than the three megadermatid genera recorded herein, the only bat genus that is known to have a sphincter colli profundus that originates from a sternohyoid raphe is *Chaerephon*, a molossid bat (Sprague, 1943). There are two hypotheses to explain the unusual posterior origin of the muscle in *Megaderma*, *Cardioderma*, and *Lavia*. First, it is possible that the sphincter colli primitively took origin from the basihyal, but shifted posteriorly in the evolution of the three genera. It could have accomplished this by "sliding" along the ventral surface of the sternohyoid, or by the sternohyoid evolving an elongated anterior portion while the sphincter colli remained firmly attached in place. Both of these suggestions might seem improbable, but Griffiths (1978a, 1982) found that similar changes had occurred (plus some that were far more improbable) in the evolution of the same group of muscles in the New World nectar-feeding bats. We have examined the innervation of the muscles in question in an attempt to confirm or refute the above hypotheses, but are unable to do either. A second possibility is one that Sprague (1943) suggested: originally in bats there were two distinct slips of the sphincter colli profundus,

one originating from the basihyal raphe and one from the sternohyoid raphe. *Megaderma*, *Cardioderma*, *Lavia*, and (presumably independently) *Chaerephon* have lost the anterior slip and retained the posterior. All other known bats have done the opposite, losing the posterior and retaining the anterior. In support of this view, one of the Zaire specimens (AMNH 49383) and one of the Sudan specimens (AMNH 83390) of *Lavia frons affinis* had what appeared to be vestigial fibers of slips of an anterior sphincter colli profundus that were weakly attached to the basihyal raphe. This was in addition to a very robust sphincter colli that originated from the raphe bisecting the sternohyoid muscle. No other bat examined of any species had even a trace of a second sphincter colli profundus; each had either an anterior or a posterior slip.

From the point of view of a phylogenetic analysis, it makes no difference which of the above hypotheses is correct. If the sphincter colli origin has moved posteriorly (for either reason) in the evolution of *Megaderma*, *Cardioderma*, and *Lavia*, this would be an unquestionable synapomorphy shared by the three genera, but not by *Macroderma*. It would be a shared, derived character state that is so unusual, it would be extremely unlikely to have evolved by convergent evolution (homoplasy), and would thus be strong

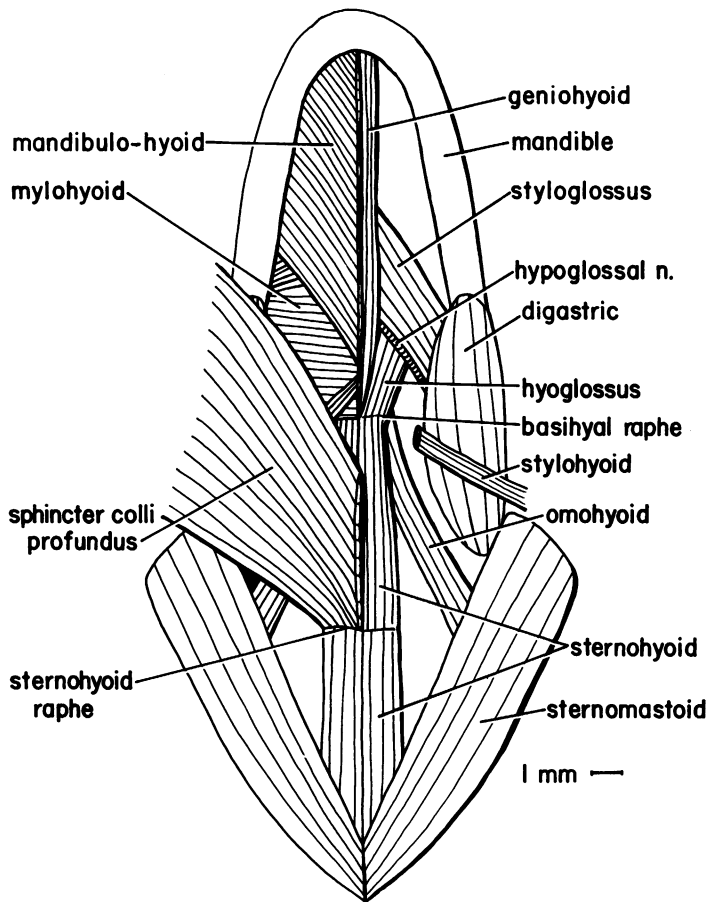


Fig. 6. Ventral view of the superficial hyoid muscles of *Lavia frons*. Deeper muscles are shown on the right (the bat's left side).

evidence for the close relationship of the three genera. Alternatively, loss of the anterior slip and retention of the posterior would also be a synapomorphy uniting the three genera, whereas the opposite condition would be an autapomorphy of *Macroderma*. The same phylogenetic tree would result in either case because of the uniqueness of the muscle morphology in *Macroderma*. We have incorporated our observations on the sphincter colli profundus as characters 1 and 2 in table 1.

M. stylopharyngeus

Figures 3, 5, 7, 9

ORIGIN: From the posteromedial surface of the stylohyal element at about the same point as the styloglossus takes origin (about half-way along the length of the stylohyal).

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

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: The muscle is the same in all known bats (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991).

M. ceratohyoideus

Figures 3, 5, 7, 9

ORIGIN: From the anterior surface of the thyrohyal element.

INSERTION: Onto the posterior surface of the ceratohyal element and onto the medial tip of the epihyal in most specimens of *Megaderma* examined. However, in some *Megaderma lyra*, the insertion is onto the posterior

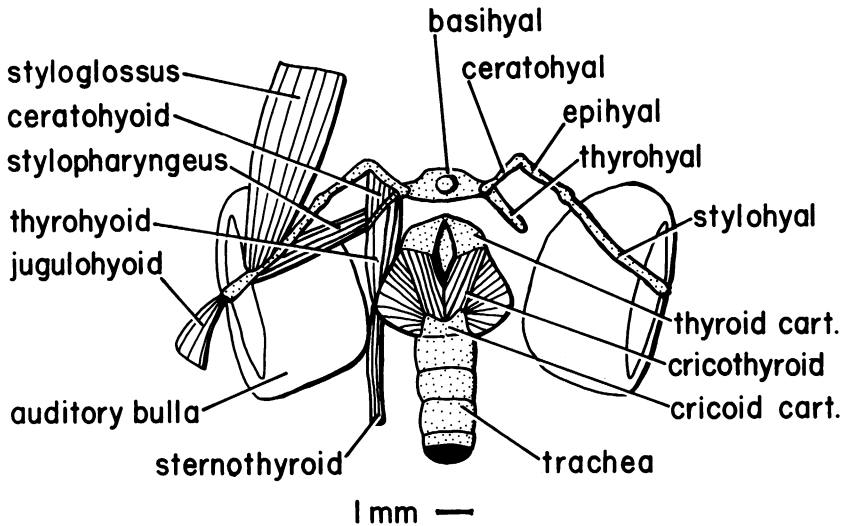


Fig. 7. Ventral view of the deep hyoid muscles and the hyoid apparatus of *Lavia frons*.

surface of the entire ceratohyal and the entire epihyal.

OTHER MEGADERMATIDS: In all *Macroderma* examined, the muscle inserts on the posterior surface of the ceratohyal and onto the posterior surface of the medial half of the epihyal. In *Cardioderma*, the insertion is quite reduced; it is restricted to the posterior surface of the ceratohyal alone. In *Lavia*, the insertion is variable: in most the ceratohyoid inserts on the entire ceratohyal and medial tip of the epihyal, while in others it inserts on the entire ceratohyal and the medial one-half of the epihyal (AMNH 49383).

COMMENTS: Griffiths (1982), Griffiths and Smith (1991), and Griffiths et al. (1991) have summarized the known variation in morphology of this muscle in Old and New World families of bats. The muscle is exceedingly variable, and it is impossible to determine the plesiomorphous state for Chiroptera with certainty (Griffiths and Smith, 1991). Because of these difficulties, we did not use this muscle in our analysis.

PHARYNGEAL CONSTRICTOR GROUP

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

M. hyopharyngeus
Not figured

ORIGIN: From the connective tissue (fascia) in the region of the pterygoid processes.

INSERTION: Into the connective tissue of the dorsal pharyngeal midline.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: The muscle is the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

M. thyropharyngeus
Not figured

ORIGIN: From the dorsal surface of the thyrohyal element.

INSERTION: Into the dorsal pharyngeal midline (the most superficial fibers insert directly into their antimere).

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: The muscle is the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

M. cricopharyngeus
Not figured

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

INSERTION: Into the dorsal pharyngeal midline (the most superficial fibers insert directly

into their antimeres). The anteriormost fibers run deep to the thyropharyngeus.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: The muscle is essentially the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

MYOTOMIC MUSCULATURE

LINGUAL GROUP

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

M. genioglossus

Not figured

ORIGIN: From the posterior surface of the mandible just lateral to the mandibular symphysis, deep to the origin of the geniohyoid.

INSERTION: Into the ventral midline of the tongue for much of the length of the tongue (there is no lateral swing of the posteriormost fibers as they insert).

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: This is a layered muscle; there appear to be a number of distinct slips to it. With minor variations in size and shape, this muscle is the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

M. hyoglossus

Figures 2, 4, 6, 8

ORIGIN: The origin of this muscle is complex. The ventral fibers (the bulk of the muscle) take origin from the connective tissue raphe (the basihyal raphe) that the hyoglossus shares with the sternohyoid and geniohyoid. There is a short tendon that passes deep to the basihyal from the raphe; thus the origin is indirectly from the basihyal by tendon. The dorsalmost muscle fibers originate from the lateral basihyal and the anterior surface of the thyrohyals. These are few in number and weakly developed in both species of *Megaderma*.

INSERTION: Into the posterolateral tongue, deep to the hypoglossal nerve and the styloglossus muscle.

OTHER MEGADERMATIDS: In *Cardioderma* and *Macroderma*, the origin of the muscle has not become as completely detached from

the basihyal element. Rather, the origin is from the basihyal raphe and from the lateral basihyal, and there is a separate set of fibers that take origin from the anteroventral surface of the thyrohyals. In *Lavia*, the hyoglossus is similar to that of *Megaderma*, except that there are no fibers originating from the thyrohyal element. The hyoglossus has no direct attachment to any part of the hyoid apparatus.

COMMENTS: In having an origin on the raphe shared with the sternohyoid and geniohyoid, megadermatid bats have developed a condition that is similar to that found in phyllostomid bats; Griffiths (1982) termed it the "free-floating" condition. *Cardioderma* and *Macroderma* possess a hyoglossus morphology that is derived with respect to outgroup genera (Griffiths and Smith, 1991), but primitive for the Megadermatidae family. In these two genera, the hyoglossus has begun to "lift off" the hyoid apparatus, but has retained a strong direct attachment to the basihyal. In *Megaderma* (both species) and *Lavia*, the hyoglossus has almost completely lifted free, becoming "free-floating." In *Megaderma*, there are some separate, lateralmost fibers that originate from the thyrohyal element, but in *Lavia* even this last attachment to the hyoid apparatus is lost. *Cardioderma* and *Macroderma* have a hyoglossus that closely resembles that of phyllostomine bats (for example, *Phyllostomus* or *Macrotus*; Griffiths, 1982). *Megaderma* and *Lavia* have gone substantially farther in the evolution of their hyoid muscle morphology. The hyoglossus of these two genera resembles that found in the more primitive nectar-feeding phyllostomid bats (for example, *Glossophaga*, *Monophyllus*, or *Lichonycteris*). Had they also evolved the advanced nectarivore tongue (Griffiths, 1982; Griffiths and Criley, 1989), there is no morphological barrier to their becoming nectarivorous.

We have coded the condition found in *Cardioderma* and *Macroderma* as a "+" in table 1 (character 5), indicating that the morphology is derived with respect to outgroups. *Megaderma* is coded as a "++" and *Lavia* as a "+++" indicating that we believe that the free-floating morphology was developed in the ancestor of *Lavia* and *Megaderma* from the condition found in the other megader-

matids, and that the ancestors of *Lavia* then lost the thyrohyal fibers of this muscle.

M. styloglossus

Figures 2–9

ORIGIN: From the ventral, lateral, and dorsal surfaces of the stylohyal element at approximately the midpoint of the element (opposite the stylopharyngeus origin).

INSERTION: Into the posterior half of the ventrolateral tongue surface.

OTHER MEGADERMATIDS: In *Megaderma* (both species), the muscle is unusual in two ways: first, the origin is unusually broad; and second, there are strips of tissue that we are unable to positively identify that run along the medial and lateral edges of this muscle (not illustrated). *Lavia* possesses both of these unusual features, but *Cardioderma* and *Macroderma* do not. In all four megadermatid genera, the muscle inserts rather posteriorly on the tongue, as compared with outgroup genera (Griffiths and Smith, 1991).

COMMENTS: As in the nectarivorous New World phyllostomids (Griffiths, 1982), the styloglossus of megadermatids inserts posteriorly on the tongue. This may be an adaptation that necessarily accompanies the "free-floating" condition of the sternohyoid, geniohyoid, and hyoglossus muscles. Griffiths (1978a, 1982) suggested that the free-floating condition was an adaptation permitting hyperextension of the tongue, and the far posterior insertion of the styloglossus might also facilitate this hyperextension. Whatever the functional reason for the condition, it is interesting that it is found in both the Old World and New World leaf-nosed bats. There is no sign of a double bellied origin of this muscle (as was found in some mormoopids and vespertilionids, Griffiths, 1982, 1983), though the origin is very broad.

The posterior insertion of this muscle into the tongue, found in all megadermatids, is coded as character 6 in table 1. The strips of unidentifiable tissue bordering the muscle are coded as character 7.

MEDIAL VENTRAL CERVICAL GROUP

The muscles of this group are innervated by a complex of nerves originating in the an-

terior cervical region, except for the geniohyoid which is innervated by N. hypoglossus (XII).

M. geniohyoideus

Figures 2, 4, 6, 8

ORIGIN: From the posterior surface of the mandible just lateral to the mandibular symphysis. The origin is fleshy (nontendinous).

INSERTION: Into the connective tissue raphe connecting the geniohyoid, the sternohyoid, and the hyoglossus, and by tendon to the basihyal element. There is also a direct attachment to the basihyal by a number of deep geniohyoid fibers.

OTHER MEGADERMATIDS: In *Lavia* the morphology is similar to that of *Megaderma* in that the geniohyoid retains a weaker, deep attachment directly to the basihyal (in addition to the stronger superficial insertion on the connective tissue raphe). *Macroderma* has a weak attachment on the raphe and a strong attachment directly on the basihyal. *Cardioderma* has a strong attachment on the basihyal and virtually no attachment onto the superficial raphe. The muscle is fused to its antimer for its entire length in all genera.

COMMENTS: Again, the megadermatids resemble the neotropical phyllostomid bats, though the morphology is not identical in the two families. *Cardioderma* has a completely plesiomorphous morphology, and *Macroderma* is very close to this, with only a few superficial fibers inserting into the basihyal raphe. We code *Cardioderma* as plesiomorphous in table 1 (character 8), and *Macroderma* as being slightly derived. *Lavia* and *Megaderma* (both species) are quite derived in losing all but a minimal direct attachment to the basihyal.

M. sternohyoideus

Figures 2, 4, 6, 8

ORIGIN: From the anterodorsal surface of the manubrium of the sternum (not from the lateral manubrium or from the clavicle).

INSERTION: Into the raphe connecting the sternohyoid to the geniohyoid and hyoglossus and, indirectly, by tendon to the basihyal.

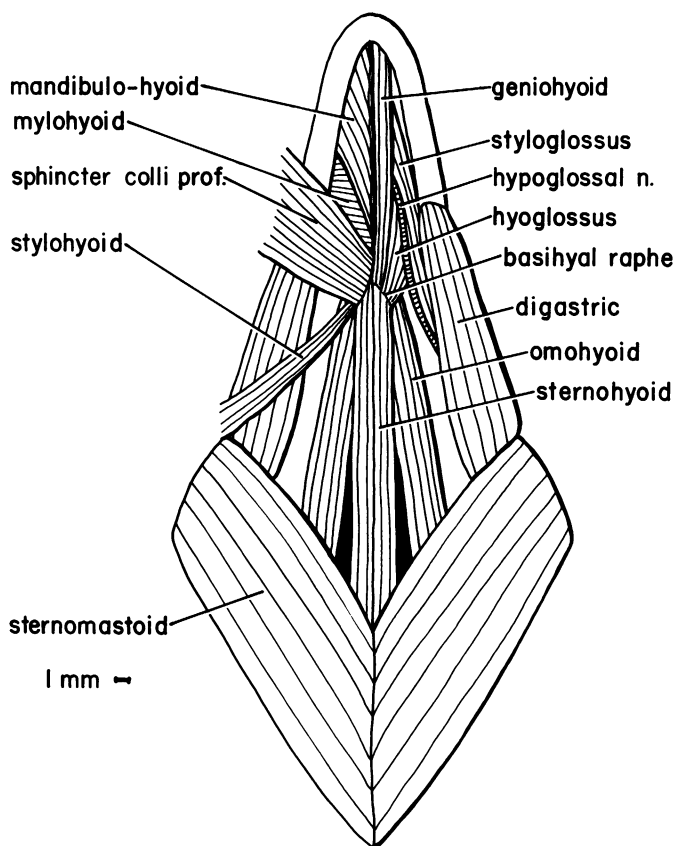


Fig. 8. Ventral view of the superficial hyoid muscles of *Macroderma gigas*. Deeper muscles are shown on the right (the bat's left side).

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: The muscle begins as a broad muscle, but narrows markedly as it passes anteriorly. About halfway along its length, the sternohyoid is crossed by a prominent raphe from which, in *Megaderma*, *Cardioderma*, and *Lavia*, the sphincter colli profundus takes origin. Anterior to the raphe, the two anteriores of the sternohyoid are fused into a single muscle.

There are three possible apomorphies. The first, found in all megadermatids, is the origin of the sternohyoid from the medial manubrium of the sternum. Primitively in the Chiroptera, the sternohyoid takes origin from the entire manubrium and in some species from the medial head of the clavicle (Sprague, 1943). Thus the origin from the medial manubrium is a derived trait found in all mega-

dermatids (table 1, character 9) and shared with *Rhinopoma*, *Nycteris*, and all known rhinolophids (rhinolophines and hipposiderines) (Griffiths and Smith, 1991). The second apomorphy (table 1, character 10) is found in all megadermatids: the lack of a direct attachment to the basihyal. A similar condition has been reported only in phyllostomids (Griffiths, 1978a, 1982), where it probably evolved by parallel evolution (see Discussion). The final possible apomorphy is the development of a new anterior portion of the sternohyoid in *Megaderma*, *Cardioderma*, and *Lavia*. This could explain why the sphincter colli profundus takes origin so far posteriorly in these three genera (although other possibilities are considered under "M. sphincter colli profundus" above). We have coded for this possibility under character 1 in table 1.

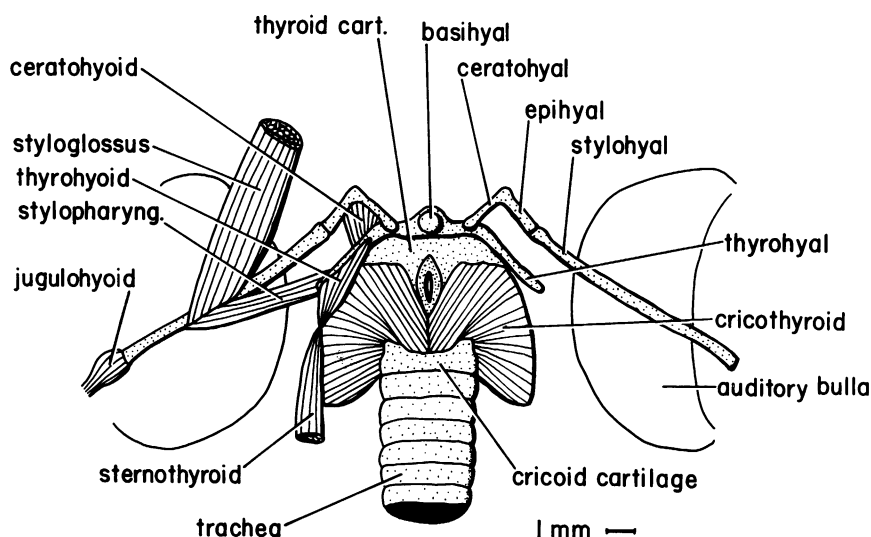


Fig. 9. Ventral view of the deep hyoid muscles and the hyoid apparatus of *Macroderma gigas*.

M. sternothyroideus

Figures 3, 5, 7, 9

ORIGIN: From the lateral manubrium of the sternum, lateral and slightly dorsal to the origin of the sternohyoid.

INSERTION: Onto the lateral surface of the posterior process of the thyroid cartilage, immediately posterior to the origin of the thyrohyoid.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids except *Macroderma*. In *Macroderma*, it originates from the lateralmost part of the manubrium, just medial to the sterno-clavicular articulation. In one specimen of *Macroderma* (AMNH 197210), the muscle originated slightly more laterally, from the sterno-clavicular articulation itself.

COMMENTS: This is a weak muscle, not well developed except in *Macroderma*. Comparison with all other known yinochiropteran genera (Griffiths and Smith, 1991) demonstrates that *Megaderma*, *Lavia*, and *Cardioderma* share the derived condition of "medial shift of origin and reduction of sternothyroid." We code this as character 4 in table 1.

M. omohyoideus

Figures 2, 4, 6, 8

ORIGIN: From the anterior surface of the midpoint of the clavicle.

INSERTION: Onto the posterolateral surface of the basihyal element.

OTHER MEGADERMATIDS: In all other megadermatids the muscle is the same.

COMMENTS: The unusual origin of the muscle from the midpoint of the clavicle (and not the scapula) is shared with emballonurids, rhinopomatids, and nycterids. This has been thoroughly discussed and evaluated by Griffiths and Smith (1991), and further comments on this will be made under Discussion in this paper. The trait is coded as apomorphic for all megadermatids as character 11 (table 1).

M. thyrohyoideus

Figures 3, 4, 5, 7, 9

ORIGIN: From the lateral thyroid cartilage.

INSERTION: Onto the posterior surface of the thyrohyal element.

OTHER MEGADERMATIDS: The muscle is the same in all megadermatids.

COMMENTS: The muscle is the same in all known bats (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991).

DISCUSSION

At some time prior to the late Eocene, perhaps 50 million years ago, we suggest that a minor evolutionary event occurred in one line of bats that was to have consequences in their

descendent's feeding, echolocation, and other activities. A small hyoid muscle, the omohyoid, that nominally runs from the anterior scapula in the shoulder to the hyoid bone of the throat, shifted its origin from the scapula to the midpoint of the clavicle. In the experience of the senior author, muscles evolve to become larger or smaller in an evolutionary line, they sometimes split into two or more bellies, and they frequently will shift their attachments slightly along a bone. But it is an uncommon event for a muscle to shift its origin from one bone to another across a joint. Thus we argue that it is exceedingly unlikely that such an event occurred twice independently, and because we observe the shifted origin in emballonurid, rhinopomatid, nycterid, and megadermatid bats (Sprague, 1943; Griffiths and Smith, 1991; Griffiths et al., 1991), we believe that it occurred once in a common ancestor of all four families (Griffiths and Smith, 1991). Such an ancestor must have lived prior to the divergence of the four families. Because fossil representatives of emballonurids, megadermatids, and possibly the other two families are known from late Eocene strata of Europe, the common ancestor must have lived prior to the late Eocene.

Whether or not the above hypothesis is correct, it is an observed fact that the omohyoid originates from the midpoint of the clavicle in all emballonurids, rhinopomatids, nycterids, and megadermatids that have been examined (Sprague, 1943; Griffiths and Smith, 1991; Griffiths et al., 1991). An omohyoid that originates from the clavicle rather than the scapula parallels the function of the sternohyoid much more closely; both run side-by-side from nearly the same origin (the clavicle versus the manubrium of the sternum) to virtually identical insertions on the hyoid apparatus. The omohyoid duplicates the function of the sternohyoid, providing posterior pull on the hyoid apparatus. We suggest that the shift of origin of the omohyoid and the resulting duplication of function freed the sternohyoid for other functional activities. Griffiths and Smith (1991) and Griffiths et al. (1991) reported on the most astonishing of these activities: in emballonurid bats, the sternohyoid has become attached to the posterior larynx and apparently functions as

an extrinsic laryngeal muscle. This very unusual adaptation is found in all emballonurid genera, but reaches the peak of development in the Old World genera *Coleura*, *Emballonura*, and *Mosia* (Griffiths et al., 1991), and in the New World genera *Peropteryx* and *Peronymus* (Griffiths and Smith, 1991). In rhinopomatids the duplication of function has allowed the sternohyoid to decrease dramatically in size (Griffiths and Smith, 1991) while the omohyoid assumes the primary responsibility for posterior pull on the hyoid apparatus. In all known nycterids (Sprague, 1943; Griffiths and Smith, 1991), apparently both the sternohyoid and omohyoid share equally the posterior pull function; both muscles are robust. And in the megadermatids, the assumption of the posterior pull function by the omohyoid has allowed the sternohyoid to detach from the hyoid apparatus, bearing some resemblance to the condition in New World phyllostomid bats that Griffiths (1982) termed "free-floating."

In all megadermatid genera, the sternohyoid has lost its direct connection to the basihyal (character 10, table 1). Accompanying this condition, the hyoglossus has at least partially detached from the hyoid apparatus, taking origin instead from the insertion of the sternohyoid via the connective tissue of the basihyal raphe (character 5, table 1). In *Megaderma* and *Lavia*, the hyoglossus is progressively more and more free of the hyoid bone (fig. 10, character state 5+), reaching the condition in *Lavia* where there are no fibers at all of the hyoglossus remaining attached (5++). Some megadermatids also have paralleled the phyllostomids in the development of a nearly free-floating geniohyoid (character 8, table 1). In *Cardioderma*, the geniohyoid is plesiomorphous in inserting directly onto the basihyal element. In *Macroderma*, most of the muscle attaches to the basihyal, but a few fibers pass superficial to the element to insert into the connective tissue of the basihyal raphe. In *Lavia* and *Megaderma*, most of the muscle inserts on the raphe, with only a small insertion onto the hyoid apparatus. This is the condition that parallels most closely the condition found in phyllostomids (Griffiths, 1978a, 1982). As in the phyllostomids, the styloglossus has

TABLE 1
Summary of the Apomorphies Used in Constructing the Cladogram (fig. 10)

(+ = apomorphic character state; - = plesiomorphic character state). Outgroups used are described in Griffiths and Smith (1991) and Griffiths et al. (1991).

Character State	Taxon				
	Meg	Car	Lav	Mac	OUT
1. Loss of anterior slip of sphincter colli profundus (or posterior "sliding" of sphincter colli profundus as the sternohyoid develops a new anterior part)	+	+	+	-	-
2. Loss of posterior slip of sphincter colli profundus (or retaining the plesiomorphous position of the sphincter colli profundus)	-	-	-	+	+
3. Loss of jugulohyoid	-	+	-	-	- ^a
4. Medial shift of origin and reduction of sternothyroid	+	+	+	-	-
5. Development of detached hyoglossus origin	++	+	+++	+	-
6. Posterior insertion of styloglossus	+	+	+	+	-
7. Strips of tissue bordering styloglossus (or unusually broad origin of styloglossus)	+	-	+	-	-
8. Development of detached geniohyoid insertion	++	-	++	+	-
9. Origin of sternohyoid from medial manubrium	+	+	+	+	+/- ^b
10. Development of detached sternohyoid insertion	+	+	+	+	-
11. Origin of omohyoid from clavicle midpoint	+	+	+	+	+/- ^c

Meg = *Megaderma* (both species), Car = *Cardiaderma*; Lav = *Lavia*; Mac = *Macroderma*; OUT = outgroup genera in Rhinopomatidae, Emballonuridae, Rhinolophidae, and Nycteridae.

^a Apomorphic in the derived emballonurid genera *Diclidurus*, *Balantiopteryx*, *Saccopteryx*, *Cormura*, *Peropteryx*, and *Peronymus* (Griffiths and Smith, 1991).

^b Apomorphic in rhinopomatids, nycterids, and known rhinolophids; plesiomorphic in emballonurids (Griffiths and Smith, 1991).

^c Apomorphic in rhinopomatids, nycterids, and emballonurids; plesiomorphous in known rhinolophids (Griffiths and Smith, 1991).

shifted its insertion posteriorly (character 6, table 1) in all megadermatids.

It might be tempting for persons in search of unusual or controversial chiropteran phylogenies to interpret the development of a "free-floating" strap muscle morphology as a synapomorphy (or synapomorphies) shared by phyllostomids and megadermatids. We believe that this is almost surely not the case because the free-floating condition appears to have developed in a different fashion in the two families. In phyllostomids, all three muscles (the sternohyoid, hyoglossus, and geniohyoid) seem to have "lifted off" the basihyal together. In every phyllostomid examined, although the degree of detachment might be different between different phyllostomid taxa, within each taxon the three muscles were always dissociated from the basihyal to the same degree (Griffiths, 1982). In contrast, in mega-

dermatids the three strap muscles appear to have dissociated from the basihyal at different times and rates. In all four genera, the sternohyoid is completely dissociated, implying that this event occurred relatively early on in the evolution of the family (and, as we suggest, we believe that this dissociation was facilitated by the omohyoid assuming the function of the sternohyoid, something that did *not* occur in the phyllostomid line). However, the hyoglossus and especially the geniohyoid vary widely in their degree of dissociation (= lifting off) from the basihyal. In *Cardiaderma* there is virtually no dissociation of the geniohyoid, and in *Macroderma* there is relatively little. The hyoglossus is completely dissociated from the basihyal in *Lavia*, but shows a lesser degree of dissociation in the remaining megadermatid genera. Unless one is prepared to argue that megader-

matids are diphyletic and the genera *Megaderma* and *Lavia* are more closely related to phyllostomids than either is to *Cardioderma* and *Macroderma*, the differences in the degree of development we have observed in phyllostomids and megadermatids strongly suggest that the "lifting off" from the basihyal occurred independently in the two lineages.

The most interesting of all megadermatid apomorphies is perhaps the unusual position of the sphincter colli profundus in three genera. In *Lavia*, *Megaderma*, and *Cardioderma*, the sphincter colli profundus takes origin from a raphe which bisects the sternohyoid muscle (figs. 2, 4, 6), whereas in *Macroderma*, the origin is from the basihyal raphe (fig. 8), as in virtually all other known bats. It is possible that primitively there were two original slips to this muscle, the anterior one originating from the basihyal raphe and the posterior one originating from the sternohyoid raphe. If this is the case, *Macroderma* lost the posterior slip and the other three genera lost the anterior one in their respective phylogenetic lines (characters 1 and 2, table 1). There are two problems with this idea. First, if two slips existed originally, why haven't more bat genera retained the posterior slip? The only other genus of bat known to have "retained" a posterior slip is *Chaerephon*, a molossid bat (Sprague, 1943). None of the dozens of other mega- or microchiropteran bat genera that have been examined show any trace of the putative posterior slip (Sprague, 1943; Griffiths, 1978a, 1978b, 1982, 1983; Griffiths and Smith, 1991; Griffiths et al., 1991). Second, if two slips existed originally, why is there no trace of a vestigial posterior slip in *Macroderma*, and no trace of an anterior slip except for a few fibers in two specimens of *Lavia frons* that might equally well be explained in another way (see below)? An alternative explanation is that there was a single slip of the sphincter colli profundus originating from the basihyal raphe in the ancestral megadermatid. *Macroderma* alone among the extant genera has retained the plesiomorphous condition. In the line leading to *Megaderma*, *Lavia*, and *Cardioderma*, a new anterior part of the sternohyoid developed, lengthening the muscle and displacing the sphincter colli posteriorly as it did so. The few fibers observed in two specimens of *Lavia* could have been left

in an anterior position as ontogenetic lengthening of the new anterior part of the sternohyoid occurred, and in fact, careful observation of the position and orientation of the anterior fibers in the two specimens of *Lavia* suggests that this possibility is likely. We have examined the innervation of the anterior sternohyoid and the sphincter colli profundus carefully to see if there is evidence for or against this hypothesis, but we are unable to confirm or deny it. In any event, whichever hypothesis is correct, the phylogenetic consequences are the same. Under either hypothesis, *Megaderma*, *Lavia*, and *Cardioderma* share a synapomorphy. *Macroderma* either has an autapomorphy or the plesiomorphous character state, but in either case is a sister group to the other three genera.

A summary of all shared derived characters is presented in table 1. The cladogram based on these is shown in figure 10. All four extant genera share the derived character states of detached hyoglossus origin (5), posterior insertion of the styloglossus (6), origin of the sternohyoid from the medial sternal manubrium (9), development of a detached sternohyoid insertion (10), and origin of the omohyoid from the clavicular midpoint (11). Character states 5, 6, and 10 are all part of the "free-floating" strap muscle condition, found only in megadermatids among all emballonuroid or rhinolophoid families. They would be synapomorphies supporting the monophyly of the family. Derived character state 11 is shared by emballonurids, rhinopomatids, and nycterids, and is shown as a synapomorphy uniting that group of families (as it is in Griffiths and Smith, 1991). Derived character state 9 is shared by rhinopomatids, nycterids, and rhinolophids, but not emballonurids (Griffiths and Smith, 1991). In the present study we treat it as a synapomorphy, but are unsure whether or not it is due to homoplasy. If treated as a synapomorphy, the emballonurids would need to have undergone a reversal of this trait (fig. 10). In figure 11, we present an alternative cladogram illustrating what the phylogeny of these families of bats might be if character state 9 is a synapomorphy of nycterids, rhinolophids, megadermatids, and rhinopomatids that never evolved in the ancestors of emballonurids. The families Nycteridae, Rhinolophi-

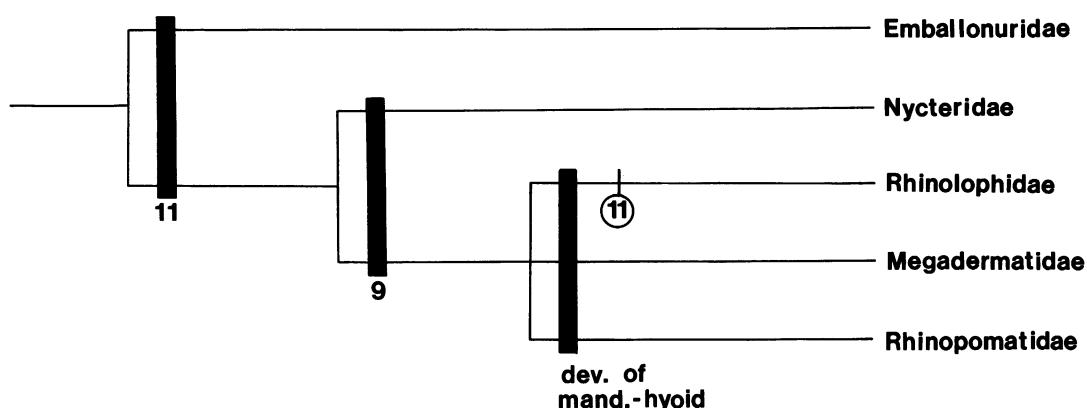


Fig. 11. An alternative interpretation of interfamilial relationships. See text for explanation. Numbers refer to synapomorphies listed in table 1. No convergent events are necessary, and only one reversal (circled) is necessary in character state 11.

ically distant from the rest of the family, whereas dental data suggest that it is a highly derived species that is closely related to *Megaderma lyra* (Hand's conclusions prompted her to resurrect the old name *Lyroderma lyra* for this species). Conversely, our hyoid data suggest that *Lavia frons* is apomorphic in a variety of ways, and is closely related to both species of *Megaderma*. Hand's dental data suggest that *Lavia* is plesiomorphous and phylogenetically distant from other living forms. We do agree that both species of *Megaderma* (or *Megaderma* and *Lyroderma*, following Hand) are derived, and that *Cardioderma cor* is intermediate in the cladogram for the family. We also strongly agree with Hand's (1985) statement that "There is little to suggest a close special relationship between these two living African species [*Cardioderma cor* and *Lavia frons*]." The fundamental difference in the two cladograms involves the placement of *Lavia frons* and *Macroderma gigas*. Reverse the position of these two species in either cladogram and the two cladograms will be more similar.

The family Megadermatidae is evolutionarily very old. If the throat morphology is an accurate indicator, the Australian genus *Macroderma* is phylogenetically distant from the remainder of the family. Its hyoid morphology, while derived in comparison with outgroups, is the most primitive of any megadermatid's. *Macroderma* is at a less-developed grade of evolution, and it may be that the

genus was isolated on Australia at a very early stage of morphological development in the family. Perhaps the family continued to develop the "free-floating" strap muscle morphology, the posteriorly displaced sphincter colli, and the other adaptations on the mainland while *Macroderma* remained at the primitive stage of its evolution. Within the remaining three genera, there is strong evidence that *Megaderma* (both species) and *Lavia* are phylogenetically very close. Not only do they share derived morphological features of the hyoid region, but also they possess a number of unique, apparently derived, features of the larynx (not described in this work). *Cardioderma* appears to be at an intermediate grade of evolution, between *Macroderma* and the *Megaderma-Lavia* group.

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