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Variation in the Bats of the Genus *Harpyionycteris,* with the Description of a New Race

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The genus *Harpyionycteris*, established by Thomas (1896) with *H. whiteheadi* as the type species, was based on a single specimen of unknown sex (BMNH 97.5.2.7) from Mindoro Island in the Philippine Islands. The holotype was collected by J. Whitehead at 5,000 feet altitude in December, 1895. Thomas (1898) later provided an illustration, in colour, of the type and figured the skull. Miller (1907) was unable to establish any close relationship of this genus, with its multicuspid dentition, with any other known taxa in the family Pteropodidae and proposed a distinct subfamily, Harpyionycterinae, to contain this most aberrant genus of the family. Andersen (1912) provided an illustration of the holotype skull (Fig. 78, p. 800) as well as excellent details of the dentition (Fig. 79, p. 802).

The holotype remained the only known specimen of the genus until Miller and Hollister (1921) described *H. celebensis* from a single adult female (USNM 219349) collected by H. C. Raven on 23 August 1917 from Gimpoe, middle Celebes. This new taxon was said to be ... "like *Harpyionycteris whiteheadi* Thomas, of Mindoro, but molars with crowns lower and cusps relatively higher, and PM^3 with a conspicuous secondary cusp on each side of main outer cusp" (Miller and Hollister, *op. cit.*, p. 99).

Tate (1951) reviewed the genus and provided data on additional specimens, six from the Buitenzorg Museum collection from Roeroekan, north Celebes, collected at 1,000 metres (3,300 ft.) in January, 1931, by G. Heinrich (Buitenzorg Mus. 2828–33), a male from Tanko Salokko, Mengkoka Mountains, south Celebes (AMNH 153590; examined by us) collected by G. Heinrich in 1932 at 1,500 metres (4,950 ft.), and a female from Negros Island, Philippines (FMNH 66302 ♀). The latter specimen from Mambaho Cave, Pagyabunan, Bais, Negros Island, collected by D. S. Rabor on 13 May 1949, was also listed by Sanborn (1952), who provided detailed measurements and a sketch of the palate. The altitude of this locality was not stated by the above authors and is not included on the data accompanying the specimen (examined by us). However, judging by maps available to us, the general region appears to be well above 1,000 feet in elevation. A specimen in the Zoologisk Museum, Copenhagen, taken at Kaatoan, Katanglad Volcano at an altitude of about 4,000 feet, Bukidnon Province, Mindanao, and previously reported by Sanborn (1953), was examined and the skull restored sufficiently to obtain several measurements. The forearm, hind foot and tibia lengths were ascertained by radiograph.

The collections of the ROM now contain

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eight additional specimens from the Philippine Islands, including one (♂ skin and skull) collected by D. Empeso on 26 May 1967 at Caterman, Mount Mamajao, Langoangon, Camiquin Island (off Mindanao, elevation between 2,500 and 3,000 feet), and seven taken by the same collector on 7 and 8 January 1968 between 500 and 1,000 feet at Balanan, Saiton, Negros Island. The latter series, together with FMNH 66302 ♀, represents an age spectrum from subadult to middle age and provides an opportunity to detail certain changes that take place in the skull during the aging process of *H. whiteheadi*.

Cranial Variation with Age—This series from Negros Island, represented by three females and five males, is not sufficiently large to detect any consistent cranial characteristics to distinguish the sexes. An attempt was made to arrange the series in an age-developmental sequence from youngest to oldest, and certain characteristics are summarized in Table I. From this series, six have been selected to show some of the more apparent aging characteristics illustrated in Fig. 1. The change in the angle of deflection of the occiput, from a strong deflection as shown in the two youngest individuals, to a more moderate one in the older specimens, is particularly noteworthy, as this angle of deflection has been used as a taxonomic character in several pteropodid genera.

The fusion of sutures follows a fairly consistent pattern if our sequence has been correctly arranged by age (see Table I). There is a general increase in size with age (as expressed by forearm length, condylobasal length, zygomatic and mastoid breadths), although, as might be expected, these increases in size are not entirely concordant with the sequence of fusion of sutures.

An inverse ratio is apparent in the width of the postorbital constriction. There is an obvious decrease in width with age, from 6.8 mm in the subadult to 5.3 mm in the mature adult. This increased constriction with age is also coincident with changes in the fronto-parietal region and the development of a sagittal crest (Fig. 1).

Specimens FMNH 66302 ♀ (not illustrated) and ROM 46146 ♀ agreed well in age characteristics. Specimen ROM 46148 ♂ (not illustrated in Fig. 1), similar in age to ROM 46150 ♀, was the most narrow in zygomatic breadth and equal to the most narrow in mastoid breadth of the series. It had an aberrant occiput with a malformed occipital condyle, and this deformity probably accounts for the aberrant width measurements in the affected areas of the skull.

It is likely that the age span in our younger series (all but specimen ROM 46149 ♂) represents a fairly short period of time (perhaps only a few weeks) beyond the juvenile stage, by which time they have become volant and independent but have not yet reached full maturity. The three youngest specimens could be classified as subadults and are characterized as follows: occiput strongly deflected, fronto-parietal and basisphenoid-basioccipital sutures unfused, and metacarpo-phalangeal joints noticeably swollen and cartilaginous. The absence of any appreciable wear on the dentition of specimen ROM 46149 ♂ suggests that even this individual was no more than middle age (possibly no more than two or three years old). Of other known specimens, the holotype of *H. whiteheadi* appears to be comparable to ROM 46149 ♂ in age characteristics, perhaps even slightly younger. Specimen ROM 43669 ♂ from Mindanao exhibits the same suture-fusion characteristics as 46149, except that the jugal-temporal suture is only partially fused, and the frontal-parietal ridges are not fused into the sagittal crest as far anteriorly. This specimen was judged on cranial characters to be slightly younger, and when the skin was subsequently examined by radiograph the metacarpo-phalangeal joints clearly had cartilaginous pads not yet completely fused to the bone ends as in 46149 ♂. The specimen from Mindanao in the Zoologisk Museum, Copenhagen, ZM 2371 ♀, was an old individual with well worn teeth (particularly the molars) and a well developed sagittal crest. The appearance of the mammae suggests that it may have been lactating at the time of collection. The articulating ends of the metacarpo-phalangeal joint are completely ossified (verified by X-ray). The specimen AMNH 153590 ♂ from the Celebes is the oldest specimen seen by us and

TABLE I

Changes in cranial morphology related to age in *Harpyionycteris whiteheadi* from Negros Island

	Subadult ROM 46146 ♀	Subadult FMNH 66302 ♀	Subadult ROM 46151 ♂	Young adult ROM 46152 ♂	Young adult ROM 46147 ♂	Young adult ROM 46150 ♀	Young adult ROM 46148 ♂	Adult ROM 46149 ♂
Internasal suture	PF	PF	PF	PF	PF	PF	PF	F
Interparietal suture	O	O	PF	PF	F	F	F	F
Deflection of occiput	Strong	Strong	Strong	Moderate	Moderate	Moderate	Moderate	Moderate
Fronto-parietal suture	O	O	O	PF	PF	F	F	F
Basisphenoid-Basioccipital suture	O	O	O	PF	PF	F	F	F
Lachrymal sutures	O	O	O	O	PF	PF	PF	F
Maxillary-Jugal suture	O	O	O	O	O	O	PF	F
Jugal-Temporal sutures	O	O	O	O	O	O	O	F
Nasal sutures	O	O	O	O	O	O	O	F
Fronto-maxillary suture	O	O	O	O	O	O	O	F
Basisphenoid-Presphenoid	O	O	O	O	O	O	O	F
Greatest length of skull (mm)	40.3	41.8	41.5	40.6	41.1	40.4	42.3	43.7
Condylobasal length	38.6	40.8	40.3	39.1	40.2	39.3	40.7	42.6
Zygomatic breadth	22.2	21.1	22.3	22.8	22.0	22.7	21.0*	23.1
Mastoid breadth	14.4	14.6	14.3	14.7	15.0	14.4	14.3*	14.8
Postorbital constriction	6.8	6.5	6.6	6.8	6.3	6.1	5.9	5.3
M^2—M^2 breadth	10.5	10.6	10.5	10.5	10.6	10.4	10.2	11.0
Interorbital width	6.2	5.8	6.0	6.1	6.2	6.2	6.2	6.1
C—M^2 length	16.1	16.8	16.5	16.3	16.9	15.8	16.4	17.8

O = Open sutures PF = Partially fused F = Sutures completely fused ROM = Royal Ontario Museum FMNH = Field Museum of Natural History

*Deformed occipital condyle with some skull distortion

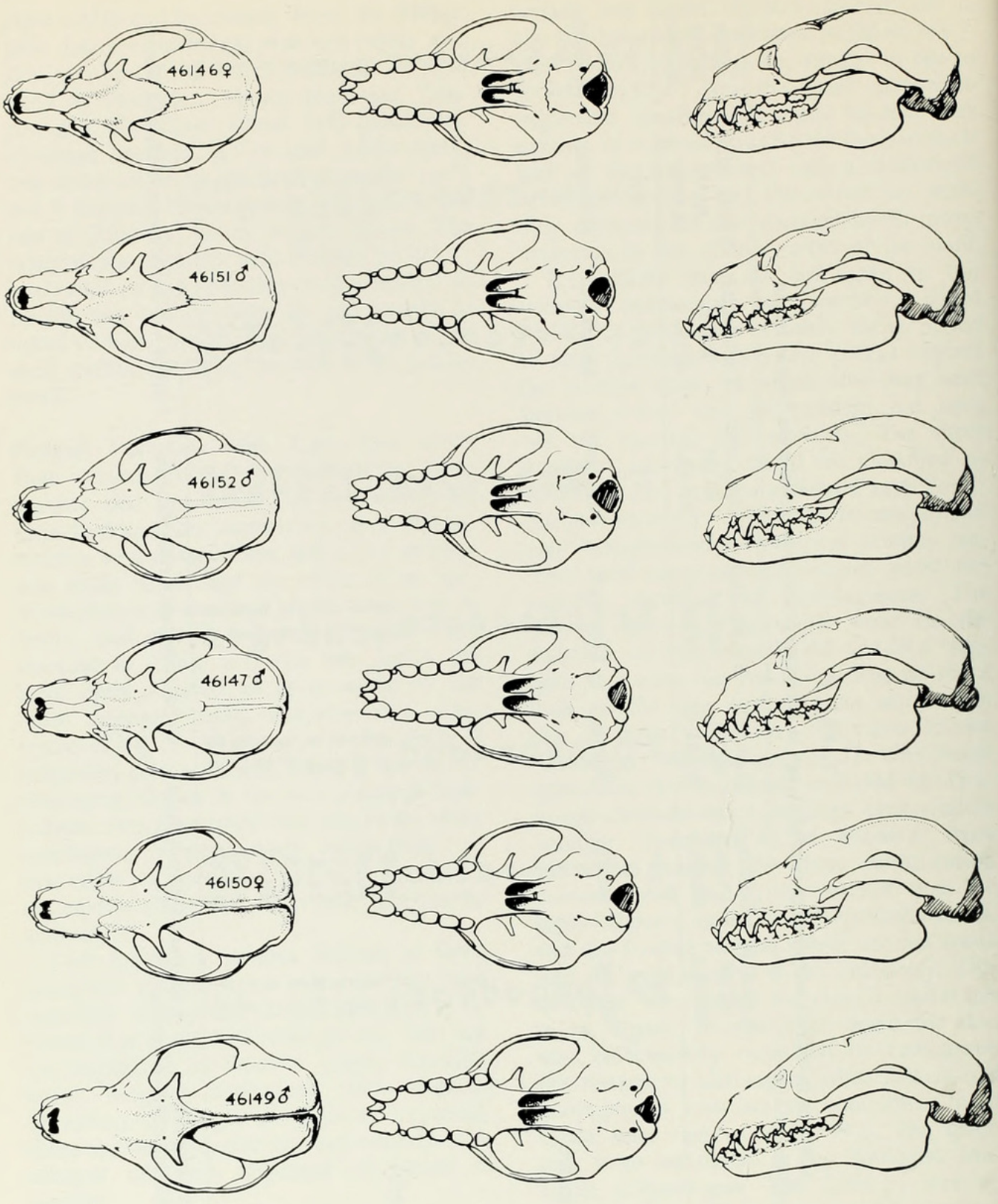

Figure 1
Changes in cranial morphology with advancing age in *Harpyionycteris whiteheadi* from Balanan, Saiton, Negros Island, Philippine Islands. See Table I for additional data.

is characterized by excessive wear on all teeth (Fig. 4). In other respects it exhibits the same age characteristics as specimen ROM 46149 ♂ from Negros Island. Tate (1951) did not see this skull, as he listed the specimen as a skin only. Buitenzorg Museum specimen 2833, illustrated by Tate (1951), is obviously a subadult. Judging by the measurements of the northern Celebes specimens given by him, one was a juvenile, and the other five were all probably subadults. Almost certainly none were older than young adult.

Wing Variation with Age—Measurements of the wing elements of the Negros series are summarized in Table II. The metacarpophalangeal joints are normally quite swollen in appearance in many pteropodid bats, but the joints of three youngest alcoholic specimens (ROM 46146 ♀, 66302 ♀ and 46151 ♂) are obviously less ossified than those of older individuals when examined externally. Radiographs were taken on the entire Negros series, and the swollen cartilaginous pads are clearly evident in the three subadults, somewhat less swollen but clearly distinct in all four young adults and absent in the adult. The length of the forearm varies from 82 to 86.5 mm in the subadult-young adults, as compared to 89.5 mm in the mature adult. The length of the humerus, as determined by radiographs, is fairly consistent in the Negros series. The subadults and young adults vary from 51.2 to 55.0 mm, whereas the adult is 56.0 mm. It is apparent that the thumb with claw (pollex) and second digit elements (with claw) reach maximum length early in life, and no further growth is obvious in this series. Moreover, there is little change in the length of the elements of the third, fourth and fifth digits in the younger series. The mature adult, however, has all of these elements consistently longer. Of the six north Celebes specimens measured by Tate (1951), one was a juvenile, and the other five, thought by us to be subadults, had forearms varying from 79 to 84 mm in length, whereas the holotype of *H. celebensis* was listed as 90 mm and the old adult from south Celebes as 91 mm (92.5 by us). These measurements are remarkably consistent with those of our Negros series. The humerus of the south Celebes specimen (AMNH 153590 ♂) is 58.5 mm long compared with 56.0 in the adult from Negros (ROM 46149 ♂; both measured by radiograph).

Variation in Hind Limbs—The genus *Harpyionycteris* is characterized by a short tibia. Unfortunately, precise measurements are difficult to obtain by ordinary methods in either study skins or preserved specimens. Radiographs taken with the feet and tibias positioned as near horizontal as possible yield much greater accuracy. The Negros series is notably consistent in lengths of both hind feet and tibias, and both are virtually identical in length, varying from 22.0 to 23.5 mm in both cases. It is obvious that these members, like the thumb or first digit of the wing, reach maximum size early in life with no apparent increase beyond the subadult age.

The femur is only slightly shorter than the tibia in five of the Negros series (properly exposed for measuring), varying from 21.0 to 22.0 mm. The Camiquin specimen (ROM 43669 ♂) measures 21.6 mm and the Mindanao specimen (ZM 2371 ♀) measures 22.0 mm. By contrast the Celebes specimen (AMNH 153590 ♂) has a femur length of 25.0 and a tibia length of 26.0 mm, both above the upper limits observed in Philippine specimens. The holotype of *H. celebensis* is said to have a tibia length of 30 and hindfoot length of 29 mm. Tate (1951) shows measurements of AMNH 153590 ♂ from south Celebes as tibia, 31, and hindfoot, 22 mm, whereas by X-ray technique these prove to be 26 mm in both cases. It seems likely that, by using our X-ray technique, these measurements for the holotype will prove to be somewhat less and to be closer to those of the south Celebes specimen.

Individual Variation in Dentition—The cusp and dental patterns of mammal teeth tend to be relatively stable elements and have long been relied on for species discrimination, especially in fossils. The only basic distinguishing character ascribed to *H. celebensis* by the original authors was the development of an extra cusp on P^3 and the greater height development of the cusps in general. The series of eight specimens from

TABLE II

Variation in wing and hind limb structures as related to age in *Harpyionycteris whiteheadi* from Negros Island

	ROM 46146 ♀	FMNH 66302 ♀	ROM 46151 ♂	ROM 46152 ♂	ROM 46147 ♂	ROM 46150 ♀	ROM 46148 ♂	ROM 46149 ♂ **
Forearm	82.0	81.4	85.1	80.0	84.0	86.5	86.0	89.5
Humerus*	53.0	53.6	51.9	51.2	54.1	55.0	—	56.0
Thumb, including claw	36.0	35.5	36.2	32.0	34.0	35.0	35.5	35.0
2nd Digit: Metacarpal	40.5	39.9	38.5	37.0	38.5	40.5	40.5	41.0
1st Phalanx	10.9	11.0	12.0	10.0	10.0	11.0	10.5	10.0
2nd Phalanx (i.c.)	12.5	12.5	12.5	12.0	12.0	13.0	13.0	12.5
3rd Digit: Metacarpal	61.0	58.0	59.5	58.5	60.0	61.0	60.5	64.5
1st Phalanx	45.0	43.2	44.0	43.0	44.5	44.0	42.5	46.0
2nd Phalanx	55.0	55.5	54.0	54.5	56.0	57.0	57.0	62.0
4th Digit: Metacarpal	56.8	56.5	57.0	56.5	57.0	57.5	58.0	62.5
1st Phalanx	36.0	34.8	36.0	35.0	35.5	36.0	35.0	36.8
2nd Phalanx	35.0	35.5	35.5	35.5	35.5	35.5	34.5	39.6
5th Digit: Metacarpal	59.0	58.5	59.5	57.5	58.5	59.0	59.5	64.4
1st Phalanx	29.0	27.6	28.5	28.5	29.0	28.4	29.0	30.5
2nd Phalanx	30.0	30.6	29.0	30.5	30.0	32.0	29.5	34.0
Femur*	21.0	21.0	22.5	21.2	—	—	22.0	—
Tibia*	23.0	23.5	23.0	22.0	23.0	23.0	23.0	23.5
Hindfoot*	23 .0	23.5	23.0	22.0	22.0	22.0	23.0	23.5
Age	Subadult	Subadult	Subadult	Young adult	Young adult	Young adult	Young adult	Adult

*Measurement verified by X-ray **Holotype — *H. w. negrosensis*

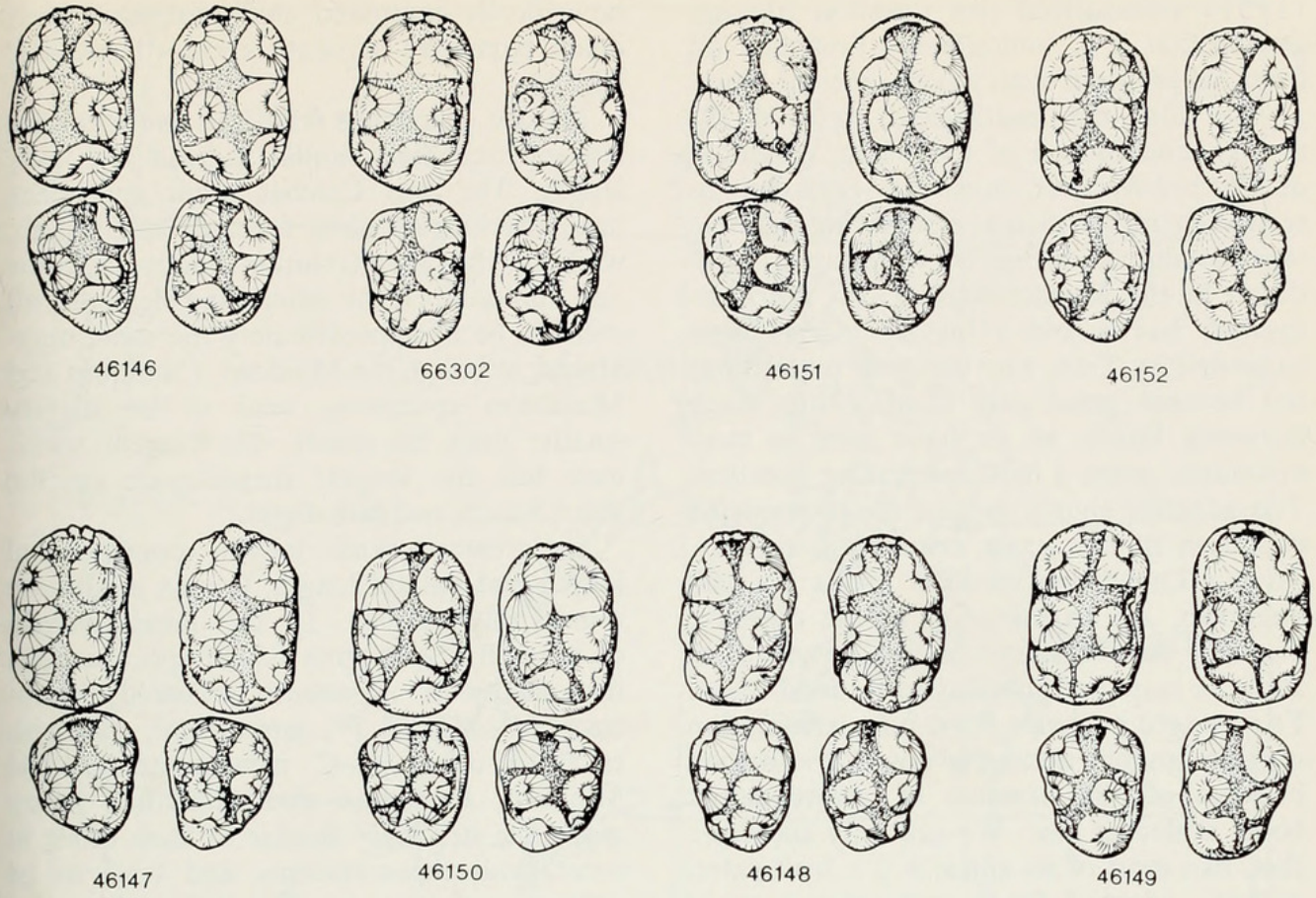

Figure 2
Variation in the cusp pattern of M^1 and M^2 of *Harpyionycteris whiteheadi* from Negros Island, Philippine Islands. No. 66302 is from Mambaho Cave, Pagyabunan, Bais (FMNH); all others are from Balanan, Saiton (ROM). See Table I for sex and age development of each specimen.

Negros affords an opportunity to assess the range of individual variation in dental pattern. A careful examination of M^1 and M^2 shows the cusp pattern to be extremely variable (see Fig. 2). In fact, no two of the eight specimens can be said to be even close to identical. The basic pattern of six cusps as defined by Andersen (1912, pp. 801–3) is altered in this genus by the addition of accessory cusps or by the division of primary cusps into two. Not only do the cusps vary in size, position and number in each individual, but there is also a comparable amount of difference in the left and right teeth of individuals. Minor variations are apparent in the other teeth as well. None show even a trace of the secondary cusp on the buccal side of P^3 seen in *H. celebensis*. Tate (1951) was in error when he stated that the Negros Island specimen (FMNH 66302 ♀) had the supplemental cuspule on P^2 [= P^3] as in *celebensis*. The known examples of that taxon, as well as the holotype of *H. whiteheadi* and ROM 43669 ♂ from off Mindanao, have a well-developed anterior supplemental cuspule on P_3. In the Negros series this cuspule is absent from three specimens and weakly developed in five, none being as distinct as in the above examples. The single pair of lower incisors are quite small and probably non-functional. Of the specimens seen by us, the holotype of *H. whiteheadi*, FMNH 66302 ♀ and ROM 46151 ♂ have only one incisor (on one side only) present, and all others have none.

Although individual variation in dental patterns is normal and to be expected, as in many species of mammals, the variability in the cusp patterns exhibited by *Harpyionycteris* is unique among bats and must certainly rank high among all mammals.

Adaptive Significance of Dentition—There has been some speculation as to the affinities of *Harpyionycteris* with other bats. Tate

(1951) summarized this question by suggesting that it ..."undoubtedly branched off from the pteropid stem in very ancient times. ... and that the multicuspid state of the molars, and indeed of the whole dentition, of *Harpyionycteris* must be regarded as secondary rather than as a surviving example representing a formerly widespread condition in the Megachiroptera." If *Harpyionycteris* has as old a history as has been suggested by Tate, why the cusp pattern has not become genetically fixed within much narrower limits, as we have seen in most mammals, poses a most interesting question. The adaptive significance of the multicuspid condition in the genus remains a mystery. To our knowledge its food habits are still unknown. An examination of the digestive tracts of the ROM specimens showed them all to be empty of any diagnostic food items. The meagre evidence from our examination suggests animal matter is not a prime food because of the absence of insect chitin, bone, scales or hair. We can only speculate that, like most of its allies, it is a fruit eater, perhaps adapted for a particular type of tough-textured fruit for which the multicusp teeth would be advantageous in extracting the juice. Possibly the fruit fibres are discarded and not normally ingested – this might explain the absence of diagnostic material in the digestive tracts! This suggests that *Harpyionycteris* may represent yet another line of highly specialized feeders – fruit juice-feeding bats.

Geographic Variation—The known range of the genus *Harpyionycteris*, based on 18 specimens, extends from Mindoro (1 specimen) in the north, southward through Negros Island (8 specimens), Camiquin Island, offshore from Mindanao (1 specimen), Mindanao Island (1 specimen) to the Celebes, including the north (6 specimens), middle (1 specimen) and south portions of the island (1 specimen) (Fig. 3). Of this total, only six are mature adults that can be critically compared, and these have been taken from five separate areas (Table III; Fig. 4).

Mature specimens from the five localities are approximately similar in head and body length. The two Celebes adult specimens have the longest tibia, forearm and thumb, while one has the maximum lengths of femur and humerus. Of the other wing elements, all seem to be of approximately the same magnitude, although the Mindoro, Camiquin and Mindanao specimens tend to be slightly smaller than the others. The Negros specimen has the longest metacarpals on the third, fourth and fifth digits.

In greatest skull length, condylobasal length and palatal length, the six adults are remarkably similar. In the measurements of breadth, the Negros Island specimen has the narrowest zygomatic, mastoid, braincase, M^2–M^2, P^3–P^3, interorbital, postorbital and upper C–C measurements. The Mindoro, Camiquin and Mindanao specimens are strikingly similar to each other in most skull measurements and tend to be either equal to or smaller in breadth measurements than the Celebes specimens. Maximum size is found in the latter in the mastoid, braincase, P^3–P^3, interorbital and the upper C–C breadth measurements.

In the length of the lower jaw, all adults are similar. However, the Negros specimen has the lowest height of ascending ramus and is lighter in build, having the least depth between P_4 and M_1 as well as behind M_3. In the dentition, the length of C–M^2 and C–M_3 tend to be similar in all adults, although there are a number of variations in the conformation of the individual teeth.

The Camiquin specimen (ROM 43669 ♂) has been compared with the holotype of *H. whiteheadi* and agrees remarkably well in all essential details of both the skull and the skin (including colour of pelage). Even in the highly variable M^2 the cusp pattern agrees well, with only a better development of the posterior buccal cusp (pc, of Ander-

Figure 3
Map of the Philippines-Celebes area showing the distribution of the known specimens of *Harpyionycteris*. 1. Mindoro Island (type locality of *H. whiteheadi whiteheadi*). 2. Mambaho Cave, Pagyabunan, Bais, Negros Island. 3. Balanan, Saiton, Negros Island (type locality of *H. whiteheadi negrosensis*). 4. Caterman, Mount Mamajao, Langoangon, Camiquin Island. 5. Kaatoan, Katanglad Volcano, Bakidnon, Mindanao. 6. Gimpoe, middle Celebes (type locality of *H. celebensis*). 7. Tanko Salokko, Mengkoka Mountains, south Celebes. 8. Roeroekan, north Celebes.

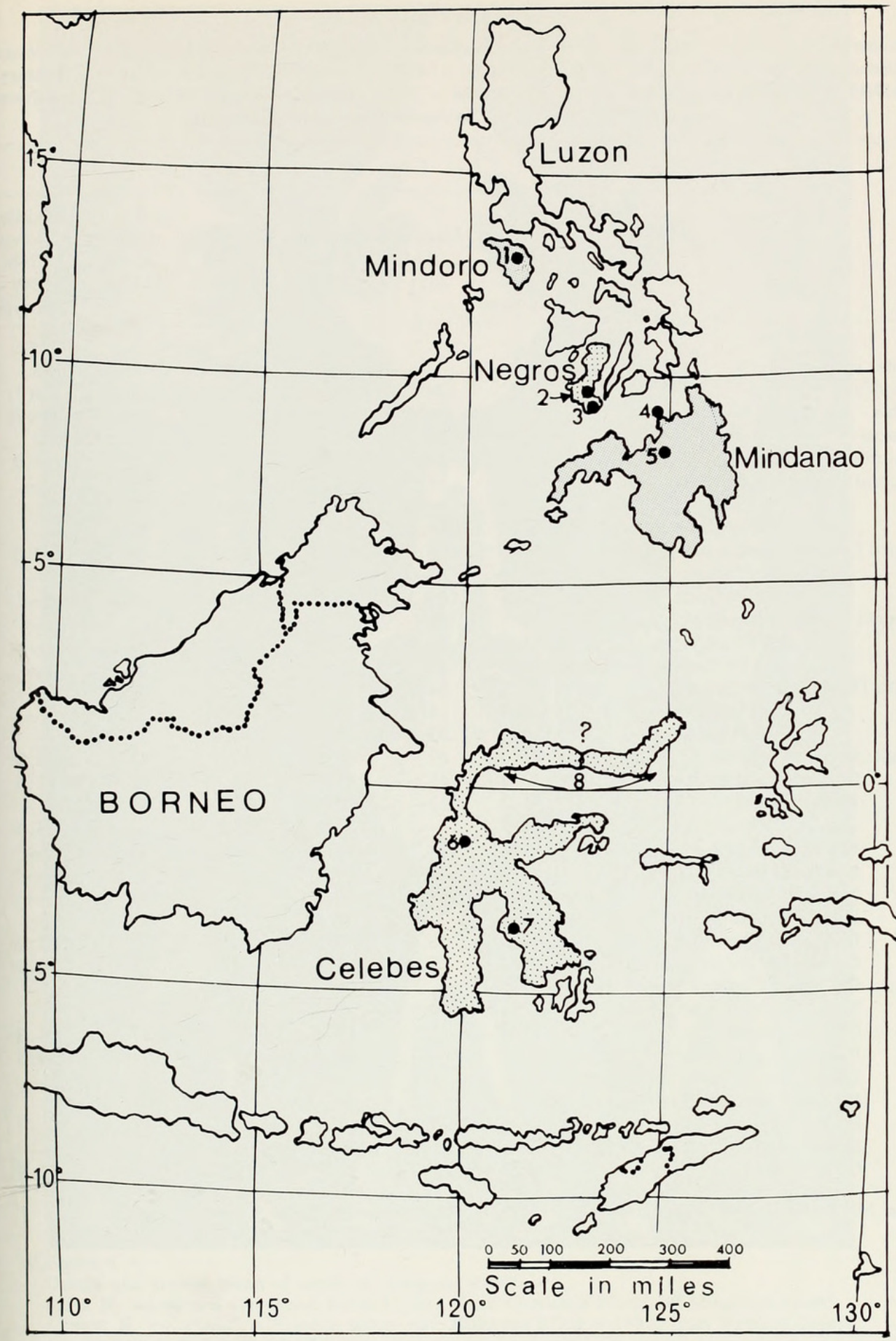
Luzon
Mindoro
Negros
Mindanao
BORNEO
Celebes
1
2
3
4
5
6
7
8
?
15°
10°
5°
0°
5°
10°
110°
115°
120°
125°
130°
0 50 100 200 300 400
Scale in miles

TABLE III

Measurements (in mm) of the known full adult specimens of the genus *Harpyionycteris*: 1. *H. whiteheadi whiteheadi* 2. *H. w. negrosensis* 3. *H. celebensis*. AMNH = American Museum of Natural History; BMNH = British Museum (Natural History); ROM = Royal Ontario Museum; USNM = United States National Museum; ZM = Zoologisk Museum, Copenhagen.

	1.			2.	3.	
	Mindoro BMNH 97.5.2.7 Holotype	Mindanao ZM 2371 ♀	Camiquin ROM 43669 ♂	Negros ROM 46149 ♂ Holotype	South Celebes AMNH 153590 ♂	Middle Celebes USNM 219349 ♀ Holotype
						*
Total length	140	—	145	152	143	153
Hindfoot	23	24†	23.5†	23.5†	26†	29(?)
Tibia	24.5	24†	23.5†	23.5†	26†	30(?)
Forearm	82.5	84	85	89.5	92.5	90
Thumb with claw	33.0	31±	33.7	35.0	36.1	39.0
Second Digit: Metacarpal	36.5	38.2	40.0	41.0	43.7	—
1st Phalanx	11.5	8.0	10.0	10.0	11.7	—
2nd Phalanx	13.0	11.5	11.3	12.5	12.0	—
Third Digit: Metacarpal	59.0	60±	60.0	64.5	64.4	63.0
1st Phalanx	43.5	44.0	43.1	46.0	50.2	—
2nd Phalanx	54.0	59.5	55.0	62.0	58.0	—
Fourth Digit: Metacarpal	54.5	56±	57.0	62.5	60.7	—
1st Phalanx	35.5	36.6	36.0	36.8	42.5	—
2nd Phalanx	36.0	36.7	36.5	39.6	37.?	—
Fifth Digit: Metacarpal	55.5	54±	59.0	64.4	61.0	—
1st Phalanx	29.0	28.5	27.9	30.5	32.6	—
2nd Phalanx	29.0	30.8	30.5	34.0	35.4	—
Skull: Greatest length	43.0±	43±	43.1	43.7	43.5±	43.0
Condylobasal length	40.0±	41±	41.7	42.6	42.0±	41.6
Palatal length	23.0	23±	22.5	22.3	23.5±	—
Zygomatic breadth	24.0	—	24.3	23.1	24.3	24.0
Mastoid breadth	15.6	15.5±	15.7	14.8	16.0	—
Braincase breadth	16.7	16.5±	16.5	15.7	16.9	—
M^2 — M^2 breadth	11.6	—	11.2	11.0	11.6	—
P^3 — P^3 breadth	9.2	—	9.3	8.9	9.5	—
Interorbital breadth	6.5	6.4±	6.9	6.1	7.0	7.0
Postorbital constriction	6.0	5.9±	6.4	5.3	5.6	6.2
Canine — Canine (upper)	7.8	—	7.8	7.4	7.9	—
Height of braincase	13.5	14.6	14.0	13.4	13.6	—
C — M^2 length	17.8	17.5	17.6	17.8	17.5	16.6
Length of mandible	35.0	34.8±	33.1	34.0	34.0	35.0
Height of ascending ramus	16.5	16.8	16.3	15.8	16.1	—
Depth of mandible between P_4 and M_1	4.4	4.4	4.4	3.7	4.1	—
Depth of mandible behind M_3	5.6	5.6	6.1	5.0	5.4	—
C — M_3 length	19.2	19.3±	18.8	19.4	18.9	17.8

**vide* Miller and Hollister (1921) and Tate (1951) †determined by X-ray

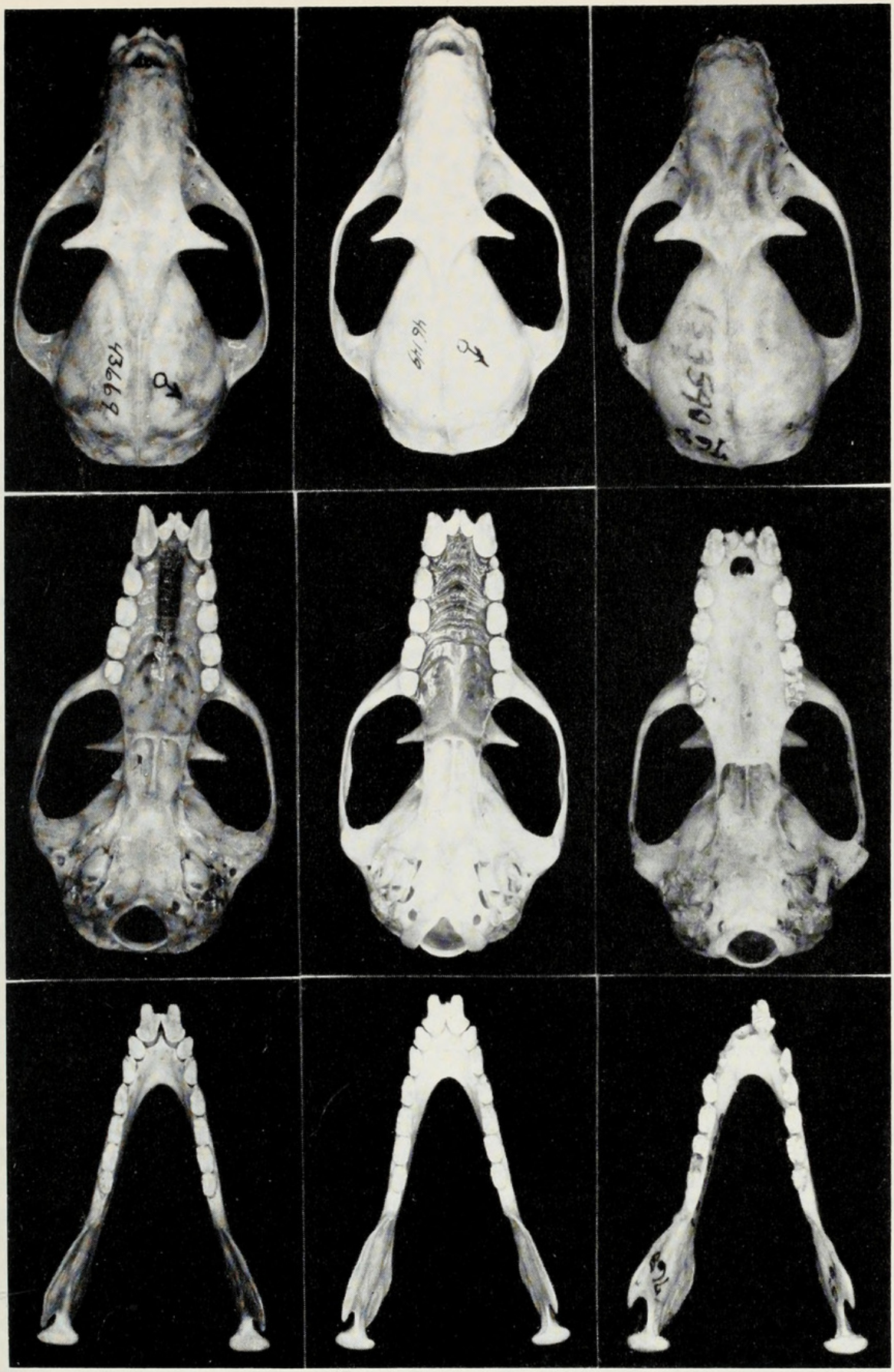

Figure 4
Dorsal and ventral views of skulls of *Harpyionycteris*.
Left: *H. whiteheadi whiteheadi* ROM 43669 ♂ from Camiquin Island, off Mindanao Island.
Centre: *H. whiteheadi negrosensis* subsp. nov. Holotype ROM 46149 ♂ from Balanan, Saiton, Negros Island, Philippine Islands.
Right: *H. celebensis* AMNH 15390 ♂ from Tanko Salokko, Mengkoka Mountains, South Celebes.

sen, 1912). The palatal ridges of the Camiquin specimen (Fig. 4), however, do not conform with the illustrations of the Negros Island specimen given by Sanborn (1952). Even though there are minor individual differences among our specimens, all, including our Negros series, are similar in having five undivided anterior ridges and three pairs of divided posterior ridges, the latter exhibiting the greatest variation in length, shape and position. There is also an undivided ridge near the posterior edge of the palate in all the specimens.

Figure 5
Details of the face of *H. w. negrosensis* ROM 46150, young adult female, prior to extraction of skull. Note lateral deflection of the nostrils.

The Negros Island population appears to have been isolated a sufficient length of time to have developed distinctive characteristics consistent with subspecific variation and may be known as

***Harpyionycteris whiteheadi negrosensis*, subsp. nov.**

Holotype—ROM No. 46149 adult male preserved in alcohol with skull extracted; collected on 7 January 1968 between 500 and 1,000 feet elevation at Balanan, Siaton, Negros Island, Philippines, by D. E. Empeso (see Figs. 1, 2, 4, and 6).

Range—Known only from Negros Island, Philippine Islands.

Diagnosis—Allied with *H. whiteheadi whiteheadi* and of the same general size but with narrower skull proportions, including zygomatic breadth, mastoid breadth, rostrum breadth (C–C and P^3–P^3), interorbital breadth, and breadth of braincase. Nasal aperture, viewed from the front, noticeably higher than deep rather than as wide or wider than deep. Mandibles are lighter in build, shallower at the junction of P_4 and M_1 and behind M_3 (see Table III). The last upper molars (M^2) lie much closer to the shelf of the zygomatic plate.

Measurements—See Tables I, II and III.

Comparisons—The pelage coloration is unknown from fresh skins, but preserved specimens, including the holotype, ROM 46150 ♀, and one skin prepared from a preserved specimen (ROM 46148 ♂) are darker than *H. w. whiteheadi*, with the underparts approaching Bister (Ridgway, 1912) rather than Buffy Brown or Dresden Brown. The dorsum is more rusty coloured, approaching Angus Brown or Brussels Brown rather than Sepia or Prout's Brown. In general the fur appears to be somewhat longer and thicker, both above and below. Light spots are also present on the wings but are more pinkish than yellowish in colour; these as well as pelage characters may be of limited taxonomic significance.

The darker pelage coloration is closer to *H. celebensis* as represented by AMNH 153590 ♂, but the length of the fur, both above and below, is noticeably shorter and is more nearly unicolour on the middle of the back, rather than bicolour, with a much paler base.

The ears of *H. w. negrosensis* are narrower and more pointed than either *H. w. whiteheadi* or *H. celebensis*.

The great variability in the dental cusps, as illustrated in the Negros Island series, suggests that caution should be exercised in using dental characters in this genus for taxonomic discrimination. The well-developed extra cusp on P^3 found in *H. celebensis* has not been observed in any Philippine specimen and may prove to be a genetically fixed character of taxonomic value. Examination of AMNH 153590 ♂ and the illustrations provided by Tate (1951) sug-

gest the possibility that the distinctive shape and angle of projection of the upper canine may be equally significant, if not more so, to distinguish *H. celebensis* from *H. whiteheadi* (see Fig. 6). In *H. celebensis* the upper canine is relatively shorter and broader with a less anterior angle of forward projection and has a much wider posterior cusp (viewed from the side).

Systematic Discussion—The past paucity of specimens of the genus *Harpyionycteris* has precluded any meaningful analysis of taxonomic characters and evolutionary trends. The addition of eight new specimens helps in an assessment of some trends but still falls far short of an adequate appraisal. If our assignment is correct, there are still only three examples of the nominate taxon now known, the holotype from Mindoro, the specimen from Mindanao (UZ 2371 ♀) and our specimen from Camiquin. These represent two widely separated localities lying both north and south of Negros Island but apparently separated by smaller water gaps from each other than from Negros Island. This presupposes that ultimately this species will be found in suitable habitat, should it exist, on the islands of Leyte, Samar and southern Luzon. If our suspicion concerning its food habits is confirmed, then its distribution may well be correlated with a specific type of fruiting plant, probably occurring primarily at higher elevations (about 1,000 feet or more).

The systematic relationships of the known populations of *Harpyionycteris* pose interesting problems common to other insular taxa. Tate (1951) suggested that the Celebes population probably represents only a subspecies of *H. whiteheadi*, a view also accepted by Laurie and Hill (1954). Such a conclusion would presuppose that there is, or has been in the recent past, some gene flow between these insular populations. If it is assumed that the species exists throughout Mindanao, the distance between the southernmost point of land and northernmost Celebes would be about 250 miles. Although there are small islands between that might serve as "stepping stones," there are still nearly 100 miles of open water to be traversed—a distance usually more than adequate to serve as an effective barrier with most species of bats. If the diet of these bats proves to be a specialized one requiring high altitude species of fruit, the smaller islands would be of limited value as "step-

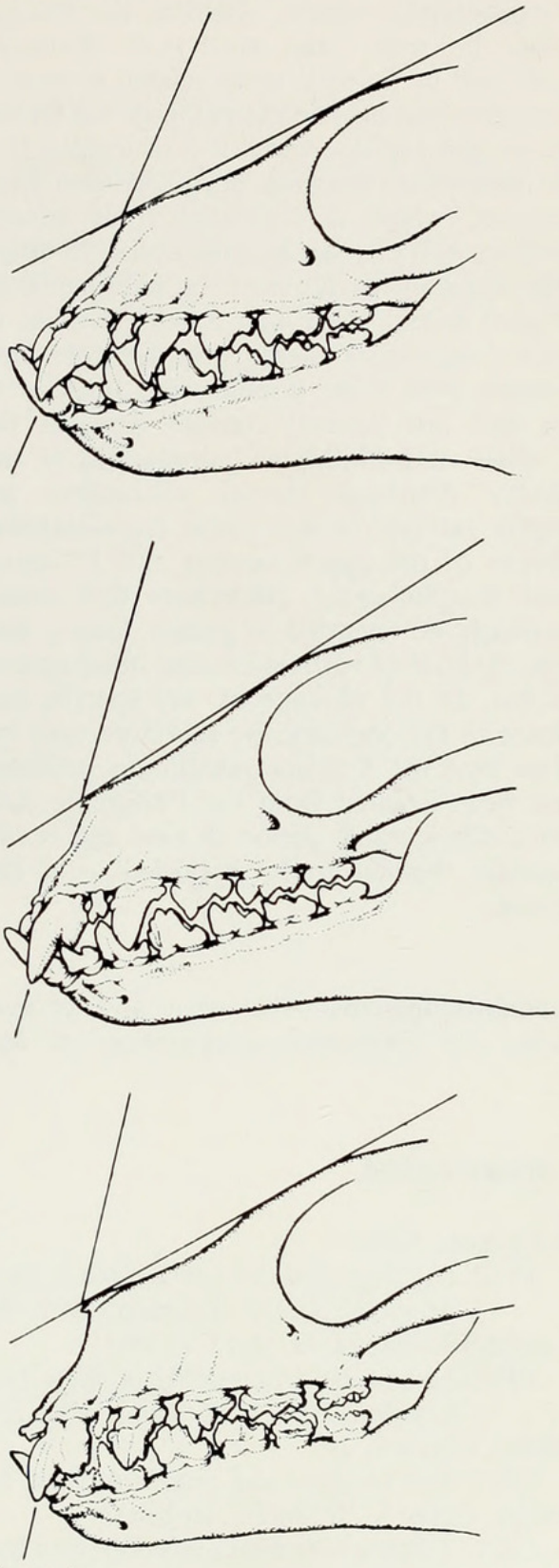

Figure 6
Diagram comparing the shapes of the rostrums and dentitions of *H. w. whiteheadi* (ROM 43669 ♂), top; *H. w. negrosensis*, Holotype, centre; *H. celebensis* (AMNH 153590 ♂), bottom.

ping stones" between the widely separated populations of *Harpyionycteris*. Celebes lies east of Wallace's Line and its fauna normally has been associated with the Australian zoogeographic region, whereas the Phillippines lie west (and north) of Wallace's Line and its fauna is more related to that of Borneo as an insular extension of the Oriental zoogeographic region. It is of interest that no *Harpyionycteris* has been recorded from Borneo, which is separated from nearest contact with Celebes by only about 75 miles. The apparent isolation of the population on Negros Island, with only 25 or 30 miles of water separating them from possible land contact with other populations, suggests to us that any normal contact between the Celebes and Philippine populations is unlikely. Although dental characters are highly variable in this genus, the distinctive shapes of the upper canines and P^3 represent morphological differences that would normally be regarded as greater than a subspecific level of variation in any other species of bat. In the absence of any specific evidence to the contrary, we therefore take the view that the Celebes population probably has been isolated from the Philippine ones for a considerable period of time and is sufficiently distinct to be regarded as a full species.

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