Considerations of the Osteology and Myology of the Upper Cervical Region in the Phyllostomatidae

Gloria M. Walton and Dan W. Walton*

Phyllostomatidae科 박쥐의 上頸部에 대한 骨學 및 筋學的 考察

글로리아 엠 왈톤·단 떠불류 왈톤

摘　　要

Phyllostomatidae科 박쥐의 第1頸椎骨에 關한 骨學的 考察을 하였다. 2個의 顯著한 腹棘狀突起, 1個의 中央腹板隆起 및 橫突起上의 附屬突起의 存在에 關하여 記述하였다. Artibeus lituratus 박쥐에 對한 第1頸椎骨과 連關된 上頸部 筋肉과의 機能에 關하여 論하였고 系統遺傳學的 의의에 관한 여러면을 考察하였다.

INTRODUCTION

The osteology and myology of the cervical region in bats are poorly known. Details of osteology are available only for *Miniopterus schreibersii* (Barbu, 1960) and *Chilonycteris psilotis* (Walton and Walton, 1970a). General osteological information for the Chiroptera is presented by Walton and Walton (1970b) who note variation in atlas form and draw attention to the presence of characteristic ventral spines on the atlas of most phyllostomatid genera.

Myological studies in the cervical region of bats are incomplete. Willie (1954) and Vaughan (1959; 1970a; 1970b) consider portions of this region and Winge (1941) and Gressé (1955) briefly discuss the cervical musculature of Chiroptera. More complete studies of cervical osteology and myology are available for other terrestrial small mammals (e.g., Parsons, 1894, 1896; Gaughran, 1954; Rinker, 1953, 1963; Klingemer, 1964).

This study presents information on the form of the atlas exhibited among phyllostomatid species and comparisons are made to atlas configuration of other chiropteran families. In relating atlas function, discussion of head position (Jepsen, 1970), brain weight relative to body weight (Pirlot, 1969) and skull size

---

and shape (Miller, 1907; Walker, 1964) are considered.

Nomenclature of taxa discussed in this paper follow Simpson (1945) and the various genera studied are considered to be representative of their respective subfamilies. Osteological terminology follows Walton and Walton(1970a) and that of myology follows Hyman (1922), Rinker (1954) and Gaughran (1954).

Phyllostomatid genera considered in the osteological portion of this study are *Chilonycteris* and *Mormoops* (Chilonycterinae), *Phyllostomus* (Phyllostomatinae), *Glossophaga*(Glossophaginae), *Caroillia*(Carollinae), *Sturnira*(Sturnirinae), *Vampyrops* and *Artibeus*(Stenoderminae) and *Phyllonycteris*(Phyllonycterinae). The Desmodontidae have been closely linked, osteologically, to the Phyllostomatidae (Walton and Walton, 1968; 1970a). *Desmodus*, therefore, is included and considered to be a phyllostomatid. Other genera examined include *Rousettus*, *Pteropus*, *Cynopterus*, *Macroglossus*(Pteropidae), *Nycteris*(Nycteridae), *Hipposideros*(Hipposideridae), *Megaderma*(Megadermatidae), *Saccopteryx*(Emballonuridae), *Myotis*, *Euderma*, *Lasiurus*, *Antrozous*(Vespertilionidae), *Tadarida*(Molossidae) and *Mystacina*(Mystacinidae). Obviously, many other genera could be considered. Those chosen are thought to adequately represent the general spectrum of diversity among the Chiroptera. Illustrations of the atlas of genera other than the phyllostomatid genera selected for this study are presented only where necessary for a particular consideration.

The myology portion of the study is based on dissections of *Artibeus lituratus*. The particular animal was selected for three reasons: the atlas, osteologically, is considered typical of the phyllostomatid genera examined, size is ideal, and several specimens of both sexes were available for dissection.

OSTEOLOGY

The phyllostomatid atlas (see generalized phyllostomatid atlas presented in Fig. 1), including that of *Desmodus*, is oval to round in outline. The anterior facets that articulate with the occipital condyles are large, oblong in shape, and smooth, but the boundaries of the facets are not distinct in *Mormoops* and *Chilonycteris* (Fig.2). The facets occupy approximately three-fourths of the anterior surface of the slightly V-shaped arch in all genera examined. Two prominent ventral spines (cervical ribs) are continuous with the anterior margin of the ventral arch and situated directly below the bases of the transverse processes equidistant on either side of the midventral line. These spines are sturdy in appearance except in *Sturnira* (Fig. 3 G+H) where they are greatly reduced and in *Mormoops* where they are completely absent. In *Glossophaga* (Fig. 3 C+D) and *Vampyrops* (Fig. 4 A +B) the spines are hooked medially; the most pronounced hook is in *Vampyrops*. The spines are blunt in all other genera.
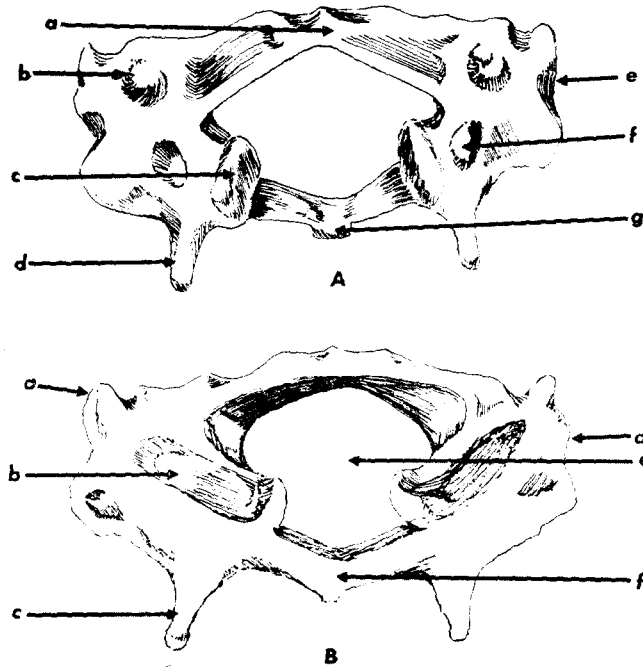
Fig. 1. Generalized phyllostomatid atlas. A. Posterior view. The parts are as follows: a. dorsal arch, b. atlantal foramen, c. articular facet for axis, d. ventral spine (cervical rib), e. transverse process, f. transverse foramen, g. mid-ventral tubercle. B. Anterior view. The parts are as follows: a. lateral tubercle of the transverse process, b. articular facet for the occipital condyle, c. ventral spine (cervical rib), d. transverse process, e. neural canal, f. ventral arch.
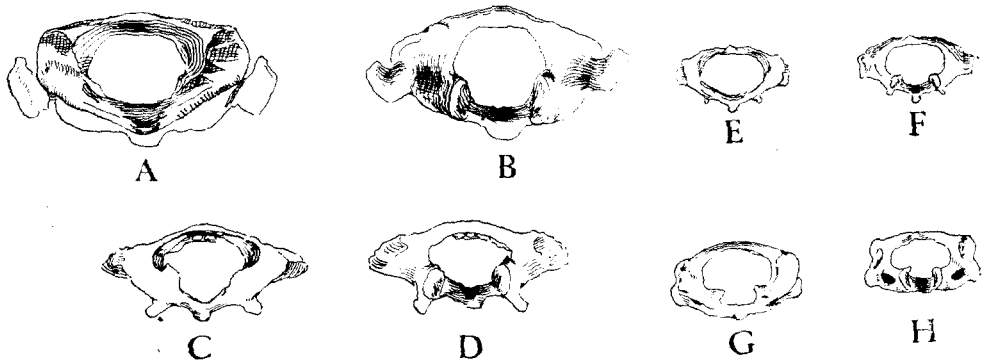

Fig. 2. Anterior and posterior views of the atlas of *Hipposideros*(A & B), *Saccopteryx* (C & D), *Chiloncteris*(E & F) and *Mormoops*(G & H).
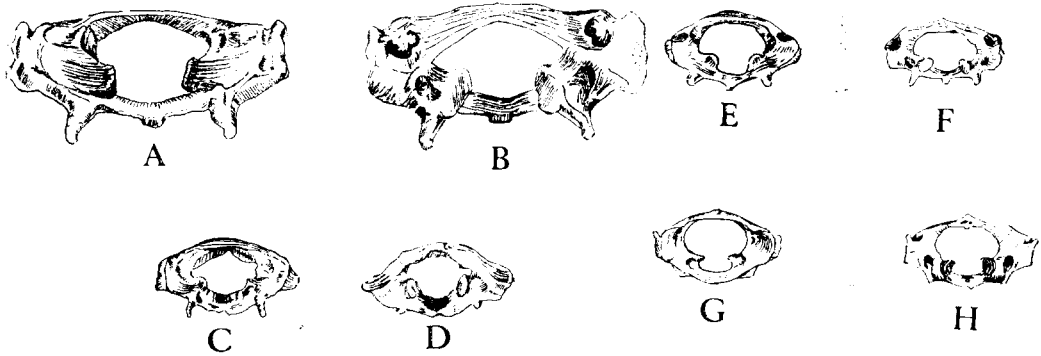
Fig. 3. Anterior and posterior views of the atlas of *Phyllostomus*(A & B),*Glossophaga* (C & D), *Carollia* (E & F) and *Sturnira*(G & H).
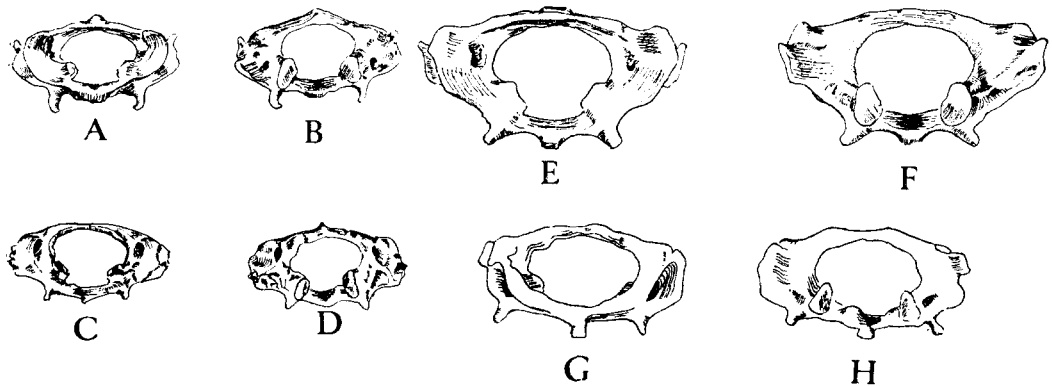
Fig. 4. Anterior and posterior views of the atlas of *Vampyrops* (A & B), *Phyllonycteris* (C & D) and *Desmodus*(E & F), *Tadarida*(G & H).

A conspicuous blunt tubercle extends ventrad from the midventral line and forms the apex of the V of the ventral arch in *Chilonycteris, Mormoops, Phyllostomus*(Fig. 3 A+B), *Carollia*(Fig. 3 E+F) and *Desmodus*(Fig. 4 E+F). This tubercle is poorly developed and inconspicuous in other genera.

The dorsal arch is the same width (anteroposteriorly) as the ventral arch, but more flattened (dorsoventrally) in appearance. In side view the dorsal arch appears concave anteriorly and slightly convex posteriorly.

The transverse processes are broad (dorsoventrally) and squared off with blunt edges. A small tubercle arises from the dorsal portion of the lateral border of each of the transverse processes in *Phyllostomus, Sturnira, Vampyrops Artibeus* and *Desmodus*. These tubercles project dorsad and slightly caudad. Other genera lack tubercles on the transverse processes.

The posterior articular facets are oval to round in shape and one-third to one-half the size of the anterior articular surfaces. The transverse foramina exhibit complete penetration of the atlas in *Mormoops*, but appear as large, round fossae in *Phyllostomus, Carollia, Sturnira, Vampyrops, Artibeus*, and *Desmodus*. They are shallow depressions in *Chilonycteris, Glossophaga* and *Phyllonycteris*.

Dorsolaterad to the transverse foramina lie the atlantal foramina. These foramina appear inconspicuous or as very shallow fossae in *Chilonycteris, Glossophaga, Sturnira, Vampyrops, Artibeus* and *Desmodus*. They are exhibited as complete foramina only in *Phyllonycteris* (Fig. 4 C+D).

Comparison of the phyllostomatid atlas with those of genera of other families reveals a number of interesting points. The orientation of the transverse processes varies considerably. In the phyllostomatids they are expanded dorsoventrally while those found in *Cynopterus, Macroglossus, Nycteris, Hipposideros* and *Lasiurus* are dorsoventrally flattened. All other non-phyllostomatid genera have dorsoventrally expanded transverse processes. In *Hipposideros* the transverse processes terminate in a peculiar secondary process(see Fig. 2, A&B). Midventral tubercles are distinct in *Nycteris, Hipposideros, Megaderma, Saccopteryx, Euderma, Tadarida* and *Mystacina*. The two prominent ventral spines (cervical ribs) are present only in *Sacropteryx*(see Fig. 2 C+D). Processes similar in appearance are seen in *Tadarida* but here the processes are laterally displaced and more closely associated with the transverse processes than with the ventral arch (Fig. 4 G+H). The transverse foramina are complete in *Cynopterus, Nycteris, Megaderma, Tadarida* and *Mystacina*. The atlantal foramina are complete only in *Megaderma*.

MYOLOGY

Superficial Spino-occipital Group (Fig. 5)

M. splenius

Origin-along the ligamentum nuchae at the level of the first and second thoracic vertebrae.

Insertion-onto the ridge formed by the lateral part of the parieto-interparietal suture and onto the lambdoidal crest as far laterad as the mastoid process of the squamosal.

Remarks-this muscle turns the head. When this muscle pair functions in concert, the head is elevated.

Deep Costo-spine-scapular Group (Figs. 5&6)

M. levator scapulae ventralis.

Origin-the short ventral spine at the base of the transverse process of the atlas.

Insertion-along the vertebral border of the scapula next to the posterior end of the anteromedial flange.

Remarks-near its insertion, this muscle joins the anterior portion of the *M. levator scapulae.* The action of this muscle is to pull the scapula forward and ventrad.

M. levator scapulae

Origin-by four large slips from the transverse processes of cervical vertebrae two through seven.

Insertion-along the vertebral border of the scapula from the posterior end of the *M. levator scapulae ventralis* inserton to the junction of the spine and vertebral of the scapula.

Remarks-only the first slip of this muscle is sketched(Figs. 5 & 6); it originates on the transverse process of the axis and the third cervical vertebra and the insertion is the same as described above. The action of this muscle is to pull the scapula forward and ventrad. When in flight, the scapula rocks back and forth with the action (Vaughan, 1959). Vaughan also notes that the origin of this muscle is cervical vertebrae four through seven. This study found the origin to be more craniad.

M. omocervicalis

Origin-from the short ventral spine at the base of the transverse process of the atlas.

Insertion-on the anteromedial surface of the clavicle.

Remarks-this muscle draws the scapula forward in most mammals (Rinker, 1954; Vaughan, 1959) but in *Artibeus* and *Macrotus* it serves to draw the clavicle up and mediad. This may facilitate the greater movement of the head relative to the shoulders.
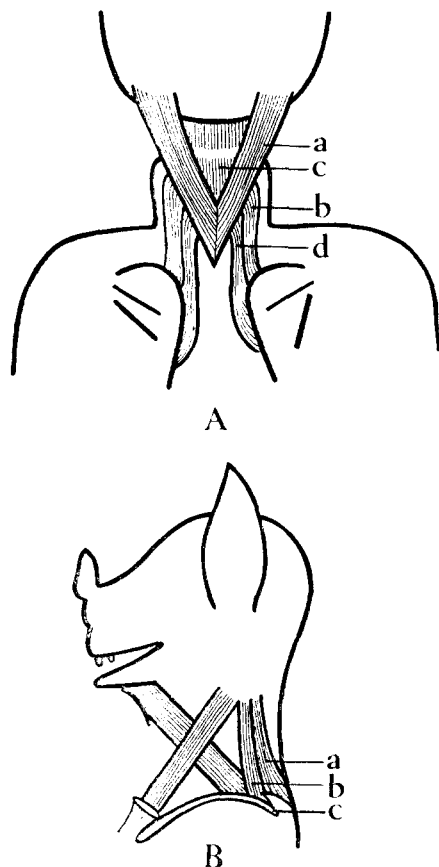
Fig. 5. Cervical musculature. A. Dorsal view of superficial cervical musculature. The parts are as follows: a. *M. splenius* b. *M. levator scapulae ventralis*, c. epaxial musculature, d. *M. levator scapulae* B. Lateral view of superficial cervical musculature. The parts are as follows: a. *M. levator scapulae ventralis*, b. *M. omocervicalis*, c. clavicle.
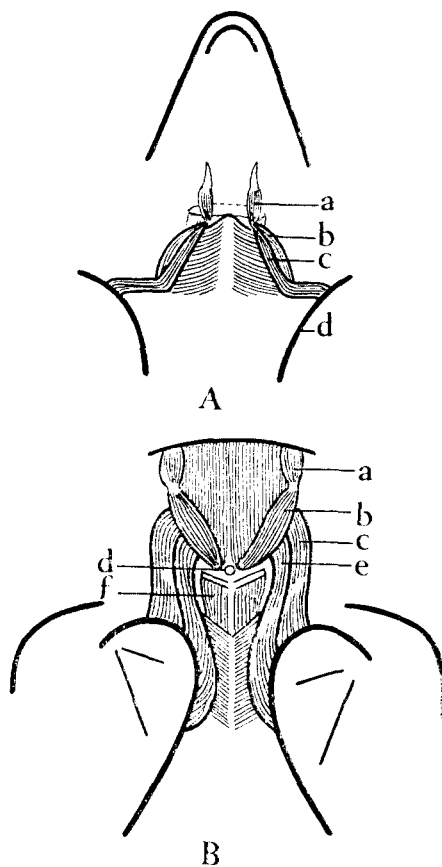
Fig. 6. Cervical musculature. A. Ventral view of the deep cervical musculature. The parts are as follows: a. *M. rectus capitus anterior*, b. *M. levator scapulae ventralis*, c. *M. omocervicalis*, d. clavicle. B. Dorsal view of the deep cervical musculature. The parts are as follows: a. *M. obliquus capitis superior*,, b. *M. obliquus capitis inferior*, c. *M. levator scapulae ventralis*, d. axial neural spine, e. *M. levator scapulae*, f. epaxial musculature.

Suboccipital Group (Fig. 6)

M. rectus capitis posterior major

Origin–from the anterolateral surface of the tip of the neural spine of the axis.

Insertion–on the lateral supraoccipital region.

Remarks–the movement of this muscle is associated with movement of the epaxial musculature.

M. rectus capitis posterior minor

Origin-from the anterolateral surface of the tip of the neural spine of the axis.

Insertion-on the lateral supraoccipital region.

Remarks-the movement of this muscle is associated with movement of the epaxial musculature.

M. rectus capitis posterior minor

Origin-from the anteromedial surface of the dorsal arch of the atlas.

Insertion-on the supraoccipital region, deep and medial to the *M. rectus capitis posterior major*.

Remarks-the movement of this muscle is associated with the movement of the epaxial musculature.

M. obliquus capitis superior

Origin-from the anterodorsal part of the transverse process of the atlas.

Insertion-on the exoccipital, just lateral to the insertion of *M. rectus capitis posterior major* and posteromediad to the caudolateral corner of the occiput.

Remarks-this muscle helps raise the head.

M. obliquus capitis inferior

Origin-from the entire dorsolateral surface of the neural spine of the axis.

Insertion-on the dorsoposterior surface of the transverse process of the atlas.

Remarks-an unusually strong muscle which aids in keeping the cervical region rigid and in turning the neck as the head is turned.

Deep Cervical Prevertebral Group (Fig. 6)

M. rectus capitis anterior

Origin-from the anteroventral margin of the transverse process of the atlas and a portion of the ventral arch just mediad to the transverse process.

Insertion-on the posterolateral part of the ventral surface of the basioccipital.

Remarks-this muscle aids in pulling the chin down toward the chest.

DISCUSSION

Ventral spines of atlas are found in all genera of the Phyllostomatidae except *Mormoops*. They are lacking in other families except Emballonuridae where they are well-developed in *Saccopteryx*. Although *Tadarida* has ventral spines on the atlas, they are laterally displace. This displacement may be associated with the general dorsoventral compression of the body seen in molossids. They probably serve a similar function as those seen in the phyllostomatid genera and *Saccopteryx*.

A conspicuous midventral tuberosity is found in *Chilonycteris, Mormoops,*

Phyllostomus, Carollia & Desmodus. The transverse processes are dorsoventrally expanded in the Phyllostomatidae and in *Megaderma, Saccopteryx, Tadarida* and *Mystacina.* In all other genera the processes are expanded anteroposteriorly. Accessory processes on the transverse processes are present in the phyllostomid genera *Phyllostomus, Sturnira, Vampyrops, Artibeus* and *Desmodus.* These processes do not appear among genera of other families although the transverse processes are quite unique in *Hipposideros.*

The *M. obliquus capitis inferior* and *M. obliquus capitis superior* in their association with the transverse processes of the atlas aid in raising and turning the head. These muscles also work with the epaxial musculature to maintain stability of the cervical region.

Phyllostomatids, in general, give the appearance of being "heavy-headed", i.e., large head relative to body size. Pirlot(1969) divided genera of four families into the following categories: Sanguivores (desmodontids), Vegetariens (phyllostomatids), Piscivores(noctilionids) and Entomophages(vespertilionids). He noted that the ratio of brain weight to body weight was highest among the sanguivores and vegetarians. Miller(1907) and Walker(1964) have both noted enlarged or heavy skulls in some genera of the Phyllostomatidae. Thus in positioning of a "heavy-head", the ventral spines, midventral tuberosity and expanded transverse processes with accessory tubercles of the atlas would serve to vastly increase muscle attachment surface area and facilitate head placement during flight/feeding activity and while at rest. In those genera where the transverse processes are expanded anteroposteriorly, head positioning should differ markedly from those bats with dorsoventrally expanded transverse processes.

All microchiropteran bats roost in a head-down position and some are quite alert in the roost, often raising their head upright (Jopsen, 1970). Extensive head movement is seen in the flight and feeding of phyllostomatid bats(Gould, 1959; Vaughan, 1959). The *M. omocervicalis* facilitates head movement by its origin on the ventral spines of the atlas and insertion on the clavicle instead of the scapula as described by Vaughan (1959) in other families (Vespertilionidae and Molossidae). This muscle attachment pattern aids in tucking the upper neck region against the clavicles and possibly facilitating movement of the clavicles during flight/feeding activity and while at rest. Head placement relative to the clavicles during flight must be variable and controlled, in part, by the *M. omocervicalis.*

The *M. levator scapulae ventralis* originate on the ventral spines of the atlas and they, with the *M. levator scapulae,* allow and control the rocking motion of the scapulae during flight. This rocking motion is described by Vaughan (1959).

who gives the origin of the first slip of the *M. levator scapulae* as the fourth and/or fifth cervical vertebra in *Macrotus*. This study found the origin to be the transverse process of the axis and the third cervical vertebra. The rocking motion of the scapulae undoubtedly produces movement of the clavicles.

Among the phyllostomatid genera examined *Mormoops* exhibits the greatest osteological divergence from the general pattern seen throughout the family. The unique atlas of *Mormoops* is consistent with the divergence noted by Walton(1968) for other skeletal features. The configuration of the atlas as presented herein does not shed light, however, on justification for according chilonycterine bats familial status as proposed by Koopman (1970) and suggested by Koopman and Jones (1970), but it does support the view presented by Walton and Walton(1968) that within the chilonycterines, two distinct groups(*Chilonycteris/Pteronotus* and *Mormoops*) exist.

The atlas of *Desmodus* appears typically phyllostomatid. This additional evidence supports the view of Walton(1968) and Koopman(1970), that the desmodontid bats could be regarded as a subfamily of the Phyllostomatidae.

Of the non-phyllostomatid genera examined, the atlas of *Saccopteryx* is most similar to that of the Phyllostomatidae. This smilarity supports the suggestions by Walton(1968) and Slaughter (1970) that the relationship between the Emballonuridae and Phyllostomatidae may be closer than is generally supposed.

In summary, the presence of ventral spines on the atlas of phyllostomatid bats is thought to serve to increase muscle attachment surface area and alter origin-insertion muscle patterns to facilitate positioning of a "heavy-head" and, with possible exception of certain emballonurid genera, the presence of ventral spines on the atlas is unique to and characteristic of bats of the family Phyllostomatidae.

SUMMARY

The osteology of the atlas of phyllostomatid bats is considered. The presence of two prominent ventral spines, a midventral tubercle and accessory processes on the transverse processes are noted. Functional consideration of the atlas is presented by a study of the myology of the upper cervical region of *Artibeus lituratus*. Consideration is given to possible phylogenetic implications.

ACKNOWLEDGEMENTS

are indebted to these individuals and their respective organizations. This work was initiated while the authors were at Southern Methodist University and Christian College of the Southwest, Dallas, Texas.

REFERENCES

Barbu, P., 1960. Contributii la studiul monografic allui *Miniopterus scheibersii* Kuhl. Bucharest Univ. 'C. I. Parlov'. *Anal. Ser. Stu. Nat.* **24** : 83-107.

Gaughran, G., 1954. A comparative study of the osteology and myology of the cranial and cervical regions of the shrew, *Blarina brevicaudu*, and the mole, *Scalopus aquaticus. Misc. Publ. Mus. Zool Univ. Mich.* **80** : 1-82.

Gould, E., 1959. Flight behavior in leaf-nosed bats. *J. Mamm.* **41** : 268.

Grasse, P.P., 1955. Anatomie. *In:* Traite de Zoologie, Tome XVII, Sec., Fasc. Masson et Cie, Paris. pp. 1729-1733.

Hyman, L.H.,1922. A Laboratory Manual for Comparative Vertebrate Anatomy. Univ. Chicago Press, Chicago.

Jepsen, G.L., 1970. Bat origins and evolution. *In:* Wimsatt, W.A.(Ed.), Biology of Bats. Vol. I., Academic Press, New York. pp. 51-53.

Klingener, D., 1964. The comparative myology of four dipodoid rodents (Genera *Zapus. Napaeozus, Sicista, Jaclus*). *Misc. Publ. Mus. Zool. Univ. Mich.* **124** : 1-100.

Koopman, K.F., 1970. Zoogeography of bats. *In:* Slaughter, B.H. and D.W. Walton (Eds.), About Bats. Southern Methodist. Univ. Press, Dallas. pp. 29-50.

Koopman, K.F. and J.K. Jones, 1970. Classification of bats. *In:* Slaughter, B.H. and D.W. Walton (Eds.), About Bats. Southern Methodist Univ. Press, Dallas. pp.22-28.

Parsons, F.G., 1894. On the myology of the sciuromorphine & hystricomorphine rodents. *Proc. Zool. Soc. London.* 251-296.

Parsons, F.G., 1896. Myology of rodents. *Proc. Zool. Soc. London.* 159-192.

Pirlot, P.,1969. Relations ponderalis entre l'encéphalon et les corps chez les chiroptéres. I. Espéces Néo-tropicales. *Rev. Can. Biol.* **28** : 127-136. (Reprinted *In: Tran. Biol. Univ. Montreal.* no. 49).

Rinker, G.C.,1954. The comparative myology of the mammalian genera *Sigmodon, Oryzomys, Neotoma* and *Peromyscus*(Cricetinae), with remarks on their intergeneric relationships. *Misc. Publ. Mus. Zool. Univ. Mich.* **83** : 1-124.

———1963. A comparative myological study of 3 subgenera of *Peromyscus. Occ. Pap. Mus. Zool. Univ. Mic.* **632** : 1-18.

Simpson, G.G.,1945. The principles of classification and a classification of

mammals. *Bull. Amer. Mus. Nat. Hist.* **85** : 54-61.

Slaughter, B.H.,1970. Evolutionary trends of chiropteran dentitions. *In*: About
Bats (Slaughter, B.H. and D.W. Walton Eds.). Southern Methodist Univ. Press,
Dallas. pp.51-83.

Vaughan, T.A., 1959. Functional morphology of three bats: *Eumops*, *Myotis*,
Macrotus. Univ. Kan. Publ. Mus Nat. Hist. **12** : 1-153.

————1970a. Functional morphology of the forelimb of mormoopid bats. *J.
Mamm.* **51** : 217-235.

————1970b. The skeletal system. *In*: Wimsatt, W.A. (Ed.), Biology of Bats.
Academic Press, New York. pp.98-139.

Walton, D.W. and G.M. Walton, 1969. Comparative osteology of the pelvic and
pectoral girdles of the Phyllostomatidae (Chiroptera; Mammalia). *J. Grad. Res.
Cen., S.M.U.* **37** : 1-135.

————1970a. Post-cranial osteology. *In*: About Bats (Slaughter, B.H. and D.W.
Walton. Eds.). Southern Methodist Univ. Press. Dallas. pp. 93-126.

Walton, G.M. and D.W. Walton., 1970b. Post-cranial osteology of *Chilonycteris
psilotis. Rev. Biol. Trop.*(Costa Rica). **17**(2) : 147-163.

Wille, A.,1954. Muscular adaptation of the nectar-eating bats. (Subfamily Glosso-
phaginae). *Trans. Kan. Acad. Sci.* **57** : 315-325.

Winge, H.,1941. The Interrelationships of the Mammalian Genera. Vol. I.
(Translated by E. Deichmann and G.M. Allen). C.A.Reitzels, Forlag, Copenhagen.
pp. 253-319.