KOREAN JOURNAL OF ZOOLOGY
Vol. 30, No. 1, pp. 79-88 (1987)

Identification of Bats belonging to the Pteropodidae (Megachiroptera) Collected from Southeast Asia by the Humeral Characters

Myung Hee Yoon
(Department of Biology, Pusan Sanub University)

上腕骨의 特徵에 의한 東南아시아產 과일박쥐류(大翼手亞目)의 分類·同定

尹 明 熙
(釜山產業大學校 理科大學 生物學科)
(Received October 10, 1986)

요 약

東南아시아에서 採集된 大翼手亞目 Megachiroptera, 과일박쥐科 Pteropodidae에 屬하는 5屬, 6種 1亞種에 대하여, 上腕骨의 特徵을 記載했다. 또한, 系統的으로 下等한 大翼手亞目 Megachiroptera과 高等한 小翼手亞目 Microchiroptera 間의 飛翔適應性의 差異에 대하여, 上腕骨의 形態, 上腕骨의 DW/PW(遠位端幅의 近位端幅에 대한 比率) 및 翼型率(第3指長의 第5指長에 대한 比率)을 通하여 考察했다.

INTRODUCTION

One of the most noticeable characteristics of bats is their ability to fly. It has been thought that bats have evolved toward adaptation for flight, and there are many studies concerning the adaptive degree for flight, i.e. functional morphology of wings (Kuramoto, 1972; Kuramoto and Uchida, 1976; Vaughan, 1959, 1966, 1970a, b; Yokoyama *et al.*, 1975; Yokoyama and Uchida, 1979a) and histology of muscles (Ohtsu *et al.*, 1978; Ohtsu and Uchida, 1979a, b; Yokoyama and Uchida, 1979b; Yokoyama *et al.*, 1979), etc. Furthermore, it has been well known that the humerus, one of the most important apparatus for flight, exhibits the property of the family, subfamily, genus and species (Miller, 1907; Revilliod, 1922; Lawrence, 1943; Vaughan, 1959, 1970a; Sigé, 1971; Yoon *et al.*, 1981, 1984a, b; Yoon and Uchida, 1983a, b). In this connection, Yoon and Uchida (1983a, b) made clear the fact that the microchiropteran species including 23 species of nine genera belonging to the Vespertilionidae and 11 species of three genera belonging to the Rhinolophidae can be classified even by only the humeral characters. They also dealt with the adaptability for flight within each taxon of the Vespertilionidae and the Rhinolophidae using the value of DW/PW (the ratio of the distal epiphysis width to the proximal one) as well as the wing-type ratio (the third finger to the fifth one).

The aim of the present study was to classify the members of the Pteropodidae belonging to the suborder Megachiroptera by the humeral characters. Furthermore, I discussed the difference in the humeral morphology and the adaptability for flight between the Megachiroptera and the Microchiroptera.

MATERIALS AND METHODS

I studied the right humeri, as a rule, of six species and one subspecies that were available, belonging to five genera of the Pteropodidae. Since I found no difference between two subspecies of ***Pteropus dasymallus yayeyamae*** and ***P.d. formosus***, they were included together in the species concerned.

With respect to the humeri of the species examined, the humerus length(HL) was measured by a caliper with 1/20mm precision, and the ratio of the distal epiphysis width to the proximal one (DW/PW) was calculated. The wing-type ratio also was estimated (Table 1). Terminology of humerus by Yoon and Uchida (1983a, b) was used for descriptions.

Table 1. Comparison of the humerus and the wing-type in the species examined the Pteropodidae.

Species	N	HL (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Rousettus leschenaulti	3	44.6~49.4 (47.5)	1.16~1.27 (1.23)	1.29~1.33	Thailand India
Pteropus dasymallus	3	89.4~100.6 (95.2)	1.25~1.28 (1.26)	1.41*	Taiwan Japan
Cynopterus sphinx	2	34.8, 36.6	1.24, 1.27	1.30, 1.32	Thailand
C. brachyotis	2	43.2, 46.6	1.25, 1.26	1.32, 1.33	Indonesia
Megaerops ecaudatus	1	29.7	1.18	1.30	Thailand
Aethalops alecto	1	25.6	+	1.40	Indonesia

HL, humerus length; DW/PW, ratio of the distal epiphysis width to the proximal one of the humerus; III/V, ratio of the third finger to the fifth one.
* The value was based on one specimen collected from Taiwan.
+ The value could not be calculated because of a damaged trochin.

DESCRIPTIONS

Suborder Megachiroptera
Family Pteropodidae
Subfamily Pteropodinae

1. **Genus** *Rousettus*

(1) *Rousettus leschenaulti* (Fig. 1)

The species belonging to the most primitive genus in the Pteropodidae is moderate in size (HL, 44.6~49.4 mm, N=3). The humeral shaft flattened distally is sigmoid in lateral view, and the proximal half is slightly tilted mediad in antero-posterior view. The head moderate in size exhibits an oval. The small trochiter is slightly higher than the head, and does not articulate with the secondary glenoid fossa of the scapula. The trochin is larger in size, but the same in height, as compared with the trochiter. The anterior pit (the pit immediately anterior to the head) is very shallow. Both the medial ridge and the lateral knob are developed moderately. The high pectoral ridge, roof-like in appearence, is about one third of the humerus in length. At the distal epiphysis, the capitulum consists of the inner and lateral ridges divided by a shallow, ill-defined lateral groove. The inner ridge is about three times as wide as the lateral one. The trochlea sharp on the margin is as wide as the capitular lateral ridge, and divided by a moderately deep groove with the capitular inner ridge. The flattened and wide medial epicondyle projects mediad, and bears distally the knob-like spinous process ended at higher level than distal end of the trochlea. The

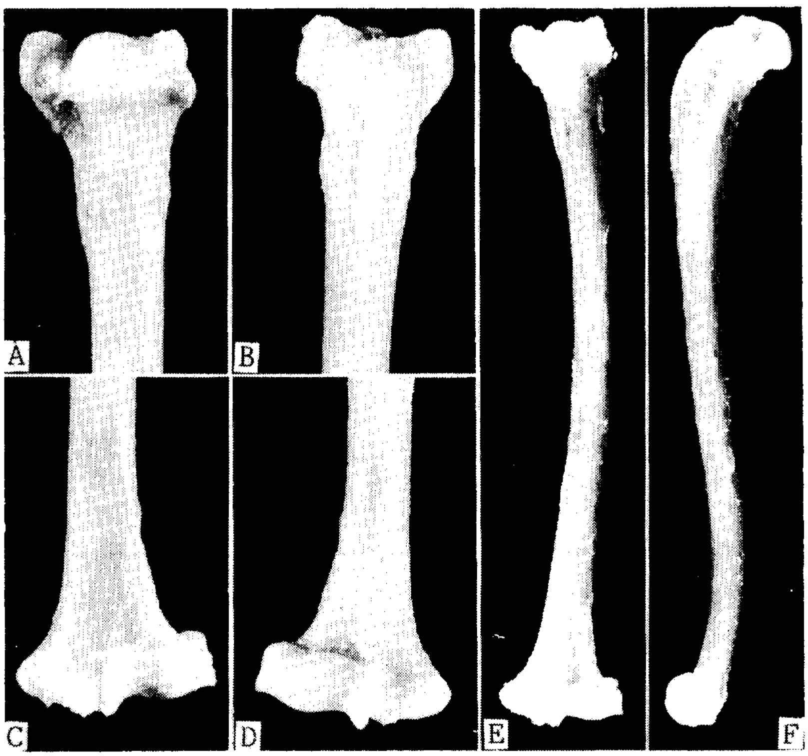

Fig. 1. Right humerus of *Rousettus leschenaulti*, showing posterior (A, C) and anterior (B, D) views of proximal and distal ends, respectively, and the whole posterior (E) and medial (F) views. A-D×3.0, E-F×2.0.

distal epiphysis is very wide and the values of DW/PW are 1.16~1.27. The distal articular surface is remarkably eccentric outward against the humeral axis. The lateral epicondylar crest is absent, and both the olecranon and the radial fossae are very shallow. The wing-type ratios are 1.29~1.33.

2. Genus *Pteropus*

(1) ***Pteropus dasymallus*** (Fig. 2)

The species is large in size HL (89.4~100.6 mm, N=3). The humeral shaft flattened distally is sigmoid in lateral view as in *R. leschenaulti*, but the proximal half is less tilted than in the species mentioned above. The large head presents an angulate ovum. The undeveloped trochiter being slightly lower than the head in height is ill-defined in its outline, especially at the boundary between it and the head. The trochin as high as the head is larger and slightly higher than the trochiter. The anterior pit is less shallow as compared with that of *R. leschenaulti*, and both the medial ridge and the lateral knob are vestigial. The roof-like pectoral ridge is low in height and is about one-third of the humerus in length. The distal epiphysis is quite similar in appearence to that of *R. leschenaulti*. The values of DW/PW are 1.25~1.28 and the wing-type ratio is 1.41(N=1).

Fig. 2. Right humerus of *Pteropus dasymallus*. Alphabetical symbols as in Fig. 1. A-D ×2.8, E-F ×1.05.

3. **Genus** *Cynopterus*

(1) *Cynopterus sphinx* (Fig. 3)

The species is small in size (HL, 34.8 and 36.6 mm, N=2). The humeral shaft flattened distally exhibits a distinctive sigmoid flexure in lateral view, and proximal one-third of the shaft is strongly curved mediad in antero-posterior view. The undeveloped small trochiter is as high as the large head taking a form of an oval and the large trochin. The anterior pit is very shallow, and both the medial ridge and the lateral knob are vestigial. The high, roof-like pectoral ridge is two-fifth of the humerus in length, and has a distinct medial border. It is characteristic that the region between the lateral and medial borders of the pectoral ridge is slightly concaved. The distal epiphysis resembles in appearence that of the above-mentioned two species, but both the olecranon and radial fossae are vestigial. The values of DW/PW are 1.24 and 1.27, and the wing-type ratios are 1.30 and 1.32.

Fig. 3. Right humerus of *Cynopterus sphinx*. Alphabetical symbols as in Fig. 1. A-D ×4.3, E-F ×3.75.

(2) *Cynopterus brachyotis*

The species is moderate in size(HL, 43.2 and 46.6 mm, N=2). The humerus is similar in shape to that of *C. sphinx* except for the following points: the proximal shaft of the humerus curves less mediad in antero-posterior view; the pectoral ridge is slightly lower and not concaved on its surface. The value of DW/PW (1.25 and 1.26) and the wing-type ratio (1.32 and 1.33) are also similar to those in *C. sphinx*.

4. **Genus** *Megaerops*

(1) *Megaerops ecaudatus* (Fig. 4)

The species is small in size (HL, 29.7 mm, N=1). The humerus is slightly different in appearance from those of the species mentioned above, although the general shape is similar to their humeri. The proximal one-third of the humeral shaft is fairly curved mediad in antero-posterior view as in *C. brachyotis.* The head taking the form of an inverted triangle with rotundity is as high as the small trochiter and the large trochin. The anterior pit is shallow, and both the medial ridge and the lateral knob are absent. The roof-like pectoral ridge is very low in height. The distal epiphysis width is relatively narrow and the value of DW/PW is 1.18. The wing-type ratio is 1.30.

Fig. 4. Right humerus of *Megaerops ecaudatus.* Alphabetical symbols as in Fig. 1. A-D ×5.7, E-F ×2.9.

5. **Genus** *Aethalops*

(1) *Aethalops alecto* (Fig. 5)

The species is one of the smallest pteropodids (HL, 25.8 mm, N=1). The humerus is similar in appearance to that of *M. ecaudatus*, especially in the shape of the head and the pectoral ridge. As compared with *M. ecaudatus*, the proximal one-third of the humerus curves more strongly in antero-posterior view as in *C. sphinx.* The lower pectoral ridge is vestigial. The capitular inner ridge is as wide as the lateral one, and the shallow radial fossa is well-defined. The distal epiphysis width is very wide and the value of DW/PW could not be calculated because of a damaged trochin. The wing-type ratio is 1.40.

Fig. 5. Left humerus of *Aethalops alecto.* Alphabetical symbols as in Fig. 1. A-D ×5.7, E-F ×3.4.

DISCUSSION

The humeri of bats have the important diagnostic characters. They reflect the phylogenetic characteristics and the adaptive characters for flight. In this connection, Yoon and Uchida (1983a, b) discussed the functional significance of the microchiropteran humeral morphology and the adaptation of bats for flight within each taxon belonging to the more advanced Vespertilionidae and the less advanced Rhinolophidae. There are essential differences in the humeral morphology between the phylogenetically primitive members of the Megachiroptera (Pteropodidae) having simple and straight flight modes and the advanced members of Microchiroptera (Rhinolophidae and Vespertilionidae) developing various flight modes from slow, highly maneuverable flight to rapid, enduring flight. First, the trochiter is very different in shape and size between the two suborders. In the Megachiroptera, the trochiter being ill-defined in its outline and lower than the head forms the single articulation, because it dose not articulate with the secondary glenoid fossa of the scapula. It suggests that the Megachiroptera has weak shoulder joints. In contrast, the Microchiroptera has strong shoulder joints, because the well-developed trochiter projecting beyond the head forms the double articulation. That is, the enlarged trochiter of the humerus locks against a depression on the dorsal surface of the scapula at the upper limit of the upstroke, transferring the force of the upstroke to the scapula and tending to tip the lateral border of the scapula upward (Vaughan, 1970a).

Secondly, the pectoral ridge in the Pteropodidae (Megachiroptera) is quite different in shape from that in the Vespertilionidae, but similar to that of the Rhinolophidae (Microchiroptera); such a difference is associated with the amount of muscles of the upper arm. The reduction of weight of the wings is a major evolutionary trend common to all flying animals. In the Pteropodidae bearing a well developed pectoral muscle, as well as in the Rhinolophidae, its anterior division inserts on the lateral border of the roof-like or knife-like pectoral ridge, whereas in the Vespertilionidae that of the thin pectoral muscle inserts on the pedestal-like ridge. Thus, the thick biceps muscle passes through a wide surface in the Megachiroptera and the Rhinolophidae, while the thin biceps muscle runs along a deeper and narrower groove in the Vespertilionidae.

Another important characteristic related closely to flight lies in the value of DW/PW, which is the most important criterion exhibiting the degree of adaptation for flight, as well as the wing-type ratio. It is generally higher in the primitive Pteropodidae (1. 16~1. 32) and the less advanced Rhinolophidae (0. 99~1. 33) than in the more advanced Vespertilionidae (0. 64~1. 12). The higher ratio indicates that the mobile force originating from the scapula and the sternum is transmitted to the upper arm more dispersedly and thus the wing-beat power becomes weaker, because the force passes through the wide distal epiphysis of the humerus bearing the broad insertion surface for muscles (Yoon and Uchida, 1983a). That is, the higher the ratio, the lower the adaptability for flight in bats. The wing-type ratio in the Pteropodidae (1. 30~1. 41), however, is higher than in the Rhinolophidae (1. 10~1. 29) which is a low-speed flier with high maneuverability, although lower than in the Vespertilionidae (1. 19~1. 75) developing various flight modes, in general. In this connection, pteropodids would be expected to be faster flier than are rhinolophids. In fact, frugivorous bats are strong and direct fliers, but are not highly maneuverable (Vaughan, 1970b).

Judging from the above facts, it seems that insectivorous microchiropteran bats, using echolocation accomplished, first of all the slow and highly maneuverable flight to pursue and capture small insects that have extremely erratic flight patterns, and then have developed a variety of styles of flight, such as fast and sustained flight etc, as they have diverged into differentiated genera and species. On the contrary, in most of the frugivorous megachiropteran bats, development of highly specialized flight modes with extreme maneuverability or endurance, is not necessary for foraging or obstacle avoidance, because most of them, with the exception of ***Rousettus*** (Novick, 1958), orient visually rather than acoustically (Vaughan, 1970b).

ABSTRACT

The humeral characteristics of six species and one subspecies of five genera belonging to

the Pteropodidae of the Megachiroptera were described. Further, I discussed differences in the adaptability for flight of the bats between the phylogenetically primitive Megachiroptera and the advanced Microchirotpera, taking the humeral morphology, the value of DW/PW (the ratio of the distal epiphysis width to the proximal one) and the wing-type ratio (the third finger to the fifth one) into consideration.

ACKNOWLEDGEMENTS

I wish to thank Professor T.A. Uchida of Kyushu University for comments on the manuscript and his kind supply of the specimens which were offered him by Mr. M. Harada of Osaka City University.

REFERENCES

Kuramoto, T., 1972. Studies on bats at the Akiyoshi-dai Plateau, with special reference to the ecological and phylogenic aspects. ***Bull. Akiyoshi-dai Sci. Mus.*** (8):7-119.

Kuramoto, T., and T.A. Uchida, 1976. An approach by functional morphology to Chiropteran phylogeny, with special reference to the adaptation for fiight. ***Biological Science*** **28**:22-29.

Lawrence, B., 1943. Miocene bat remains from Florida, with notes on the generic characters of the humerus of bats. ***J. Mamm.*** **24**:356-369.

Miller, G.S., 1907. The families and genera of bats. ***Bull. U.S. natn. Mus.*** **57**:1-282.

Novick, A., 1958. Orientation in paleotropical bats. II. Megachiroptera. ***J. Exp. Zool.*** **137**:443-462.

Ohtsu, R. and T.A. Uchida, 1979a. Further studies on histochemical and ultrastructural properties of the pectoral muscles of bats. ***J. Fac. Agr., Kyushu Univ.*** **24**:145-155.

Ohtsu, R. and T.A. Uchida, 1979b. Correlation among fiber composition and LDH isozyme patterns of the pectoral muscles and fiight habits in bats. ***J. Fac. Agr., Kyushu Univ.*** **24**:157-163.

Ohtsu, R., T. Mōri and T.A. Uchida, 1978. Electron microscopical and biochemical studies on the major pectoral muscles of bats. ***Comp. Biochem. Physiol.*** **61A**:101-107.

Revilliod, R., 1922. Contribution à l'étude des chiroptères des terrains tertiaires. Troisieme partie et fin. ***Mém. Soc. Paléontol. Suisse*** **45**:131-195.

Sigé, B., 1971. Anatomie du membre antérieur chez un chiroptère molossidé (***Tadarida*** sp.) du Stampien de Cereste (Alpes-de-Haute-Provence). ***Paleovertebrata*** **4**:1-38.

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

Vaughan, T.A., 1966. Morphology and flight characteristics of molossid bats. ***J. Mamm.*** **47**:249-260.

Vaughan, T.A., 1970a. Adaptation for Flight in Bats. ***In:*** About Bats (H. Slaughter and D.W. Walton, editors). Southern Methodist Univ Press, Dallas, pp. 127-143.

Vaughan, T.A., 1970b. Flight Patterns and Aerodynamics. ***In:*** Biology of Bats (W.A. Wimsatt, editor). Academic Prese, New York and London, pp. 127-143.

Yokoyama, K. and T.A. Uchida, 1979a. Funtional morphology of wings from the the standpoint of adaptation for flight in Chiroptera. II. Growth and changes in mode of life during the young period in ***Rhinolophus cornutus cornutus. J. Fac. Agr., Kyushu Univ.*** **23**:185-198.

Yokoyama, K. and T.A. Uchida, 1979b. Ultrastructure of postembryonic development of the pectoral muscles in the Japanese lesser horseshoe bat, ***Rhinolophus cornutus cornutus*** from the standpoint of adaptation for flight. *J. Fac. Agr., Kyushu Univ.* **24**:49-63.

Yokoyama, K., T.A. Uchida and S. Shiraishi, 1975. Functional morphology of wings from the standpoint of adaptation for flight in Chiroptera. I. Relative growth and ossification in forelimb, wing loading and aspect ratio. *Zool. Mag.* **84**:233-247.

Yokoyama, K., R. Ohtsu and T.A. Uchida, 1979. Growth and LDH isozyme patterns in the pectoral and cardiac muscles of the Japanese lesser horseshoe bat, ***Rhinolophus cornutus cornutus*** from the standpoint of adaptation for flight. *J. Zool., London* **187**:85-96.

Yoon, M.H. and T.A. Uchida, 1983a. Identification of recent bats belonging to the Vespertilionidae by the humeral characters. *J. Fac. Agr., Kyushu Univ.* **28**:31-50.

Yoon, M.H. and T.A. Uchida, 1983b. Identification of recent bats belonging to the Rhinolophidae by the humeral characters. *J. Fac. Agr., Kyushu Univ.* **28**:135-146.

Yoon, M.H., T. Kuramoto and T.A. Uchida, 1981. Studies on taxonomy and phylogeny of bats' fossils from the Akiyoshi-dai Plateau. I. ***Plecotus auritus*** and ***Barbastella leucomelas darjelingensis*** belonging to the tribe Plecotini. *Bull. Akiyoshi-dai Sci. Mus.* (16):35-53.

Yoon, M.H., T. Kuramoto and T.A. Uchida, 1984a. Studies on Late Pleistocene bats including two new extinct ***Myotis*** species from the Akiyoshi-dai Plateau, with reference to the Japanese microchiropteran faunal succession. *Bull. Akiyoshi-dai Mus. Nat. Hist.* (19):1-14.

Yoon, M.H., T. Kuramoto and T.A. Uchida, 1984b. Studies on Middle Pleistocene bats including ***Pleistomyotis*** gen. et sp. nov. and two new extinct ***Myotis*** species fom the Akiyoshi-dai Plateau. *Bull. Akiyoshi-dai Mus. Nat. Hist.* (19):15-26.