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A Taxonomic Study of Pteropodid Bats (Megachiroptera) Collected from Southeast Asia Based on the Humeral Characters and Their Adaptation for Flight*

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Based on the humeral morphology of six frugivorous species of five genera (Pteropodinae) and three nectar-feeding species of two genera (Macroglossinae) belonging to the Pteropodidae, keys to the genera (tribes) and species were presented. Further, the adaptation for flight within each taxon was discussed, taking the humeral morphology, the value of DW/PW and the wing-type ratio into consideration. As the result, it was revealed that the Pteropodinae and the Macroglossinae may have been adapted to high-speed and low-speed flights, respectively, as they have changed their food habits.

INTRODUCTION

It has been well known that the humerus of bats exhibits characteristics of the family, subfamily, genus and species, and reflects the adaptation for flight. Such studies have been extensive on the Microchiroptera (Miller, 1907 ; Revilliod, 1922 ; Lawrence, 1943 ; Vaughan, 1959, 1970 ; Sigé, 1971; Kuramoto, 1972 ; Felten et al., 1973). Especially, Yoon and Uchida (1983a, b) made clear the fact that bats can be identified by the humeral characters alone, presented the keys based on the humeral characters of 23 species belonging to the Vespertilionidae and 11 species belonging to the Rhinolophidae, and discussed the adaptability for flight on the microchiropteran bats examined, 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 account. Further, Yoon et al. (1984a, b), on the basis of the humeral morphology of the recent bats, identified the fossil bats found from the Akiyoshi-dai Plateau and then inferred the Japanese microchiropteran fauna1 succession.

However, there have been only a few such studies for the Megachiroptera (Miller, 1907 ; Vaughan, 1970), including a report on the species level (Yoon, 1987). The aim of the present study is to describe humeral characters and arrange the keys to six frugivorous species of five genera (Pteropodinae, Pteropodidae) and to three nectar-feeding species of two genera (Macroglossinae, Pteropodidae) based on the humeral morphology, and to discuss the adaptation for flight within each taxon of the Pteropodidae.

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MATERIALS AND METHODS

The right humeri, as a rule, of available Pteropodidae, including six species and one subspecies of five genera belonging to the Pteropodinae, and three species of two genera belonging to the Macroglossinae were used in the present study (see Table 1). Because of no difference in the hurneral morphology 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 humeral length (HL), proximal epiphysis width (PW) and distal epiphysis width (DW) were measured by a caliper with 1/20 mm precision, and the ratio of the distal epiphysis width to the proximal one (DW/PW) was calculated. The wing-type ratio also was estimated.

DESCRIPTIONS

Family Pteropodidae

This family belonging to the Megachiroptera consists of two subfamilies, the Pteropodinae and the Macroglossinae. The humeri of the Pteropodidae examined possess the following characteristics. The humeral shaft flattened distally is sigmoid in lateral view, and the proximal one-third or half is fairly tilted mediad in antero-posterior view. The head exhibits an oval, ellipse, angulate oval or inverted triangle with rotundity. The undeveloped trochiter is smaller than the trochin, and does not articulate with the secondary glenoid fossa of the scapula. The anterior pit (the pit immediately anterior to the head) is very shallow. Both the medial ridge and the lateral knob are undeveloped or vestigial. The pectoral ridge, taking the form of a roof or a knife, is about one-third to two-fifths of the humerus in length. The capitulum consists of the inner and lateral ridges divided by a shallow, ill-defined lateral groove. The trochlea sharp on the margin is separated from the capitular inner ridge by a shallow or moderately deep groove. The flattened and wide medial epicondyle projects mediad, and bears distally the knob-like spinous process ending at higher level than the distal end of trochlea. The distal epiphysis is very wide and the values of DW/PW are 1.16-1.41 (Table 1). 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 or vestigial.

There are no distinct differences in the humeral morphology between the two subfamilies, except for the value of DW/PW (Pteropodinae, 1.16-1.28; Macroglossinae, 1.23-1.41) (Table 1).

Subfamily Pteropodinae

The humeral characteristics of five genera belonging to two tribes are as follows (Fig. 1).

Key to the genera (tribes) and species of Pteropodinae examined on the basis of the humeral morphology

1. Proximal half of humeral shaft slightly tilted mediad in antero-posterior view ; pectoral ridge one-third of humerus in length …… (Pteropodini)

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

Species	N	HL (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Subfamily Pteropodinae					
Tribe Pteropodini					
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*	Thailand Japan
Tribe Cynopterini					
Cynopterus ***sphinx***	2	***34.8, 36.6***	1.24. 1.27	1.30, 1.32	Thailand
C. brachyotis	2	***43.3, 46.6***	1.25. 1.26	1.32, 1.33	Indonesia
Megaerops *ecaudatus*	1	***29.7***	1.18	1.30	Thailand
Aethalops abcto	1	***25.6***		1.40	Indonesia
Subfamily Macroglossinae					
Tribe Macroglossini					
Eonycteris spelaea	1	***40.7***	1.23	1.40	Thailand
Macroglossus minimus	3	***25.7-27.8 (27.0)***	1.33-1.41 (1.39)	1.32	Indonesia
M. lagochilus	1	***27.2***	1.40	1.34	Malaysia

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

2. Humeral length less than 50 mm ; head oval, moderate in size ; both trochiter and trochin higher than head ; both medial ridge and lateral knob moderately developed ; anterior pit very shallow ; high pectoral ridge sharp roof- or knife-like in appearance. DW/PW : 1.16-1.27 ..... *Rousettus* ***leschenaulti***

2'. Humeral length about 90-100 mm ; head angulate oval, large in size ; trochiter slightly lower than head which is as high as trochin ; both medial ridge and lateral knob vestigial ; anterior pit less shallow ; low pectoral ridge taking the form of a roof with a gentle inclination in appearance. DW/PW : 1.25-1.28 ..... *Pteropus dasymallus*

1'. Proximal one-third of humeral shaft considerably curved mediad in antero-posterior view ; pectoral ridge two-fifths of humerus in length ..... (Cynopterini)

3. Head oval ; pectoral ridge with a sharp lateral margin relatively high.

4. Proximal shaft strongly curved ; pectoral ridge concave on the surface. DW/PW : 1.24, 1.27 ..... *Cynopterus sphinx*

4'. Proximal shaft less curved ; pectoral ridge not concave on the surface. DW/PW 1.25, 1.26 ..... *Cynopterus brachyo tis*

3'. Head taking the form of an inverted triangle with rotundity;

pectoral ridge roof-like and very low.

5. Pectoral ridge low but distinctive ; capitular inner ridge three times as wide as lateral one. DW/PW: 1.18 ····· *Megaerops ecaudatus*

5'. Pectoral ridge vestigial ; capitular inner ridge as wide as lateral one ····· *Aethalops alecto*

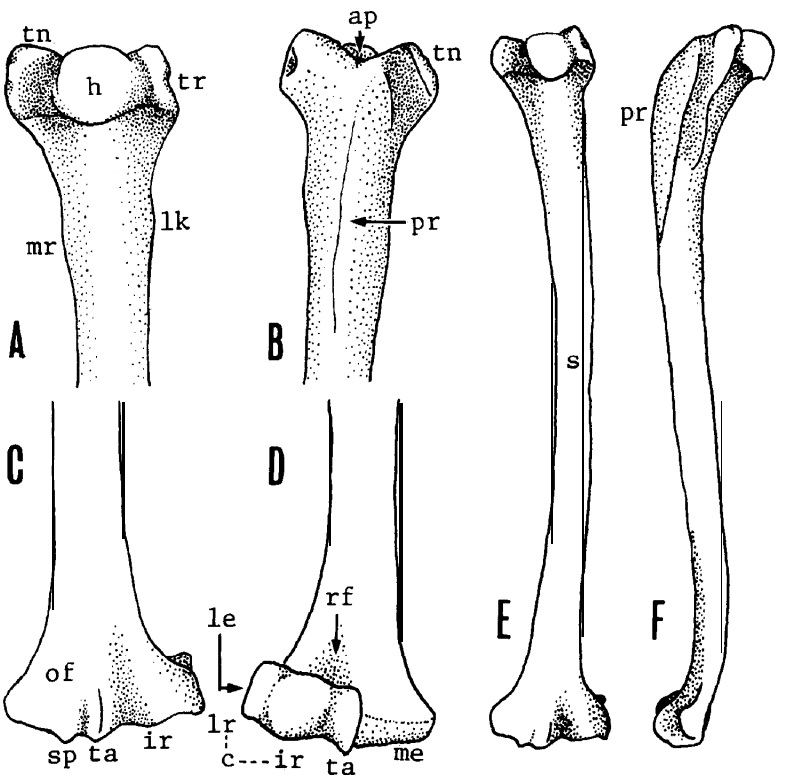

Fig. 1. Right humerus of *Rousettus leschenaulti,* showing posterior (A, C) and anterior (B, D) views of proximal and distal ends, respectively, and the whole posterior (E) and medial (F) views. A-D x *3.0,* E-F x 2.0. Abbreviations : ap, anterior pit ; c, capitulum ; h, head ; ir, inner ridge of capitulum ; le, lateral epicondyle ; lk, lateral knob ; lr, lateral ridge of capitulum ; me, medial epicondyle ; mr, medial ridge ; of, olecranon fossa ; pr, pectoral ridge ; rf, radial fossa ; s, shaft ; sp, spinous process ; ta, trochlea ; tn, trochin ; tr, trochiter.

Subfamily Macroglossinae

The humeral characteristics of two genera belonging to the Macroglossini are as follows (Fig. 2).

Key to the genera and species of Macroglossinae examined on the basis of the hurneral morphology

1. Humeral length about 40 mm : shaft slightly curved mediad at proximal half in antero-posterior view ; both trochiter and trochin slightly higher than head ; high and sharp pectoral ridge one-third of humerus in length. DW/PW: 1.23 ..... *Eonycteris spelaea*

1'. Humeral length about 27 mm ; shaft strongly curved mediad at proximal one-third in antero-posterior view ; both trochiter and trochin not higher than head ; low pectoral ridge two-fifths of humerus in length. DW/PW: 1.33-1.41.

2. Head oval ; both trochiter and trochin moderate in size and as high as head ; roof-like pectoral ridge with a gentle inclination very low ; capitular inner ridge about three times as wide as lateral one ; groove between capitular inner ridge and trochlea moderately shallow. DW/PW: 1.33-1.41 ..... *Macroglossus minimus*

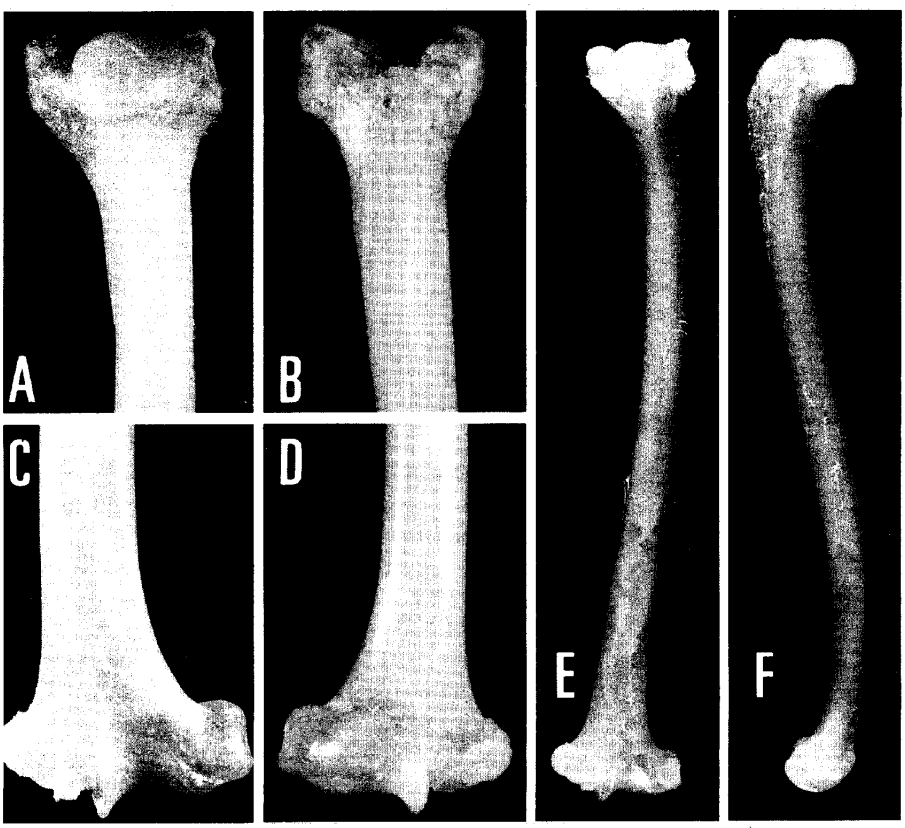

Fig. 2. Right humerus of *Eonycteris spelaea.* Alphabetical symbols as in Fig. 1. A-D x4.7, E-F x2.5.

2'. Head ellipsoidal ; both trochiter and trochin very small in size and lower than head ; roof-like and relatively high pectoral ridge with a steep inclination and a sharp margin at lateral border ; capitular inner ridge about twice as wide as lateral one ; groove between capitular inner ridge and trochlea very shallow. DW/PW : 1.40 ..... *Macroglossus lagochilus*

DISCUSSION

Phylogeny within the Pteropodidae has been studied mainly by Anderson (1912) and somewhat modified afterwards by Koopman and Jones (1970). According to them, the Pteropodinae and the Macroglossinae may have diverged before the evolution of the various genera within the Pteropodinae and a common ancestor of the two subfamilies is presumably a *Rousettus*-like form ; *Rousettus* and *Eonycteris* have been regarded as the most primitive genus in the Pteropodinae and Macroglossinae, respectively. These views have led to a karyological presumption that the ancestral form of the family may have possessed the same karyotype (2n= 36, FN =68) as those of *Rousettus* and *Eonycteris* (Andō, 1982).

Also from the viewpoint of the humeral morphology, *Rousettus* and *Eonycteris*, each presumed to be the most primitive genus in their respective subfamilies, resembled each other. Within each subfamily belonging to the Pteropodidae, the humeri of the bats examined had the following characters : the more the genus took a high phylogenetic position, the stronger the proximal shaft of the humerus was curved, the smaller the trochiter was, and the longer and lower the roof-like pectoral ridge was. In the two genera mentioned above, however, the proximal shaft of the humerus curved slightly, trochiter was relatively high, and the short pectoral ridge was high roof- or knife-like in appearance. Further, they showed a similarity in the value of DW/PW. Judging from these facts, the ancestral form of the Pteropodidae appears to have borne the *Rousettus*-like humeri and flight pattern. However, the ancestral form may have been adapted to feed on not only fruits but also nectar and pollen, so that *Eonycteris,* the most primitive form of the Macroglossinae, may have branched off from the pteropodid ancestor, then the specialized *Macroglossus* have derived, and eventually the humeral characters and the attributive flight modes of pteropodid bats have been altered with changes in food habit.

In fact, frugivorous pteropodinine bats fly linearly with strong flaps, but nectar-feeding macroglossinine bats fly slowly, with hovering through the dense vegetation of tropical forests. Bats of both the two subfamilies, however, are not so maneuverable as are certain insectivorous bats (Vaughan, 1970). The adaptation for flight of the Pteropodidae may be inferred, taking the humeral morphology, the value of DW/PW and the wing-type ratio into consideration, as follows. In all the members of the family, since the relatively small trochiter does not form a secondary articulation with the scapula (Miller, 1907), an angle for a wing-beat becomes larger : accordingly, much energy is needed for strong flight in the Pteropodinae, but for hovering in the Macroglossinae (Vaughan, 1970). Further, the two subfamilies were very similar also in other humeral cahracters to each other. On the other hand, it is suggested that the Pteropodinae is more advanced in the adaptation for high-speed flight than is the

Macroglossinae, judging form the higher value of DW/PW in the former (cf. Yoon and Uchida, 1983a, b).

Such a difference in the adaptation is due to the disparity in feeding habit. That is, the frugivorous Pteropodinae which is visually oriented seems to have been sdapted to increase the speed of flight, instead of acquiring greater maneuverability. Accordingly, the wing may become comparatively longer and narrower : especially in each tribe, the higher the genus was in the phylogenetic position, the longer and narrower the wing was (Table 1). However, the bats of the family vary little between the subfamilies and tribes in the humeral morphology and the value of DW/PW. As suggested by Vaughan (1970), the flight apparatus in the Pteropodinae seems not to have been specialized because of short periods of flight used during foraging and reduced maneuverability.

On the other hand, the Macroglossinae, which chooses nectar and pollen as its food because of failure in competition for limited fruits, has advanced to a narrower space for foraging, and consequently may have come to develop maneuverable and hovering flight. As a result, the transition of mobile force to the upper arm seems to have gradually changed with flight patterns, and the value of DW/PW became larger. In fact, the specialized *Macroglossus* has a higher value of DW/PW than the primitive *Eonycteris,* i. e. the higher the phylogenetic position, the higher the degree of maneuverability. This fact is backed up also with the wing-type ratio which is lower in *Macroglossus*. Therefore, the macroglossinine bats have been adapted to a type of flight involving low-speed and skillful hovering.

To sum up, although the pteropodid ancestral form has the *Rousettus*-like humerus and flight pattern, the frugivorous Pteropodinae may have been adapted to rather high-speed flights, but the netter-feeding Macroglossinae to butterfly-like low-speed flights with hovering, as they have changed their food habits.

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