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HARPYIONYCTERIS, A GENUS OF RARE FRUIT BATS

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During the past few years opportunities have arisen to study the types of the two known species of *Harpyionycteris*, *H. whiteheadi* and *H. celebensis*, as well as other material from Celebes, and recently a specimen from Negros Island, Philippines. *Harpyionycteris* differs from all other genera of Pteropodidae by the possession of multicuspid molar teeth. It was placed in a separate subfamily by Miller (1907) and by Andersen (1912). The nostrils open laterally on either side of the broad septum as in *Pteropus* and *Dobsonia*. They are not prolonged into tubes as in *Nyctimene*. The ears display no special characters; their tips are rounded. The pelage is dense and soft, and is carried along the humerus to a little beyond the elbow and down the leg to the ankle. The claw of the second digit remains fully developed as in *Pteropus* and *Nyctimene;* in *Dobsonia* it is virtually obsolete. The relative shortness of the tibia is extreme, though the foot appears normal. The tail is lost, also as in *Nyctimene* and *Pteropus*. In *Dobsonia*, the tail is still present, though very short.

SKULL

The median nasal suture can be distinguished both in *Dobsonia* and in *Harpyionycteris celebensis* (not in *H. whiteheadi*). On the other hand, in quite young specimens of *Nyctimene* (*N. celaeno*, A.M.N.H. No. 152438), in which the naso-maxillary and naso-frontal sutures are still completely open, the nasals are so solidly fused together that no trace of the median suture remains.

The premaxillae, which are narrowed above, are completely fused in our material and in the type of *Harpyionycteris whiteheadi*. In the youngest *Nyctimene* examined, these bones are already completely fused. In *Dobsonia*, as in most other pteropodid genera, the premaxillae do not become fused together.

The septum separating the incisive foramina is strongly developed in the type of *celebensis* and in our series, but appears to be obsolete, or is possibly broken, in the type of *whiteheadi*.

Arching of the skull, so characteristic a feature of the "long-faced" Pteropodidae (Tate, 1942, p. 332) is moderately well developed in *Harpyionycteris*. The rostrum is substantially longer than are the rostra of *Dobsonia* and *Nyctimene*. Neither the arching nor the length of muzzle is so pronounced as in *Pteropus* and its close allies.

The anteorbital canal is short: only 1.1 mm. in *H. whiteheadi*, 1.0 in the Negros specimen, 0.9 in A.M.N.H. No. 2833 from Celebes.

DENTITION

Both upper and lower incisors are limited in number to one pair. The upper incisor is a rather large tooth, the lower an extremely minute, functionless peg. The upper tooth is both broad and thick at its base and towards the median line is lengthened into a stout cusp. The two cusps of opposite teeth are in contact and function together.

Those upper incisors, with their exaggeratedly inturned cusps, slightly suggest those of *Nyctimene*, though in it the cusps are shorter and not in contact and descend only slightly. In *Dobsonia* the right and left incisors are widely separated and conform to those of *Pteropus* which retains the second pair.

The lower incisors on the contrary nearly match the tiny incisors of *Dobsonia*. In *Nyctimene* they are not developed.

The canines in the Pteropodidae commonly develop accessory cusps. In both the upper and the lower canines of *Harpyionycteris* such accessory cusps are present. In the upper canines a strong posterior cuspule is also seen. In the lower tooth, not only the posterior cusp but also a pronounced internal one occurs, and the internal cusps of either side come into contact above the reduced lower incisors. Strong internal cingula appear in both upper and lower teeth. The lower canines, moreover, are rotated, slightly procumbent, and incisoriform. They

seem to function as incisors. In both *Nyctimene* and *Dobsonia* the canines show some degree of approximation; in the former the lower canines are fully in contact. But the flattening and the procumbent position of the teeth seen in *Harpyionycteris* are little more than foreshadowed in either; internal accessory cusps are not present on the lower incisors of either.

The premolars in *Harpyionycteris* number $\frac{3}{3}$.[1] The first upper premolar approaches the vestigial, being much reduced, with a small main cusp and a minute posterior accessory cusp. The first lower premolar on the contrary is a well-developed tooth and functions with the incisoriform canine. The upper and lower second premolars are nearly premolariform, as commonly understood, particularly the lower tooth, for the upper one is already in process of becoming multicuspid. The third premolars, upper and lower, are markedly altered in the direction of the multicuspid condition of the true molars.

Little resemblance can be found between the premolars of *Dobsonia* (with *Nyctimene*) and *Harpyionycteris*. In the first place absolutely no tendency towards a multicuspid state can be seen. In both *Dobsonia* and *Nyctimene*, p^1 has disappeared, and p_1 is already greatly reduced in *Dobsonia* and is missing in *Nyctimene*. *Nyctimene* has advanced further. It has already greatly reduced p_2^2.

The molars in *Harpyionycteris* have the formula $\frac{2}{3}$. (In *Dobsonia* m_3^3 are much reduced.) This formula (absence of m^3) is preserved in many Megachiroptera. The multicuspid condition to be seen in *Harpyionycteris* is not even suggested in any other genus. Andersen (1912, p. xxix) explains it as the result of the interaction of four distinct modifications.

RELATIONSHIPS

The affinities of *Harpyionycteris* remain obscure; the evidence offered by its structure is conflicting. It has undoubtedly branched off from the pteropodid stem in very ancient times.

Characters shown by *Harpyionycteris* that are common in the Megachiroptera include retention of the claw in d2, reduction of the tail, elongation of the palate behind the molars, the small size of the audital bullae, the large size of the postorbital processes, and the wholly fused mental symphysis.

[1] I have used the terminology p_{1-3}^{1-3}, though this can be shown instead as p_{-4}^{2-4}.

Characters shared with the "long-faced" Pteropodidae are the moderately elongate rostrum and slightly arched skull.

Characters shared with the "short-faced" Pteropodidae are the narrowing of the premaxillae above, a tendency towards reduction of the number of incisors, and a modification of the remaining teeth.

Characters shared with *Nyctimene* are the fusion of the two premaxillae and the fact that the lower canines are in contact with each other.

Characters unique in *Harpyionycteris* are the very short tibiae, the specialization of the single upper incisor, the near obsolescence of the single lower incisor (same stage as in *Dobsonia*), the large size of p_1, the multicuspid character of the molars, and the large size of m_3^3.

How many of these features are secondary and how many are of old phylogenetic origins are unknown.

Andersen (1912, figs. 2, 6) associated *Harpyionycteris* and *Dobsonia* on a common branch of his "*Rousettus* section." I feel assured that they are less closely related, and Andersen himself later became likewise convinced, because at the end of the same work (1912, p. 799) he separated *Harpyionycteris* as a subfamily. I am also doubtful whether or not *Dobsonia* should be kept in association with *Rousettus* and *Pteropus*, as I believe that the fusion of the premaxillae and the contact of the lower canines, common to both *Harpyionycteris* and *Nyctimene*, are definitely significant. Looking at the megachiropteran assemblage as a whole, I suspect 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.

HARPYIONYCTERIS THOMAS

Hapryionycteris THOMAS, 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 18, p. 243; 1898, Trans. Zool. Soc. London, vol. 14, p. 384. ANDERSEN, 1912, Catalogue of the Chiroptera in...the British Museum, ed. 2, pp. li, 799–805.

TYPE: *Harpyionycteris whiteheadi.*

Only two species, or more probably subspecies, of *Harpyionycteris* are known: *whiteheadi* and *celebensis*. They differ by extremely slight characters. The yellowish markings on the wings of *whiteheadi* may be significant. The tooth row of the type of *whiteheadi* is longer than that of any example of *celebensis* I have

measured. There appear also to be slight differences in the proportions of the cusps of the premolars and molars. In the type of *whiteheadi*, compared with *celebensis*, the cuspule just behind the main cusp of p^2 is obsolete; the third (posterior) external cusp of p^3 is much reduced in size; the same cusp of m^1 is divided. However, not all these characters hold in the Negros Island specimen, so they may not be valid.

Harpyionycteris whiteheadi Thomas

Harpyionycteris whiteheadi THOMAS, 1896, Ann. Mag. Nat. Hist., ser. 6, vol. 18, p. 244; 1898, Trans. Zool. Soc. London, vol. 14, p. 384 (colored plate). WHITEHEAD, *in* Thomas, 1898, Trans. Zool. Soc. London, vol. 14, p. 385 (description of collection of specimen). ANDERSEN, 1912, Catalogue of the Chiroptera in the . . . British Museum, ed. 2, pp. li, 799–805, figs. 78, 79.

TYPE: B.M. No. 97.5.2.7, sex undetermined, from Mindanao Island, Philippines, 5000 feet.

MATERIAL: Mindanao, one female, in alcohol, skull cleaned (C.N.H.M. No. 66302).

Through the kindness of Mr. T. C. S. Morrison-Scott, I was able to examine the type in London. The general body color is virtually the same as that of *celebensis*—dark brown, paler in the area of the mantle. The specimen was originally prepared as a skin, not skinned from alcohol. On the wings are faint yellowish markings somewhat like those on the wings of *Nyctimene* but smaller. The measurements are given in tables 1 and 2.

Mr. C. C. Sanborn, Curator of Mammals at the Chicago Natural History Museum, has kindly lent me the female specimen recently acquired from Negros Island. I am not able to compare it with the type of *whiteheadi*, but, compared with our series from Celebes, the presphenoid-basisphenoid suture lies considerably farther back from the hind edge of the palate (4.3:3.2).

The posterior, supplemental cuspule on p^2, obsolete in the type, is present in the Negros specimen, as it is in *celebensis*. The cingular cusp at the back of the same tooth is present in all.

Harpyionycteris celebensis Miller and Hollister

Harpyionycteris celebensis MILLER AND HOLLISTER, 1921, Proc. Biol. Soc. Washington, vol. 34, p. 99. RAVEN, 1935, Bull. Amer. Mus. Nat. Hist., vol. 68, p. 183 (mention only).

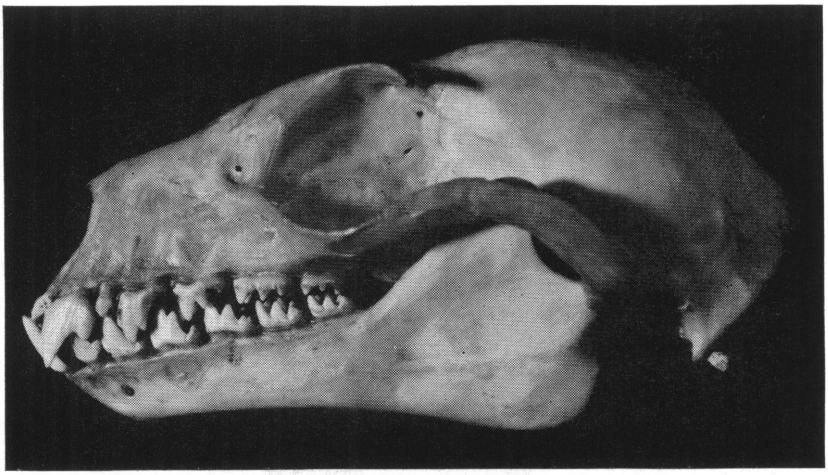

FIG. 1. *Harpyionycterus celebensis* (Buitenzorg Museum, No. 2833), lateral view to show occlusal pattern.

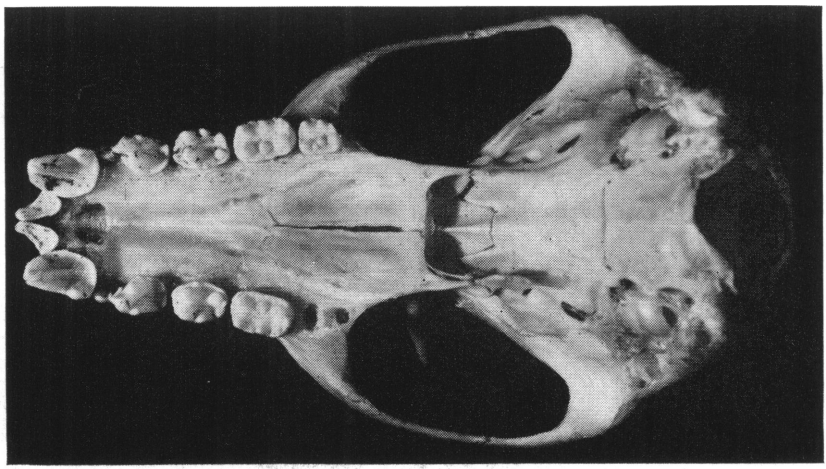

FIG. 2. *Harpyionycteris celebensis* (Buitenzorg Museum, No. 2833), palatal view.

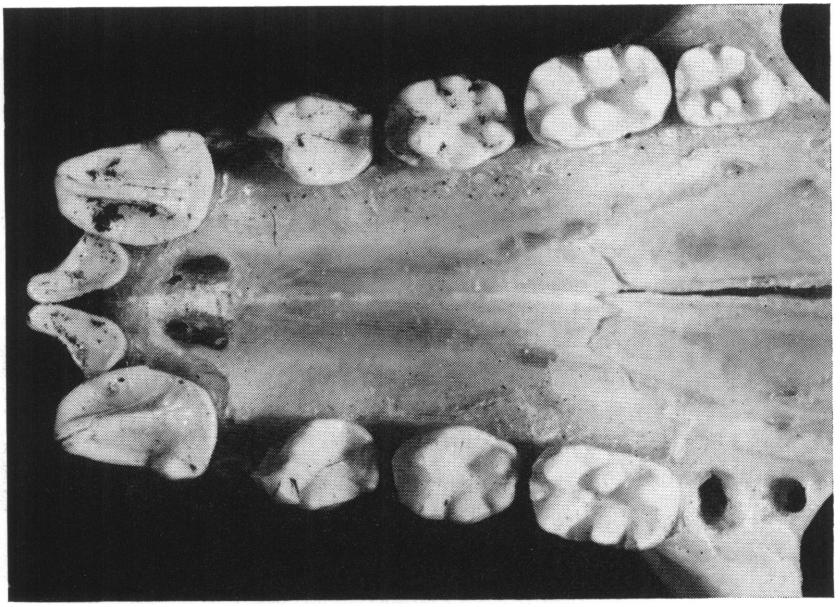

FIG. 3. *Harpyionycteris celebensis* (Buitenzorg Museum, No. 2833), enlarged to demonstrate the multicuspid condition of the molars.

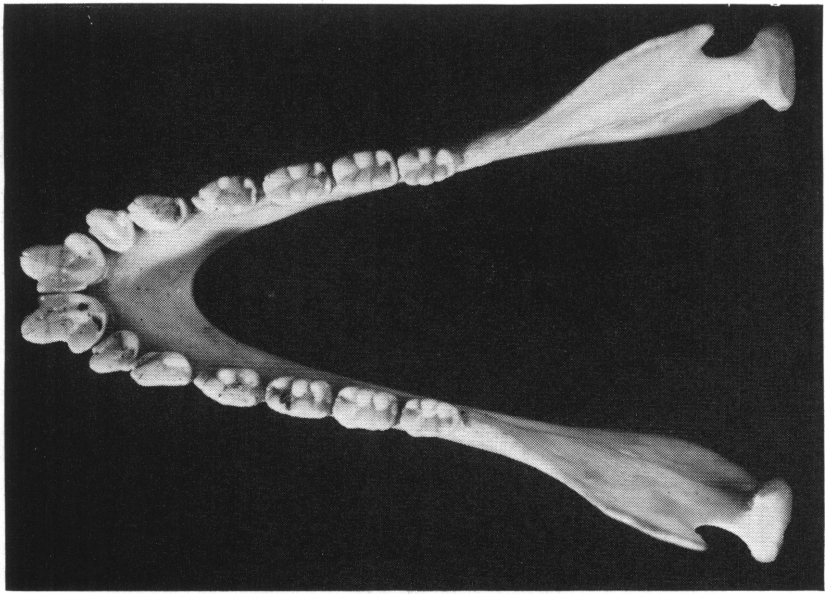

FIG. 4. *Harpyionycteris celebensis* (Buitenzorg Museum, No. 2833), mandible, showing cusps of lower teeth.

TYPE: U.S.N.M. No. 219349, adult female, from Gimpoe, middle Celebes, collected by H. C. Raven, August 23, 1917.

Among material on deposit in the American Museum from the Buitenzorg Museum are six specimens from Roeroekan, north Celebes, 1000 meters, collected by G. Heinrich in January, 1931. The Buitenzorg numbers are 2828 to 2833. Heinrich's field numbers, still attached to all specimens but one, are: 169, female; 178, male?; 182, male; 186, male; 188, male. Number 2828 (169) is obviously juvenal, but the skull carrying that number is mismatched. The single pair of pectoral nipples in the female are plainly visible. In addition, we have a single male skin without skull from Tanko Salokko, Mengkoka Mountains, south Celebes, 1500 meters, taken also by Heinrich (A.M.N.H. No. 153590).

Dr. David H. Johnson has recently kindly permitted me to reëxamine and remeasure the type in Washington.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF *Harpyionycteris*

	Length of Head and Body	Fore-arm	Tibia	Condylo-basal Length	Zygo-matic Width	Width of Post-orbital Process	Length, c–m[2]
whiteheadi,[a] type B.M. No. 97.5.2.7	±150	83	±27	±40	23.5	12.0	17.4
whiteheadi,[b] Negros I. C.N.H.M. No. 66302	—	79.5	±25	40	21.3	12.4	16.8
celebensis, type, female, U.S.N.M. No. 219349	153	90	30	41.6	24	—	16.6
Male, Buitenzorg No. 2831	134	79.5	27.5	—	21.4	12.5	16.4
Male, Buitenzorg No. 2832	136	79.0	—	—	22.6	±11	16.0
Buitenzorg No. 2830	—	79.5	29	37	23	±13	16.4
Male, Buitenzorg No. 2833	132	82	30	36.3	22.4	14.5	16.4
Buitenzorg No. 2829	124	84	30.5	—	22.5	14.0	15.5
Female,[c] Buiten-zorg No. 2828	117	70.5	30	—	—	—	—
Male,[c] A.M.N.H. No. 153590	143	91	31	—	—	—	—

[a] Interorbital width, 6.5 mm.; intertemporal width, 5.8 mm.

[b] Interorbital width, 6.0 mm.; intertemporal width, 6.7 mm.

[c] Skulls either mismatched or lost.

TABLE 2

CROWN DIMENSIONS (IN MILLIMETERS) OF THE CHEEK TEETH IN *Harpyionycteris*

	whiteheadi Type		*whiteheadi* from Negros Island		*celebensis* Type	
	Length	Width	Length	Width	Length	Width
p^1	1.0	0.9	1.1	0.9	1.2	1.0
p^2	2.6	2.0	2.8	2.0	2.8	2.1
p^3	3.1	2.1	2.9	2.0	3.0	2.2
m^1	3.3	2.1	3.2	2.1	3.5	2.2
m^2	2.3	1.9	2.5	1.9	2.5	2.0
p_1	1.7	1.7	1.7	1.7	1.7	1.7
p_2	2.3	1.4	2.3	1.5	2.2	1.4
p_3	2.5	1.6	2.7	1.6	2.8	1.7
m_1	2.6	1.6	2.5	1.6	2.6	1.7
m_2	2.5	1.7	2.5	1.7	2.6	1.8
m_3	2.3	1.5	2.3	1.6	2.4	1.7

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