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## RESULTS OF THE ARCHBOLD EXPEDITIONS. No. 36

### REMARKS ON SOME OLD WORLD LEAF-NOSED BATS

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When reviewing recently the genus *Hipposideros*,<sup>1</sup> it became necessary to study other available hipposiderine genera, to re-examine *Rhinolophus*, and to some extent to study the remaining leaf-nosed bats, the Megadermidae and Nycteridae.

Material referable to *Asellia*, *Anthops*, *Clootis*, *Triaenops*, *Coelops*, *Rhinolophus*, *Megaderma*, *Lavia*, *Nycteris*, *Lyroderma* was examined. (*Rhinonycteris* is apparently unrepresented in American collections.) Notes made upon their comparative structures are presented herewith. The hipposiderine genera are considered first, then briefly the Nycteridae and Megadermidae. The isolated position of *Coelops* is pointed out. Only incidental remarks are offered on the Rhinolophinae, reviewed two years ago<sup>2</sup> and now in course of extensive revision by C. C. Sanborn.

A list of materials belonging to these genera contained in the Archbold collections is appended.

#### Hipposiderinae

##### ANTHOPS THOMAS

*Anthops* THOMAS, 1888, Ann. Mag. Nat. Hist., (6) I, p. 156; 1888, Proc. Zool. Soc. London, p. 477.—MILLER, 1906, Bull. U. S. Nat. Mus., LVII, p. 113.

GENOTYPE.—*A. ornatus* Thomas from Aola Guadalcanar.

Thomas distinguished *Anthops* from *Hipposideros* by its short tail, which Miller says is less than half the length of the femur and contains four caudal vertebrae, and by the projections of the transverse noseleaf being "rounded and hollow behind." Miller indicated the larger size of

the cochleae (not so large, however, as in *H. muscinus*).

Many of the following notes are based upon specimens kindly lent us by the Curators of Mammals at Washington, Chicago and Cambridge.

##### *Anthops ornatus* Thomas

U.S.N.M. 123441, Guadalcanar.

Ears much as the "emarginate ears" of members of *Hipposideros*, but with anti-tragal fold somewhat larger. Horseshoe with two lateral leaflets, the inner quite small, the outer large. Transverse leaf with three raised, rounded processes, each hollowed out behind and each representing the extension of the three thickened septa which in front support the leaf (as in *H. larvatus*). The transverse leaf subtended by two small lateral leaflets of its own, separate from those margining the horseshoe. Traces of a small frontal sac. Tail very short.

Skull of the short, massive type seen in *Hipposideros speoris* and *larvatus*. Broken. The rostral portion triangular, the rostral swellings at the apices of the triangle not extremely prominent. Infraorbital foramen inclosed by a bar. Intertemporal constriction pronounced. Cochlea and ring not greatly enlarged (diameters 3.4 and 2.8). Back of palate level with m<sup>2</sup>. Incisive foramina closed by maxilla. Back of premaxillae rounded. External lobe of incisors virtually obsolete; c with low posterior cusp; p<sup>2</sup> neither greatly reduced (cingulum length, 0.7) nor wholly out of tooththrow; m<sup>3</sup> with partly reduced W-pattern; rami of mandibles at symphysis forming a narrow inverted V; outer incisors slightly thickened, inner ones strongly overlapping;

<sup>1</sup> "Results of the Archbold Expeditions. No. 35." 1941, Bull. Amer. Mus. Nat. Hist., LXXVIII, Art. 5.

<sup>2</sup> Tate and Archbold, 1939, Amer. Mus. Novit., No. 1036, pp. 1-12.

$p_2$  unreduced,  $\frac{\text{cingulum length } p_2}{\text{cingulum length } p_4} = \frac{1.10}{1.15}$ .  
Back of skull destroyed.

Sanborn records the species from Choisul, Troughton from Ysabel and Bougainville Islands.

Contrary to statements by authors, *Anthops* is not very close to *Asellia*. It differs in several features: its much heavier incisors, the retention of  $p^2$ , the form of rostrum and sagittal crest, the less reduced  $m^3$  and  $p_2$ .

The type of *A. ornatus*, B.M. 88.1.5.16, old adult female, two paratypes, B.M. 88.1.5.17 and 88.1.5.28, female and male, and a juvenal male topotype, B.M. 89.4.3.5, all in alcohol, were examined by me. The forearms measured 50, 51, 48.5 and 37 mm., respectively.

My measurements of the type skull are: greatest length, 20.0 mm.; zygomatic breadth, 10.4; mastoid breadth, 9.0; breadth of braincase, 8.4; least interorbital width, 2.0; cochlea, 3.0;  $c-m^3$ , 7.0.

**"Rhinolophus" tricuspidatus** Temminck

A.M.N.H. 109987, Hollandia, Dutch New Guinea.

A quite small species with horseshoe unnotched in front, two lateral leaflets, the outer pair connecting with the transverse leaf above and uniting in front beneath the horseshoe; no lateral cells as in *Triaenops*; no papilla-like process on "sella;" transverse leaf divided into three parts somewhat as in *Asellia tridens*, but the lateral processes much less elevated. Ears shaped as in *H. galeritus*, although somewhat narrower and more acute and thus approaching *H. muscinus* in form. Tail considerably exserted beyond membrane.

Skull somewhat narrow, the zygomata only slightly exceeding mastoid width, and rostral expanse only slightly less. Rostral swellings large, high. Zygomatic eminence rising gradually in front; high behind. Cochlea rather large and fairly close together (2.1 : 1.0). Premaxillae weakly united, their contact with palate V-shaped.

Upper incisors clearly bilobate, but very small and with the roots exceedingly delicate, divergent, placed at the outer corners of the premaxillae as in *Asellia* and *H. commersonii*;  $p^2$  still with small cusp and retained in tooththrow;  $m^3$  less reduced than in *Asellia tridens*; tooththrows almost parallel as in *H. muscinus*. Lower incisors, as in *H. muscinus*, scarcely at all imbricated;  $p_2$  unreduced, its cingulum length actually greater than that of  $p_4$  (0.9 : 0.8), but markedly compressed laterally (width, 0.5 to 0.6).

*Tricuspidatus*, placed by Dobson and by Peters in a special division of *Hipposideros*, betrays affinities with *Anthops*, *Asellia*, *Triaenops* and *Clootis* by the division of the upper edge of the noseleaf into three points. It appears nevertheless to represent a distinct line of development which may be distinguished as

**ASELLISCUS NEW GENUS**

GENOTYPE.—*Rhinolophus tricuspidatus* Temminck from Amboina.

DESCRIPTION.—A Hipposiderine genus of bats with upper margin of transverse noseleaf divided into three points, no papilla on the sella, two lateral leaflets margining horseshoe, no frontal sac in either sex, tail extending considerably beyond membrane, as in *Asellia*.

Skull with large separate rostral inflations, premaxillary bones divergent in front, cochlea rather large.

Teeth. Incisors bilobed, small, divergent; canine with low posterior cusp;  $p^2$  included in tooththrow;  $m^3$  scarcely reduced;  $p_2$  low, uncrowded, laterally compressed. Tooththrows parallel.

It seems probable that *stoliczkanus*<sup>1</sup> and

<sup>1</sup> Since this manuscript was completed a small series of "*Asellia*" *wheeleri* Osgood from Chipwi, northern Burma, has been examined. The species is a little smaller than *tricuspidatus*, with forearm, 49 mm., instead of 54; the ear less elongated and more like the ear in the *H. galeritus* group; the tail elongate instead of short (40 mm. : 25 mm.) and its tip extends two or three millimeters beyond the membrane.

The noseleaf, surrounded by rather dense facial hair, somewhat as in *Coelops*, is very like that of *tricuspidatus*, with three small points on the transverse leaf, which terminate three supporting ribs or septa. There are two lateral leaflets. The front of the horseshoe shows indications of a cleft. No frontal sac is present in the male. *Wheeleri* and *stoliczkanus* appear closely related.

The skull is slightly reminiscent of the skull of *Coelops*, in that it is low, and the canine-bearing portion and premaxillae are elongated; while the canines are strongly proodont, though devoid of the strongly developed supplemental cusps of *Coelops*.

The skull represents a quite advanced Hipposiderine near *Aselliscus*; the premaxillae though longer preserve the same relations with the upper incisors,

*trifida* Peters from the Malay and Burma region must also be referred to *Aselliscus*.

The new genus is distinguished from *Anthops* and *Triaenops* by its very different premaxillae, zygoma and upper incisors, from *Cloeotis* by its relatively low jugal eminence and much deeper skull, from *Asellia* (*tridens*) by its lower sagittal crest, much inflated rostrum, pore-like infraorbital foramen and parallel toothrows, and from *Rhinycteris* by the several characters given for the last by Dobson (1878).

The geographical range of *A. tricuspιδatus* includes Amboina, Buru (Dammerman), the north coast of Dutch New Guinea, Batjan (Peters), Duke-of-York Island (Dobson), Morty Island, New Britain, and New Ireland (Dobson), Kei (Peters and Doria), Aola, Guadalcanar (Thomas), Woodlark Island (Thomas), Trobriand Island (Heller), Solomon Island and Santa Cruz Island (Sanborn).

#### RHINYCTERIS GRAY

*Rhinycteris* GRAY, 1847, Proc. Zool. Soc., London, p. 16.

*Rhinycteris* GRAY, 1866, Proc. Zool. Soc., London, p. 81.

GENOTYPE.—*Rhinolophus aurantius* Gray, from North Australia.

*Rhinycteris* is unrepresented in our collection. Study of the illustration of the noseleaves shown by Dobson, 1878 (Pl. VIII, fig. 2), shows a few cellular structures lateral to the transverse leaf, development of the anterior process of the internasal septum and a medial pit in front of the transverse leaf, much like those of the *Triaenops*. But the transverse leaf is simple and rounded above, slightly pointed at the middle. There appears to be a median papilla on the "sella." The horse-

shoe is broadened to form two angled expansions. The ears are simple, somewhat acute and appear to be slightly emarginate.

which are similarly delicate in structure; the molar series are parallel; p<sup>2</sup> is similar in size, shape and position; m<sup>3</sup> has the W-pattern similarly unreduced. It differs in possessing a quite large posterior zygomatic eminence somewhat as in *Triaenops*, *Asellia* and *Cloeotis* and in the reduced, compressed form of p<sup>2</sup>.

From *Triaenops* it is distinguished by its much narrower rostrum in proportion to braincase and in other characters (see *T. persicus* beyond). From *Cloeotis* and *Asellia* (both described beyond) it exhibits a number of distinguishing characters. Perhaps it should be accorded generic separation.

The status of *stoliczkanus* Dobson can be cleared up only by restudy of the type. Dobson's illustration (1878, pl. 8), of the face of *stoliczkanus*, which may be poorly drawn, seems to differ from *wheeleri* in several particulars.

shoe is broadened to form two angled expansions. The ears are simple, somewhat acute and appear to be slightly emarginate.

Canine with large secondary cusp; and peculiarities of premaxillae, rostrum, zygoma and sagittal crest (Miller, 1907).

*R. aurantius* is found chiefly in northern and northwestern Australia. Wood-Jones writes that it occurs rarely in South Australia.

#### TRIAENOPS DOBSON

*Triaenops* DOBSON, 1871, J. Asiatic Soc. Bengal, XL, 2, p. 455.

GENOTYPE.—*Triaenops persicus* Dobson, from Shiraz, Persia.

Additional forms named:

<i>afer</i> Peters	Mombasa
<i>furcula</i> Trouessart	W. Madagascar
<i>humbloti</i> Milne Edwards	E. Madagascar
<i>rufus</i> Milne Edwards	E. Madagascar
<i>aurita</i> Grandidier	Diego Suarez
<i>furinea</i> Trouessart	Aldabra Islands
<i>?wheeleri</i> Osgood	Tonkin

With the exception of *wheeleri* Osgood,<sup>1</sup> already dealt with under *Aselliscus*, this genus is indigenous to the part of the world which includes Persia, Arabia, East Africa and the Mascarene group of islands.

#### *Triaenops persicus* Dobson

U.S.N.M. 123439, Arabia.

Ears short, acute, very like the emarginate ear in the *galeritus* group, but with a well-developed fold at anterior edge, also a low tragus inside antitragal lobe. Horseshoe not cleft, but interrupted by flat rectangular process from internasal septum. Supplemental leaflets two, the inner interrupted at each side near front, and its anterior parts uniting smoothly in advance of horseshoe. The posterior half divides and anastomoses to form a complex system of six cells between the eye, the horseshoe and the transverse leaf. The outer leaflet small and broad. The transverse leaf modified into three high, pointed processes, much as in *Cloeotis*. In front of the central one of the processes a large median pit, and in front of the pit the "sella," upon which stands a high, pointed, laterally compressed papilla, the

<sup>1</sup> 1932, Mammals of the Kelly-Roosevelt Expedition, p. 224.

equivalent of similar organs in *Cloeotis* and *H. muscinus*.

Skull rather high and with high rostrum, canine-bearing part extended forwards (as in *H. pratti*); rostrum broad, the swellings individual and their inflations in the frontal rather than in the maxillary portion of the rostrum; jugal eminence very large and high, occupying almost the whole length of the zygoma; squamosal roots of zygomata little expanded; premaxillae indistinct (not described); roofs of pterygoid and narial canals with step-like discontinuity as in *H. armiger*; cochlea rather large; a foramen developed in the web of bone tying together the angular and articular processes of mandible.

Outer lobe of upper incisor well developed, and teeth convergent, approximated, placed towards center of combined premaxillae; canine with definite posterior cusp to half its length;  $p^2$  excluded, not extremely reduced;  $m^{1-3}$  with W-pattern only slightly reduced. Outer of three lobes of outer lower incisor obsolescent;  $p_2$  low but cingulum length not reduced.

#### CLOEOTIS THOMAS

*Cloeotis* THOMAS, 1901, Ann. Mag. Nat. Hist., (7) VIII, p. 28.

GENOTYPE.—*Cloeotis percivali* Thomas from British East Africa.

Additional form since named: *australis* Roberts.

#### *Cloeotis percivali* Thomas

U.S.N.M. 154589, Rhodesia, South Africa.

A very small bat with forearm 34 mm. Ears short, low, rounded, only the suspicion of a "tip" perceivable. Horseshoe deeply cleft in front, the two sides of the cleft raised and produced as two small processes. Two lateral leaflets, the outer larger, coalesce upwards to form a single fold which reaches the side of the transverse leaf. Transverse leaf modified into three high pointed processes which rise from the three septa. Transverse leaf subtended on each side by large lateral papilla, which low cutaneous ridges connect with inner canthus of eye and with transverse leaf. Sella with small clubbed process at center

and between center and outer margin a small eminence (on each side). Thumbs quite small. Frontal sac? Tail not reduced (7 joints).

Skull short, low, broad (like *Hipposideros dyacorum*). Rostral swellings moderate, rostrum low; intertemporal constriction marked; premaxillae not clearly visible; palate to half  $m^{2-2}$  only, with a broad spine; zygomata wide, jugal eminences, contrary to Thomas' description large, and unlike those of *Asellia*, inclined backwards, limited to portion of zygoma directly over glenoid; glenoid surfaces broad and flat; Eustachian tubes well developed; cochlear spirals visible (large); tympanic rings not enlarged; angular processes connected by web of bone with articular; coronoid low.

Upper incisors two-lobed but very small, the roots above the crowns very slender as in *Aselliscus*;  $c$  with posterior cusp descending for half its length;  $p^2$  greatly reduced, excluded;  $p^4$  well developed; hypocones weak, internal interdental spaces large;  $m^3$  with W-pattern almost complete.  $P_2$  not much reduced, low, but its cingulum length not shortened.

#### ASELLIA GRAY

*Asellia* GRAY, 1838, Mag. Zool. Bot., II, p. 493; 1843, List Spec. Mamm. British Mus., p. 24; 1866, Proc. Zool. Soc. London, p. 81.

GENOTYPE.—*Rhinolophus tridens* Geoffroy (by monotypy) from Egypt.

Additional forms since described:

<i>murraiana</i> J. Anderson	Karachi, India
<i>patrizii</i> de Beaux	Ethiopia
<i>italosomaliae</i> de Beaux	Italian Somaliland
<i>pallida</i> Laurent	French Morocco
<i>diluta</i> Andersen	Algerian Sahara

*Asellia*, excluding *tricuspidata* and its allies for which the genus *Aselliscus* has now been proposed, is seen to range across arid northern Africa, Arabia and Iraq to northwest India.

Below is a redescription of *A. tridens murraiana* J. Anderson, 1881, based upon material at the Field Museum of Natural History.

#### *Asellia tridens murraiana* J. Anderson

F.M.N.H. 48728, ♂, Baghdad.

Ears much like *H. speoris*, with anti-tragal notch and groove, no tragus, outer

edge emarginate, no costal fold as *Tri-aenops*.

Horseshoe weakly notched in front, no trace of process from internarial region; lateral leaflets two, the inner smaller; transverse leaf with three processes, the median high and narrow, the lateral ones nearly as high but much broader; no papilla on sella (see *Tri-aenops*, *Cloetis*, and *H. muscalis* and *cylops*), no complex of cells lateral to noseleaves (*Tri-aenops*). Tail extending considerably (one joint) beyond uropatagium.

Skull with well-expanded zygomata, jugal eminence not enlarged as in *Tri-aenops*, rostrum wide and almost as high as braincase without sagittal crest; premaxillae strongly fused, rounded posteriorly at contact with palate, their lateral processes nearly contiguous with maxilla and not enclosing incisive foramina; back of palate level with backs of  $m^{3-3}$ ; cochlea more than twice as wide as their distance apart (2.8 : 1.0).

Upper incisors peg-like (outer lobe obsolete), divergent, placed at outer corners of premaxillae; canine with posterior cusps descending below middle of tooth, much as *Tri-aenops*; absolutely no indication of  $p^2$ ;  $p^4$  large; interdental spaces somewhat reduced;  $m^3$  with much reduced W-pattern; outer lower incisor considerably thicker than the inner, the outer lobe unreduced (compare *Tri-aenops*). Anterior lower premolar considerably reduced, and moved slightly outwards in the toothrow.

#### COELOPS BLYTH

*Coelops* BLYTH, 1848, J. Asiatic Soc. Bengal, XVII, 1, p. 251.

*Chilophylla* MILLER, 1911, Proc. U. S. Nat. Mus., XXXVIII, p. 395.

GENOTYPES.—*Coelops*, *frithii* Blyth from "Soonderbuns" = Sandarbans (Dobson), Bengal; *Chilophylla*, *hirsuta* Miller from Mindoro.

The following further systematic work on *Coelops* has been done:

1862, PETERS, Archiv f. Naturg., II, p. 117.  
1865, PETERS, Monatsber. Akad. Berlin, pp. 641-648, described *C. bernsteini*.

1871, PETERS, *op. cit.*, pp. 330-332, reviewed the genus, synonymizing his own species.

1878, DOBSON, Cat. Mamm. Brit. Mus., pp. 152-153, reviewed *Coelops*.

1907, MILLER, Bull. U. S. Nat. Mus., LVII, pp. 113-114, reviewed *Coelops*.

1908, BONHOTE, J. Fed. Malay States Mus., III, p. 4, described *C. robinsoni* from Pahang.

1911, MILLER, *loc. cit.*, described *Chilophylla hirsuta* from Philippines.

1912, MILLER, P. Biol. Soc. Wash., XXV, p. 117, remarked on dentition and skull of "*Chilophylla hirsutum*," not from Philippines but from Federated Malay States (thus probably *C. robinsoni*).

1928, HORIKAWA, Trans. Nat. Hist. Soc. Formosa, XVIII, No. 98, described *C. formosanus*.

1928, G. M. ALLEN, Amer. Mus. Novit., No. 317, p. 4, described *C. sinicus* from Szechwan.

1928, MILLER, P. Biol. Soc. Wash., XLI, p. 85, synonymized his *Chilophylla* with *Coelops* (in footnote) and described as new *C. inflata* from Fukien.

1929, OSGOOD, Field Mus. N. H., Zool., XVIII, pp. 226-228, discussed the genus. He indicated the supplementary canine cusps.

The named forms of *Coelops* may be listed as follows:

<i>frithii</i> Blyth	Bengal
<i>bernsteini</i> Peters	Java
<i>robinsoni</i> Bonhote	Pahang, Malay
<i>inflata</i> Miller	Fukien
<i>sinicus</i> G. M. Allen	Szechwan
<i>formosanus</i> Horikawa	Formosa
<i>hirsuta</i> Miller	Philippines

The following remarks on *Coelops* are based upon examination of *Coelops* "*robinsoni*," U.S.N.M. 175000, Malay States.

*Coelops* represents a type of bat very different from the Hipposiderine genera previously described. Horseshoe, if it may be so called, with deep anterior median notch reaching back to the internasal septum, each lateral portion of horseshoe parted into two greatly overlapped lobes, the outer over the inner, the inner extended farther forwards than the outer one. Lateral leaflets apparently absent, or else obscured by a dense development of stiff hairs which margin the nasal area. Transverse leaf rather low, posteriorly pocketed, with, however, a small median eminence. "Sella" with slight median raised ridge connecting internasal area with middle of transverse leaf. No visible frontal sac (Dobson says it is present). Ear short, rounded, with antitragal lobe, devoid of strengthening "ribs" as in

*Hipposideros*, etc. Thumb with metacarpal extraordinarily lengthened, its length to that of basal phalanx = 5.7 : 1.2. Tail extremely short, if not absent. Calcar much shortened, its length to that of tibia = 3 : 15 mm.

The skull is correspondingly peculiar: braincase short and rounded; intertemporal region narrow; rostral area with inflations confined to maxillary portion, the nasal portion uninflated, flat; zygomata short, little expanded, without jugal eminence; infraorbital foramen a pore, not enclosed by a bar, as in most *Hipposideros*; tooth-bearing portion of maxilla greatly extended forwards, carrying the tooththrow with it so that the back of the premaxillae is level with the middle of  $m^2$ ; premaxillae correspondingly extended to allow the incisors to be in line with the fronts of the proödont canines; back of palate slightly behind  $m^3$ ; cochlea and tympanics not modified; but basicranial foramina enormously enlarged. Mandibles, with toothrows parallel, U-shaped at symphysis.

Upper incisors minute, convergent, the outer lobe obsolescent; canine highly proödont, provided with two accessory cingulum cusps, each of which extends more than posterior down the body of the tooth; the posterior cusp, common to many Hipposiderinae and Megadermidae, and an internal cusp;  $p^2$  small but still with cusp, retained in tooththrow;  $p^4$  rather weaker than in most Hipposiderinae;  $m^3$  with W-pattern virtually complete; lower incisors not imbricated, retaining all three cusps; lower canines small, vertical;  $p_2$  unreduced, compressed, somewhat as in *tricuspidata*, moved slightly outwards in tooththrow.

The skull of this specimen was used in 1912 by Miller to describe the "cranial and dental characters of *Chilophylla*" and again by Taylor<sup>1</sup> for the same purpose.

Besides the skull of "*robinsoni*" just mentioned, I have before me for study the type skull of *sinicus*, two specimens from Tonkin marked *inflata* (F.M. 32232-3), and five from Bali (A.M.N.H. 107508-12); and in addition photographs of the skulls of the types of *bernsteini* and *robinsoni*.

*C. robinsoni* with forearm 37 mm. was stated by Bonhote to be the smallest of the genus. The forearm of U.S.N.M. 175000 is said by Taylor to measure only 33.5. The skull of this specimen differs sharply from all others seen not only in its small size but in the obsolescence of the customary large pocket or recess inside the maxillary root of the zygoma, anterior to the temporal fossa and directly above the roots of  $m^4$  and the posterior half of  $m^3$ . This pocket in U.S.N.M. 175000 (*robinsoni*?) is reduced to a small pore. Further, the upper edge of the zygoma terminates abruptly on meeting the rostrum level with the back of  $m^2$ , while in other species examined the zygomatic edge runs upwards and forwards onto the rostrum to terminate almost level with the back of  $m^1$ .

Again, the pterygoids are placed much nearer the back of the palate than in any other form examined: in "*robinsoni*" the distance from back of palate to back of hamulus of pterygoid = 1 mm., and in others the distance is 1.5 mm. or greater.

*C. inflata* was compared chiefly with *robinsoni*. It and *bernsteini* of Java appear to be related; the forearm length in each is 35.5. The tooththrow of *bernsteini*, measured against a millimeter rule photographed with the type skull, amounts to 6.1 mm.; that of *robinsoni*, obtained in the same way, to 4.9 mm. Also it can be seen clearly that the zygoma does not merge with the rostrum as described above for *robinsoni*. Our series from Bali is apparently near *bernsteini*: tooththrow, 5.6-5.8 mm.; forearm, 38, and greatest width of braincase, 7.6. In *sinicus* the tooththrow,  $c-m^3$  attains 6.2 mm.; the forearm, 36; width of braincase, 8.0.

The relationship of *frithii* from Bengal and *hirsuta* from the Philippines to the Indo-China and Javanese forms can be cleared up only when the type of the former has been re-examined and topotypes of the latter secured and studied. *Formosanus* is probably close to *inflata* or *sinicus*.

It has long been customary to place *C. bernsteini* of Java in the synonymy of *C. frithii* of Bengal. But considering the

<sup>1</sup> 1934, Taylor, "Philippine Land Mammals," pp. 247-248.

new forms which have been distinguished in the Malay region, China and Philippines, I doubt whether the practice should be longer held to, at least until the synonymy can be re-established by direct comparison of topotypes of each. Therefore the name *bernsteini* is here revived and applied to the Archbold series from Bali, just east of Java.

## NYCTERIDAE

### NYCTERIS GEOFFROY

*Nycteris* GEOFFROY, 1803, Cat. Mamm. Mus. Nat. Hist., p. 64.

*Petalia* GRAY, 1838, Mag. Zool. Bot., II, p. 484.

*Petalia* GRAY, 1866, Proc. Zool. Soc. London, p. 83.

*Nycterops* GRAY, 1866, Proc. Zool. Soc. London, p. 83.

GENOTYPES.—*Nycteris*, *Vespertilio hispidus* Schreber, Africa. *Petalia* (*Petalia*), *Nycteris javanica* Geoffroy, Java. *Nycterops*, *Nycterops pilosa* Gray, Africa.

When Gray set up *Nycterops* and further characterized "*Petalia*," he exemplified *Nycteris* Geoffroy by *N. thebaica* instead of *N. hispidus*. Allen<sup>1</sup> shows *hispidus* from Senegal and *thebaica* from Egypt as distinct species. He lists a total of 22 full species from Africa. Only *javanica* and *tragata* are recorded from the Orient. So *Nycteris* is to be regarded as primarily African with a subgeneric offshoot (*Petalia*) in the East Indies.

Although in some African species, for example, *arge*, *hispidus*, *major*, considerable further reduction of the posterior lower premolar is attained, and in *major* it becomes vestigial, neither of the Javanese species shows this modification.

*Nycteris* was reviewed by Peters<sup>2</sup> and by Dobson.<sup>3</sup> Peters appended an excellent plate to his paper, showing lower jaws and the condition of the lower teeth in eight species. Reduction and displacement of the posterior lower molar are clearly seen in many of them. He classified the species by their ears, the cusps of the incisors, the state of  $p_4$ . His system resulted

in the association of *grandis* from Guinea (West Africa) and *javanica*.

Dobson made his first division on characters of the tragus and his subsidiary ones on the structure of incisors, ears and lower premolars. His plan brought *Javanica* closest to *aethiopica* and next to *grandis*.

*N. tragatus* Andersen, 1912, differs from *javanica* chiefly by characters of the tragus and greater size of the teeth. The fourth premolar is similarly unreduced. The East Indian species compared with most African are unspecialized *Nycteris* with scarcely reduced  $p_4$ , and unenlarged ears. They are specialized, in that the outer lobes of the originally trifold lower incisors are obsolete.

Our collections contain both *javanica* and *tragata*, the latter represented by two specimens from Macarah Doewa, Palembang, Sumatra. The conspicuously larger teeth ( $c-m^3$ , 8.9 and 8.8 mm.) and  $p_4$  even less reduced in proportion to  $p_2$ , and the slightly larger palate and rostrum distinguish *tragata* from *javanica*, in addition to other features published by Andersen. We have photographs of the skull of *N. tragata*.

## MEGADERMIDAE

### MEGADERMA GEOFFROY

*Megaderma* GEOFFROY, 1810, Ann. Mus. Hist. Nat. Paris, XV, p. 197.

*Spasma* GRAY, 1860, Proc. Zool. Soc. London, p. 83.

GENOTYPES.—*Megaderma*, *Vespertilio spasma* Linnaeus. *Spasma*, *Vespertilio spasma* Linnaeus.

*Megaderma* and allied genera have been reviewed repeatedly. Probably the clearest way to present the taxonomic work done on the genera is to trace it chronologically:

1838, GRAY, Mag. Zool. Bot., II, pp. 490-491, proposed *Lavia*, with type *M. frons* Geoffroy.

1847, HODGSON, S. Asiatic Soc. Bengal, XVI, p. 891, proposed *Eucheira* for *M. lyra* Geoffroy. As shown later by Miller (1907) this is a homonym of *Eucheira* Westwood, 1836, Trans. Entom. Soc. London, I, p. 44.

1872, PETERS, Monatsber. Akad. Wiss. Berlin, pp. 192-196, reviewed *Megaderma*, described *M. cor.* and erected *Lyroderma* for *M. lyra*.

<sup>1</sup> 1939, Bull. Mus. Comp. Zool., LXXXIII, pp. 67-71.

<sup>2</sup> 1870, Monatsber. Akad. Wissen. Berlin, pp. 900-914.

<sup>3</sup> 1878, Cat. Chir. Brit. Mus., pp. 161-167.

- 1873, PETERS, *op. cit.*, p. 488, proposed *Cardioderma* for *cor*.
- 1878, DOBSON, Coll. Chirop. Brit. Mus., pp. 154-160, treated all foregoing names as subgenera of *Megaderma*.
- 1880, DOBSON, Proc. Zool. Soc. London, p. 461, described *M. gigas*.
- 1906, MILLER, Proc. Biol. Soc. Wash., XIX, p. 84, proposed *Macroderma* for *Megaderma gigas*.
- 1907, ANDERSEN AND WROUGHTON, Ann. Mag. Nat. Hist., (7) XIX, pp. 129-145, reviewed the family Megadermidae, proposing several new species and races. They attempted to revive *Eucheira* and discussed the wing structure and general relationships of the genera.
- 1907, MILLER, Bull. U. S. Nat. Mus., Wash., LVII, pp. 101-106, recognized the genera *Megaderma*, *Lyroderma*, *Macroderma*, *Lavia* and *Cardioderma*. He showed *Eucheira* Hodgson to be a homonym.

Since that time the generic situation has remained static.

The named forms of the Oriental subgenera *Megaderma* and *Lyroderma* are shown in the accompanying list:

<i>Megaderma</i>	
<i>spasma</i> Linnaeus	Ternate Island
<i>trifolium</i> Geoffroy	Java
<i>carinatae</i> Miller	Karimata Island
<i>natunae</i> Andersen and Wroughton	Natuna Island
<i>philippinense</i> Water- town	Philippines
<i>horsfieldi</i> Blyth	"Continental India"
<i>lasiae</i> Lyon	Lasia Island
<i>niasense</i> Lyon	Nias Island
<i>siumatis</i> Lyon	Siumat Island
<i>pangandarana</i> Sody	S. Central Java

<i>medius</i> Andersen	Singapore
<i>majus</i> Andersen	Lower Chindwin
<i>minus</i> Andersen	Cambodia
<i>ceylonense</i> Andersen	Trincomalee, Ceylon
<i>Lyroderma</i>	
<i>lyra</i> Geoffroy	"probably E. coast of Madras"
<i>caurina</i> Andersen and Wroughton	Surat, India
<i>sinense</i> Andersen and Wroughton	Amoy, China
<i>carnatica</i> Elliot	S. Martha Country
<i>schistacea</i> Hodgson	N. E. Bengal
<i>spectrum</i> Wagner ?	Kashmir

We have photographs of the type skulls of *Megaderma natuna*, *majus*, *medium minus*, *pangandarana* and of *Lyroderma sinense* and *caurina*.

Our material from Celebes appears inseparable from our series from Cheribon, Java. In *pangandarana* Sody seems to have named a series of bats which average very slightly larger than usual. And in spite of the extraordinary differences Geoffroy<sup>1</sup> has shown in their nasal leaves, it remains questionable whether *trifolium* of Java is significantly different from *spasma*. Topotypes from Ternate, type locality of *spasma*, are needed. *Spasma* was founded upon a figure in Seba.

On the other hand, a specimen from Burma, A.M.N.H. 54815, referable to *majus*, has decidedly larger molar teeth (c-m<sup>3</sup>, 10.3; m<sup>1-3</sup>, 5.9 mm.), compared with 9.1 and 5.2 in Cheribon (Java) material.

#### ON THE INTER-RELATIONSHIPS OF THE LEAF-NOSED BATS

The affinity of *Anthops*, *Aselliscus*, *Rhinonycteris*, *Triaenops*, *Cloetis*, *Aselha* and *Coelops* to *Hipposideros* rather than to *Rhinolophus* is indicated chiefly by reduction of their pedal phalanges to two and by lack of ps. Further they are well differentiated from the megadermid and nycterid bats.

In the Megadermidae and Nycteridae a tendency for the ears to become enlarged and united is developed. Various types of nasal appendages are seen. The tragus is present, bifid. *Megaderma*, *Lavia* and *Lyroderma* resemble *Rhinolophus* in possessing high posterior noseleaves, but in

*Nycteris* the posterior leaf is so much reduced as to be rudimentary. A true horse-shoe, with broadened, shield-like inter-narial septum appears in *Lyroderma* and *Megaderma spasma*, but in *Lavia* there is no internarial development. The number of phalanges of the toes is complete in all. None shows the special modifications of the thumb to be seen in *Coelops*.

In its skull, *Nycteris* alone has developed the extreme shortening of the palate common in *Rhinolophus*, but this condition cannot show relationship, since the pre-

<sup>1</sup> 1810, Ann. Mus. Hist. Nat. Paris, XV, pp. 187-198.



maxillae and rostrum are formed in wholly different ways. Two pairs of bifid upper incisors and three of trifid lower incisors can be seen. In the mandible of *N. revouillii*  $p_3$ , very minute, is found beneath the outside of the adjoining cingula of  $p_2$  and  $p_4$ , but  $p_3$  is absent from *N. javanica* and *arge*. The angular process of the mandible is much reduced, a unique character among the bats being discussed.

*Megaderma* and *Lyroderma* should perhaps not be separated more than subgenerically. Tragus very large (as in *Lavia*; in *Nycteris* quite small); tail obsolescent (also in *Lavia*, but well developed in *Nycteris*). Skull in many ways unspecialized—e.g., palate, *basis cranii*, rostral region—but premaxillae apparently never ossified and upper incisors entirely wanting. Canine possessing the large, posterior cusp, so frequent among Hipposiderinae;  $p^2$  minute, inside  $c$  and  $p^4$ ; W-pattern of  $m^3$  much reduced; lower incisors (3-lobed) two;  $p^3$  absent,  $p^2$  unreduced.

*Lavia* has developed expanded post and anteorbital processes and a low rostral region, similar to the depressed frontal area of *Nycteris*. But, like *Megaderma*, it has lost the premaxillae and upper incisors. Posterior canine cusp large;  $p^2$  obsolete;  $m^3$  much reduced; lower incisors two;  $p$  obsolete. The angular processes are unreduced in *Lavia*, *Megaderma* and *Lyroderma*.

As was pointed out under *Hipposideros* the lines of development of the several structures usually employed in classification of the leaf-nosed bats seem to function and change independently. Some of these structures are traced below, as they appear in some genera of the Nycteridae, Megadermidae and Rhinolophidae.

The transverse noseleaf is seen in very simple form in *Nycteris* and in the *bicolor* and *calcaratus* groups of *Hipposideros*. In *Hipposideros* it is primarily a flat, rounded structure with three "septa" supporting it in front. In the *H. diadema*, *armiger* and *pratti* groups it becomes lobed and enlarged. In *Anthops* the lobes are further developed, the apex of each lobe being also the termination of a correspond-

ing "septum." The noseleaf of *Asellia* is somewhat similar.

At this stage one of two courses is followed: the three lobed or raised parts of the leaf become higher and acutely pointed as with *Cloeotis* and *Triaenops*; or else, the median one of the three becomes enormously enlarged while the lateral ones degenerate, as in *Rhinolophus* and the Megadermid bats. Contrary to all of the foregoing, the transverse noseleaf of *Coelops* develops twin points instead of one or three.

In conjunction with the transverse noseleaf special cells or pockets develop: the median, anterior pouch and the honeycomb of lateral pits found in *Rhinonycteris* and *Triaenops*; the frontal sac in *Hipposideros*.

The ear develops along two wholly different lines of specialization. In the Megadermidae and in *Hipposideros megalotis* the ears become enlarged and united across the forehead by a common fold of skin. But also in the Megadermidae the large bifid tragus is retained, whereas in the Hipposiderinae it becomes obsolete. Folds strengthening the pinna of the ear, which appear in all genera with large ears, are non-existent in *Coelops*. In it the ears are small, rounded and uniform in structure. They are commonly described as "funnel-shaped."

The rostral region of the skull remains broad, flat and relatively unspecialized in *Megaderma* and in the *Hipposideros armiger* group. In most of *Hipposideros* and allied genera and in *Rhinolophus* the rostrum is raised and variously inflated, the swelling affecting usually both nasal and maxillary portions. On the other hand, a marked dorsal depression or pit occupies the whole frontal area in *Nycteris* and *Lavia*. *Coelops* manifests a similarly depressed rostrum.

The premaxillae are in course of reduction by three methods. In *Megaderma* the premaxillary bones remain cartilaginous. In *Nycteris* the outer portions, each carrying two incisors, become ossified and more or less completely fused to the maxillae laterally. In all Rhinolophidae it is the center of the combined premaxillae which ossifies (bearing one incisor only on

each side), while the space laterally between maxillae and the palatal branch of premaxillae tends to remain open.

Of the upper premolars  $p^2$  is rudimentary in all families except Nycteridae. It is obsolete in *Nycteris*, rudimentary and displaced inwards from the toothrow in *Hipposideros* and *Rhinolophus*. In the lower jaw of *Rhinolophus*  $p_3$ , greatly reduced, is seen on the outer side of the ramus, displaced by the contiguous  $p_2$  and  $p_4$ . The tooth is absent in all other genera.

In most genera  $p_2$ , although wholly different in shape from  $p_4$ , due to its being single-rooted instead of double-rooted, is about as large as  $p_4$ . It becomes slightly reduced in *Lavia*, *Rhinolophus*, *Triaenops*, *Asellia* and *Hipposideros*, and quite markedly so in *H. muscinus* and in *Clootis*. But in the exceptional case of *Nycteris*  $p_4$  is absent, while  $p_2$  takes its place as the large functioning premolar, with  $p_3$  much or slightly reduced behind it (*N. javanica* and *arge*), or even vestigial and concealed beneath the cingulum of  $p_2$  (*N. thebaica*).

The W-pattern of  $m^3$  remains fairly complete in *Clootis*, *Coelops*, *Triaenops*, *Rhinolophus* and in *Hipposideros muscinus*. It is more or less reduced in the majority of *Hipposideros*, and in *Nycteris*, *Lavia*, *Megaderma*, *Asellia*.

Obviously most modifications in the six sets of structures just discussed are of ancient origin and have operated with varying intensities upon the species of the three families just discussed, which Weber<sup>1</sup> unites as the superfamily Rhinolophoidea. When character changes turn up indiscriminately through the three families and their genera, those same characters are unlikely to prove universally valuable as indicators of relationships. For example, because progressive reduction of the pattern of  $m^3$  shows in all groups, the condition of the tooth is significant chiefly when the W-pattern is unreduced. But characters marking a distinct, irrefutable departure from type, which are confined to a small group of species, such as shows in the premolars of *Nycteris*, are of value. Neither the Nycteridae because of their

premaxillae and premolars, nor the Megadermidae because of their exaggerated transverse noseleaves and total obsolescence of premaxillary bones can show direct relationship to the hipposiderine genera. But they still exhibit a number of those character trends which were constantly in operation during the evolution of the superfamily taken as a whole. Enlargement of the rostrum,<sup>2</sup> non-ossification of the lateral connections of the premaxillae to the maxillae, the tendency for the ears to remain free, obsolescence of the tragus—these are characters of the Rhinolophidae which the Megadermidae and Nycteridae lack.

The single large genus *Rhinolophus*, commonly given subfamily rank, differs from the remainder chiefly by non-coalescence of the toes of the feet to make two joints instead of three (all Hipposiderinae); by the exaggerated development of the posterior noseleaf into a tall blade and the development of corresponding modifications of the "sella" region; and by the pronounced shortening of the palatal bridge. Further characters of *Rhinolophus*, which, however, are duplicated by other genera and by one or another of the species groups of *Hipposideros*, are: linear arrangement of the lower incisors (also in *H. muscinus* and *Coelops*), wide separation of the upper incisors (*H. commersonii*, *Asellia*, *Aselliscus*), large size and approximation of cochlea (*H. muscinus*). Thus some of the conspicuous features which distinguish certain Hipposiderine bats are "standard" characters in *Rhinolophus*.

Out of the large number of characters usable for defining a species only a very few are absolute characters of kind. The preponderance represent merely differences of degree which frequently fluctuate among the species composing the genera whose phylogeny one seeks to trace out. Although the fluctuating characters ought to carry much weight in estimating phylogenetic relationships it is the few absolute ones which in practice are seized upon. Because *Coelops* has but two joints to the toes of its hind feet it is placed with the

<sup>1</sup> 1927, "Die Säugetiere," I, p. xiv.

<sup>2</sup> In *Coelops*, incipient only.

Hipposiderinae. But apart from its specialized feet, it shows several quantitative characters and at least two qualitative—the depressed frons and the highly individual type of noseleaves—which suggest it may belong elsewhere and that the fusion of the tarsals indicates a case of convergence.

*Coelops* is, in fact, so remote from other hipposiderine bats that it may be desirable

to grant it subfamily rank, the *Coelopsinae*. Its unique characters are listed:

- 1.—Structureless condition of the ear pinna.
- 2.—Strongly differentiated "horseshoe."
- 3.—Enormously elongated first metacarpal.
- 4.—Absence of tail.
- 5.—Greatly extended canine-bearing portion of maxilla.
- 6.—Much fenestrated *basis cranii*.
- 7.—Internal as well as posterior supplemental canine cusps.
- 8.—U-shaped symphyseal portion of combined mandibles.

#### LEAF-NOSED BATS, OTHER THAN *RHINOLOPHUS* AND *HIPPOSIDEROS*, IN THE ARCHBOLD COLLECTIONS

NYCTERIDAE		
<i>Nycteris javanica</i>	Cheribon, Java	41
<i>Nycteris javanica</i>	Noesa Penida, Bali	18
<i>Nycteris tragata</i>	Macarah Doewa, Sumatra	2
MEGADERMIDAE		
<i>Megaderma spasma</i>	Cheribon, Java	6
<i>Megaderma spasma</i>	Taliaboe Island, Moluccas	2
<i>Megaderma spasma</i>	Togian Island, Celebes	1
<i>Megaderma spasma</i>	Wawo, S. Celebes	1
HIPPOSIDERINAE		
<i>Aselliscus tricuspidata</i>	Hollandia, Dutch New Guinea	44
COELOPINAE		
<i>Coelops</i>	Oeboed, Bali	5

Species occurring in the New Guinea-Australian region but not obtained by the Archbold expeditions are: *Anthops or-*

*natus*, *Rhinonycteris aurantia* and *Macroderma gigas*.

