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The Systematic Relationship of *Emballonura nigrescens* to other Species of *Emballonura* and to *Coleura* (Chiroptera: Emballonuridae)

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ABSTRACT

Dissection of the hyoid musculature and examination of ear, penial, and skull morphology of eight species of *Emballonura* and one species of *Coleura* reveal that, with the exception of *Emballonura nigrescens*, all species share a derived character of the hyoid region. The sternohyoid muscle in all species except *nigrescens* is deflected dorsally and laterally by a prominent postlaryngeal tracheal expansion. Additionally, *E. nigrescens* is clearly derived in having a distinctive penis, in contrast

with other species of *Emballonura* as well as *Coleura*. These observations strongly suggest that non-*nigrescens* species of *Emballonura* are more closely related to species of *Coleura* than either is to *Emballonura nigrescens*. We conclude therefore that the available generic name *Mosia* Gray, 1843, should be used for the species currently called *Emballonura nigrescens*. We continue to recognize *Coleura* as a valid third genus.

INTRODUCTION

The species that is known today as *Emballonura nigrescens* was first described as *Mosia nigrescens* by Gray (1843). Peters (1867) included *nigrescens* in the genus *Emballonura*.

Dobson (1878) followed Peters in placing the species in *Emballonura*. However, he recognized that *nigrescens* was morphologically distinct from other *Emballonura* species. On

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the basis of facial and tooth characters, he placed *nigrescens* in the subgenus *Mosia*, while including *atrata*, *monticola* (including *alecto*), and *semicaudata* in the nominate subgenus. *Mosia* was characterized by: nostrils widely separated, opening by elliptical apertures placed obliquely; upper lip not projecting in front; lower incisors filling space between canines. The subgenus *Emballonura* was represented as having: nostrils close together in front, opening by circular apertures directed anteriorly; upper lip projecting beyond the lower; lower incisors separated on each side from the canines. Tate and Archbold (1939) figured skulls of emballonurid bats, but did not recognize *Mosia* even as a subgenus. *Emballonura nigrescens* was characterized as: size very small, marked shortening of skull, nasal sulcus undeveloped, postorbital crests strongly developed, molar tooth series slightly convergent anteriorly, and rostrum flattened.

In this paper, we present evidence from our studies of the hyoid region musculature, penis form, skull morphology, and tragus shape suggesting that *Emballonura nigrescens* should be excluded from the genus *Emballonura* and placed in the resurrected genus *Mosia*. Derived characters (apomorphies) of the hyoid region, shared by all species of *Emballonura* except *nigrescens*, and by species within the genus *Coleura* support the hypothesis that *nigrescens* is the sister group of the *Emballonura-Coleura* group, and deserves full generic status as *Mosia nigrescens*.

MATERIALS AND METHODS

Fluid-preserved museum specimens of the following bat species were examined. Family Emballonuridae: *Coleura afra*: American Museum of Natural History (AMNH) 188268, 188269, 237325; Museum of Comparative Zoology, Harvard (MCZ) 49800 (for penis characters); *Emballonura alecto*: Field Museum of Natural History (FMNH) 80373, 80375; *E. atrata*: FMNH 74199, 74203; *E. beccarii*: AMNH 192816 (for penis and tragus characters), 257111, FMNH 54862, 54869; *E. monticola*: AMNH 216794, FMNH 44149; *E. nigrescens*: AMNH 143879, 144055 (for penis characters), 144057, FMNH 33665 (for tragus charac-

ters), 33696 ("n. solomonsis"); *E. raffrayana*: AMNH 193598, 193599, 193604, FMNH 54843 (for penis and tragus characters); *E. semicaudata* (including *sulcata*⁴): AMNH 68833, 87135 (for penis and tragus characters), FMNH 54850, 54853, 65582; *Taphozous georgianus*: AMNH 197189 (for penis and tragus characters); *T. melanopogon*: AMNH 237735, 237736; *T. nudiventris*: AMNH 208127, FMNH 11121.

Skeletal specimens of the following species were examined. *Coleura afra*: AMNH 82237, 187346, 188255; *Emballonura alecto*: AMNH 106860, 153215, 241781, 254543; *E. beccarii*: AMNH 192817; *E. furax*: AMNH 221958; *E. monticola*: AMNH 103873, 247237; *E. nigrescens*: AMNH 105343, 194336; *E. raffrayana*: AMNH 99485, 99487, 101939; *E. semicaudata* (including *sulcata*⁴): AMNH 3285, 87136, 87188, 256514; *Taphozous mauritanus*: AMNH 257150; *T. nudiventris*: AMNH 27391; *T. theobaldi*: AMNH 241412.

ACKNOWLEDGMENTS

We thank Bruce Patterson of the Field Museum of Natural History for access to specimens and for the use of facilities and equipment at the museum. We thank David Klingener of the University of Massachusetts; Robert DuBose of Washington University, St. Louis; and John Edwards Hill, recently retired from the British Museum (Natural History) for their extremely helpful reviews of the manuscript. We are grateful to DuBose for his PAUP analysis of our data, confirming our hand-generated cladogram; and to Hill for sharing some of his unpublished observations on *Emballonura*. Artist Carolyn N. Gray produced the originals of figures 8 and 9 while working for Starrett. These were recopied in slightly different form by Andrea L. Smith of Illinois Wesleyan University for the present study. Pam Sponholtz of IWU assisted in the production of figure

⁴ *Emballonura sulcata* is here included in *E. semicaudata* because KFK has found that although *sulcata* can be distinguished from *E. s. semicaudata* by several characters, these break down when *E. s. palauensis* and *E. s. rotensis* are considered.

10. All other illustrations are originals by TAG.

DESCRIPTION OF THE HYOID APPARATUS

Sprague (1943) and Wassif and Madkour (1968–69) provided the only detailed previous descriptions of the elements of the emballonurid hyoid apparatus. In general, our observations agree with theirs. The basihyal of all species examined by us is roughly diamond-shaped (figs. 2, 4, 6), similar to the basihyal of *Taphozous perforatus* described by Wassif and Madkour (1968–69). The thyrohyals are paddle-shaped and strongly fused to the basihyals. The ceratohyal (=“hypohyal” of Sprague, 1943, and Wassif and Madkour, 1968–69) is a small, well-formed element that articulates with the basihyal and epihyal by a freely moveable synchondral joint. The epihyal (=“ceratohyal” of Sprague, 1943, and Wassif and Madkour, 1968–69) is approximately 1½ times as long as the ceratohyal in *Taphozous*, and about twice as long as the ceratohyal in all species of *Emballonura*. It articulates via a synchondral joint with the stylohyal. The stylohyal is the longest element of the anterior cornu. In all specimens examined, it extends from its articulation with the epihyal to the posterolateral rim of the auditory bulla, where it expands to form a flattened paddle (figs. 2, 4, 6). There is a pronounced bend in the stylohyal at about the point where the styloglossus and stylopharyngeus muscles originate. The bend is not visible in figure 4 because of the orientation of the stylohyal, but it is present.

The anatomy of the larynx is not described in detail in this work, but a few features of tracheal and laryngeal anatomy should be noted here. The larynx of all specimens examined has a large, complex cricothyroid muscle which takes origin from an elongated cricoid cartilage (figs. 2, 4, 6). The trachea of all species of *Taphozous* is typically mammalian, but in *Emballonura* and *Coleura* the tracheal rings immediately posterior to the larynx are expanded to form a large, postlaryngeal chamber (noted also by Sprague, 1943, in *Emballonura semicaudata*). In *Emballonura nigrescens*, the tracheal expansion is present in some (but not all) specimens ex-

amined. It was not present in the Field Museum specimens examined. When present, it appears to be located more dorsally on the sides of the trachea (fig. 7) than in other *Emballonura*. It is probable that the postlaryngeal chamber of *E. nigrescens* is not homologous with that of other species of *Emballonura*.

DESCRIPTION OF THE HYOID MUSCLES

Each muscle is described as it appears in specimens of *Emballonura raffrayana* dissected. Unless otherwise noted under Exceptions, the muscle is similar in all other specimens of *Emballonura* and *Coleura*, and in all species of *Taphozous* dissected.

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, 7

ORIGIN: From the medial surface of the mandible for much of the length of the mandibular body.

INSERTION: Into its antimeres along the ventral midline raphe and, posteriorly, onto the ventral tip of the basihyal and the ventral surface of the thyrohyal.

EXCEPTIONS: None.

COMMENTS: In all specimens, the mylohyoid is thickest anteriorly and posteriorly and thinnest between these two extremes. However, it is never aponeurotic or broken into distinct anterior and posterior parts, as was found in some phyllostomid bat genera (Griffiths, 1982).

M. mylohyoideus profundus

This muscle is absent in all specimens dissected. The term “mylohyoideus profundus” was coined by Griffiths (1978a) to describe a deep, posterior piece of the mylohyoid which seemed to have become a separate muscle in phyllostomid bats. This deep mylohyoid ap-

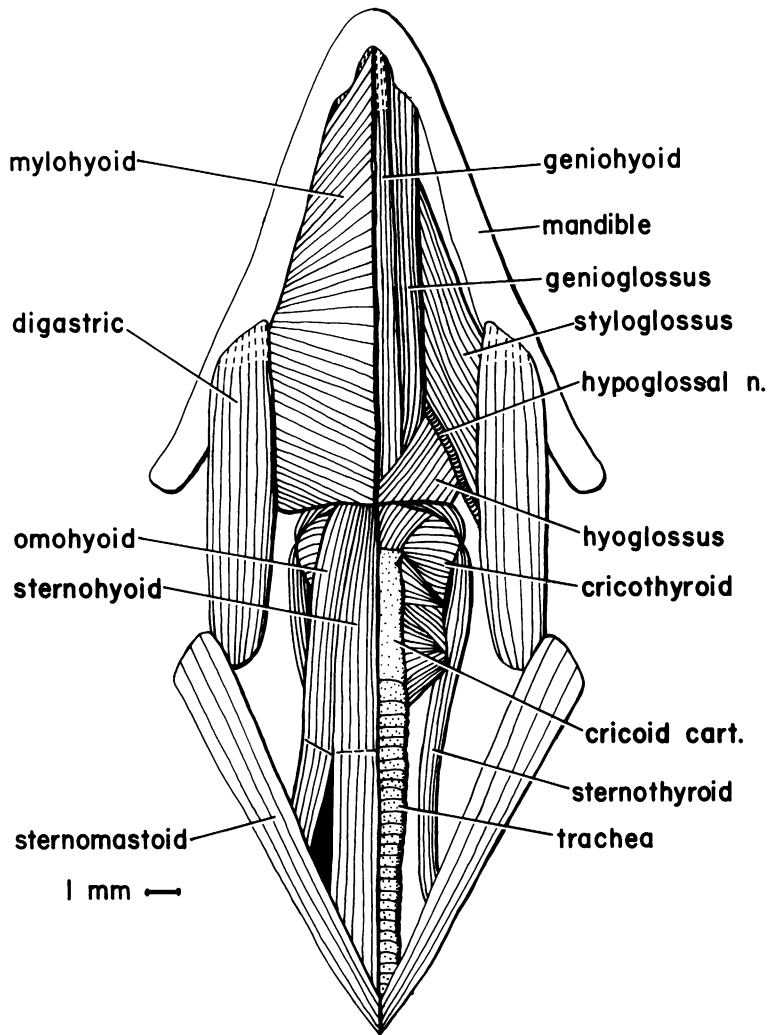


Fig. 1. Ventral view of the hyoid region of *Taphozous melanopogon*. The mylohyoid, sternohyoid, and omohyoid are removed on the right side to expose deeper muscles.

parently had remained attached to the basihyal as the remainder of the mylohyoid was displaced superficially by the development of a "free-floating" sternoglossus complex.

Griffiths (1982) mistakenly used the term "mandibulo-hyoideus" to describe his "mylohyoideus profundus" of 1978, believing that Sprague (1943) had previously described the deep mylohyoid under that term. Additional dissections of other bat species revealed that Sprague was describing another muscle, and "mandibulo-hyoideus" should be reserved for that muscle. All written descriptions and

figures in Griffiths (1982) are accurate, except that wherever the term "mandibulo-hyoideus" is used in that paper, "mylohyoideus profundus" should be substituted.

M. mandibulo-hyoideus (sensu Sprague, 1943)

This muscle is absent in all specimens dissected.

HYOID CONSTRICTOR GROUP

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

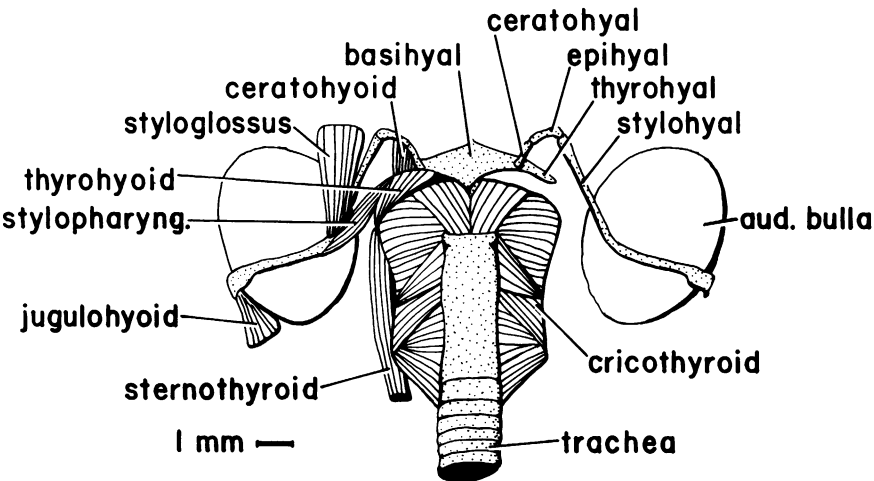


Fig. 2. Ventral view of the hyoid apparatus, deep hyoid muscles, larynx, and trachea of *Taphozous melanopogon*.

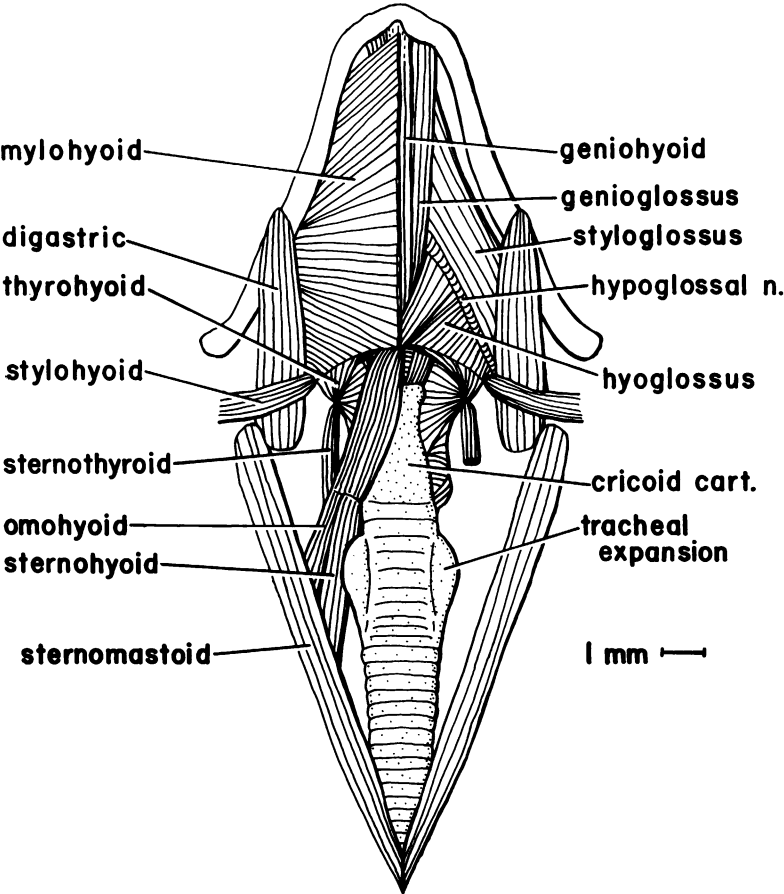


Fig. 3. Ventral view of the hyoid region of *Emballonura raffrayana*. Superficial hyoid muscles are removed on the right side.

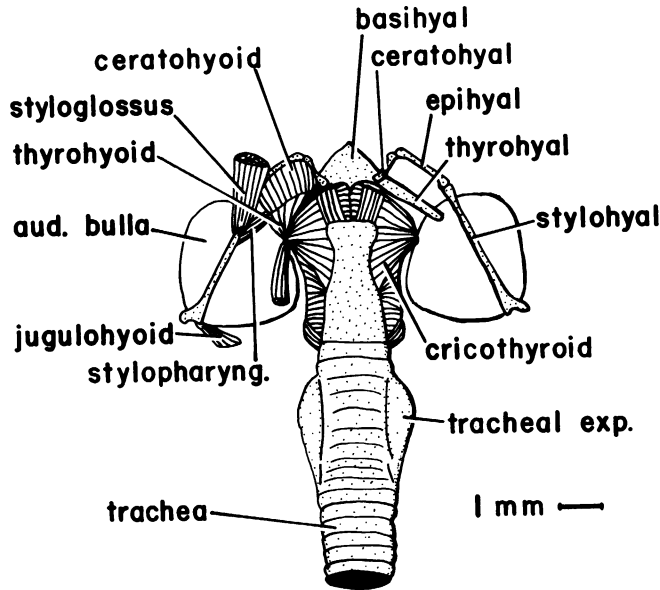


Fig. 4. Ventral view of the hyoid apparatus, deep hyoid muscles, larynx, and trachea of *Emballonura raffrayana*.

M. stylohyoideus

Figures 3, 5, 7

ORIGIN: By short tendon from the medial surface of the distal expansion of the stylohyal.

INSERTION: The muscle passes medially and curves around the ventral surface of the digastric to insert on the lateral tip of the thyrohyal.

EXCEPTIONS: The muscle is absent in all specimens of *Taphozous* dissected, but is otherwise the same in all other species dissected.

COMMENTS: Sprague (1943) suggested that among the bats he dissected, only *Rhinopoma* had a significantly long tendinous origin from the stylohyal. The stylohyoid of *Emballonura* was described as "mostly fleshy." Our findings differ from his; there is a significant length of tendon in *Emballonura* too. Sprague (1943) noted the absence of this muscle in *Taphozous nudiventris*.

M. jugulohyoideus

Figures 2, 4, 6

ORIGIN: From the paroccipital shelf just posterior to the auditory bulla.

INSERTION: Onto the expanded lateral tip of the stylohyal.

EXCEPTIONS: None.

M. sphincter colli profundus

This muscle is completely absent in all specimens dissected.

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, at about the same level as the origin of the styloglossus, or slightly distal to it (there is some interspecific variability).

INSERTION: Into the lateral wall of the pharynx, passing into the pharynx wall just anterior to the course of the thyropharyngeus.

EXCEPTIONS: None.

COMMENTS: In phyllostomid bats (Griffiths, 1982), the origins of the stylopharyngeus and styloglossus muscles are much more distally located on the stylohyal element.

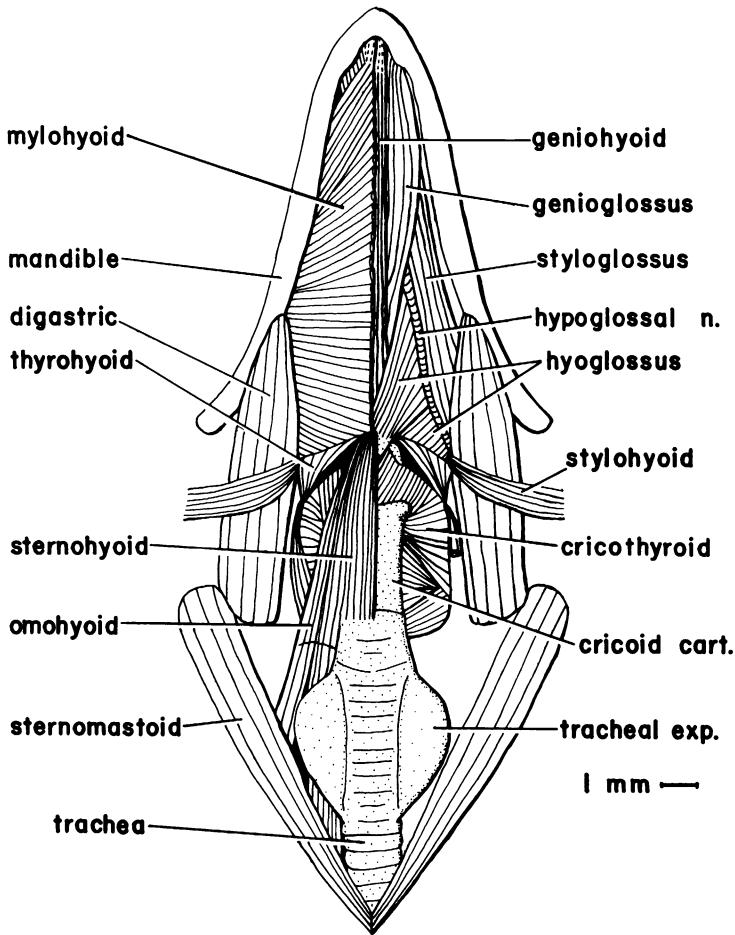


Fig. 5. Ventral view of the hyoid region of *Coleura afra*. Superficial hyoid muscles are removed on the right side.

M. ceratohyoideus

Figures 2, 4, 6

ORIGIN: From the anterior surface of the thyrohyal bone.

INSERTION: Onto the posterior surface of the ceratohyal, epihyal, and medial tip of the stylohyal bones.

EXCEPTIONS: In *Coleura* and in all other species of *Emballonura* (including *nigrescens*) the muscle is the same: the ceratohyoid inserts on the posterior surfaces of the ceratohyal, epihyal, and the medial epihyal. In *Taphozous melanopogon* the origin is the same, but the insertion is onto the posterior surface of the ceratohyal and onto the pos-

terior surface of the medial one-half of the epihyal. In *T. nudiventris*, the insertion is onto the posterior surface of the ceratohyal alone.

COMMENTS: It is difficult to know how much significance to give to the variation in the insertion of this muscle. All elements in the anterior cornu are closely linked by synchondral joints. It would appear that the ceratohyoid could easily extend its insertion across a joint, thus inserting on two (or more) elements rather than one. Nevertheless, the insertion of the muscle onto all three anterior cornu elements in species of *Emballonura* and *Coleura* might be a synapomorphy uniting those species. Additionally, the variation in morphology between species of *Taphozous*

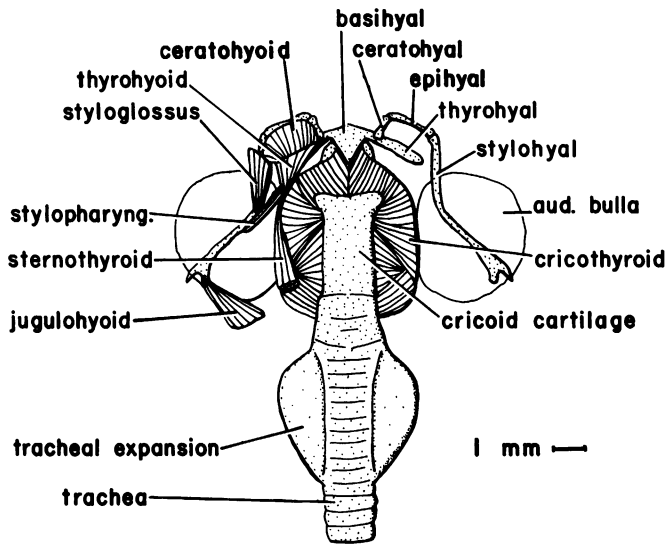


Fig. 6. Ventral view of the hyoid apparatus, deep hyoid muscles, larynx, and trachea of *Coleura afra*.

ultimately might prove valuable in working out systematic relationships within the genus.

PHARYNGEAL CONSTRICTOR GROUP

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

M. hyopharyngeus
Not figured

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

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

EXCEPTIONS: None.

COMMENTS: Though this muscle is more robust than in any phyllostomid bat dissected (Griffiths, 1982, 1983), it is still one of the less well-developed hyoid muscles. It consists of muscle fibers running in the fascia of the dorsoposterior pharynx.

M. thyropharyngeus
Not figured

ORIGIN: From the dorsal surface of the tip of the thyrohyal bone.

INSERTION: Into the dorsal midline of the pharynx.

EXCEPTIONS: None.

M. cricopharyngeus
Not figured

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

INSERTION: Into the dorsal midline of the pharynx.

EXCEPTIONS: None.

MYOTOMIC MUSCULATURE

LINGUAL GROUP

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

M. genioglossus
Figures 1, 3, 5, 7

ORIGIN: From the posterior surface of the anterior mandible, just dorsal and slightly lateral to the origin of the geniohyoid. In all species examined, there is a small process on the ventromedial surface of the mandible from which the genioglossus takes origin.

INSERTION: Into the ventral surface of approximately the posterior one-third of the tongue; the most posterior fibers turn laterally and pass deep to the hyoglossus to insert laterally in the posterior tongue.

EXCEPTIONS: This muscle is the same in all

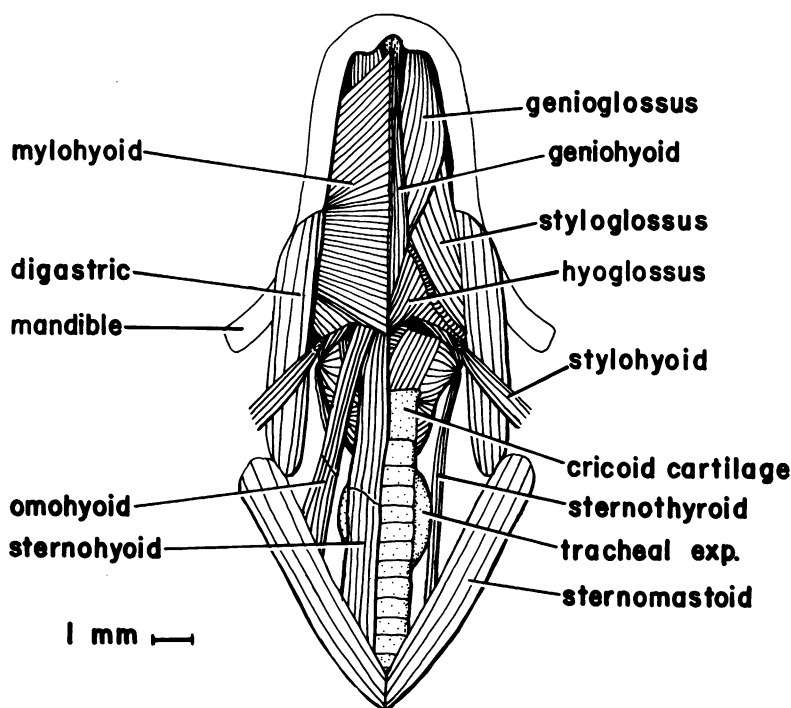


Fig. 7. Ventral view of the hyoid region of "*Emballonura*" *nigrescens*. Superficial hyoid muscles are removed on the right side.

specimens dissected. It is particularly robust in *nigrescens* (fig. 7).

COMMENTS: In all emballonurids examined, this muscle is very easy to see. It requires very little dissection to reach it, other than the removal of the mylohyoid. The reason for this is that the geniohyoid, which covers the genioglossus in other bat taxa (Sprague, 1943; Griffiths, 1978a, 1982) is markedly reduced in emballonurids.

M. hyoglossus
Figures 1, 3, 5, 7

ORIGIN: The anteriormost fibers originate from the connective tissue connecting the hyoglossus with its antimere; more posteriorly, from the ventrolateral part of the basihyal bone; the posteriormost fibers, from the ventral surface of the thyrohyal bone.

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

EXCEPTIONS: None.

COMMENTS: The hyoglossus is a particu-

larly broad muscle in all emballonurids dissected.

M. styloglossus
Figures 1, 3, 5, 7

ORIGIN: From the ventral surface of the proximal stylohyal bone.

INSERTION: Into the lateral surface of the tongue.

EXCEPTIONS: This muscle is the same in all specimens dissected, except that in one specimen of *Taphozous nudiventris* from the Field Museum, some fibers of styloglossus took origin from the fascia of the medial auditory bulla.

COMMENTS: The origin of this muscle in emballonurids is from a point much more anteriorly (and medially) located on the stylohyal than in phyllostomid bats (Griffiths, 1982).

MEDIAL VENTRAL CERVICAL GROUP

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

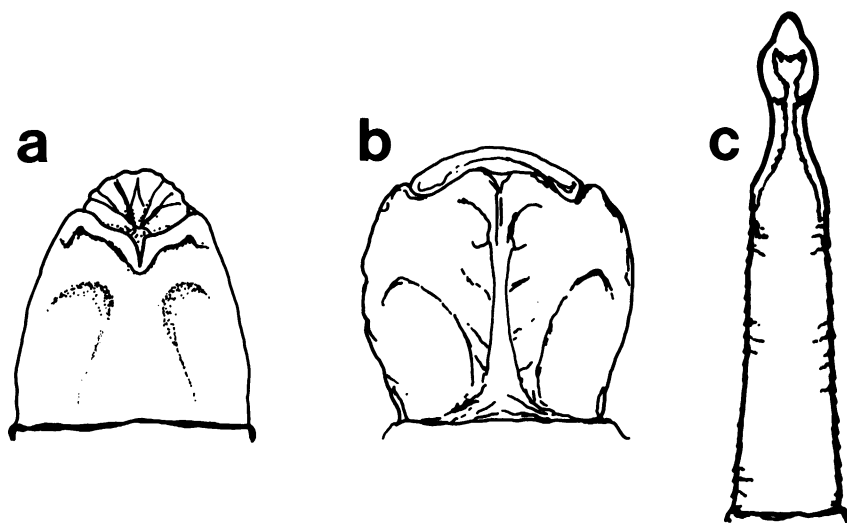


Fig. 8. Ventral view of the caudally directed penises of *Coleura afra* (a), *Emballonura raffrayana* (b), and "*E.*" *nigrescens* (c); spines omitted.

terior cervical region, except for the geniohyoid which appears to be innervated primarily by N. hypoglossus (XII).

M. geniohyoideus

Figures 1, 3, 5, 7

ORIGIN: By tendon, from the posterior surface of the mandible, just lateral to the mandibular symphysis.

INSERTION: Onto the anterior surface and ventral tip of the basihyal bone.

EXCEPTIONS: None.

COMMENTS: In all specimens of *Emballonura* and *Coleura* examined, the geniohyoid is reduced in size and fused to its antimeres except at the tendinous origin. In all specimens of *Taphozous* the muscle is robust. In *Taphozous*, the tendon of origin of the geniohyoid is often fused with an overlying connective tissue sheet extending from the mylohyoid raphe to the symphysis of the jaw. This is not the case in smaller emballonurid species examined.

M. sternohyoideus

Figures 1, 3, 5, 7

ORIGIN: By two slips, the medial from the anterior surface of the manubrium of the sternum; the lateral, from the proximal head of the clavicle (closely associated with the origin of the sternothyroid).

INSERTION: In all specimens of *Emballonura*, there is a strong attachment to the posterior larynx in the region of the posterior cricoid cartilage/first tracheal ring. To reach this attachment point, in all species except *nigrescens*, the muscle passes dorsal to a well-developed tracheal expansion (fig. 3). After the attachment, the muscle continues anteriorly to ultimately insert on the posterior edge of the basihyal bone.

EXCEPTIONS: In *Coleura* the muscle is attached and runs the same way. The attachment of the anterior sternohyoid to the posterior larynx is especially well developed (fig. 5). The fibers of the anterior sternohyoid have extended medially along the cartilage, apparently to obtain a stronger attachment to this region. In *Taphozous* there is a weaker attachment to the posterior larynx, and the muscle is not dorsally deflected by a postlaryngeal expansion. In *Emballonura nigrescens* the attachment is strong, as in other *Emballonura*, but there is no dorsal deflection.

COMMENTS: In all species of *Emballonura* except *nigrescens*, and in *Coleura*, the course of the muscle is very unusual. The two antimeres of the muscle do not lie together as is the case in most mammals. Each sternohyoid antimeres passes anteriorly in a position that is lateral and dorsal to the expanded tracheal expansion (figs. 3, 5). The muscle then passes ventrally and anteriorly to attach to

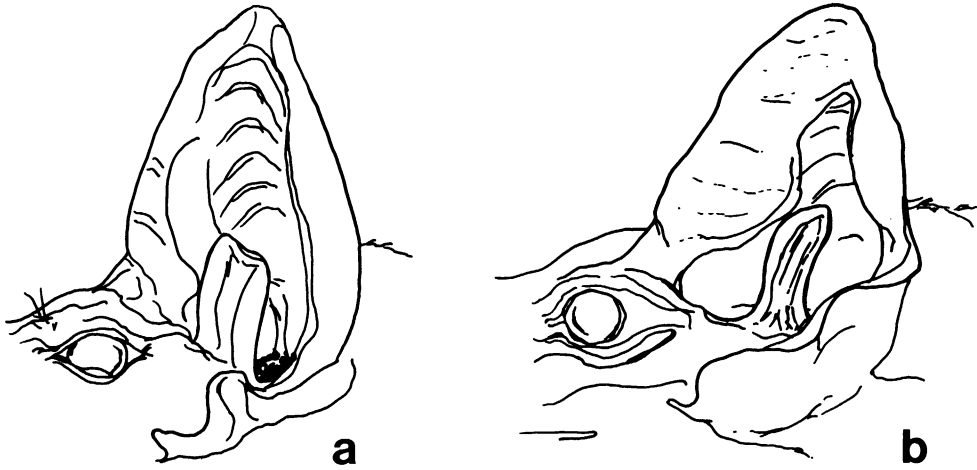


Fig. 9. Lateral view of the left ear of *Emballonura raffrayana* (a) and "*E.*" *nigrescens* (b) showing difference in tragus shape.

the posterior larynx on the cricoid/first tracheal ring. At about this point, the omohyoid becomes strongly associated (almost fused) with the sternohyoid, and they both continue anteriorly to insert on the basihyal. It is tempting to speculate that in the ontogeny of the tracheal expansion, the sternohyoid is pushed laterally and dorsally, although this cannot be known without study of a developmental series of specimens. In *nigrescens* (fig. 7), the course of the muscle is much more typical of other bats. The sternohyoid is not closely associated with its antimere, though they are closer than in the bats described above. However, the sternohyoid passes ventral to the tracheal expansion rather than dorsal, and the omohyoid and sternohyoid never become strongly associated. Clearly, the dorsal position of the sternohyoid in non-*nigrescens* *Emballonura* and in *Coleura* is a shared derived character, or synapomorphy. This character state does not occur in other emballonurid bat genera (Griffiths, unpubl.) or in other bats that have been examined (Sprague, 1943; Griffiths, 1978a, 1978b, 1982, 1983).

M. sternothyroideus
Figures 1, 2, 3, 4, 5, 6, 7

ORIGIN: From the anterior surface of the medial head of the clavicle, just lateral and

slightly dorsal to the origin of the lateral slip of the sternohyoid.

INSERTION: Onto the lateral surface of the thyroid cartilage.

EXCEPTIONS: None.

M. omohyoideus
Figures 1, 3, 5, 7

ORIGIN: From the anterior surface of the mid-clavicle.

INSERTION: Onto the lateral basihyal bone, just lateral to the insertion of the sternohyoid.

EXCEPTIONS: None.

COMMENTS: In all genera examined, the anterior omohyoid becomes closely associated (almost fused) to the anterior sternohyoid. The two muscles are difficult to separate. The omohyoid is also unusual in taking origin from the mid-clavicle region. In virtually all other groups of mammals, the omohyoid originates from the scapula, usually from the anterior edge.

M. thyrohyoideus
Figures 1, 2, 3, 4, 5, 6, 7

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

INSERTION: Onto the posterior surface of the thyrohyal bone.

EXCEPTIONS: None.

TABLE 1
Summary of the Apomorphies Used in Constructing the Cladogram (fig. 10) (+ = apomorphic character state; - = plesiomorphic character state; ++ = strong expression of the apomorphy; +/- = variable expression of trait)

Character state	Taxon											
	nig	atr	mon	ale	bec	raf	fur	sem	Col	Tap		
1) nasal sulcus present ^a	-	+	+	+	+	+	+	+	-	-		
2) lateral rostral swelling ^b	-	-	+	+	++	+	++	+	+	-		
3) basal pits confluent ^c	+/+	-	-	-	+	+/-	+	+/-	+	-		
4) ant.-lat. extension of bas. pits ^d	-	-	+	+	-	+	+	+	+	-		
5) post. recession of bas. pits ^e	+	-	+	-	+	++	+	-	++	+		
6) upper incisors reduced in no.	-	-	-	-	-	-	-	-	+	+		
7) sternohyoid attach. post. larynx	++	++	++	++	++	++	++	++	++	+		
8) omohyoid clavicular origin	+	+	+	+	+	+	+	+	+	+		
9) loss of stylohyoid	-	-	-	-	-	-	-	-	-	+		
10) extended insertion of ceratohyoid	+	+	+	+	+	+	+	+	+	-		
11) reduct. and fusion of geniohyoid	+	+	+	+	+	+	+	+	+	-		
12) dorsal deflection of sternohyoid	-	+	+	+	+	+	+	+	+	-		
13) wormlike penis	+	-	-	-	-	-	-	-	-	-		

^a Members of the genus *Emballonura* (s.s.) always seem to have the nasal sulcus at least slightly better developed than in the other genera here considered. However, the difference between *nigrescens* (absent) and some *semicaudata* (present) is admittedly rather subtle.

^b The extreme swelling appears different in *furax* and *beccarii*, but this seems to be caused by the autapomorphic lengthening of the rostrum in *furax*. The presence or absence of rostral swelling in *atrata* is not entirely clear from Tate and Archbold's (1939) figure.

^c There is great variation of this character in *nigrescens*, *semicaudata*, and *raffrayana*, and the character may be of dubious utility.

^d Scored on whether or not the pits extend lateral to a line from the pterygoid processes to the tympanic bone. Based on this criterion, anterolateral extension is very slight in *semicaudata* and *furax*.

^e Hill (personal commun.) would score *E. monticola* as "-" for this character. See text for discussion of this observation.

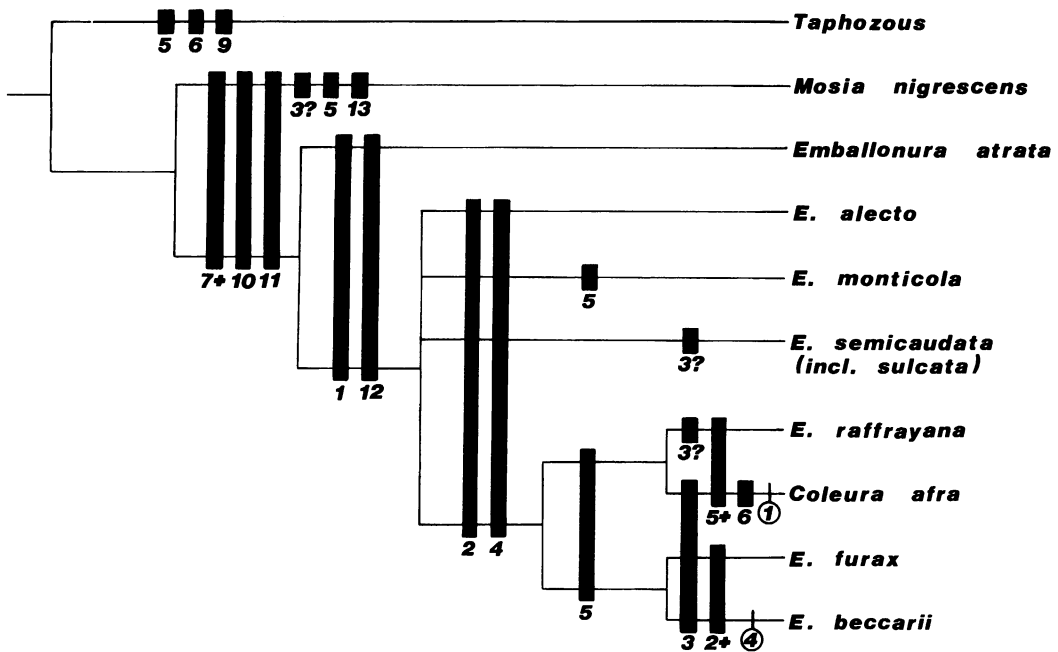


Fig. 10. Strict consensus cladogram (PAUP analysis) showing relationships among species discussed. Bars show apomorphic character states used in producing the cladogram: numbers refer to character state numbers in table 1. "+" next to a number refers to a strong expression of a trait in table 1; "?" means the character is variable. A circled number indicates a postulated reversal of a character state.

DISCUSSION

Compared with other, non-emballonurid bats examined by Griffiths (1978a, 1978b, 1982, 1983, unpubl.), there are four major apomorphic traits of the emballonurid hyoid region. The first two, found among all bats examined herein, are the unusual laryngeal attachment of the sternohyoid and the clavicular origin of the omohyoid (characters 7 and 8, table 1). These traits are of minimal taxonomic value to this study because they are found in all bats examined, but they are mentioned here for completeness. However, among all *Emballonura* and *Coleura* dissected there is a secondarily derived strong attachment of the sternohyoid (as opposed to the weaker attachment in *Taphozous*). This character state (7+ in fig. 10) is a synapomorphy common to all *Emballonura* and *Coleura* studied (including *nigrescens*). The third major apomorphic trait, the reduction of the geniohyoid and fusion to its antimer, is found among all *Coleura* and *Emballonura* (including *nigrescens*), but is also a character state

of New World emballonurids (Griffiths, unpubl.). It thus links the *Emballonura*-*Coleura* group with the New World genera. The fourth apomorphy, the dorsal deflection of the sternohyoid by the postlaryngeal tracheal chamber, is found in all species of *Emballonura* except *nigrescens*, and in all *Coleura* examined. The presence of this trait as a synapomorphy in the above species supports strongly the close phylogenetic relationship of species of *Coleura* and *Emballonura*, excluding only *E. nigrescens*.

There are two other apomorphic character states of the emballonurid hyoid region. The stylohyoid muscle has been lost in all specimens of *Taphozous* examined (and in *Saccolaimus*, Griffiths, unpubl.). This observation (character 9) supports a close phylogenetic relationship between *Taphozous* and *Saccolaimus*, but for the present study may be regarded merely as an autapomorphy of the *Taphozous* line (fig. 10). Additionally, the unusual insertion of the ceratohyoid muscle onto all three anterior cornu

elements in all *Emballonura* (including *nigrescens*) and in *Coleura* probably is a synapomorphy uniting these species (fig. 10, character 10).

There are two external characters which set *nigrescens* apart from all other *Emballonura* and *Coleura* studied. The first is the long, slender (wormlike) penis, as opposed to the short and broad penis of other *Emballonura*, *Coleura*, and *Taphozous* (fig. 8). This trait is surely an autapomorphy of *nigrescens*. Second, the tragus of *nigrescens* differs from that of all other specimens examined in being longer, narrower, and thinner (fig. 9). In this case, however, the character polarity is less clear. There is some diversity among the other species examined. At one extreme is *Taphozous* with a very short, square-ended tragus. This is less extreme in *E. beccarii* and *semicaudata* and of medium length in *alecto*, *monticola*, *raffrayana*, and *Coleura*.

Skull characters in *Emballonura* give a very confused picture. Tate and Archbold (1939) used skull characters exclusively in their dendrogram. We have reexamined these characters and scored them (table 1) as apomorphic or plesiomorphic for all species of *Emballonura* listed by Tate and Archbold, including *E. atrata* (which Tate and Archbold figure) and *Coleura*, using those characters which can be discriminated clearly. Scoring the characters required many subjective judgments; there is apparently some intraspecific variability which has not been previously analyzed. *Emballonura nigrescens* agrees with *atrata* and *beccarii* in its small skull size; with *Coleura* in the absence of a nasal sulcus; with *atrata* in the absence of lateral rostral swellings; with *atrata*, *monticola*, *alecto*, and some *semicaudata* and *raffrayana* in the presence of a septum separating the basal pits of the two sides; with *atrata* and *beccarii* in the absence of anterolateral extensions of the basal pits; and with *beccarii*, *furax*, and *monticola* in the moderate retrenchment of the basal pits posteriorly into the basioccipital, this being more pronounced in *raffrayana* and *Coleura* and absent in *alecto* and *semicaudata*. *Coleura* agrees with *furax* in its very large size; with *nigrescens* in the absence of a nasal sulcus; with *atrata* and *nigrescens* in the absence of lateral rostral swellings; with *beccarii*, *furax*, and some *nigrescens*, *raffrayana*,

and *semicaudata* in the absence of a septum separating the basal pits of the two sides; with *monticola*, *alecto*, *raffrayana*, *furax*, and *semicaudata* in the presence of anterolateral extensions of the basal pits; and with *raffrayana* in the pronounced retrenchment of the basal pits posteriorly into the basioccipital. The only skull character that clearly distinguishes *Coleura* from all *Emballonura* is the loss of the posterior upper incisor, which we here interpret as an autapomorphy of that line (fig. 10). Miller (1907) mentioned a few other characters in passing, but we find none to be consistently reliable.

J. E. Hill, in reviewing a presubmission version of this paper, very kindly shared some of his published and unpublished observations on cranial characters of emballonurid bats. *Emballonura diana*, the one species of *Emballonura* that was unavailable to us, is described by Hill (1958; personal commun.) as having a strongly developed nasal sulcus, rostrum laterally greatly inflated, basal pits divided by a moderately developed bladelike septum, strong anterior-lateral extension of the basisphenoid pits, and strong posterior recession of the basisphenoid pits. We have not included *E. diana* in our cladogram (fig. 10), but if included, it would seem most closely allied with *E. raffrayana* or *E. furax* (assuming, of course, that it possessed the requisite characters of the hyoid region, which seems a reasonable assumption).

Hill (personal commun.) disagrees with us in our observation that *Emballonura monticola* has posteriorly recessed basisphenoid pits (character state 5 in table 1 and fig. 10). His observations (on a different set of specimens) show that the basisphenoid area of *monticola* is most similar to that of *alecto*. We note that there is a great deal of variation in our own observations, and acknowledge that Hill may well be correct. However, lacking direct observations on Hill's specimens, we chose to retain our original interpretation in table 1 and figure 10. Part of the problem may be one of definition. In *E. monticola* there is clearly a lesser degree of recession than in *E. raffrayana*, but we see more than in *E. alecto*, where it is essentially nonexistent. In our original hand-generated cladogram, we placed *E. monticola* as a third line in the *raffrayana* to *beccarii* clade based on

our observation that *E. monticola* shared the derived (apomorphic) condition of character state 5. As part of the review process for this paper, we asked Dr. Robert DuBose of Washington University to run a PAUP analysis of our data, and the consensus tree produced (fig. 10) was identical to our hand-generated cladogram except for the placement of *E. monticola*. Our original cladogram was clearly more parsimonious than the PAUP consensus cladogram (fig. 10) because it required one fewer convergent event (i.e., the PAUP version assumes independent acquisition of posteriorly recessed basisphenoid pits). We considered presenting our original tree herein rather than the PAUP tree, but did not do so for two reasons. First, if Hill is correct that most *E. monticola* lack the posterior recession of the basisphenoid pits, then figure 10 becomes the most parsimonious cladogram (character state 5 would not be an apomorphy on the *monticola* line in fig. 10 or in table 1). Second, we present the PAUP tree because more people trust a PAUP cladogram than a hand-generated cladogram. However, we emphasize that if our observations on *E. monticola* are correct, it would be more parsimonious to place *E. monticola* as a third line in the *raffrayana* to *beccarii* clade.

Barghoorn (1977) and Robbins and Sarich (1988) have studied relationships of *Emballonura* and *Coleura* to one another and to other emballonurid genera. Barghoorn (1977) suggested that the loss of an incisor in *Coleura* and in New World emballonurid genera was a synapomorphy, and he placed *Coleura* in a clade with the highly derived genera *Peropteryx*, *Peronymus*, and *Balantiopteryx*. *Emballonura* was placed as a sister group to the entire *Coleura*-New World genera clade. We agree with the placement of *Emballonura*, but our data unequivocally support a close relationship between *Coleura* and *Emballonura*. In particular, the highly unusual (perhaps unique) dorsal deflection of the sternohyoid found in *Coleura* and all species of *Emballonura* except *nigrescens* supports this conclusion. It seems highly improbable that such an unusual feature would evolve twice independently.

Robbins and Sarich (1988), in the only other cladistic study to date of relationships between emballonurid genera, placed *Coleura*

in a clade with all species of *Emballonura* they analyzed, including *nigrescens*. We agree in many respects with Robbins and Sarich, but our data do not support their conclusion that *Coleura* is a sister taxon to a clade containing *Emballonura nigrescens*. Rather, we find that *Coleura* is most parsimoniously placed among the more derived species of *Emballonura*, while *nigrescens* appears to be excluded from the clade comprising the remaining *Emballonura* and *Coleura* (fig. 10).

We have produced a cladogram (fig. 10) that incorporates hyoid muscle characters, skull characters, and a penis character. Skull characters, as we have analyzed them here, can be used to produce other cladograms that are nearly as parsimonious as our figure 10. However, in no case is *nigrescens* parsimoniously included in a clade with "other" species of *Emballonura*. It always falls outside the *Coleura*-*Emballonura* group. As indicated above, the generic name *Mosia* Gray, 1843 is available for *nigrescens* if generic separation is warranted. We believe it is in this case, because *nigrescens* is separable from all other *Emballonura* in at least one derived character (penis form), whereas all other *Emballonura* plus *Coleura* differ from *nigrescens* in the clearly derived hyoid character state of dorsal deflection of the sternohyoid muscle. As indicated above, Dobson (1878) recognized *Mosia* as a subgenus and, judging by present standards, his genera were considerably lumped because *Peropteryx*, *Balantiopteryx*, and *Centronycteris* were all included in *Saccopteryx* as subgenera. It is not clear why the name *Mosia* was dropped, but we suggest that later-described species of *Emballonura* (Dobson knew of only four) caused the characters Dobson used to break down *E. beccarii* in particular keys out to *Mosia* using Dobson's characters, though our data clearly place it with typical *Emballonura*.

Interestingly, our grouping of species of *Emballonura* has some similarity to the groups shown in Tate and Archbold's (1939) dendrogram. We agree that *atrata* is the most primitive of the *Emballonura* and that it is paraphyletic to all other *Emballonura* species (but not to *nigrescens*). We also agree that *raffrayana*, *furax*, *beccarii*, and possibly *monticola* (if we are correct about character state 5, see above) form a closely related

group, though exact relationships of species are different. However, our analysis indicates that *Coleura afra* may also be a part of the group, and we do not support Tate and Archbold's conclusion that *alecto* is part of it. Finally, we agree that *sulcata* and *semicaudata* are closely related, but we suggest that they in fact are not separable into distinct species. We suggest that they all should be recognized as *E. semicaudata*. We do not agree with Tate and Archbold that *nigrescens* is closely related to *E. semicaudata*.

We have generated a number of different cladograms in our analysis of the conflicting skull data. In some of these possibilities based on skull characters (including our fig. 10), certain characters support the placement of *Coleura* with various species of *Emballonura*. A case could be made for reducing *Coleura* to at least subgeneric rank, but we hesitate to do this because of the conflicting nature of the skull evidence, because of the great variability we have observed in skull characters, and because Robbins and Sarich's (1988) protein data seem to support placing *Coleura* not only outside the genus *Emballonura*, but outside our proposed *Mosia-Emballonura* clade as well. Our data strongly argue against the latter hypothesis, but because of the conflict, we do not choose at this time to change the status of *Coleura*. We thus recognize a clade within the family Emballonuridae with three genera: *Mosia* (containing the single species *Mosia nigrescens*), *Emballonura*, and *Coleura*.

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