A NEW SPECIES AND SUBSPECIES OF BAT OF THE
HIPPOSIDEROS BICOLOR-GROUP FROM PAPUA NEW GUINEA,
AND THE SYSTEMATIC STATUS OF HIPPOSIDEROS
CALCARATUS AND HIPPOSIDEROS CUPIDUS (MAMMALIA:
CHIROPTERA: HIPPOSIDERIDAE)¹

James Dale Smith²
and J. Edwards Hill³
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A NEW SPECIES AND SUBSPECIES OF BAT OF THE HIPPOSIDEROS BICOLOR-GROUP FROM PAPUA NEW GUINEA, AND THE SYSTEMATIC STATUS OF HIPPOSIDEROS CALCARATUS AND HIPPOSIDEROS CUPIDUS (MAMMALIA: CHIROPTERA: HIPPOSIDERIDAE)

James Dale Smith and J. Edwards Hill

ABSTRACT. A new species of bat of the Hipposideros bicolor-group is described from New Guinea and the Bismarck Archipelago. The description of this new taxon was prompted by the study of recently acquired specimens from the Bismarck Islands of New Britain and New Ireland. In addition, this new material has allowed for the clarification of a long-standing problem concerning Hipposideros calcaratus Dobson 1877 and Hipposideros cupidus Andersen 1918. We find these latter two species to be conspecific and referable to Hipposideros calcaratus (by priority) and distinguishable from the new taxon on the basis of numerous qualitative and quantitative features.

The geographic variation of the new taxon and Hipposideros calcaratus was assessed by computing principal component and discrimination analyses for 11 cranial and 10 wing variables. Sufficient geographic variation was found to merit recognition of geographic races in both H. calcaratus and the new species. In the former, populations from the Bismarck and Solomon Islands, as well as the island groups off the southeastern coast of New Guinea, are assigned to Hipposideros calcaratus calcaratus and populations of this species from New Guinea are assigned to Hipposideros calcaratus cupidus (new combination). The nominate race of the new species is restricted to the Bismarck Islands, and a new subspecies is described to accommodate populations of the new species from New Guinea.

INTRODUCTION

For many years, two medium-sized species of the Hipposideros bicolor-group have been thought to coexist in New Guinea, the Bismarck Archipelago, and the Solomon Islands. One of these, Hipposideros calcaratus, was described from Duke of York Island in the Bismarcks by G.E. Dobson in 1877; the other, Hipposideros cupidus, was described by Knud Andersen in 1918 from Papua (New Guinea). Andersen’s description of H. cupidus (issued on his behalf by Oldfield Thomas) was brief and basically defined it as being smaller than H. calcaratus.

In his comprehensive review of the Indo-Australian species of Hipposideros, Tate (1941) introduced the notion of apparent sympatry of these two species in New Guinea and provided diagnoses with additional characteristics to distinguish them. Tate’s assessment and conclusions regarding these two species were based primarily on collections in the American Museum of Natural History.

Sanborn and Beecher (1947:390) first reported H. cupidus from the Solomon Islands; identification of this material was credited to Tate. In first recording the occurrence of H. calcaratus in the Solomons (Rennell Island), Hill (1956) noted that, in this region, Tate’s criteria of size and height of the posterior canine cusp apparently were not reliable diagnostic features. Nevertheless, in his monographic treatment of the genus Hipposideros, Hill (1963) adopted most of Tate’s other diagnostic characteristics to distinguish between these two species. At the time, Hill’s assessment was limited to specimens in the collections of the British Museum (Natural History), which included the type material of H. cupidus and H. calcaratus and some specimens from the Solomons. Since then, additional material has been obtained from the Solomons (Hill 1971, and BMNH) and Papua New Guinea (McKean 1972). This material was reported and identified primarily on the basis of Tate’s diagnostic features.

In the summer of 1979, the Taylor South Seas Expedition from the Natural History Museum of Los Angeles County, led by one of us (Smith), conducted extensive field investigations on the bat fauna of New Ireland and New Britain Islands (Bismarck Archipelago). In the process of identifying the species of Hipposideros in this collection, it became apparent that there were two similar taxa that differed mainly in size; one small, presumed to be H. cupidus, and the other large, presumed to be H. calcaratus. Subsequent examination and comparisons with other material, including the holotypes of both species, clearly demonstrated that Tate (1941) wrongly assigned specimens of his larger species from New Guinea and the Bismarcks to H. calcaratus, which does not possess the sphenoidal characteristics he ascribed to it. Furthermore, it is even more apparent that Tate incorrectly identified specimens of H. calcaratus from the Solomons as H. cupidus.

After considerable study, we have found that Tate’s sphenoidal character and other features that he employed to distinguish H. calcaratus from H. cupidus do not, in fact, differentiate between these two species. His diagnostic features do, however, distinguish a generally larger species from a generally smaller one. The holotypes of calcaratus and cupidus both correspond with the smaller of these two species. We propose that

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in the absence of compelling, qualitative characteristics to the contrary, there are no bases for maintaining *Hipposideros calcaratus* and *H. cupidus* as separate and distinct species. The larger species, referred by Tate (1941) and others to *Hipposideros calcaratus*, represents an undescribed species. The geographic variation and nomenclature of these taxa are considered below.

**METHODS**

Five hundred and fifty-six specimens of *Hipposideros calcaratus* (including *cupidus*) and the new species were examined in the preparation of this study. Lists of referred specimens are given under each subspecific account. Institutional abbreviations are as follows: American Museum of Natural History, New York (AMNH); Bernice P. Bishop Museum, Honolulu (BBM); British Museum (Natural History), London (BMNH); Universitets Zoologiske Museum, Copenhagen (CN); Field Museum of Natural History, Chicago (FMNH); Natural History Museum of Los Angeles County, Los Angeles (LACM); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Natur-Museum Senckenberg, Frankfurt (SMF); United States National Museum, Washington (USNM); Museum Für Naturkunde der Humboldt-Universität zu Berlin, Berlin (ZMB). In these lists of referred specimens, localities are reported within provincial boundaries or islands (arranged alphabetically) and within these, localities are listed from north to south, the westernmost listed first in cases where two localities lie at or near the same latitude. As indicated in the lists, some localities were not plotted on the distribution maps because undue crowding of symbols would have resulted. Also, localities where sympatry was noted between *H. calcaratus* and the new species described in this paper are noted.

Specific and subspecific variation were assessed on the basis of qualitative features and quantitative measurements taken from the skull and wing. Eleven cranial measurements included: zygomatic breadth; breadth of the braincase; mastoid breadth; breadth of the interorbital constriction; condylocanine length; breadth across the canines; length of the maxillary toothrow; breadth across the last upper molars (M3/); length of the palatal bridge; length of the mandibular toothrow; and length of the mandible. Ten alar measurements included: length of the forearm; length of the third, fourth, and fifth metacarpals; length of the proximal phalanx of the third, fourth, and fifth digits; and length of the distal phalanx of the third, fourth, and fifth digits (see Smith and Starrett 1979). These measurements were taken with dial calipers and were recorded to the nearest tenth of a millimeter. All measurements given in the text are in millimeters, and dental notations follow Miller (1907).

Statistical analyses of the data were carried out at the computer center of the University of Southern California, Los Angeles, using an unpublished program of discriminant analysis (DISANAL) written by Richard A. Pimentel (Department of Biology, California Polytechnic University, San Luis Obispo). This multivariate program assesses the morphometric variation among variables by computing principal components (PCA) and discriminant analyses with classification and matrices of generalized distance. For a discussion of the program and analyses, see Pimentel (1979) and Smith and Starrett (1979).

**SYSTEMATICS**

**Order Chiroptera Blumenbach 1779**

**Suborder Microchiroptera Dobson 1875**

**Family Hipposideridae Miller 1907**

*Hipposideros calcaratus* (Dobson 1877)

Spurred leaf-nosed bat

Figures 1–4, 7–8 and Table 1
(Synonymy under subspecies)

**DISTRIBUTION.** Papua New Guinea (Bismarck Archipelago and mainland); West Irian; and Solomon Islands (Fig. 4).

**DIAGNOSIS.** Size moderate (mean length of forearm, 51.74, range 55.8–46.2; mean condylocanine length, 18.16, range 19.5–15.9). Calcar relatively short, approximately one-half length of tibia. Tail with five equal to subequal tail vertebrae; fifth tail vertebra not especially shortened. Soft palate with nine interdental ridges, area between ridges divided into numerous small cells giving palate a honeycombed appearance. Bony palate with shallow depression on each side adjacent to lingual corner of M2/ and M3/. Mastoid process moderately developed and flange-like. Upper canine moderately large, not bulbous at base; posterior supplementary cusp well developed, but small, extending from base one third or less along length of tooth. First upper premolar (P2/) small, not crowded out of toothrow; canine and second upper premolar (P4/) not in contact. Hypocone on M1/ and M2/ distinct. Lower incisors tridif, equal or subequal in size, not overly crowded between lingual cingula of lower canines. Mandibular symphysis moderately broad. Lower molars relatively broad; trigonid and talonid of M1 and M2 equal to subequal in size. Hypoconid, hypoconulid, and entoconid forming distinct cusps on M1–3. Coronoïd process moderately low; posterior margin markedly concave. Angular process long, slender, and deflected laterally. Sphenoid bridge relatively narrow and emarginated, not concealing large, round optic foramina. Basisphenoid depression shallow and troughlike.

**DESCRIPTION.** Face (Fig. 1) moderately long, narrow, and rising gently to low crown of head. Muzzle, lateral and anterior to noseleaf, with moderate number of vibrissae, which emerge from small, round, and purplish epidermal glands; vibrissae on lower lip less numerous. Noseleaf (Fig. 1B) simple, secondary leaflets absent. Lateral narial lappets not well developed, subtubular, and squared off above external nares. Intermediate noseleaf simple, medial ridge a large, prominent, conical bump, two lateral ridges smaller and less prominent. Each lateral ridge bears a long vibrissa seated in a purplish epidermal gland similar to those on muzzle and lower lip. Posterior noseleaf relatively long, with three strong vertical septa; middorsal portion of upper margin with a tiny, rounded bump. Small, wartlike
tubercle above each small eye and behind dorsolateral corner of posterior noseleaf; several long vibrissae with basal epidermal glands protrude from apex of each tubercle. Frontal sac of males relatively small, horizontal, and not much elevated above posterior noseleaf, which sometimes partially obscures it. Ears relatively long, broadly subtriangular, and funnel-shaped with rounded tips; 10 to 13 transverse ridges traversing inner surface of each pinna; short, round tragus concealed within ear conch. Antitragus relatively low, round, and moderately convex. Wing membrane attached to side of foot at level of proximal metatarsus. Calcarea short, approximately one-half length of tibia. Tail with five vertebrae, equal to subequal in length; fifth tail vertebra not noticeably short or absent.

**Pelage and coloration.** Dorsal surface (including crown and nape) with long, silky pelage; sides of muzzle sparsely haired; cheeks below eye more densely so, with relatively long hairs (Fig. 1). Ventral pelage long, dense, and woolly. Inner surface of ear moderately hairy, inner margin and antitragus more strongly so (Fig. 1). Dorsal pelage dark brown, hairs unicolored, a slight paler “V” over the shoulders; ventral pelage grayish white; wing membranes naked, blackish brown. The pelage is occasionally bleached with a reddish-orange tinge.

**Soft palate.** Nine interdental ridges traverse soft palate (Fig. 2). First ridge extends from posterior border of canine forward to a sharp point, then abruptly rearward to form a deep notch; it is fused on midline. Second ridge originates at anterior border of second premolar; middle portion of this ridge is rounded anteriorly. Third ridge extends from near protocone of second premolar and is gently bowed anteriorly. Fourth, fifth, sixth, and seventh ridges extend from sides of first molar; these are nearly straight with slight anterior bow near midline. Eighth ridge extends in a similar fashion from between first and second molars. Ninth ridge originates at anterior margin of second molar and bows gently rearward to fuse on midline. Numerous cells between palatal ridges give soft palate a distinct and characteristic honeycombed appearance (may be less pronounced or absent in young individuals). There are no interdental ridges behind level of second molar; this portion of palate is flat and granular.

**Cranium.** Skull (Fig. 7 C,D,G,H) teardrop-shaped (viewed dorsally), lightly built, and generally similar to those of other unspecialized members of the bicolor-group. Rostrum long, narrow, subtubular, only slightly broader than interorbital constriction. Anterior nasal tubercles slightly inflated, but not exaggerated above nasal profile (Fig. 8 C,D). Top of rostrum flat and lacking pits or depressions. Braincase slightly oblong (viewed dorsally), low and elongate in profile, not abruptly vaulted above facial plane. Some individuals with low sagittal crest on frontals; crest may be weak or absent on parietals; lambdoid crest weak. Infracorbital foramen relatively short and slitlike. Zygomatic arches moderately strong, not markedly arched dorsally; malar flange well developed. Mastoid process well developed and flangeliike. Premaxillaries long; anterior palatal emargination terminating posteriorly on or near line joining anterior margins of first molars. Palate moderate, its posterior emargination near a line joining rear faces of last molars, flat, with a shallow depression on each side adjacent to lingual corner of M2/ and M3/. Pterygoid wings relatively long and hooked rearward. Sphenoidal bridge narrow and noticeably emarginate (Fig. 7 G,H). Optic foramina large and rounded. When ventral aspect of skull is viewed, optic foramina extend laterally well beyond narrow sphenoidal bridge. [Tate (1941:362, 364) em-
Table 1. Means and ranges (in parentheses) of selected cranial and external measurements of *Hipposideros calcarius*. Letters in parentheses following locality names coincide with centroids plotted on the canonical graphs in Fig. 10. Superscript numbers indicate sample size different from those given in left-hand column.

<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>CONCANC</th>
<th>ZYGOMA</th>
<th>MASTOD</th>
<th>INTORB</th>
<th>CANINE</th>
<th>MAXTOH</th>
<th>PALWID</th>
<th>PALLEN</th>
<th>MANDIB</th>
<th>DENTAR</th>
<th>FORARM</th>
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<td>7.3</td>
<td>7.0</td>
<td>3.6</td>
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<td>14.1</td>
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<td>10.1</td>
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<td>6.6\textsuperscript{a}</td>
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**Hipposideros calcarius cupidus**

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<th>N</th>
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<th>MASTOD</th>
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<th>MANDIB</th>
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CONCANC, condylocanine length; ZYGOMA, zygomatic breadth; MASTOD, mastoid breadth; INTORB, breadth of the interorbital constriction; CANINE, breadth across the canines; MAXTOH, length of the maxillary tooththrow; PALWID, breadth across the last upper molars (M3/); PALLEN, length of the palatal bridge; MANDIB, length of the mandibular tooththrow; DENTAR, length of mandible; FORARM, length of the forearm.
ployed this character complex to distinguish “H. calcarius” from “H. cupidus.”] Basisphenoid constricted between cochleae (no broader than width of one cochlea). Basisphenoidal depression shallow and troughlike. Ectotympanic not especially broad; inner margin of auditory meatus without toothlike projection (Fig. 8 C.D). Mandibles lightly built, not particularly attenuated anteriorly. Chin abrupt, symphysis relatively deep. Anterior mental foramen opening anterodorsally, situated approximately halfway up on chin. Lateral mental foramen directed anterodorsally and situated below anterior margin of first premolar. Postdental portion of mandible rotated anterodorsally thus elevating articular facet above dental plane. Coronoid process moderately low, posterior margin markedly concave; masseteric fossa deep and well developed. Angular process long, slender, and deflected laterally; coronoid not so deflected.

**Dentition.** Dental formula: I 1/2; C 1/1; P 2/2; M 3/3 = 30 (Fig. 3). **Incisors.** Upper incisors slender, indistinctly bifid, curved toward midline. Lower incisors trifid, outer and inner pair equal to subequal in size, not overly crowded. **Canines.** Upper canines moderately large, with pronounced lingual shelf and faint labial cingulum. Posterior supplementary orbital well developed, but small, extending no more than one-third length of tooth from base; not forming a strong, longitudinal shear facet with main cusp of canine. Lower canines long and slender; strong cingulum circumscribes each tooth. **Premolars.** First upper premolar (P2/) single-rooted, small (nearly equal to a lower incisor in size), not excluded from toothrow, and having a low longitudinal ridge with an indistinct central cusp. Second upper premolar (P4/) triple-rooted, only slightly shorter than an upper first or second molar; central cusp moderately long, somewhat slender; posterior longitudinal blade low; labial cingulum distinct; lingual shelf well developed with pronounced protocone and hypaconic basin. First lower premolar (P/2) single-rooted, nearly equal to second lower premolar in length; longitudinal blade high, rising over well-developed central cusp, which is only slightly lower than that of second lower premolar. Second lower premolar (P/4) moderately large with strong, slender central cusp, its thin, lingually oblique blade connecting central cusp with lower, posterior lingual supplementary cusp; a strong cingulum circumscribes tooth. **Molars.** First and second upper molars (M1/ and M2/) nearly identical in size and coronal morphology; both with typical W-shaped ectoloph. On M1/, paracone and metacone nearly equal in height, metacone situated slightly more lingually than paracone. On M2/, metacone is noticeably higher than paracone. Protocone of both molars low and indistinct; pre- and postprotocrista well developed; hypoconal shelf descends abruptly to low, narrowly rounded hypaconal heel bearing a low but distinct hypocone. Last upper molar (M3/) markedly reduced in size and coronal morphology; pre- and postmetacrista of ectoloph absent, this tooth standing slightly in front of the anterior extent of postpalatal emargination. First and second lower molars (M1 and M2) nearly equal in size and coronal morphology; both moderately broad, with trigonid and talonid equal to subequal in size. Para-

**Figure 2.** Soft palate of *Hipposideros calcarius.*
signment of these bats to the smaller species (herein designated *calcarius*) was correct. However, his disregard for size in this instance led subsequent workers into confusion. Hill (1956;78 and 1963;38) commented that “criteria of size appear not to hold good in the Solomon Islands.” On the surface and in a restricted sense, as will be shown below, this statement also is true. However, these statements caused others (McKean 1972; Topal 1975; Vestjens and Hall 1977; and Koopman 1979) to adopt the erroneous notion that large individuals of the taxa under consideration here were *calcarius* and that smaller bats were *cupidus*. Actual sympathy, except in the Solomon Islands, among these taxa also has further confused the issue.

On the basis of many qualitative features, *Hipposideros calcarius* and *H. cupidus* are conspecific (herein assigned to *H. calcarius* by priority) and distinct from the new species diagnosed below. An extensive multivariate analysis of the quantitative, intraspecific variation of *H. calcarius* indicates that this species is divisible into two geographic races: *H. c. calcarius* (Bismarck Archipelago, Trobriand, and Louisiade Islands, and Solomon Islands) and *H. c. cupidus* (Japen Island and mainland of New Guinea). This distinction is based on overall size and allometric shape (shape) among the variables analyzed in this study. The results of the principal components (PCA) and discriminant function analyses of 10 wing and 11 cranial variables (analyzed separately) are shown in Figure 10 and Table 2; PCA canonical graph is not shown. Means and ranges (in parentheses) of 11 selected cranial and external variables of selected populations from throughout the geographic range of *Hipposideros calcarius* are shown in Table 1.

Cranial and wing variables exhibit separate, although similar, patterns of variation. Individuals of *calcarius* from the Bismarck and Solomon Islands are generally larger, in all respects, than those from the mainland of New Guinea (Table 1). Specimens from Kiriwina (Trobriand group) and Misima (Louisiade group) Islands agree in size with those from the Bismarcks and Solomons. This pattern may be seen in the ordination of group centroids (Fig. 10 A–H compared to I–L).

Cranial variables appear to be better discriminators of groups than are wing variables. This may be seen in the component scores shown in Table 2. The first component of the direction cosines (PCA) usually is a strong size component; that is, with coefficients having the same sign. It will be noted that the coefficients in this component vary in their sign, thus expressing their contribution to allometric shape. Only condylocanine length weighs heavily in this component axis. The second component of the PCA is more typically an overall size component with all coefficients negative in sign. In the discriminant analysis, the standardized canonical vectors (Z-scores) all express an allometric shape in the first three component axes. In the canonical graph for cranial variables (Fig. 10), Bismarck and Solomon centroids (A–H) ordinate together along the first component axis; centroids for samples from the mainland of New Guinea (I–L) ordinate farther to the left (small-size quadrant) along this axis. Solomon Island centroids (F–H) disassociate, somewhat, from Bismarck centroids (A–D) along the second component axis; the centroid for Kiriwina Island (E) ordinates with Bismarck centroids. There is little discrimination in the third canonical axis. Zygomatic breadth, breadth of the interorbital constriction, length of the mandibular toothrow, length of the dentary, and condylocanine length are the strongest discriminators among the cranial variables examined.

Although the two geographic races of *calcarius* may be identified readily on the basis of the length of the forearm (Table 1), wing variables generally exhibit a greater degree of variation. Again, the Bismarck and Solomon Island populations are generally large in overall size compared to those from the mainland of New Guinea, and their respective centroids tend to ordinate together (Fig. 10). The centroids for mainland samples are less strongly ordinated from the island samples of *calcarius*, although these (I–L) are ordinated into the small-sized quadrant of the canonical graph. The first component of the PCA (Table 2) expresses a strong overall size influence (all signs negative); the second component likewise expresses a considerable amount of overall size. Although the coefficients in the discriminant analysis exhibit allometric shape in the first three component axes, most of the ordination of centroids shown in the canonical graph (Fig. 10) appears to be related to interspecific variation.

Perhaps the most interesting aspect of the variation of wing variables is the pattern of interspecific variation. We have already commented on the apparent past confusion associated with overall size of “*calcarius*” and “*cupidus*." Until now,
large-sized individuals from the mainland of New Guinea were thought to be “calcaratus” and small-sized individuals were thought to represent “cupidus.” The former are, in fact, the new species described below. The confusion rests in the general similarity in wing size between Solomon Island samples and the large taxon (thought to be calcaratus) from the mainland of New Guinea. This interspecific variation is illustrated in the canonical graph for wing variables (Fig. 10) in which Solomon and Bismarck centroids, to a certain extent (F–H and A–E, respectively), show only a small amount of ordination from mainland centroids of the new species (P–W) along the first component axis. The generalized distance (based on wing variables) between Malaita and San Jorge (Solomons) samples of calcaratus and mainland samples of the new species average 4.28 (5.22–3.36) compared to an average distance of 3.95 (5.23–2.04) between the Solomon samples and mainland samples of calcaratus. The generalized distance between these samples, based on craniol variables, is 10.98 (14.65–7.66) and 7.45 (9.57–5.66), respectively.

**Hipposideros calcaratus calcaratus** (Dobson 1877)

**Phyllorhina calcarata** Dobson 1877:122 (Duke of York Island); Jentink 1888:168 (Duke of York Island).


**Hipposideros calcaratus** Sanborn 1931:24 (Papua New Guinea, Nissan Island); Tate 1941:362, 392 (in part: Duke of York Island); Laurie and Hill 1954:55 (in part: Duke of York Island; Russell Island; New Georgia Island; Nissan Island); Hill 1956:76 (Rennell Island); Hill 1963:37 (in part: Duke of York Island; Russell Island; New Georgia Island; Nissan Island; Rennell Island); Hill 1968:55 (Rennell Island); Hill 1971:574 (San Cristobal Island; San Jorge Island; Malaita Island).

**Hipposideros cupidus**, Tate 1941:392 (in part: Duke of York Island [no specimen cited]; Tabar Island); Sanborn and Beecher 1947:390 (New Georgia Island; Banika Island—identification of these specimens credited to Tate); Koopman 1979:9 (New Britain Island; Duke of York Island; Tabar Island).

**HOLOTYPE.** BMNH 77.7.18.13, an adult female (preserved in alcohol, skull removed) from Duke of York Island, East New Britain Prov., Papua New Guinea (lat. 4°10'S long. 152°28'E).

**DISTRIBUTION.** Papua New Guinea: Bismarck Archipelago, Trobriand Islands, Louisiade Islands, and possibly some others of the inshore islands of New Guinea; Solomon Islands (Fig. 4).

**DIAGNOSIS.** Qualitative features same as for species. Overall size large: length of forearm, 52.33 (55.8–49.0); condylocanine length, 18.50 (19.5–17.4); length of maxillary toothrow, 7.43 (8.1–6.5). See Table 1 for the mean (range) of selected cranial and external measurements.

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**Figure 4.** Geographic distribution of **Hipposideros calcaratus.** See lists of referred material for key to plotted localities.
REPEARED MATERIAL (307 specimens examined). PAPUA NEW GUINEA. BOUGAINVILLE PROV.: Nissan Island, (4°30'S 154°10'E), 1 (AMNH 99904), Bougainville Island, Toqarau, base Mt. Balbi, ca. 600 m, (5°58'S 155°4'E), 1 (BBM-NG 61370). EAST NEW BRITAIN PROV.: Duke of York Island, (4°10'S 152°28'E), 1 (BMNH 77.18.13, Holotype); Ulu Island, (4°15'S 152°25'E), 1 (AMNH 99844); New Britain Island, 1 km E Kurakakaul DPI Station, 40 m, (4°13'S 152°8'E), 21 (LACM 66348-68); Taliligap, 1000 ft, (4°19'S 152°9'E), 2 (BBM-NG 20987, 20994); Keravat, 500 ft, (4°21'S 152°2'E), 3 (BBM-NG 20879, 20881, 20884); 3 km SW Gunanur Plantation, 60 m, (4°24'S 152°15'E), 12 (LACM 66369-80); 2 km S Gunanur Plantation, 80 m, (4°24'S 152°16'E), 47 (LACM 66381-427); 5 (BBM-NG 20813, 20817, 20827, 20840, 20854); Wide Bay, Bayalong, 2500 ft, (5°15'S 152°5'E), 1 (AMNH 99823). MILNE BAY PROV.: Kiriwina Island (Trobriand Group)., 1 (MVZ 109754); New Ireland Island, Laburua Cave, 1 km S, 2 km W Laburua, 80 m, (2°53'S 151°2'E), 11 (LACM 66276-86); Lengemebung Cave, 1.3 km S, 3 km E Lakaramau Plantation, 80 m, (2°54'S 151°16'E), 5 (LACM 66287-91); Panapak Cave, 2.5 km S, 1 km E Madina High School, 80 m, (2°56'S 151°23'E), 4 (LACM 66292-95); Madina Cave, 3 km S Madina High School, 200 m, (2°56'S 151°22'E), 4 (LACM 66296-99); Riri Cave, 1 km SW Kalom, 80 m, (3°29'S 152°13'E), 20 (LACM 66300-19); Maraboke Cave, Baken Village, 40 m (3°33'S 152°21'E), 11 (LACM 66320-30); Kabis Cave, 3 km SW Suhon 2, 220 m, (3°43'S 152°30'E), 11 (LACM 66331-41); Loula Cave, 3 km S, Balai, 100 m, (3°51'S 152°38'E), 6 (LACM 66342-47); Tabar Island, (3°0'S 152°0'E), 5 (AMNH 99488-90, 99847-48).

SOLOMON ISLANDS. CENTRAL DIST.: Russell Island (Russell Group), Talaena, (9°4'S 159°12'E), 1 (BMNH 33.11.11.2); Rennell Island, (11°38'S 160°14'E), 5 (BMNH 54.878-882); Kondara Cave in Tinggoa, (11°51'S 160°38'E), 10 (CN 2863-72); San Jorge Island (Santa Ysabel Group), Talise, (8°25'S 159°35'E), 78 (BMNH 67.1957-2034). EASTERN DIST.: San Cristobal Island, confuence Warihito and Goge Rivers, ca. 6 mi inland from Wainoni Bay, (10°33'S 162°2'E), 1 (BMNH 67.1761). MALAITA DIST.: Malaita Island, Dala, ca. 20 m, (8°35'S 160°40'E), 1 (BBM-BSIP 24135); Riba Cave, near King George VI School, Auki, (8°48'S 160°44'E), 28 (BMNH 67.2035-2062). WESTERN DIST.: New Georgia Island, (8°20'S 157°30'E), 1 (BMNH 94.10.8.2); Munda Point, (8°23'S 157°15'E), 1 (FMNH 54764).

COMPARISONS. As noted above, the nominate race of H. calcaratus may be distinguished readily from H. c. cupidus solely on the basis of its larger overall size (Table 1). In a general sense, H. c. calcaratus from the Bismarckts, especially New Britain Island, is intermediate in size. Individuals of this subspecies, especially those from the Solomon Islands, approach mainland representatives of the new species in external size; cranially, this similarity in size is less pronounced (Tables 1 and 3), and the two are easily distinguished by various qualitative features outlined herein. It is worth noting here that the narrowness of the sphenoidal bridge and the greatest breadth across the optic foramina appears to be slightly more pronounced among specimens from the Solomon Islands than among other populations of either H. c. calcaratus or H. c. cupidus.

Hipposideros calcaratus cupidus Andersen 1918 new combination

(?) Phyllorhina calcarata, Peters and Doria 1880:693 (West Irian: Andai; Dorei).

(?) Hipposideros calcaratus, Jentink 1906:174 (West Irian: Andai; Doreh [ = Dorei]); Jentink 1908: 363 (West Irian: Lake Sentani).


HOLOTYPE. BMNH 97.12.6.4, a subadult male (preserved in alcohol, skull removed) collected by A.S. Anthony (presented by Lord Rothschild) from Ega, British New Guinea. Ega is apparently one of two villages now called Ega, one at lat. 7°21'S long. 148°18'E, the other at lat. 6°1'S long. 144°56'E. The first of these localities is just in West Irian, in the lowlands, the second is a little over the northern border of the former territory of Papua (now Chimbu Prov.) and seems to be the more likely as the type locality.

DISTRIBUTION. Japen Island and mainland of New Guinea (Fig. 4).

DIAGNOSIS. Qualitative features same as for species. Overall size small: length of forearm, 48.75 (51.3-46.2); condylocanine length, 16.72 (15.3-15.9); length of maxillary toothrow, 6.67 (7.4-6.3). See Table 1 for the mean (range) of selected cranial and external measurements.

REFERRED MATERIAL (52 specimens examined). WEST IRIAN. GEELINKY BAY DIST.: Japen Island, Jobi, (1°42'S 136°27'E), 3 (BMNH 86.11.3.11; USNM 18480-81); 1 mi NW Sumbaraba, 1000 ft, (1°47'S 136°39'E), 1 (BMNH-NG 22079); Dawai River Cave, Kanyon Batu, 10 mi E Sumbaraba, (1°48'S 136°45'E), 3 (BMNH-NG 22121, 22140-41); no specific locality, 9 (ZMB 54620-27, 91837). DJAYAPURA
Hippidosideros maggietaylorae new species
Maggie’s leaf-nosed bat

Figures 5–9, 11 and Table 3
(Synonym under subspecies)

**DISTRIBUTION.** Papua New Guinea (Bismarck Archipelago and mainland) and West Irian (Fig. 11).

**DIAGNOSIS.** Largest member of *Hippidosideros bicolor-group* (Hill 1963) in the Indo-Australian region (mean length of forearm, 58.41, range 67.2–50.4; mean condylocone length, 20.38, range 23.5–17.3). Resembles *H. calcaratus* in general appearance. Calcar long, more than half length of tibia. Tail with four conspicuous vertebrae; fifth tail vertebra extremely short or absent. Soft palate with 10 simple ridges. Rostrum moderately long and narrow. Bony palate lacking any noticeable depressions. Mastoid processes not well developed or flangelike. Upper canines large and bulbous at base; posterior supplementary cusp strong and well developed extending from base at least one third (usually more) along length of tooth. First upper premolar (P2/) small and crowded out of toothrow (labially) so that cingula of second upper premolar (P4/) and canine are in contact, or nearly so. Hypocone on M1/ and M2/ indistinct. Lower incisors trifid; inner pair (1/1) smaller than outer pair (1/2). Mandibular symphysis acutely narrow so that outer incisors are crowded up and behind inner pair, lingual cingula of lower canines are nearly in contact. Lower molars relatively narrow; paraconid merged anterolabially and nearly aligned with protoconid. Lower molars (M1–3) with reduced hypoconids and entoconids, hypoconids low; entoconids on M1–2 indistinct, obsolete on M3. Coronoid process well developed, subtriangular, not deflected laterally, its posterior margin only slightly concave. Angular process strong, knoblike and deflected laterally. Sphenoidal bridge relatively wide, partially or totally concealing elongate optic foramina. Basisphenoidal depression prominent and nearly as wide as long.

**DESCRIPTION.** Face (Fig. 5) short, relatively broad, and rising to high domed crown. Muzzle, lateral and anterior to noseleaf, and lower lip with numerous vibrissae, which emerge from small, round, and purplish epidermal glands. Noseleaf (Fig. 5B) simple, secondary supplementary leaflets absent. Lateral narial lappets long and slender, not ornamented. Intermediate noseleaf simple, with two ridges lateral to medial ridge; each lateral ridge bears a vibrissa seated in a purplish epidermal gland similar to those on muzzle and lower lip. Posterior noseleaf relatively short with three vertical sepa. Large wartlike tubercle above each small eye and behind dorsolateral corner of posterior noseleaf; several long vibrissae with basal epidermal glands protrude from apex of each tubercle. Frontal sac horizontal, large in males, which accentuates shortness of the face and abruptness of the forehead (Fig. 5B). Ears moderately short, subtriangular, and funnel-shaped with rounded tips; nine or 10 transverse ridges traversing inner surface of each pinna; short, knoblike tragus concealed within ear conch. Antitragus short and slightly convex. Wing membrane attached to side of foot at level of proximal metatarsus. Calcar long, more than half length of tibia. Tail with four vertebrae, equal in length; fifth tail vertebra absent or short.

**Pelage and coloration.** Dorsal surface densely furred with short (6–8 mm), woolly hairs, somewhat shorter (4–6 mm) and denser on head and upper neck than on back; ventral surface covered with thick woolly fur (6–7 mm), chin and throat less densely haired; inner surface of ear sparsely haired. Dorsal pelage grayish-brown, forming a pale diffuse "V" over shoulders; ventral pelage grayish-white, paler posteriorly; wing membranes naked, brownish-gray. Some individuals with reddish-orange tinge as the result of bleaching. Pelage of juveniles and subadults less dense than that of adults and uniformly gray in color.

**Soft palate.** Ten interdental ridges traverse soft palate (Fig. 6). First ridge extends between posterior portions of canines and is deeply notched at midline; short, pointed tubercle is situated in front of this ridge and at base of canine. Second ridge bows posteriorly, then anteriorly to midline, originating from in front of second premolar (P4/). Third ridge extends from posterior portions of P4/. Anterior three ridges are more widely spaced than are seven posterior ridges, which are tightly packed and extend between first and second molars. Fourth palatal ridge extends between first molars approximately from level of protocone. Fifth, sixth, and seventh ridges do not join on midline.

6. Locality of sympatry between *H. calcaratus* and new species (Fig. 4).
7. Locality not plotted to avoid overcrowding of symbols (Fig. 4).
and extend from hypoplastic heel of first molars. Eighth ridge does not reach midline and originates approximately from level of protocone of second molars. Ninth ridge (shortest of palatal rugae) extends from just posterior to protocone of second molars to just short of midline. Last palatal ridge is fused on midline where it is curved slightly anterior; it originates from hypoplastic heel of second molars. Eighth and tenth ridges appear to encase shorter, ninth ridge. Soft palate behind interdental ridges flat and granular.

Cranium. Skull (Fig. 7 A,B,E,F) teardrop-shaped (viewed dorsally), lightly built, and generally similar to those of unspecialized members of *bicolor*-group. Rostrum relatively long, narrow, subtubular, and not appreciably broader than interorbital portion of skull. Anterior nasal turbercles not inflated or otherwise exaggerated above nasal profile (Fig. 8 A,B); small pit on midline between turbercles. Braincase slightly elongated and roundish (viewed dorsally), low and slightly oblong in profile, not abruptly vaulted above facial plane. Some individuals with low sagittal crest; lambdoidal crest distinct. Infracristal foramen long and slitlike. Zygomatic arches strong, not markedly arched dorsally; malar flange distinct. Mastoid processes not well developed. Premaxillaries long, anterior palatal emargination terminating posteriorly on or near line joining anterior margins of first molars. Palate moderately flat and lacking any noticeable depressions or pits; its posterior emargination near a line joining rear faces of last molars. Pterygoid wings relatively long and hooked rearward. Sphenoidal bridge not emarginate (Fig. 7 E,F). Optic foramina elongate and not especially rounded. When ventral aspect of skull is viewed, broad sphenoidal bridge tends to obscure underlying optic foramina. [Tate (1941:362, 364) employed this character complex to distinguish "H. calcaratus" from "H. cupidanus."] Basiphoid broad; more than breadth of one coelum. Basiphoidal depression moderately deep, not elongated and troughlike. Ectotympanic not especially broad; tiny toothlike projection from ventral lip of auditory meatus (Fig. 8 A,B). Mandibles strongly built, sharply attenuated anteriorly. Chin abrupt, symphysis deep. Anterior mental foramen opening anteriorly and situated low on chin. Lateral mental foramen directed anterodorsally and situated directly below canine. Postdental portion of mandible rotated anterodorsally, thus elevating articular facet well above dental plane. Coronoid process high and triangular in shape; masseteric fossa deep and well developed. Angular process long, terminating with a rounded knob, moderately deflected laterally from a perpendicular through the articular process; coronoid not so deflected.

Dentition. Dental formula: I 1/2; C 1/1; P 2/2; M 3/3 = 30 (Fig. 9). Incisors. Upper incisors slender, bifid, and curved toward the midline; tips nearly in contact. Lower incisors trifid, outer pair slightly larger than inner pair. As the result of the marked attenuation of the anterior lower dental arcade, lower incisors are extremely crowded between anterior cingula of lower canines; outer pair of incisors pushed up and nearly behind inner pair. Canines. Upper canines robust and bulbous at base, with pronounced lingual shelf, and lacking labial cingulum. Posterior supplementary cusp strong, well developed, situated one third or usually more along length of tooth. A well-developed shear facet connects supplementary cusp with main cusp of canine and this engages during occlusion with longitudinal blade of lower first premolar (P/2); these shearing surfaces are moderately to heavily worn in most individuals. Lower canines not so large or robust as upper pair, main cusp long and slender; pronounced cingulum circumscribes each tooth. Bases of lower canines in close proximity as a result of acute attenuation of anterior dental arcade. Premolars. First upper premolars (P2/) small (only slightly larger than a lower outer incisor), ex-
cluded labially from toothrow. This single-rooted tooth situated in a small notch in the posterior labial portion of upper canine and has a long longitudinal ridge with an indistinct central cusp. Second upper premolar (P4/) triple-rooted, about as long as an upper first or second molar, with strong central cusp and high posterior, longitudinal blade; labial cingulum absent and posterolinguinal shelf well developed, protocone absent. Anterior cingulum of this tooth in contact with posterior portion of upper canine. First lower premolar (P2/) single-rooted, about two-thirds length of second lower premolar. Longitudinal blade of this tooth is low, yet strongly developed, and rises over a slightly developed central cusp. Second lower premolar (P4/) large with strong central cusp; short, linguolabial blade connects central cusp with lower, posterolinguinal cusp. This blade, although moderately to heavily worn in most individuals, does not exclude directly with any shearing surfaces of the upper dentition; weak cingulum circumscibes each tooth. Molars. First and second upper molars (M1/ and M2/) nearly identical in size and coronal morphology; both with typical W-shaped ectoloph. Paracone and metacone situated near the longitudinal midline of tooth; metacone slightly higher and lingual to paracone. Protoconal shelf markedly lower than either paracone or metacone, cusp not distinct, but appears as a short longitudinal ridge. Hypoconal shelf descends from protoconal shelf posteriorly as a low, broadly rounded lingual heel; hypocone absent. Last upper molar (M3/) markedly reduced in size and coronal morphology; pre- and postmetacrista of ectoloph absent; protoconal shelf low and rounded. This tooth situated behind the anterior extent of postpalatal emargination. First and second lower molars (M1/ and M2/) nearly equal in size and shape; both relatively narrow (M1/ narrowest of lower molar arcade); trigonid generally larger than talonid. Paracristid on M1/ shifted anterolabially and nearly in line with paracone; on M2/ and M3/ paracone is not so positioned. On all three lower molars, the paracristid is intricately blended with trigonid rather than being distinctly separated from the paracone and metaconid. Talonid lower than trigonid on all lower molars. Talonid cusps (hypoconid, hypoconulid, and entoconid) indistinct and absorbed into connecting commissure that encompasses talonid. Talonid of M3/ markedly reduced and laterally compressed, reflecting reduction of M3/.

ETYMOLOGY. This new species is named after Mrs. Reese (Maggie) Taylor in recognition of her interest in, and most generous sponsorship of, field research of one of us (Smith) in the Bismarck Islands in the summer of 1979.

INTRASPECIFIC VARIATION. The analysis of intraspecific variation of Hipposideros maggietaurora indicates that the species is divisible into two geographic races: the nominate subspecies H. m. maggietaurora (Bismarck Archipelago) and a second subspecies, described below, from the mainland of New Guinea. This geographic distinction, like that in Hipposideros calcaratus, is marked by a rather pronounced differential in overall size, the Bismarck populations being larger in all respects than those from the mainland (Figs. 7 and 8, Table 3).

Cranial variables, especially zygomatic breadth, length of the mandibular toothrow, and length of the dentary, are strong discriminators along the first component axis (Table 2 and Fig. 10). The crania of individuals from the Bismarck Islands are massive and more heavily built than are those of individuals from the mainland of New Guinea (Fig. 7 and 8). In profile, the forehead of Bismarck specimens appears to rise somewhat less abruptly than do those of mainland specimens. The posterior margin of the coronoid tends to be slightly more concave in mainland individuals than in those from the Bismarck.

Again, the wing variables are not as strong as cranial variables in the ordination of group centroids. However, these do separate Bismarck and mainland centroids of H. maggietaurora to a greater extent than they do those of H. calcaratus (Fig. 10). Finally, New Britain samples, while clearly assignable to H. m. maggietaurora, are somewhat intermediate in size between New Ireland populations and those from the mainland.

REMARKS. Specimens of the mainland representative (described below) of this species were identified by the late G.H.H. Tate (1941:392) as H. calcaratus, thus leading him to ascribe characters to calcaratus that it does not, in fact, possess. This misidentification resulted in further confusion in the literature, having misled authors such as Hill (1956, 1963, 1968, and 1971), McKeen (1972) and Koopman (1979). With

Figure 6. Soft palate of Hipposideros maggietaurora.
the advent of extensive additional material from New Guinea and adjacent islands, it has been possible to fully clarify this situation.

**Hipposideros maggiaylorae maggiaylorae**

*Hipposideros calcaratus*, Tate 1941:392 (Duke of York Island).

**HOLOTYPE.** LACM 66433, an adult male (preserved in alcohol, skull removed) collected 19 June 1979 by Craig S. Hood (original number 275) in Lengmebug Cave, 1.3 km south and 3 km east Lakuramau Plantation, 80 m, New Ireland Island, New Ireland Prov., Papua New Guinea (lat. 2°54′S long. 151°16′E).

**PARATYPES.** Thirty-five individuals (19 males and 16 females; LACM 66428–32, 66434–35, 66437–48, 66450–63, BMNH 80.391–92) from the type locality captured on 19 June 1979. All are preserved in alcohol; skulls removed from six males and seven females.

**DISTRIBUTION.** Papua New Guinea: Bismarck Archipelago (Fig. 11).

**DIAGNOSIS.** Qualitative features same as for species. Overall size large: length of forearm, 63.14 (67.2–69.9); condylocanine length, 21.93 (23.5–20.8); length of maxillary toothrow, 8.40 (8.8–7.8). See Table 2 for the mean (range) of selected cranial and external measurements.

**REFERRED MATERIAL.** (88 specimens examined). PAPUA NEW GUINEA. EAST NEW BRITAIN PROV.: New Britain Island, Keravat, 500 ft, (4°21′S 152°2′E), 4 (AMNH 193718, 193720, 193724–25); Toburtue Village, 40 m, (4°21′S 152°2′E), 5 (LACM 66494–98); Mt. Raiven, 1 km E Toburtue Village, 100 m, (4°21′S 152°2′E), 6 (LACM 66499–504); 2 km S Gunanur Plantation, 80 m, (4°24′S 152°16′E), 7 (LACM 66505–11). NEW IRELAND PROV.: New Ireland Island, Lengmebug Cave, 1.3 km S, 3 km E Lakuramau Plantation, 80 m, (2°54′S 151°16′E), 36 (LACM 66428–35, 66437–48, 66450–63; BMNH 80.391–92; Type series); Madina Cave, 3 km S Madina High School, 200 m, (2°56′S 151°22′E), 3 (LACM 66464–66); Lower Bunbun Cave, 3 km S Lambuso, 220 m, (3°13′S 151°49′E), 27 (LACM 66467–93).

8. Locality of sympatry between *H. calcaratus* and *H. maggiaylorae*.

9. Locality not plotted to avoid overcrowding of symbols (Fig. 11).

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**Figure 8.** Lateral view of cranium and lower jaw of: A, *Hipposideros maggiaylorae maggiaylorae*; B, *Hipposideros maggiaylorae* new subspecies (see p. 12); C, *Hipposideros calcaratus calcaratus*; and D, *Hipposideros calcaratus cupidus*. 

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Smith and Hill: New *Hipposideros* from New Guinea 13
**Hippodromas maggietailorae erroris**

**new subspecies**


**HOLOTYPE.** MVZ 138582, an adult male (skin and skull) collected 23 July 1969 by William Z. Lidicker, Jr. (original number 3045) in Yagoua Sulfur Cave, 5 mi south and 3 mi west Madang, Madang Prov., Papua New Guinea (lat. 5°17'S long. 145°45'E).

**DISTRIBUTION.** Mainland of Papua New Guinea and West Irian (Fig. 11).

**DIAGNOSIS.** Qualitative features same as for species. Overall size small: length of forearm, 54.32 (57.6~50.4); condylodecanine length, 19.59 (21.3~18.6); length of maxillary toothrow, 7.74 (8.8~7.0). See Table 3 for the mean (range) of selected cranial and external measurements.

**REFERRED MATERIAL** (109 specimens examined). WEST IRIAN. DJAYAPURA DIST.: Djayapura (= Hollandia and Sukarnapura), (2°32'S 140°42'E), 3 (AMNH 109949, USNM 295059~60).

PAPUA NEW GUINEA. CENTRAL PROV.: Javereri, Musgrave River, 220 m, (9°24'S 147°26'E), 7 (AMNH 108491~97); Mt. Diamond Mine, ca. 12 mi E Port Moresby, (9°27'S 147°28'E), 11 (BMNH 69.319~324, FMNH 110939~40, MVZ 140374~75, 140379).10 EAST SEPIK PROV.: Ambu. (4°13'S 142°50'E), 2 (McKeon 1972:24); Wag, (4°20'S 142°45'E), 15 (McKeon 1972:24);10 Kairiru Island, Kairiru Cave, near St. Xaviers Mission, (3°21'S 143°36'E), 8 (BMNH 73.2038~2045); St. Xaviers Mission, (3°21'S 143°36'E), 3 (BMNH 75.1863~865). GULF PROV.: Bulldog, Lakekama River, (7°47'S 146°25'E), 10 (SMF 24621~29, 24446); Putei, (7°48'S 146°8'E), 27 (McKeon 1972:24).

MADANG PROV.: Kaimbugu (12 mi SSW Josephstal), 460 ft, (4°55'S 144°57'E), 5 (AMNH 198773~77); near Madang, (5°12'S 145°47'E), 1 (MVZ 138589); ca. 10 km S Madang, (5°15'S 145°45'E), 2 (BMNH 78.875~876).11 Yagoua Sulfur Cave, 5 mi S, 3 mi W Madang, (5°17'S 145°45'E), 12 (MVZ 138646, 138576~84, 140384~85; type series);11 Tunnel Cave, 7 mi S, 3 mi W Madang, (5°18'S 145°45'E), 2 (MVZ 138585~86). MILNE BAY PROV.: Opaigwari, (approx. 9°37'S 149°23'E), 7 (AMNH 157420~26); Gwebmanto Cave, 1 mi N Maneau Village, 300 m, (9°41'S 149°21'E), 3 (AMNH 157415~17).11 MOROBE PROV.: Ninea (Ninea, (5°54'S 146°54'E), 1 (McKeon 1972:24);10 Wasu, 40 m, (5°57'S 147°11'E), 13 (BBMN 53062~66, 53068, 53070~73, 53075~77);10 Seborgisung Cave, near Finschhafen, 500 ft, (6°35'S 147°50'E), 4 (AMNH 194863~66); Oomsis Creek, 10 m, (6°40'S 146°48'E), 1 (AMNH 191320); Salamana, (7°3'S 147°3'E), 6 (BMNH 80.516~522). NORTHERN PROV.: Budumaga, 125 m, (9°39'S 149°18'E), 2 (AMNH 157418~19). WESTERN PROV.: Fly River, 5 mi below Palmer Junction, 80 m, (5°54'S 141°32'E), 4 (AMNH 105052~55); Fly River, north bank opposite Sturt Island, (8°10'S 142°15'E), 5 (AMNH 105536, 105539, 105540~56).

**REMARKS.** Individuals of *H. m. erroris* from the western portions of the mainland of Papua New Guinea tend to be slightly smaller, on the average, than those from the eastern parts of the island (Table 3).

**ETYMOLOGY.** The name chosen for this subspecies reflects the fact that its members have for many years been referred

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10. Locality of sympathy between *H. calcaratus* and *H. maggietailorae.*

11. Locality not plotted to avoid overcrowding of symbols (Fig. 11).
Figure 10. Canonical graphs from discriminant analyses; upper graphs 1 X 2 and 1 X 3 for 11 cranial variables and lower graphs 1 X 2 and 1 X 3 for 10 wing variables. Group centroids are plotted, with their respective confidence circles, as follows: A–H (stippled), Hipposideros calcatus calcatus; I–L (stippled), Hipposideros calcatus cupidus; M–O, Hipposideros maggieterolae maggieterolae; P–W, Hipposideros maggieterolae new subspecies (see p. 12); see Tables 1 and 3 for identity of geographic locality of centroid letter codes.
Table 2. Eigenvectors (direction cosines) of principal components (left) and standardized canonical vectors (Z-scores) from discriminant analyses (right) for 11 cranial variables (upper) and 10 wing variables (lower). Only the first three component axes are shown because most of the variation is exhibited in these components. The number in parentheses following each component score indicates the percentage of variance contributed by each variable to that respective component:

<table>
<thead>
<tr>
<th>Variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Cumulative Percent</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Cumulative Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZYGOMA</td>
<td>0.006 (0.15)</td>
<td>-0.502 (70.06)</td>
<td>0.000 (0.00)</td>
<td>70.21</td>
<td>0.576 (98.03)</td>
<td>-1.164 (0.16)</td>
<td>0.525 (0.36)</td>
<td>98.55</td>
</tr>
<tr>
<td>BRACAS</td>
<td>-0.004 (0.11)</td>
<td>-0.313 (43.56)</td>
<td>0.006 (2.15)</td>
<td>45.82</td>
<td>-0.029 (23.69)</td>
<td>0.042 (1.03)</td>
<td>0.112 (1.54)</td>
<td>26.26</td>
</tr>
<tr>
<td>MASTOD</td>
<td>0.012 (0.97)</td>
<td>-0.375 (54.27)</td>
<td>0.108 (2.35)</td>
<td>57.59</td>
<td>-0.078 (48.99)</td>
<td>0.366 (22.38)</td>
<td>-0.664 (15.56)</td>
<td>86.93</td>
</tr>
<tr>
<td>INTORB</td>
<td>0.009 (1.09)</td>
<td>-0.097 (7.98)</td>
<td>0.050 (1.11)</td>
<td>10.18</td>
<td>0.137 (85.76)</td>
<td>0.024 (0.05)</td>
<td>-0.711 (10.11)</td>
<td>95.92</td>
</tr>
<tr>
<td>CANINE</td>
<td>0.006 (0.22)</td>
<td>-0.261 (29.79)</td>
<td>0.119 (3.23)</td>
<td>33.24</td>
<td>-0.099 (71.11)</td>
<td>0.242 (8.78)</td>
<td>0.194 (1.19)</td>
<td>81.08</td>
</tr>
<tr>
<td>MAXTOH</td>
<td>-0.027 (2.46)</td>
<td>-0.235 (11.84)</td>
<td>-0.785 (69.36)</td>
<td>83.66</td>
<td>0.118 (48.54)</td>
<td>0.803 (46.20)</td>
<td>0.162 (0.40)</td>
<td>95.14</td>
</tr>
<tr>
<td>PALWID</td>
<td>0.006 (0.23)</td>
<td>-0.270 (32.86)</td>
<td>-0.113 (3.02)</td>
<td>36.11</td>
<td>-0.035 (34.93)</td>
<td>-0.218 (28.09)</td>
<td>-0.100 (1.26)</td>
<td>64.28</td>
</tr>
<tr>
<td>PALLEN</td>
<td>-0.013 (0.88)</td>
<td>-0.192 (12.51)</td>
<td>-0.052 (0.47)</td>
<td>13.86</td>
<td>0.099 (74.16)</td>
<td>0.251 (9.93)</td>
<td>-0.132 (0.58)</td>
<td>84.67</td>
</tr>
<tr>
<td>MANDIB</td>
<td>0.004 (0.06)</td>
<td>-0.188 (10.13)</td>
<td>0.553 (45.84)</td>
<td>56.03</td>
<td>0.341 (96.06)</td>
<td>-0.289 (1.43)</td>
<td>0.591 (1.26)</td>
<td>98.75</td>
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<tr>
<td>DENTAR</td>
<td>-0.021 (1.73)</td>
<td>-0.482 (53.62)</td>
<td>0.156 (2.93)</td>
<td>58.28</td>
<td>0.458 (98.54)</td>
<td>0.230 (0.51)</td>
<td>-0.209 (0.09)</td>
<td>99.14</td>
</tr>
<tr>
<td>CONCAN</td>
<td>-0.999 (99.99)</td>
<td>-0.008 (0.00)</td>
<td>0.022 (0.00)</td>
<td>99.99</td>
<td>0.078 (85.29)</td>
<td>-0.168 (8.26)</td>
<td>-0.100 (0.62)</td>
<td>94.17</td>
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</table>

Percent Trace 84.8 5.2 2.7
Cumulative Percent 84.8 90.0 92.7

<table>
<thead>
<tr>
<th>Variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Cumulative Percent</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>Cumulative Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>ZYGOMA</td>
<td>0.383 (57.28)</td>
<td>-0.171 (2.92)</td>
<td>0.131 (1.24)</td>
<td>61.44</td>
<td>-0.812 (96.54)</td>
<td>-0.617 (2.85)</td>
<td>0.331 (0.26)</td>
<td>99.65</td>
</tr>
<tr>
<td>BRACAS</td>
<td>-0.429 (65.57)</td>
<td>0.096 (0.84)</td>
<td>0.423 (11.92)</td>
<td>78.33</td>
<td>-0.171 (32.14)</td>
<td>1.067 (64.42)</td>
<td>-0.116 (0.24)</td>
<td>96.80</td>
</tr>
<tr>
<td>MASTOD</td>
<td>-0.188 (33.76)</td>
<td>-0.213 (11.08)</td>
<td>0.027 (0.13)</td>
<td>44.97</td>
<td>-0.393 (90.90)</td>
<td>0.299 (2.70)</td>
<td>0.688 (4.45)</td>
<td>98.50</td>
</tr>
<tr>
<td>INTORB</td>
<td>-0.246 (25.90)</td>
<td>-0.585 (37.28)</td>
<td>-0.522 (21.63)</td>
<td>84.81</td>
<td>0.140 (63.00)</td>
<td>-0.429 (30.16)</td>
<td>-0.091 (0.42)</td>
<td>93.58</td>
</tr>
<tr>
<td>CANINE</td>
<td>-0.554 (66.61)</td>
<td>0.625 (21.64)</td>
<td>-0.528 (11.28)</td>
<td>99.53</td>
<td>-0.039 (33.71)</td>
<td>0.120 (16.57)</td>
<td>0.022 (0.18)</td>
<td>50.46</td>
</tr>
<tr>
<td>MAXTOH</td>
<td>-0.130 (25.57)</td>
<td>-0.095 (3.46)</td>
<td>0.089 (2.24)</td>
<td>31.27</td>
<td>0.147 (61.77)</td>
<td>-0.397 (23.46)</td>
<td>-0.317 (4.68)</td>
<td>90.91</td>
</tr>
<tr>
<td>PALWID</td>
<td>-0.094 (10.73)</td>
<td>-0.258 (20.50)</td>
<td>-0.019 (0.08)</td>
<td>31.31</td>
<td>-0.195 (79.49)</td>
<td>0.296 (9.35)</td>
<td>0.406 (5.52)</td>
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</tr>
<tr>
<td>PALLEN</td>
<td>-0.448 (67.03)</td>
<td>-0.098 (0.83)</td>
<td>0.447 (12.44)</td>
<td>80.30</td>
<td>0.029 (3.56)</td>
<td>-0.254 (14.47)</td>
<td>-0.851 (50.65)</td>
<td>68.68</td>
</tr>
<tr>
<td>MANDIB</td>
<td>-0.154 (37.17)</td>
<td>-0.124 (5.52)</td>
<td>0.008 (0.02)</td>
<td>38.71</td>
<td>0.251 (83.51)</td>
<td>0.055 (0.21)</td>
<td>-0.422 (3.76)</td>
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</tr>
<tr>
<td>DENTAR</td>
<td>-0.130 (13.75)</td>
<td>-0.288 (17.30)</td>
<td>-0.210 (6.75)</td>
<td>37.80</td>
<td>-0.034 (19.42)</td>
<td>-0.169 (25.26)</td>
<td>-0.162 (7.20)</td>
<td>51.88</td>
</tr>
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</table>

Percent Trace 50.6 12.9 9.4
Cumulative Percent 50.6 63.5 72.9

ZYGOMA, zygomatic breadth; BRACAS, breadth of the braincase; MASTOD, mastoid breadth; INTORB, breadth of the interorbital constriction; CANINE, breadth across the canines; MAXTOH, length of maxillary tooththrow; PALWID, breadth across the last upper molars (M3); PALLEN, length of the palatal bridge; MANDIB, length of the mandibular tooththrow; DENTAR, length of the mandible; CONCAN, condylocanine length; FORARM, length of the forearm; META-3, META-4, META-5, length of the third, fourth, and fifth metacarpal, respectively; DIG-31, DIG-41, DIG-51, length of the proximal phalanx of the third, fourth, and fifth digits, respectively; DIG-32, DIG-42, DIG-52, length of the distal phalanx of the third, fourth, and fifth digits, respectively.
Table 3. Means and ranges (in parentheses) of selected cranial and external measurements of *Hipposideros maggietaylorae*. Letters in parentheses following locality name coincide with centroids plotted on the canonical graphs in Fig. 10. Superscript numbers indicate sample size different from those given in left-hand column.

<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>CONCAN</th>
<th>ZYGOMA</th>
<th>MASTOD</th>
<th>INTORB</th>
<th>CANINE</th>
<th>MASTOH</th>
<th>PALWID</th>
<th>Pallen</th>
<th>MANDIB</th>
<th>DENTAR</th>
<th>FORARM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Madina (M)</td>
<td>15</td>
<td>22.2</td>
<td>14.6</td>
<td>12.2</td>
<td>4.3</td>
<td>5.8</td>
<td>8.5</td>
<td>8.3</td>
<td>5.1</td>
<td>11.1</td>
<td>18.1</td>
<td>63.9</td>
</tr>
<tr>
<td>South New Ireland (N)</td>
<td>15</td>
<td>22.2</td>
<td>14.6</td>
<td>12.4</td>
<td>4.4</td>
<td>5.9</td>
<td>8.5</td>
<td>8.4</td>
<td>5.2</td>
<td>11.2</td>
<td>18.3</td>
<td>64.7</td>
</tr>
<tr>
<td>East New Britain (O)</td>
<td>13</td>
<td>21.2</td>
<td>14.3</td>
<td>12.2</td>
<td>4.3</td>
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<td>8.2</td>
<td>5.0</td>
<td>10.7</td>
<td>17.3</td>
<td>59.8</td>
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**Hipposideros maggietaylorae**

<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>CONCAN</th>
<th>ZYGOMA</th>
<th>MASTOD</th>
<th>INTORB</th>
<th>CANINE</th>
<th>MASTOH</th>
<th>PALWID</th>
<th>Pallen</th>
<th>MANDIB</th>
<th>DENTAR</th>
<th>FORARM</th>
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<tbody>
<tr>
<td>Mt. Diamond</td>
<td>10</td>
<td>19.6</td>
<td>12.3</td>
<td>11.0</td>
<td>4.0</td>
<td>4.8</td>
<td>7.9</td>
<td>7.4</td>
<td>4.5</td>
<td>9.3</td>
<td>15.5</td>
<td>52.9</td>
</tr>
<tr>
<td>Mine (P)</td>
<td>10</td>
<td>20.2</td>
<td>12.6</td>
<td>11.4</td>
<td>4.1</td>
<td>3.8</td>
<td>5.2</td>
<td>4.5</td>
<td>4.7</td>
<td>4.4</td>
<td>9.7</td>
<td>15.5</td>
</tr>
<tr>
<td>Javaneri (P)</td>
<td>6</td>
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<td>11.3</td>
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<td>3.9</td>
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<td>7.4</td>
<td>7.3</td>
<td>4.6</td>
<td>9.6</td>
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<td>Bulldog (Q)</td>
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<td>4.9</td>
<td>7.4</td>
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<tr>
<td>Palmer Junction (R)</td>
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<td>4.2</td>
<td>4.0</td>
<td>5.1</td>
<td>4.7</td>
<td>7.6</td>
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<td>4.7</td>
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<td>15.4</td>
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</tr>
<tr>
<td>Kairuru Island (T)</td>
<td>6</td>
<td>21.3</td>
<td>13.4</td>
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<td>4.3</td>
<td>3.9</td>
<td>5.3</td>
<td>4.8</td>
<td>7.9</td>
<td>7.4</td>
<td>4.9</td>
<td>10.3</td>
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<td>Salamana (U)</td>
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<td>4.3</td>
<td>3.9</td>
<td>5.1</td>
<td>4.7</td>
<td>8.7</td>
<td>7.9</td>
<td>4.6</td>
<td>10.5</td>
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<tr>
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<td>19.2</td>
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<td>4.9</td>
<td>7.5</td>
<td>7.4</td>
<td>4.3</td>
<td>9.7</td>
<td>15.4</td>
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<tr>
<td>Djayapura (W)</td>
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<td>20.1</td>
<td>13.1</td>
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<td>5.2</td>
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<td>4.5</td>
<td>10.2</td>
<td>16.1</td>
<td>54.5</td>
</tr>
</tbody>
</table>

CONCAN, condylodecanine length; ZYGOMA, zygomatic breadth; MASTOD, mastoid breadth; INTORB, breadth of the interorbital constriction; CANINE, breadth across the canines; MASTOH, length of the maxillary toothrow; PALWID, breadth across the last upper molars (M3); Pallen, length of the palatal bridge; MANDIB, length of the mandibular toothrow; DENTAR, length of mandible; FORARM, length of the forearm.
erroneously to H. calcaratus, actually represented on New Guinea by the much smaller H. calcaratus cupidus.

ACKNOWLEDGMENTS

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Special thanks is extended by one of us (Smith) to his graduate student, trusted field assistant, and tolerant companion Craig S. Hood. Susan E. Smith and Margaret Maas graciously contributed to the preparation of figures and typing of the man-
uscript, respectively. Some financial assistance to aid in prepa-
ration of the manuscript was extended by the California State
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Finally, without the early interest, encouragement, and gen-
erous support from Mrs. Reese Taylor, the new species de-
scribed herein would still be foraging, unrecognized by science,
through the green mansions of New Guinea.

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