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https://doi.org/10.5109/23777

出版情報：九州大学大学院農学研究院紀要. 28 (1), pp.31-50, 1983-09. Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., 28 (1), 31-50 (1983)

Identification of Recent Bats belonging to the Vespertilionidae by the Humeral Characters

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(Received May 9, 1983)

With the finding of many humeri of fossil bats on the Akiyoshi-dai Plateau in recent years, the investigation was carried out to determine whether bats can be classified to the species level by the humeral characters alone. Using the humeri of 23 recent species and 4 subspecies belonging to 9 genera of the Vespertilionidae including 3 subfamilies, keys based on humeral characters to various taxa from subfamily to species enabled us to identify to the species level. Furthermore, not only the functional significance of the humeral morphology but also the adaptation of bats for flight within each taxon were discussed; the higher the bat was in the degree of adaptation for flight, the lower the DW/PW ratio (the ratio of the distal epiphysis width to the proximal one) was. Consequently, it became clear that the ratio is one of the most important criteria exhibiting directly the degree of adaptation. Taking also the wing-type ratio (the third finger to the fifth one) into consideration, the adaptability for flight in bats can be estimated more exactly.

INTRODUCTION

Bats are the only mammals capable of flight. Their specialized body structure and life mode have been caused by adaptation for flight, although they have preserved primitive characteristics of the prototypic insectivore ; thus, their most diagnostic features result from variations in the foraging pattern from highly manoeuvrable flight with a low speed to sustained flight with a high speed. Careful descriptions of the flight mechanism in bats have been given by Vaughan (1959, 1966, 1970).

At the present time, the need of identification of bats to the species level by only the humeral characters becomes pressing, because a number of humeri of fossil bats, which occupy a great part of the fossil skeletons, were found on the Akiyoshi-dai Plateau of the Yamaguchi Prefecture. Only a few papers based on the humeral characters of fossil bats for identification have been published (Revilliod, 1922; Lawrence, 1943; Sigé, 1971; Yoon et ***al.,*** 1981). This investigation dealt with morphological differences amongst humeri of many recent bats accesible to determine whether they can be classified to the species level by humeri alone. Furthermore, in order to discuss the adaptability of these bats for flight, we inquired closely into the functional significance of their humeral characters, and paid our attentions to the ratio

of distal epiphysis width to proximal one (DW/PW) as the most important characteristic indicating directly the degree of adaptation for flight, as well as the wing-type ratio (the third finger to the fifth one) which would frequently be utilized.

MATERIALS AND METHODS

We studied the right humeri, as a rule, of 23 species and 4 subspecies that were available, belonging to 9 genera of the Vespertilionidae including 3 subfamilies, which represent all the genera in Japan. Since we found no difference between two subspecies of *Myotis nattereri bombinus* and ***M.*** *n. amurensis,* *Plecotus* ***auritus*** *sacrimontis* and ***P. a.*** *auritus, Pipistrellus pipistrellus pipistrellus* and ***P.*** *p. bactrianus,* and ***P. savii velox*** and ***P. s.*** *coreensis,* they were included together in the species concerned.

The humerus length (HL), proximal epiphysis width (PW) and distal epiphysis width (DW) were measured by a caliper with 1/20 mm precision, and then the ratio of DW/PW was calculated. The wing-type ratio also was estimated.

DESCRIPTIONS

Family Vespertilionidae

Members of the Vespertilionidae inhabiting Japan belong to one of three subfamilies, i. e. Vespertilioninae, Murininae and Miniopterinae. The humeral shaft of vespertilionid bats examined, which is nearly straight in lateral view, is slightly flattened distally or cylindrical over the length. The head exhibits an oval or ellipse, etc. The trochiter curves mediad, projects beyond the head and articulates with the secondary glenoid fossa of the scapula to form the double articulation. The trochin is lower and smaller than the trochiter. The depth of anterior pit (the pit immediately anterior to the head) and size of the lateral knob vary within the family, and the medial ridge is well developed. The pectoral ridge is pedestal-like in appearence. The capitulum consists of the inner and lateral ridges divided by a lateral groove. Another inner groove, which is parallel or slightly oblique to the humeral axis as well as the above one, separates the inner ridge of the capitulum from the trochlea. The trochlea is flat or slightly declined towards capitular inner ridge. The medial epicondyle, which is moderately wide or narrow, bears distally the spinous process slightly curving laterad and taking the form of a tubercle, projection or well-developed and compressed peg. The distal epiphysis is wide moderately or narrow. The distal articular surface and radial fossa are concentric or slightly eccentric outwards against the humeral axis. The size of the lateral epicondylar crest and the depth of the olecranon and radial fossae also vary with species.

Key to the subfamilies of Vespertilionidae examined on the basis of the humeral morphology

1. Groove between two ridges of capitulum shallow or moderately deep; spinous process tubercular or projection-like.
   2. Head globular, oval or ellipsoidal; trochiter extending beyond head moderately or extremely high; pectoral ridge one-sixth to one-fifth of humerus in length; medial epicondyle wide moderately, or narrow and knob-like ; spinous process terminated at slightly lower or higher level than distal end of trochlea; distal epiphysis wide moderately or narrow. DW/PW: 1.03-o. 64 ..... Vespertilioninae
   2′. Head round, flattened on surface; trochiter slightly higher than head; pectoral ridge one-quarter of humerus in length; medial epicondyle wide; spinous process ended at distal one-third level of trochlea; distal epiphysis wide. DW/PW: 1. 12-1.00 ..... Murininae
1'. Groove between two ridges of capitulum extremely deep; spinous process well-developed and compressed peg-like.. ..... Miniopterinae

Subfamily Vespertilioninae

The humeri in all the seven Japanese genera belonging to four tribes are examined in this paper.

Key to the genera (tribes) of Vespertilioninae examined on the basis of the humeral morphology

1. Shaft moderately flattened distally; radial fossa shallow. DW/PW: 1.03-0.84.
   2. Medial ridge moderately wide; lateral knob undeveloped or moderately developed; pectoral ridge curved at proximal third..... ..... *Myotis* (Myotini)
   2'. Medial ridge narrow; lateral knob well developed; pectoral ridge curved at proximal quarter..... (Plecotini)
      3. Head oval; both trochiter and trochin slightly higher than head; anterior pit shallow; medial ridge approximately two-thirds of pectoral ridge in length; inner ridge of capitulum four times as wide as lateral one; trochlea slightly declined outwards, narrower than capitular inner ridge; medial epicondyle wide moderately ; spinous process terminated at slightly higher level than distal end of trochlea; distal epiphysis relatively wide; distal articular surface slightly eccentric outwards against humeral axis; narrow olecranon fossa very shallow. DW/PW: 1. 03–0. 96 ..... *Plecotus*
      3'. Head ellipsoidal; trochiter fairly higher than head, trochin as high as head; anterior pit deep; medial ridge about three-fifth of pectoral ridge in length; capitular inner ridge as wide as lateral one; trochlea flat, as wide as capitular inner ridge; knob-like medial epicondyle narrow; spinous process terminated at slightly lower level than distal end of trochlea; distal epiphysis wide

moderately; distal articular surface nearly concentric against humeral axis; narrow olecranon fossa moderately deep. DW/PW: 0.84 ..... *Barbastella*

1'. Shaft slightly flattened distally or cylindrical over the length; radial fossa deep. DW/PW: 0.89-o. 64.

4. Lateral margin of olecranon fossa reached behind capitular lateral ridge.. ..... (Pipistrellini)

5. Shaft flattened distally; spinous process terminated at slightly lower level than distal end of trochlea. DW/PW: 0.89-o. 78 ..... *Pipistrellus*

5'. Shaft nearly cylindrical; spinous process terminated at fairly lower level than distal end of trochlea. DW/PW: 0.81-o. 64.

6. Trochiter fairly higher than head; lateral knob well developed ; lateral epicondylar crest slightly developed. DW/PW: 0.81-o. 72 ..... *Vespertilio*

6'. Trochiter extremely higher than head; lateral knob undeveloped ; lateral epicondylar crest moderately developed. DW/PW: 0.67-0. 64.. ..... *Nyctalus*

4'. Olecranon fossa restricted behind trochlea ..... *Eptesicus* (Nycticeini)

Genus Myotis

The humeri of four species out of all the 10 Japanese species and another foreign species are dealt with in this paper (Table 1 and Fig. 1). The humeri of *Myotis* have not only the characteristics shown in the above key of the genus (tribe) but also the following: the head takes the form of a globe or oval, the trochiter moderately high in general, the trochin as high as the head, the anterior pit shallow or moderately deep, the medial ridge more

Table 1. Comparison of the humerus and the wing-type in *Myotis* examined.

Species	N	HL (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Myotis nattereri	4	*22.05-24.25 (23.40)*	*0.95-O. 97 (0.97)*	*1.21-1.25*	Japan Korea
M. mystacinus glacilis	14	*20.70-22.35 (21. 40)*	*0.89-o. 96 (0.92)*	*1.21-l. 28*	Japan
*M. daubentoni ussuriensis**	8	*22.40-23.40* (23.02)	*0.85-o. 93* (0.89)	*1.21-l. 25*	Korea USSR
M. macrodactyus	21	20.90-23.00 *(22.52)*	0.87-o. 92 *(0.89)*	1.24-l. 25	Japan Korea
M. myotis myotis	1	*35.10*	*0.88*		Sweden

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.

* Although only foreign specimens were examined, the species inhabits Japan, too.

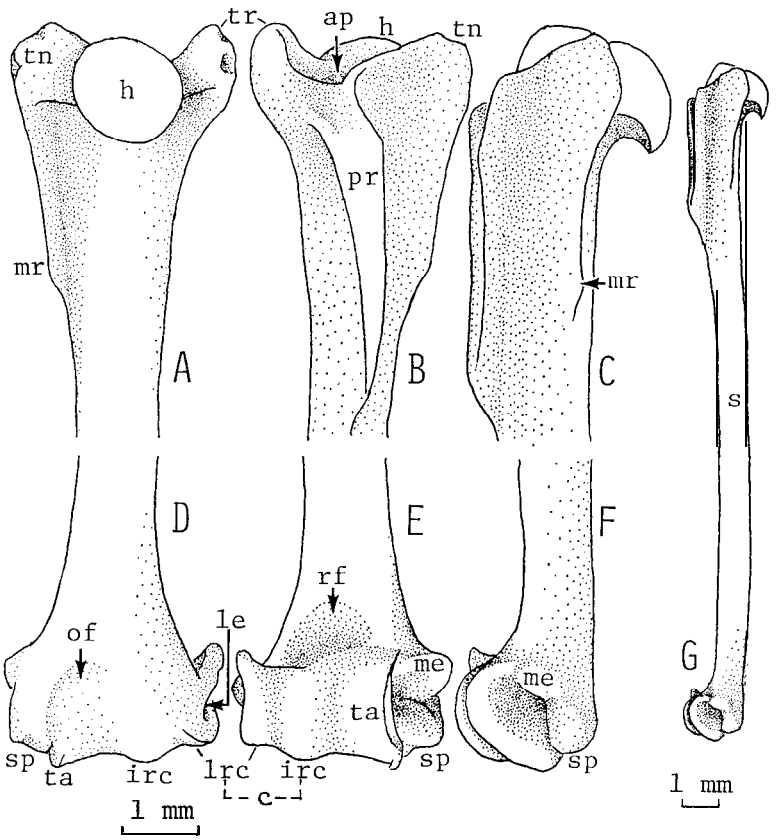


Fig. 1. Right humerus of *Myotis nattereri bombinus*, showing posterior (A, D), anterior (B, E) and medial (C, F) views of proximal and distal ends, respectively, and a whole view (G). Left and right scales are for A-F and G, respectively. Abbreviations: ap, anterior pit; c, capitulum; h, head; irc, inner ridge of capitulum; le, lateral epicondyle; lrc, 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.

than two-thirds of the pectoral ridge in length, the pectoral ridge one-sixth to one-fifth of the humerus in length; the groove separating the capitular inner ridge from the lateral one (in the ratio of two to one in width) nearly parallel to the humeral axis, the trochlea declined outwards, as large as the capitular inner ridge and separated from the inner ridge by another shallow groove running in almost parallel with the humeral axis, the medial epicondyle moderately wide, the tubercular spinous process terminated at higher level than the distal end of trochlea, the distal epiphysis wide moderately and the articular surface nearly concentric against the humeral axis, the lateral epicondylar crest undeveloped, the radial fossa shallow in general.

Key to the species of *Myotis* examined on the basis of the humeral morphology

1. Humerus length about 20-25 mm; head globular.
   2. Trochiter low; anterior pit shallow; medial ridge two-thirds of pectoral ridge in length; pectoral ridge one-fifth of humerus in length; spinous process terminated at approximately distal one-quarter level of trochlea ..... *M. nattereri*
   2'. Trochiter moderately high; anterior pit moderately deep; medial ridge three-quarters of pectoral ridge in length; pectoral ridge one-sixth of humerus in length; spinous process terminated at higher level than distal one-quarter of trochlea.
      3. Lateral knob moderately developed; olecranon fossa relatively deep ..... *M. mystacinus glacilis*
      3'. Lateral knob undeveloped; olecranon fossa extremely shallow.
         4. Posterior margin of spinous process in line with shaft, devoid of tilting back; radial fossa shallow ..... *M. daubentoni ussuriensis*
         4'. Posterior margin of spinous process tilted back, protruded from line of shaft; radial fossa moderately deep ..... *M. macrodactylus*
1'. Humerus length about 35mm; head oval ..... *M. myotis myotis*

Genus Plecotus

The humeral characteristics of the single Japanese species and another foreign species are described (Fig. 2 and Table 2). The humeri possess some characters in addition to those shown in the above key of the genus (tribe), i. e. the two shallow grooves on the distal articular surface are nearly parallel to the humeral axis, the lateral epicondylar crest undeveloped.

Key to the species of *Plecotus* examined on the basis of the humeral morphology

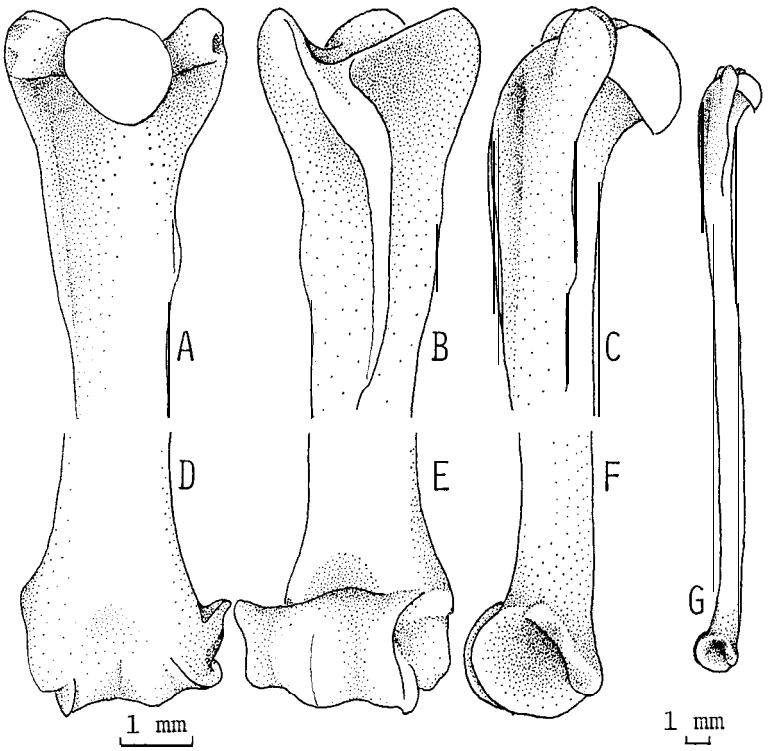
1. Anterior pit shallow; olecranon fossa vestigial. DW/PW: 1.00-o. 96 ..... *P. auritus*
1'. Anterior pit moderately deep; olecranon fossa shallow. DW/PW: 1.03 ..... *P. townsendi*

Genus Barbastella

The humeri of the single Japanese species *Barbastella leucomelas darjelingensis* are examined (Fig. 3 and Table 2). The humeri are characterized by some other properties than those given in the preceding key of the genus (tribe), i. e. two grooves on the distal articular surface are moderately deep, slightly oblique to the humeral axis, the lateral epicondylar crest undeveloped.

Genus Pipistrellus

The humeral characteristics of all the three Japanese species and another foreign species are noted (Fig. 4 and Table 3). The humeri of *Pipistrellus* have the following characters except for those shown in the above key of the ge-



Fig, 2. Right humerus of *Plecotus auritus sacrimontis*. Alphabetical symbols and scales as in Fig. 1.

Table 2. Comparison of the humerus and the wing-type in *Plecotus* and *Barbastella* examined.

Species	N	HL (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Plecotus auritus	7	*23.85-25.30* (24.68)	*0.96-l. 00* (0.99)	*1.29-l. 33*	Japan USSR
P. townsendi	*1*	*23.40*	*1.03*	*1.36*	Mexico
Barbastella leucomelas darjelingensis	3	25.50-25.85 (25.63)	0. 84*	1.36-l. 38	Japan

Abbreviations as in Table 1.

* Since the trochins of both the humeri were damaged in two specimens out of the three, the value was based on one specimen.

nus (tribe): the head is ellipsoidal, the trochiter moderately high, the trochin not higher than the head, the anterior pit deep, the medial ridge wide in general, terminating at about the same level of the distal end of the pectoral ridge, the lateral knob well developed, the pectoral ridge not less than one-sixth of the humerus length, curved at proximal third; the capitulum is divid-

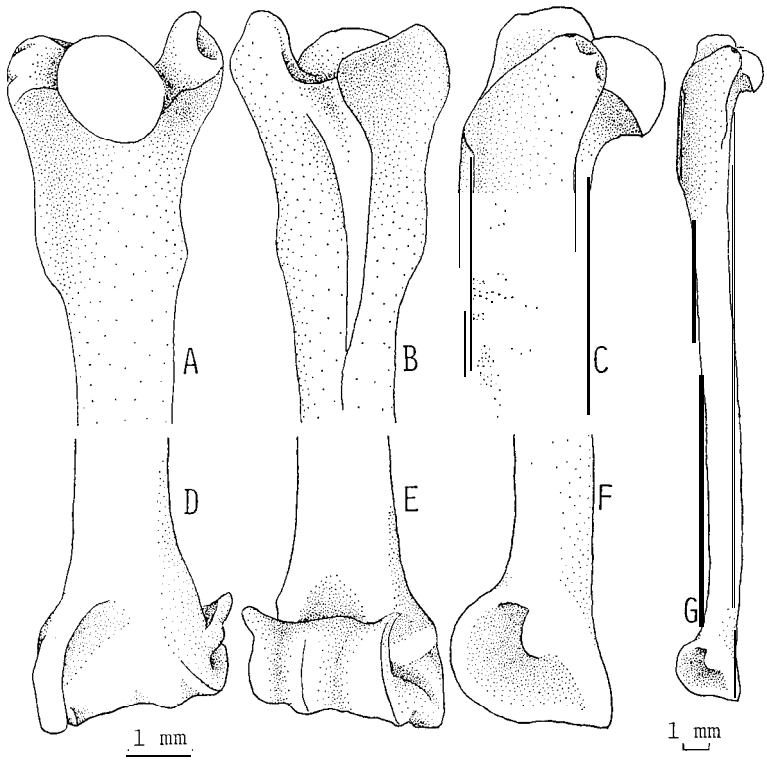


Fig. 3. Right humerus of *Barbastella* ***leucomelas*** *darjelingensis*. Alphabetical symbols and scales as in Fig. 1.

ed into inner and lateral ridges (in the ratio of two to one in width) by a moderately deep groove oblique slightly to the humeral axis, the wide and flat trochlea larger than the inner ridge, the deep groove between the trochlea and the inner ridge also slightly oblique to the humeral axis, the medial epicondyle small and knob-like, the distal epiphysis comparatively narrow, the distal articular surface almost concentric against the humeral axis, the lateral epicondylar crest well developed in general, the moderately deep olecranon fossa pocket-like.

Key to the species of *Pipistrellus* examined on the basis of the humeral morphology

1. Humerus length about 18-22 mm; medial ridge very wide; spinous process terminated at slightly lower level than distal end of trochlea.
   2. Head ellipsoidal, but flattened on upper external and lower internal sides. DW/PW: 0.85-0.78 ..... *P. pipistrellus*
   2'. Head ellipsoidal, having a rotundity. DW/PW: 0.89-o. 82.
      3. Pectoral ridge about one-sixth of humerus in length; radial fossa wide and moderately deep ..... *P. endoi*

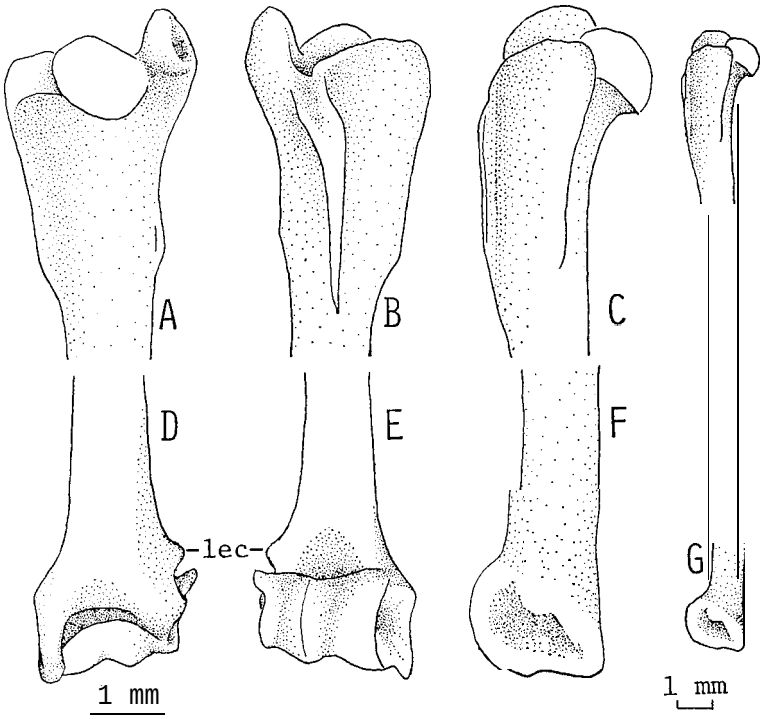


Fig. 4. Right humerus of *Pipistrellus pipistrellus pipistrellus.* Alphabetical symbols and scales as in Fig. 1. Abbreviation :lec, lateral epicondylar crest.

3'. Pectoral ridge more than one-fifth of the humerus length; radial fossa narrow and deep..... *P. abramus abramus*

1'. Humerus length not less than 22 mm; medial ridge moderately wide ; spinous process terminated at much the same level of distal end of trochlea..... *P. savii*

Genus Vespertilio

Humeral characteristics of the single Japanese species and another foreign species are observed (Fig. 5 and Table 3). The humeri of *Vespertilio* possess the following characters besides those shown in the above key of the genus (tribe) : compared with *Pipistrellus,* the head is sideways lengthened, the medial ridge narrow, terminated at higher level than the distal end of the pectoral ridge, the capitular inner ridge as long as the trochlea, the groove between the trochlea and the inner ridge moderately deep, the distal epiphysis relatively narrow, the lateral epicondylar crest undeveloped, and both the olecranon and radial fossae deep.

Table 3. Comparison of the humerus and the wing-type in *Pipistrellus*, *Vespertilio* and *Nyctalus* examined.

Sepcies	N	H L (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Pipistrellus pipistrellus	12	17.95-19.75 *(18.65)*	0.78-o. 85 (0.82)	1.35-l. 40	-France Spain USSR
*P. savii**	5	22.45-24.35 (23.35)	0.85-o. 89 (0.86)	1.36-l. 37	Korea
P. endoi	3	*18.10, 19.75*†	*0.84-o. 88 (0.86)*	1.40-l. 45	Japan
P. abramus abramus	26	*19.30-21.60* (20.61)	*0. 82-O. 89* (0.86)	*1.34-l. 35*	Japan Korea
Vespertilio murinus	2	*25.50, 26. 55*	*0.81, 0.81*	*1.40, 1.42*	USSR
V. superans superans	7	28.00-30.10 (28.96)	0.73-O. 76 (0.74)	*1.47-l. 48*	Japan
Nyctalus furvus	2	*30.80'*	0.67‡	*1.64, 1.66*	Japan
N. lasiopterus aviator	2	*37.00, 37. 20*	*0. 64, 0.65*	*1. 66, 1. 67*	Japan

Abbreviations as in Table 1.

* Although only foreign specimens were examined, the species inhabits Japan, too.

† *Since* the shafts of both the humeri *were* broken *in one* specimen out of the three. the value was based on two specimens.

‡ In one specimen out of the two, both the humeri had been used for karyotypic analyses, thus the value was based on one specimen.

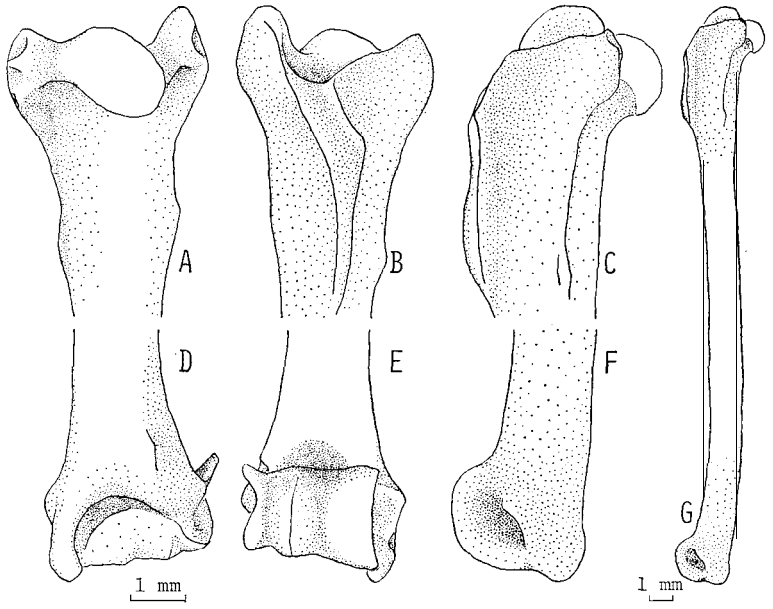


Fig. 5. Right humerus of *Vespertilio murinus*. Alphabetical symbols and scales as in Fig. 1.

Key to the species of ***Vespertilio*** examined on the basis of the humeral morphology

1. Humerus length about 26mm; head flattened on upper external and lower internal sides; anterior pit moderately deep. DW/PW: 0.81 ..... *V. murinus*

1′. Humerus length about 29 mm; head not so flattened on upper external and lower internal sides; anterior pit very deep. DW/PW: 0.76-o. 73 ..... *V. superans superans*

Genus Nyctalus

The humeral characteristics of all the two Japanese species are described (Fig. 6 and Table 3). The humeri of ***Nyctalus*** have the following characters in addition to the aforesaid diagnoses given in the above key of the genus (tribe): the head is sideways longest within the Vespertilionidae examined, the trochiter highest within the Vespertilioninae checked, the trochin nearly as high as the head, the anterior pit deepest within the subfamily examined, both the medial and the pectoral ridges similar to those of ***Vespertilio*** in shape, but the former ridge which is slightly shorter than the latter proximally wider than that of ***Vespertilio;*** the distal epiphysis is similar to that of *Pipis-*

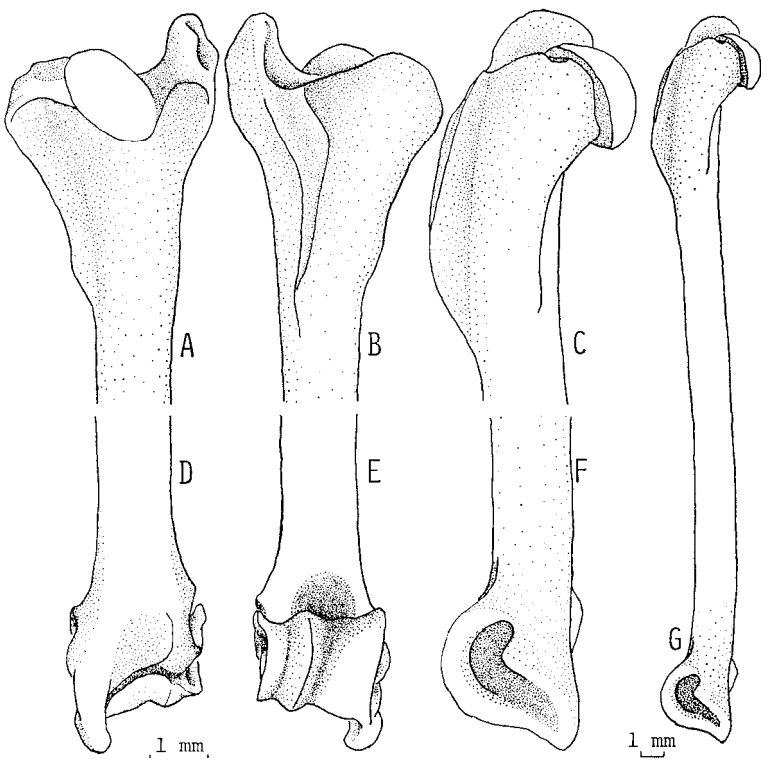


Fig. 6. Right humerus of ***Nyctalus furvus.*** Alphabetical symbols and scales as in Fig. 1.

trellus and *Vespertilio* in shape, but the trochlea which is remarkably wider than the capitular inner ridge is widest within the Vespertilionidae examined, the projection-like spinous process longer, the distal epiphysis narrowest within the Vespertilionidae checked, the olecranon fossa deeper.

Key to the species of ***Nyctalus*** examined on the basis of the humeral morphology

1. Humerus length about 31 mm; proximal part of medial ridge considerably wide, DW/PW: 0.67 ..... *N. furvus*

1'. Humerus length about 37 mm; proximal part of medial ridge moderately wide. DW/PW: 0.65–0.64 ..... *N. lasiopterus aviator*

Genus Eptesicus

The humeri of the two Japanese species and two other foreign species are dealt with (Fig. 7 and Table 4). The humeri of ***Eptesicus*** have not only the characteristics described in the above key of the genus (tribe) but also the following characters: the shaft is flattened distally, the head ellipsoidal generally, the trochiter moderately high, the trochin nearly as high as the head, the anterior pit moderately deep in general, the medial ridge moderately wide, somewhat shorter than the pectoral ridge, the lateral knob scarcely developed, the pectoral ridge nearly one-fifth of the humerus in length, curved at proximal third; the moderately deep groove which is slightly oblique to the humeral axis divides the capitulum into the inner and lateral ridges (in

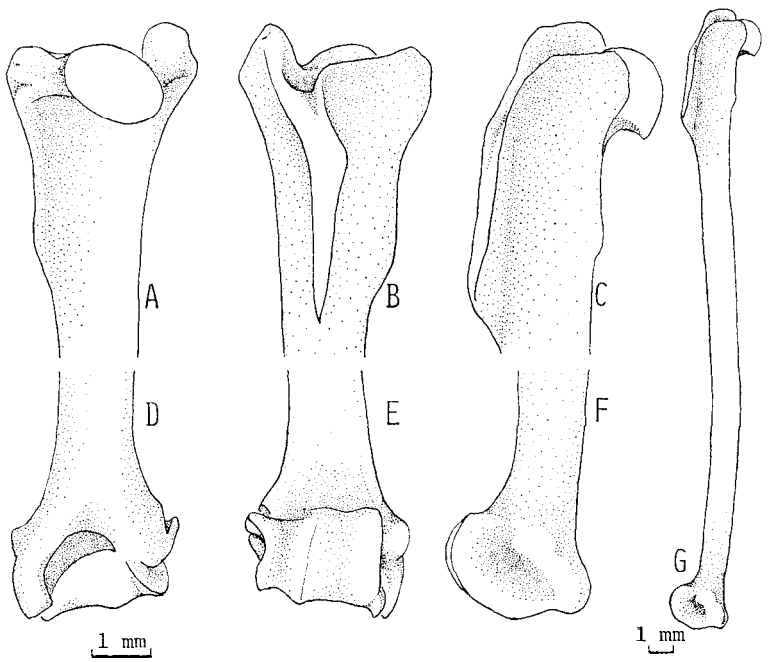


Fig. 7. Right humerus of ***Eptesicus nilssoni parvus.*** Alphabetical symbols and scales as in Fig. 1.

Table 4. Comparison of the humerus and the wing-type in ***Eptesicus*** examined.

Species	N	H L (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Eptesicus *nilssoni parvus*	***2***	***24.50, 26.20***	***0.83, 0.84***	***1.38, 1.39***	Japan
E. *japonensis*	1	25.25	0.84	1.40	Japan
E. *fuscus fucsus*	***1***	31.00	0.84	1.33	USA
E. serotinus *pallens*	***1***	***33.70***	***0.85***	***1.36***	Korea

Abbreviations as in Table 1.

the ratio of approximately two to one in width), the flat trochlea being separated from the capitular inner ridge in equal width each other by another shallow groove which is slightly oblique to the humeral axis, the medial epicondyle knob-like, the tubercular spinous process never extends to the lower level than the distal end of the trochlea, the distal epiphysis narrow and the articular surface nearly concentric against the humeral axis, the lateral epicondylar crest undeveloped, the pocket-like olecranon fossa moderately deep, the radial fossa shallow.

Key to the species of *Eptesicus* examined on the basis of the humeral morphology

1. Medial ridge moderately wide; pectoral ridge moderately curved at proximal third ..... *E. nilssoni parvus*
1'. Medial ridge narrow; pectoral ridge strongly curved at proximal third.
   2. Humerus length about 25 mm; trochiter moderately high; both anterior pit and olecranon fossa moderately deep; radial fossa shallow ..... *E. japonensis*
   2'. Humerus length not less than 31 mm; trochiter relatively low; both anterior pit and olecranon fossa relatively shallow; radial fossa very shallow.
      3. Humerus length about 31 mm; head globular; posterior margin of spinous process tilted back, protruded from line of shaft ..... *E. fuscus fuscus*
      3'. Humerus length about 34mm; head ellipsoidal; posterior margin of spinous process in line with shaft, devoid of tilting back..... *E. serotinus pallens*

Subfamily Murininae

Genus Murina

The humeri of the two species out of all the three Japanese species are treated in this paper (Fig. 8 and Table 5). The humeri of *Murina* are characterized by the following properties as well as those shown in the above key of the subfamily: the shaft is slightly flattened distally, the narrow trochin lower than the head, the anterior pit very shallow, the narrow medial ridge terminated at distal quarter level of the pectoral ridge, the lateral knob mod-

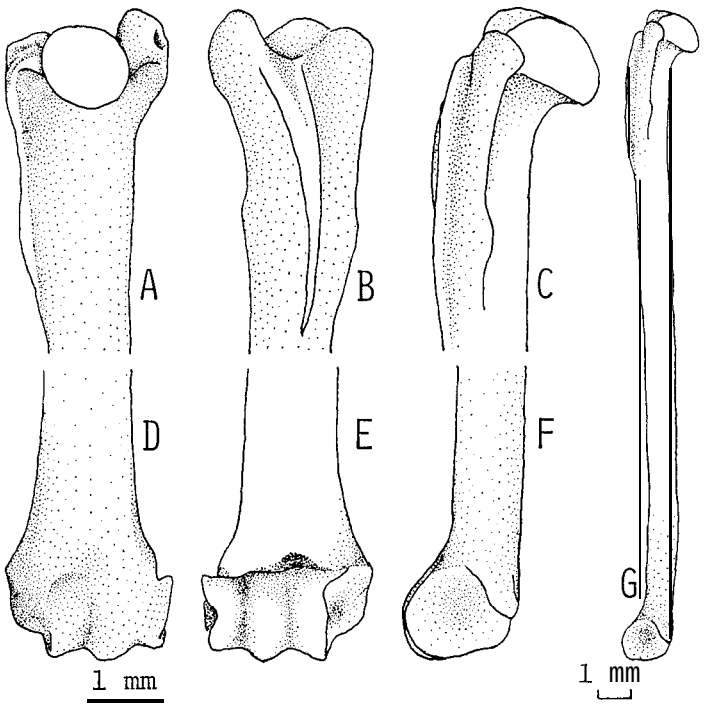


Fig. 8. Right humerus of *Murina aurata ussuriensis*. Alphabetical symbols and scales as in Fig. 1.

Table 5. Comparison of the humerus and the wing-type in *Murina* and *Miniopterus* examined.

Species	N	H L (Av. in mm)	DW/PW (Av.)	Wing-type (III/V)	Locality
Murina aurata ussuriensis	2	19.65, 20.15	1.08, 1.12	1.19, 1.21	Japan
M. leucogaster hilgendorfi	6	27.20-28.20 (27.71)	1.00-1.03 (1.02)	1.24-1.29	Japan
Miniopterus schreibersi fuliginosus	20	*26.00-27.70 (26.97)*	*0.71-0.77 (0.75)*	*1.73-1.75*	Japan

Abbreviations as in Table 1.

erately developed, the pectoral ridge low and narrow; the capitular lateral ridge is somewhat smaller than the inner one, and a moderately deep groove between them roughly parallel to the humeral axis, the trochlea declined outwards and separated from the inner ridge nearly in equal width each other by another groove approximately parallel to the humeral axis, the distal epiphysis eccentric laterad against the humeral axis, the lateral epicondylar crest vestigial, both the olecranon and the radial fossae shallow.

Key to the species of *Murina* examined on the basis of the humeral morphology

1. Humerus length about 20mm. DW/PW: 1. 12 and 1. 08..... *M. aurata ussuriensis*

1'. Humerus length about 28 mm. DW/PW: 1.03-1. 00..... *M. leucogaster hilgendorfi*

Subfamily Miniopterinae

Genus Miniopterus

The humeri of the single Japanese species are examined (Fig. 9 and Table 5). The humeri of *Miniopterus* possess the following characteristics except for the diagnoses mentioned in the preceding key of the subfamily: the shaft is cylindrical over the length, the head fairly flattened on the upper external and the lower internal sides, similar to that of *Vespertilio* in shape, the trochiter extremely high as well as in *Nyctalus*, the trochin lower than the head, the medial ridge terminated at about distal one-third level of the pectoral ridge, the lateral knob vestigial, the pectoral ridge about one-quarter of the humerus in length, curved conspicuously at proximal third; the capitulum is divided into the inner and lateral ridges in equal width by a very deep

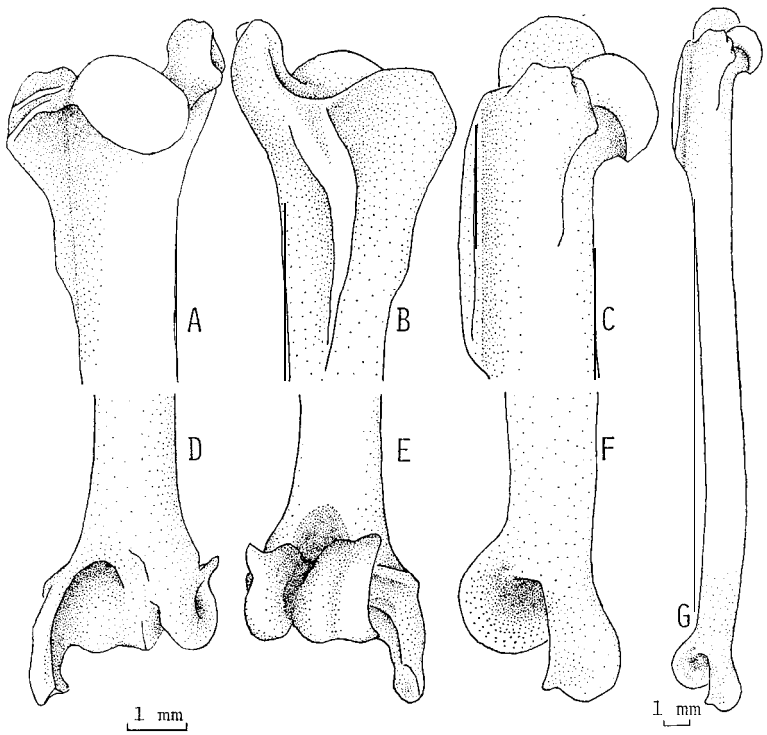


Fig. 9. Right humerus of *Miniopterus schreibersi fuliginosus*. Alphabetical symbols and scales as in Fig. 1.

groove, the trochlea which is as wide as the capitular inner ridge separated from the capitulum by another very shallow groove, and consequently both the trochlea and the inner ridge appear massive in appearence, the two grooves on the distal articular surface oblique to the humeral axis, the knob-like medial epicondyle small, the spinous process longest within the Vespertilionidae examined and concaved at the centre of the distal apex, the distal epiphysis narrowest next to ***Nyctalus,*** and the articular surface concentric against the humeral axis, the lateral epicondylar crest small, both the olecranon fossa which is limited only behind the trochlea and the radial fossa very deep.

DISCUSSION

The humeri of bats have more important diagnostic characters than expected. They reflect the phylogenetic characteristics and the adaptation for flight. Generic differences of the humeri within the Vespertilionidae (Lawrence, 1943), between three genera, *Eumops, Myotis* and *Macrotus* (Vaughan, 1959), and within the Mormoopidae (Smith, 1972) have been pointed out. Furthermore, our previous paper (Yoon ***et al., 1981)*** and this study revealed that bats can be classified to the species level by the humeral characters alone.

Adaptation for flight at the subfamily level within the Vespertilionidae

Myotis is the most primitive genus within the Vespertilionidae, and *Myotis*-like bat seems to be an ancestral form of the family (Miller, 1907; Tate, 1942), so that the ancestral form appears to be a manoeuvrable flier with short-broad or intermediate wings, which flies at a low or moderate speed.

Within the Vespertilionidae, speciation has occurred most frequently amongst members of the Vespertilioninae. As shown in the above key, the humeral characters of the Vespertilioninae have diversely varied within an intermediate range between the Murininae and Miniopterinae; the more the species is in a high phylogenetic position, the more the humeral characters are generally adapted for flight. Judging from the LDH isozyme pattern and fiber composition of the pectoral muscle, however, ***V. s.*** *superans* (Vespertilioninae) appears able to fly at a higher speed with endurance than ***M. s.*** *fuliginosus* (Miniopterinae) regarded as the most advanced form in the family (Ohtsu and Uchida, 1979). In addition, the examined members of the Vespertilioninae have various wing-type ratios (1.21-1.67) between those of the Murininae and Miniopterinae. Perhaps, vespertilionine bats might have developed various flight modes as they have diverged into many genera and species, and then each of them might have built up a territorial air through competitions for feeding space.

Although the humerus of *Murina* belonging to the Murininae is similar to that of *Myotis* (Vespertilioninae) in appearence, the differences between both the subfamilies, as shown in the key, suggest that *Murina* has weak shoulder and elbow joints, and flies at a lower speed by fluttering a higher angle. Especially, the value of DW/PW, i. e. an important characteristic related close-

ly to flight, is generally higher in the Murininae than in the Vespertilioninae. The higher ratio indicates that the mobile force originated 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. The fact is backed up with the lower wing-type ratio (1.19-1.29) of the genus. The Murininae seems to have branched off from the *Myotis*-like ancestral form very early, and to have specialized towards broader and shorter wings (Kuramoto, 1972).

In contrast, the humerus of *Miniopterus* belonging to the Miniopterinae possesses the strongest articular surfaces at both the ends and the characteristics adapted for the most fast and sustained flight within the Vespertilionidae. Especially, the spinous process is similar in shape to that of Molossidae, the most efficient flier. Probably vespertilionid bats have narrowed and extended their wings as they have evolved from the Myotis-like ancestral form towards speedy fliers, and eventually might have given rise to *M. s. fuliginosus* of which the wing-type ratio (1.73-1.75) approximates to those of *Tadarida condylular (2.10)* (Kuramoto, 1972) and *Molossus* major (1.95) (unpublished) belonging to the Molossidae having the longest and narrowest wings.

Adaptation for flight at the genus (tribe) level within the Vespertilioninae

With regard to the phylotaxanomic position within the Vespertilionidae, Tate (1942) included *Myotis*, together with the relative genera, in the tribe Myotini in a narrow sense, and *Plecotus* and *Euderma* in the tribe Plecotini, and put together the two tribes under the tribe Myotini in a broad sense, and further placed *Barbastella,* together with *Pipistrellus* and *Nyctalus* in the Pipistrelloid genera of the tribe Pipistrellini, basing on the cranial and dental characters. However, *Barbastella* was considered to have branched off from the tribe Plecotini which had derived from the *Myotis-like* form, and to be a relative of *Plecotus* and *Euderma* (Handley, 1959). Afterwards, *Barbastella* was excluded from the Pipistrellini and then included in the Plecotini (Williams *et al.,* 1970; Uchida and Andō, 1972; Kuramoto and Uchida, 1976), and Yoon *et al.* (1981) also agreed to this proposal basing on the humeral characteristics.

Also, Tate (1942) put the genera *Vespertilio* and *Eptesicus* under the Eptesicoid genera, whereas Andō (1982) regarded *Vespertilio* as a specialized form belonging to the Pipistrelloid genera of the tribe Pipistrellini. On the other hand, *Eptesicus* was considered as a primitive genus of the tribe Nycticeini (Bickham, 1979), and this concept was supported from its karyotype (Andō, 1982).

Therefore, it is indicated that *Myotis* is included in the Myotini, *Plecotus* and *Barbastella* belong to the Plecotini, *Pipistrellus*, *Vespertilio* and *Nyctalus* are members of the Pipistrellini, and *Eptesicus* is a member of the Nycticeini; this proposal is supported also by the key based on the humeral characteristics.

At first, *Myotis* belonging to the Myotini is deficient in interspecific variation of the humeral characteristics, and most of the characters are contained within the variation of those of the Plecotini. In other words, as pointed out clearly in the key, *Plecotus* is primitive in the humeral characteristic, whereas

Barbastella is superior in the adaptive characteristic for flight, compared with *Myotis*. This matter is well reflected also on the values of DW/PW: *Myotis*, *0.97-o. 85; Plecotus*, 1.03-o. 96; *Barbastella*, *0.84*. On the other hand, the wing-type ratios in the Myotini (1.21-1.28) are lower than in the Plecotini (*Plecotus*, 1.29-L 36; *Barbastella*, 1. 36-l. 38). Within the Plecotini, *Barbastella* is higher than *Plecotus* in the degree of adaptation for flight (Tables 1 and 2). *Barbastella* is similar to the genera of the Pipistrellini in the wing-type ratio and humeral morphology, but remarkably differs in the degree of flattening of the distal shaft, shape of the olecranon fossa and depth of the radial fossa.

As for the Pipistrellini, from the degree of articular reinforcement and the wing-type ratios (1.33-l. 67) (Table 3), it is assumed that the tribe is placed higher in adaptation for flight than is Myotini. The differences amongst the genera given in the key suggest that *Pipistrellus*, *Vespertilio* and *Nyctalus* are placed in ascending order of the adaptation for flight and of the reinforcement of shoulder and elbow joints. The fact can be confirmed also by the wing-type ratios: *Pipistrellus*, 1.34-l. *45*; *Vespertilio*, 1.40-l. 48; *Nyctalus*, 1.64-l. 67 (Table 3).

Although *Eptesicus* belonging to Nycticeini resembles the genera of the Pipistrellini in the humeral morphology, its humerus is different in the shape of the olecranon fossa as shown in the key. The DW/PW (0.85-0.83) and wing-type ratio (1.33-l. 40) each in the genus (Table 4), however, is included in the range of *Pipistrellus*. Hence, the flight mode of *Eptesicus* seems alike to that of *Pipistrellus*.

Adaptation for flight at the species level

As a general trend *in* evolution of Chiroptera, the mechanism considered responsible for karyotypic evolution within a genus leads to a lowering of the 2n despite a considerable constancy of the FN, and the more evolved species is characterized by the larger body size (Andō and Uchida, 1974; Andō, 1982). Further, as to the adaptation for flight, bats have a common tendency to increase the flight speed by elongation and narrowing of the wings. Such two trends are well recognized in *Vespertilio*, *Nyctalus* and *Murina* (Vespertilionidae) (Tables 3 and 5).

On the other hand, *Myotis* which is non-specialized in both the external character (Miller, 1907; Tate, 1942) and the karyotype (Baker, 1970) is poor also in the interspecific variation of adaptation for flight (Table 1). Compared the isometric two examined species of *Plecotus*, it seems likely that *P. townsendi* regarded as a specialized form from X-chromosomal morphology (Andō, 1982) is superior to *P. auritus* also in the degree of adaptation for flight. Amongst the examined members of *Pipistrellus*, small-sized *P. pipistrellus* is regarded as the most primitive species, and next in order are *P. **savii**, P. endoi* and *P. abramus*, judging from their karyotypes (Fedyk and Ruprecht, 1976; Andō *et al.*, 1977). On the basis of the DW/PW and wing-type ratio (Table 3), it is presumed that members of *Pipistrellus* derived from an ancestor which is suspected to be a moderate-speed flier with an intermediate wing-type might have gradually evolved towards slow and manoeuvrable fliers with low wing-type

ratios, except for *P. endoi* with a reverse tendency towards a speedy flier. In short, there is a complexity in the direction of adaptation for flight in the genus. On the other hand, most of the species belonging to *Eptesicus* are similar in karyotypes (Bickham, 1979), and characterized by a tendency for larger species to have broader and shorter wings, and consequently is adapted for low-speed flight.

From the results of the present study based on the humeral characteristics, it becomes clear that the humeri of bats are effectively used not only as a morphological criterion for classifying recent bats to the species level, but also as an indicator of the adaptation for flight in various taxa from subfamily to species; the DW/PW ratio is the most important character exhibiting directly the degree of adaptation for flight. Accordingly, taking also the wing-type ratio into consideration, the degree of adaptation for flight can be estimated more precisely. We believe that the information presented here will establish a useful procedure by the humeral characters for classifying fossil bats found on the Akiyoshi-dai Plateau.

ACKNOWLEDGEMENTS

We thank Dr. T. Kuramoto of the Akiyoshi-dai Museum of Natural History for his valuable advice, and Professor E. W. Jameson, Jr. of the University of California for comments on the manuscript. Foreign specimens were kindly supplied to one of the authors, T. A. Uchida by Professor R. E. Mumford of the University of Prudue and Dr. 0. L. Rossolimo of the Zoological Museum of MGU (Moscow), Professor S. W. Son of the Kyungnam University, Dr. H. Felten of the Forschungs-Institut Senckenberg and Dr. K. Andō of the University of Ryukyus.

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