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A Key to the Bats of the Philippine Islands

Nina R. Ingle

Lawrence R. Heaney

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A Key to the Bats of the Philippine Islands

Nina R. Ingle

Department of Natural Resources
Fernow Hall
Cornell University
Ithaca, New York 14853

Lawrence R. Heaney

Department of Zoology
Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496

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Table of Contents

List of Illustrations

List of Tables

A Key to the Bats of the Philippine Islands

Nina R. Ingle and Lawrence R. Heaney

Abstract

An identification guide is presented for the six families and 70 species of bats now known from the Philippine Islands, based on a key and a set of standardized measurements. Most critical characters are illustrated, and detailed drawings are provided of the skulls of 42 species.

Introduction

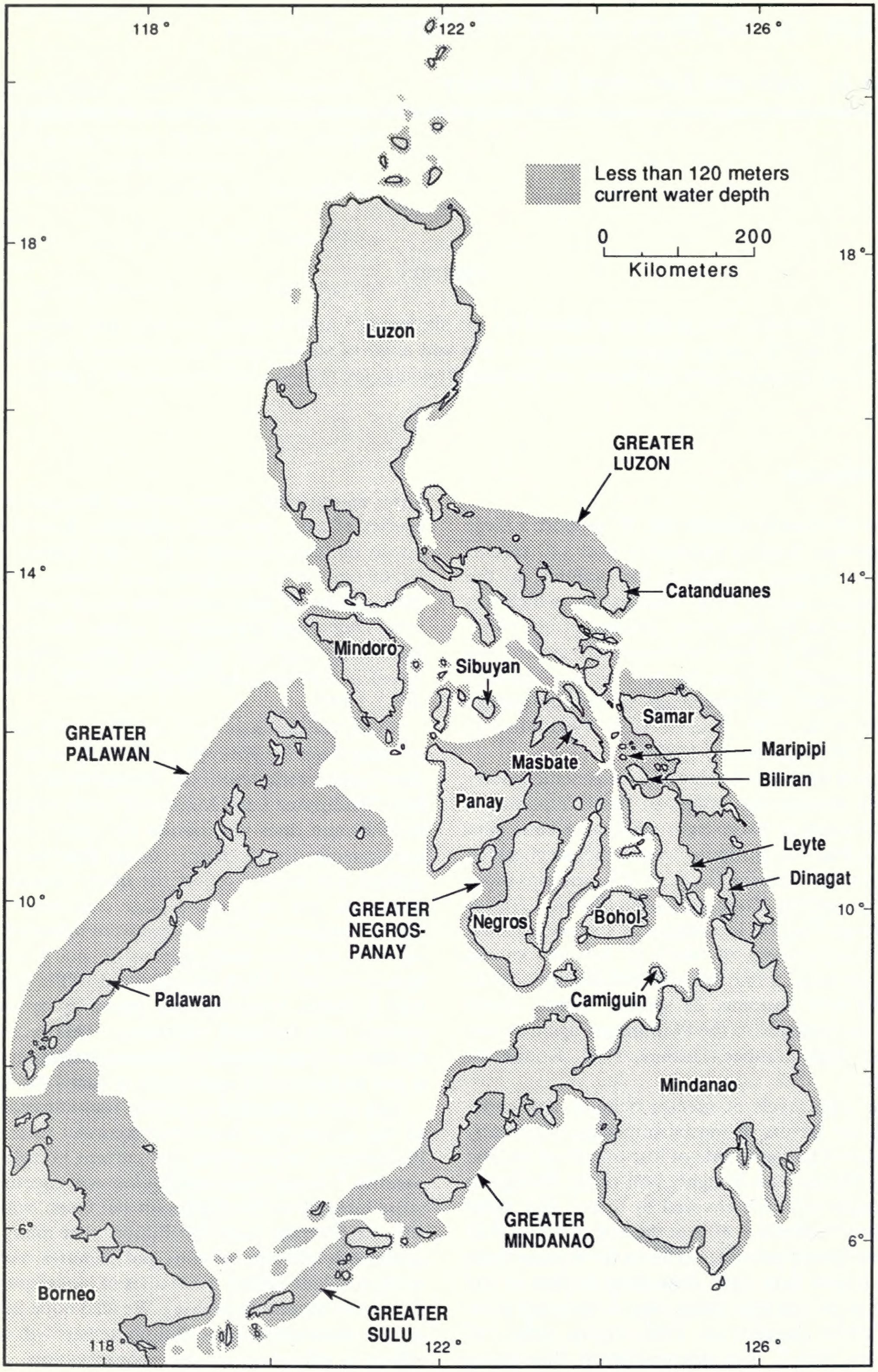
The Philippine Islands (fig. 1) support a large and diverse fauna of mammals: over 170 species are now known, compared, for example, to the 105 species known from Madagascar, which has nearly twice the land area (Heaney et al., 1987; Jenkins, 1987). About 100 species are endemic to the Philippines, giving the country an unusually high number and percentage of unique species (Hauge et al., 1986; Heaney, 1986, 1991; Heaney et al., 1987; Koopman, 1989).

One of the most diverse and, in general, poorly known mammalian orders in the Philippines is the Chiroptera. Sixty-eight species of bats were known from the Philippines when the last checklist was prepared (Heaney et al., 1987), and two more are now known (*Pteropus dasymallus* and *Harpiocephalus harpia*). In number of species, bats exceed even rodents, of which 67 are now known (Heaney et al., 1987; Musser and Heaney, 1992). By our best estimate, 22 species of bats, about 31%, are endemic to the Philippines, again an unusually high number (Heaney, 1991; Koopman, 1989).

The high levels of species richness and endemism are factors of special importance currently because of the rapid rate of loss of natural habitat in the Philippines. Roughly 94% of the Philippine land area was once covered by forest; that figure had been reduced to 40% at the end of World War II, and current estimates of forest cover range from 25% to less than 20%, depending in part on the amount of degraded forest that is included (Collins, 1990; Hauge et al., 1986; Myers, 1988; Utzurrum, 1991). The ongoing forest destruction poses an especially grave problem because many species of bats, especially endemics, depend primarily on forest (Heaney et al., 1987; Heaney and Utzurrum, 1991; Heideman and Heaney, 1989). Two species of bats (*Acerodon lucifer* and *Dobsonia chapmani*) are believed to have become extinct in the last 100 years, and many others are threatened (Heaney and Heideman, 1987; Heaney et al., 1987).

No identification guide to the 70 species of bats recorded from the Philippines currently exists. The most recent work describing Philippine bats, Taylor's "Philippine Land Mammals", was published in 1934 and does not include the many species subsequently described or recorded from the Philippines, nor does it reflect the many changes in taxonomy that have taken place over nearly 60 years. Moreover, Taylor's keys were intended for use with museum study specimens, not live animals in the field. Thus, identification of Philippine bats in recent years has been primarily by comparison with museum specimens. This requires access to a comprehensive reference collection and is not an option for researchers in many places.

This key is intended to permit identification of all bat species that have been recorded from the Philippines, to the extent that current knowledge permits. It is our hope that this key will encourage more research on the Philippine bat fauna, which, with its diversity and distribution over many islands with differing habitats and climates, serves as an excellent subject for studies of biogeography and many aspects of ecology. We also hope that a greater knowledge about Philippine bats will contribute to efforts toward their conservation.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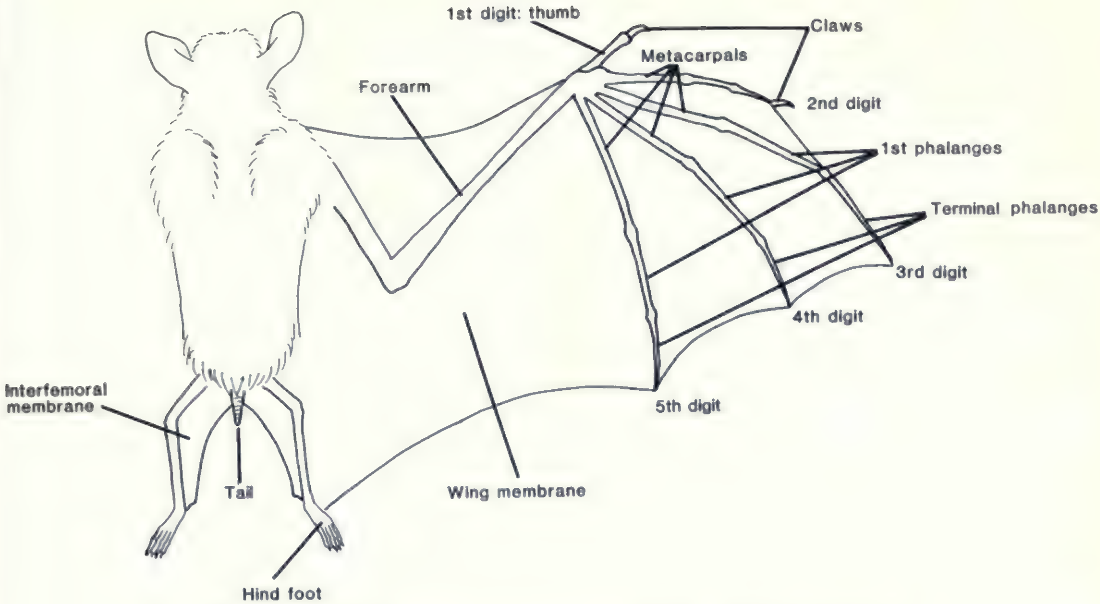

FIG. 2. Generalized pteropodid bat, with important structures indicated.

Methods

The descriptions and measurements in this key have been based primarily on examination of specimens in the American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), Royal Ontario Museum (ROM), Philippine National Museum (PNM), Silliman University Museum of Natural History (SU), University of Michigan, Museum of Zoology (UMMZ), and United States National Museum of Natural History (USNM). Our descriptions and measurements are based on Philippine specimens except in a few cases involving species that are rare in collections; in those cases, specimens from elsewhere or characters from published accounts were utilized.

For standard external measurements we relied preferentially on data from animals that we had collected, but we also utilized data on specimen labels and measured specimens in collections. We took cranial measurements with dial or digital calipers following deBlase and Martin (1974) and Heaney and Peterson (1984); these measurements are described briefly in the following section, Anatomy and Measurements of a Bat.

We consulted a variety of publications as aids in building the keys and descriptive sections, relying heavily on Harrison (1966), Hill (1983), Lawrence (1939), Lekagul and McNeely (1977), Medway (1969), Miller (1907), Payne et al. (1985), and Taylor (1934). These publications, the references cited in Hill (1983), and publications referred to in the sections for each bat family should be consulted for descriptions of characters not treated in the key.

Anatomy and Measurements of a Bat

Familiarity with basic terminology on the anatomy of a bat is necessary to use this key; Figure 2 shows the most important external structures. The external ear (pinna) has two structures that can be useful for identification. The tragus is a

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FIG. 1. Map of the Philippines. Recent islands are outlined by continuous lines, and the extent of late Pleistocene islands is indicated by the shaded areas.

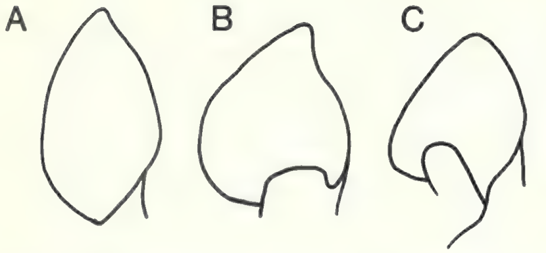

FIG. 3. Left external ears (pinnae) of representative bats. **A,** Pteropodidae; **B,** Rhinolophidae; **C,** Vespertilionidae.

projection from the base of the ear (fig. 3C); this structure is absent in members of the Pteropodidae (fig. 3A) and Rhinolophidae (fig. 3B) and is quite small in the Molossidae. The antitragus is the flap along the lower posterior margin of the ear (figs. 3B, 12); it is especially well developed in rhinolophids and most molossids. Rhinolophids and megadermatids have noseleaves, structures formed from elaborate folds of skin on their noses (figs. 8B,C, 12); bats of other families have no such structure.

All bats have four types of teeth: incisors, canines, premolars, and molars (fig. 5). All bats possess a pair of large, sharp, conical teeth called canines on the upper and lower jaws. The smaller teeth at the front of the mouth, anterior to the canines, are incisors. Posterior to the canines are the premolars and molars, collectively called cheek teeth. The large teeth in this series are referred to as molariform teeth. Molariform teeth are usually low and broad with cutting or grinding surfaces; the anterior cheek teeth are tiny pegs in some species.

External and cranial measurements provide substantial aid in identification; we have therefore included tables containing typical adult measurements. The definitions of standard external measurements are illustrated in Figure 4. The cranial measurements included in the tables are shown in Figure 5 and are defined as follows: condylobasal length (CBL), distance from the posterior edge of the occipital condyles to the anterior tip of the premaxillaries; condylocanine length (CCL), distance from the posterior edge of the occipital condyles to the anterior edge of the base (alveolus) of the canines; and maxillary toothrow (C^1 to last M), distance from the posterior edge of the last upper molar to the anterior edge of the upper canine, taken along the bone line of the alveolus.

Use of the Key

Using the key most effectively requires several steps that are explained in detail in the following sections. First, the bat should be identified as to

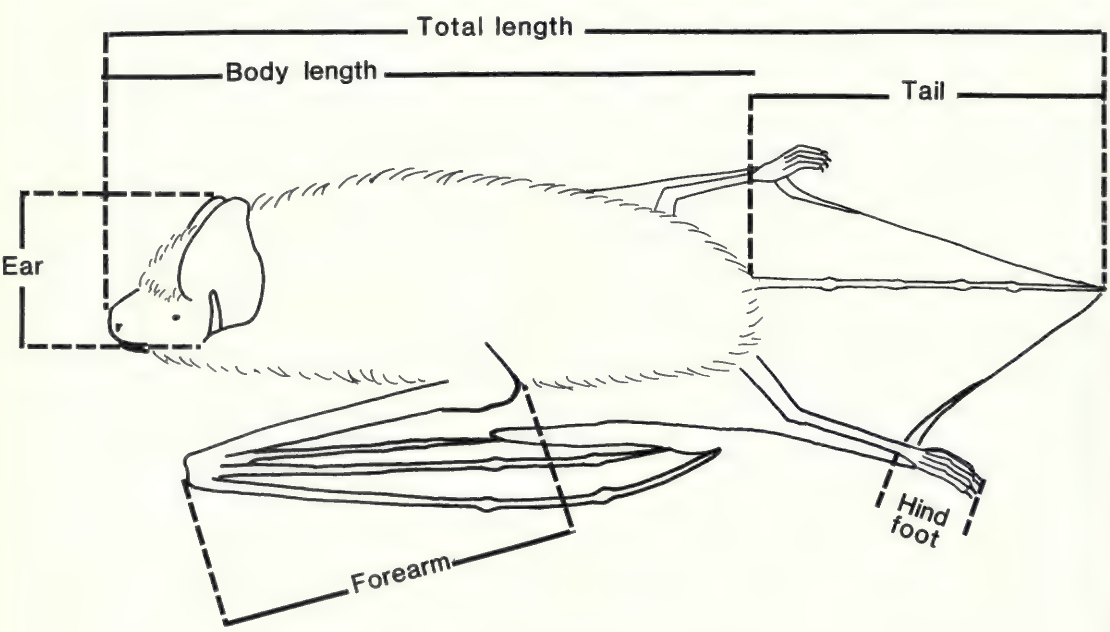

FIG. 4. Bat with external measurements indicated.

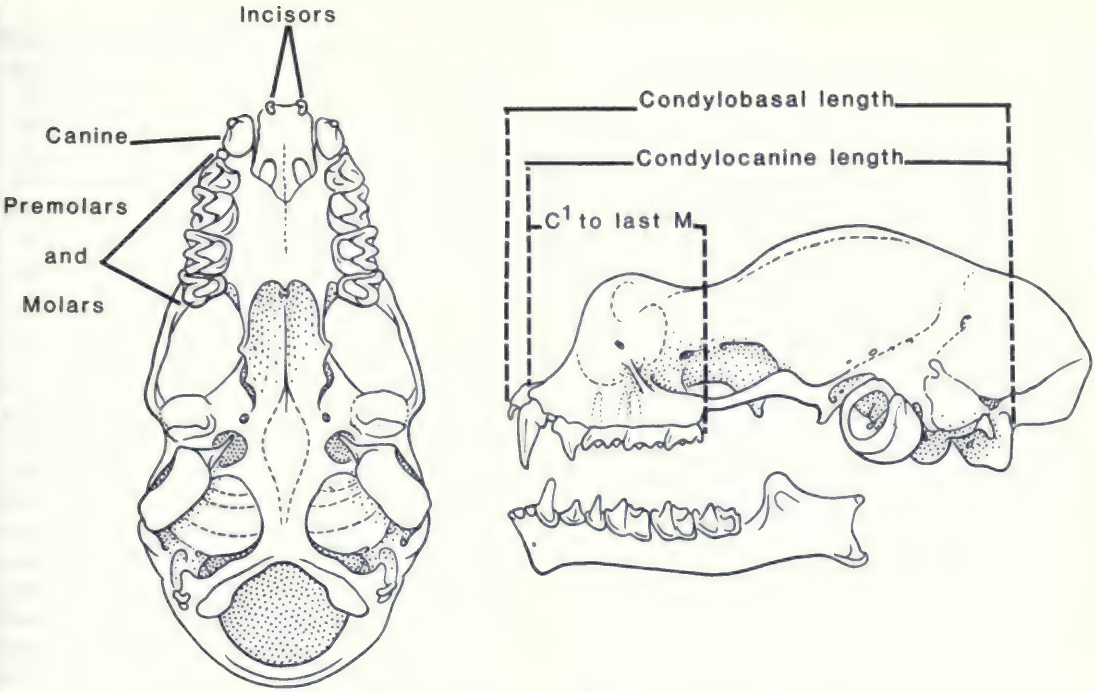

FIG. 5. Bat skull with teeth and cranial measurements indicated.

age and sex. It should then be identified to family with the Key to Families, and then to species with the key to that family. Next, all external measurements should be taken and matched against those in the tables of measurements; if the measurements do not match, the identification is questionable and the process should be begun again from the first step. Finally, if a skull is available, it should be visually compared with Figures 19–60 to see if it matches the features of that species or genus.

Determination of Age and Sex

The age of bats can be estimated by the degree of ossification of the joints in the digits of the wing (Anthony, 1988). In juvenile bats, the joints have cartilaginous discs where growth takes place. When a light is shown through the wing of a live bat, the bands of cartilage at the joints appear partly translucent (fig. 6B). In adult bats, the bones are fully ossified and the joints appear opaque (fig. 6A). The shape of the joints of the digits also differs between juvenile and adult bats; this is especially useful in determining the age of animals prepared as stuffed skins or fluid-preserved specimens. In juvenile bats the joints are swollen and tapered (fig. 6B), whereas in adult bats the joints are knobby and more distinct from the bone shaft (fig. 6A).

Bats can be sexed by examination of the external genitalia. Males have a conspicuous penis (except

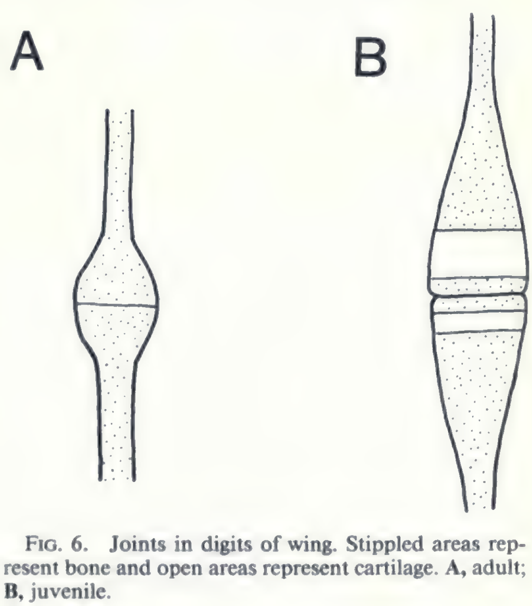

FIG. 6. Joints in digits of wing. Stippled areas represent bone and open areas represent cartilage. **A,** adult; **B,** juvenile.

subadult male *Rousettus,* in which the penis is retracted into the abdomen). Both sexes possess axillary nipples on the upper chest, usually near the armpit (axilla). However, the nipples of adult females are more prominent than those of males. In female rhinolophids and megadermatids, a pair of inguinal papillae that look like nipples is present just anterior to the genitals.

Identification to Family and Species

Following determination of age and sex, the bat should be identified to family with the Key to Families, and then to species with the key for the appropriate family. The keys consist of sets of alternatives arranged in order of increasing restrictiveness. Alternatives belonging to the same set are preceded by the same number with different superscripts (e.g., 1, 1′, 1″). For each set, the user should choose the best alternative; this indicates either the next set of alternatives to be considered, or the name of the family or species. All distinguishing characters should be checked carefully before a choice is made. This will minimize the likelihood of incorrectly identifying a bat. Researchers should bear in mind that this key includes only those species now known from the Philippines, and that discovery of undescribed species and previously unreported species is likely.

Figures illustrating important descriptive characteristics are referred to in the key and should be consulted. Fur coloration can be useful in identification; it should be observed on a dry animal or study skin.

Use of Measurement Tables

Once a bat has been identified to species, it is good practice to check if its measurements agree with those given in the tables. Cranial measurements should be taken with calipers. External measurements can be taken with a ruler, although calipers provide more accurate measurements of forearm length and of small structures such as parts of the noseleaves of rhinolophids.

Because forearm length is a very useful measurement for identifying adult bats, ranges for forearm length are given in the keys for each species, usually at the end of the final description for that species. Note that forearm lengths are given even when overlap in the ranges of two or more species means that the measurement cannot be used to fully distinguish between the species. When other measurements are particularly useful for separating similar species, they are also given in the key. Measurements should not be used to identify juvenile bats, although hind foot length is sometimes useful because the feet of juvenile bats approach adult size long before most other structures have ended growth.

Comparison with Skull Drawings

Skulls are very important in identification of bats. Thus, although we have written this key with the intention that live animals and preserved specimens can be identified without examination of their skulls, we have included skull drawings of common Philippine bats (figs. 19–60). The drawings will aid in identification of museum specimens with cleaned skulls and will provide a means of verifying an identification based on external characteristics. The skull drawings also serve as a guide to head shape. Even if use of the key yields an apparently unambiguous identification, it is always best if a skull can be examined from a voucher specimen. The skull should be compared with the figures, and cranial measurements should be taken and compared with those in the tables. Dentition, although most easily visible on a skull, can also be observed, at least partially, on a live animal and should be examined when possible. The mouth can be gently pried and held open by a toothpick, and the lips can be lifted to view the cheek teeth. With small bats a magnifying lens is a great help. Note that if the jaws are closed, some teeth, particularly the canines, may obstruct the view of others.

Users of this key should not overlook the fact that variation in both quantitative and qualitative characters is present in all species. Whenever possible, samples of more than one individual for each species should be examined and the most common character states used in the key.

The identities of a few species of Philippine bats that are extremely poorly represented in collections (sometimes only by the holotype) are uncertain. When possible, these species have been included in the key on the basis of whatever descriptions are available, and further comments on their identification are provided in the Notes section. We also comment briefly on two new records of bats for the Philippines in this section.

Collecting and Preserving Voucher Specimens

In any study, several individuals of each species should be preserved as voucher specimens and deposited in a museum collection. Voucher specimens are necessary to verify identification, since many species can be identified definitively only after careful study of the external and cranial morphology. Such specimens are invaluable for adding to our current, very limited knowledge of Philippine bats, particularly of distribution and inter- and intraspecific variation. Specimens should be collected and prepared carefully, following all regulations for the scientific study of wildlife.

Bats are most easily preserved in fluid. They should be killed in a quick and painless manner, examined for reproductive condition, and weighed, and their standard external measurements taken (total length, tail length, ear length, and hind foot length). The date, habitat, collection locality, elevation, collector, collector's field number, and external measurements should be recorded in India ink (which is best) or pencil (which is usually acceptable), *not* with other kinds of ink (which are not permanent). These data should accompany the specimen as part of the permanent record. The specimen should have a permanent label attached that bears the collector's name and field number; other data may go onto the same label or into a field catalog. The specimens should then be rinsed lightly with soapy water, injected with a 10% solution of formalin, and immersed in a 10% solution of formalin. After about three days, they can be rinsed with clean water and transferred to 70% alcohol (methanol is best) for permanent storage. Skulls can be extracted and cleaned in the museum.

The Philippine National Museum, University of the Philippines at Los Baños, Silliman University, and a number of other institutions maintain research collections and accept voucher specimens for their permanent collections, and the staff may be able to help with identifications.

Key to Families of Philippine Bats

1. Interfemoral membrane is absent or reduced, forming narrow margin along insides of legs; tail short (up to 20% of body length) or absent, never completely enclosed by interfemoral membrane (fig. 7A); both thumb and second finger with claw (except *Eonycteris* and *Dobsonia*; fig. 2); both tragus and antitragus absent (figs. 3A, 8A); ear margin forms continuous ring . . . Megachiroptera: Pteropodidae

1′. Interfemoral membrane is a continuous expanse of skin stretching between legs (figs. 7B–F; except *Coelops*, which has a concave posterior margin to the membrane and no tail); tail present (except *Megaderma* and *Coelops*, which both possess noseleaves, structures not present in any pteropodids), usually comprising more than 20% of body length; the second finger does not have a claw; either tragus (fig. 3C) or antitragus (fig. 3B) or both present; ear margin does not form continuous ring . . . . . . (Microchiroptera) 2

2. Noseleaf present (figs. 8B,C) 3

2′. Noseleaf absent (figs. 8D–F) 4

3. Large ears connected at top of forehead (fig. 8B); tragus long and forked; external tail absent but interfemoral membrane well developed (fig. 7B) . . . . . . Megadermatidae

3′. Ears not connected across top of forehead; tragus absent, but antitragus usually well developed (fig. 3B); tail present, enclosed by interfemoral membrane except at extreme tip (fig. 7D; except *Coelops*, which has no tail and a reduced interfemoral membrane . . . . . . Rhinolophidae

4. Tail extends to posterior margin of interfemoral membrane (extreme tip may project 1–2 mm beyond membrane; fig. 7C); ears variable, usually not fleshy (fig. 8F); anterior edge of bony palate deeply emarginate . . . . . . Vespertilionidae

4′. Tail emerges dorsally from interfemoral membrane but is shorter than membrane when legs and membrane are outstretched (fig. 7F); ears not noticeably thick and fleshy (fig. 8D); anterior edge of bony palate deeply emarginate . . . . . . Emballonuridae

4″. Tail projects beyond posterior margin of interfemoral membrane for over half its length (fig. 7E); ears thick and fleshy (fig. 8E); anterior edge of bony palate continuous, not emarginate . . . . . . Molossidae

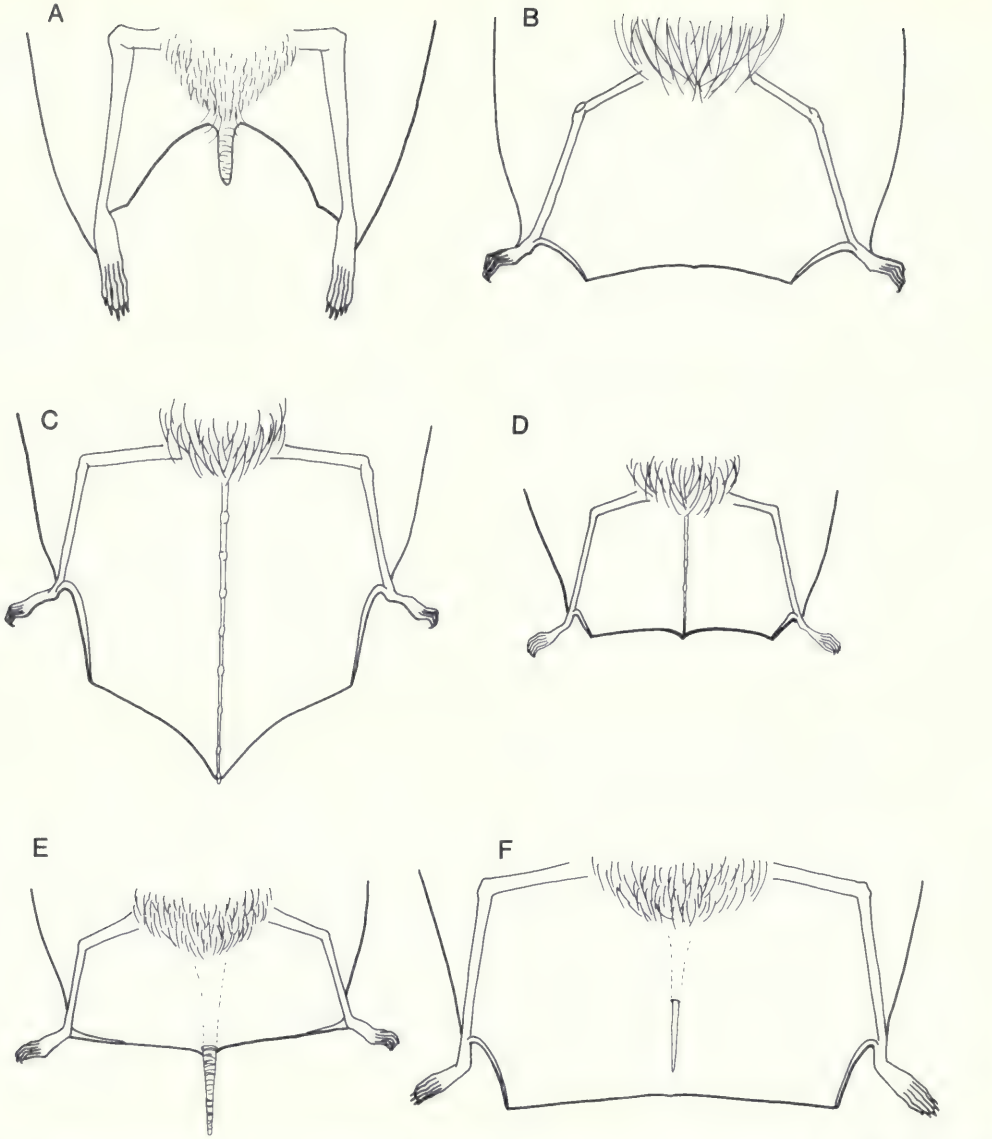

FIG. 7. Tails of representatives of Philippine bat families. **A,** Pteropodidae (*Rousettus*); **B,** Megadermatidae (*Megaderma*); **C,** Vespertilionidae (*Miniopterus*); **D,** Rhinolophidae (*Rhinolophus*); **E,** Molossidae (*Chaerephon*); **F,** Emballonuridae (*Taphozous*).

Family Pteropodidae: Fruit Bats

All fruit bats are characterized by dog-like heads (fig. 8A), with eyes that are proportionately larger than those of most other bats; the large eyes are associated with their dependence on vision for orientation and their lack of echolocation (sonar) systems (except for the very simple and limited one used by *Rousettus*). They do not have the elaborate

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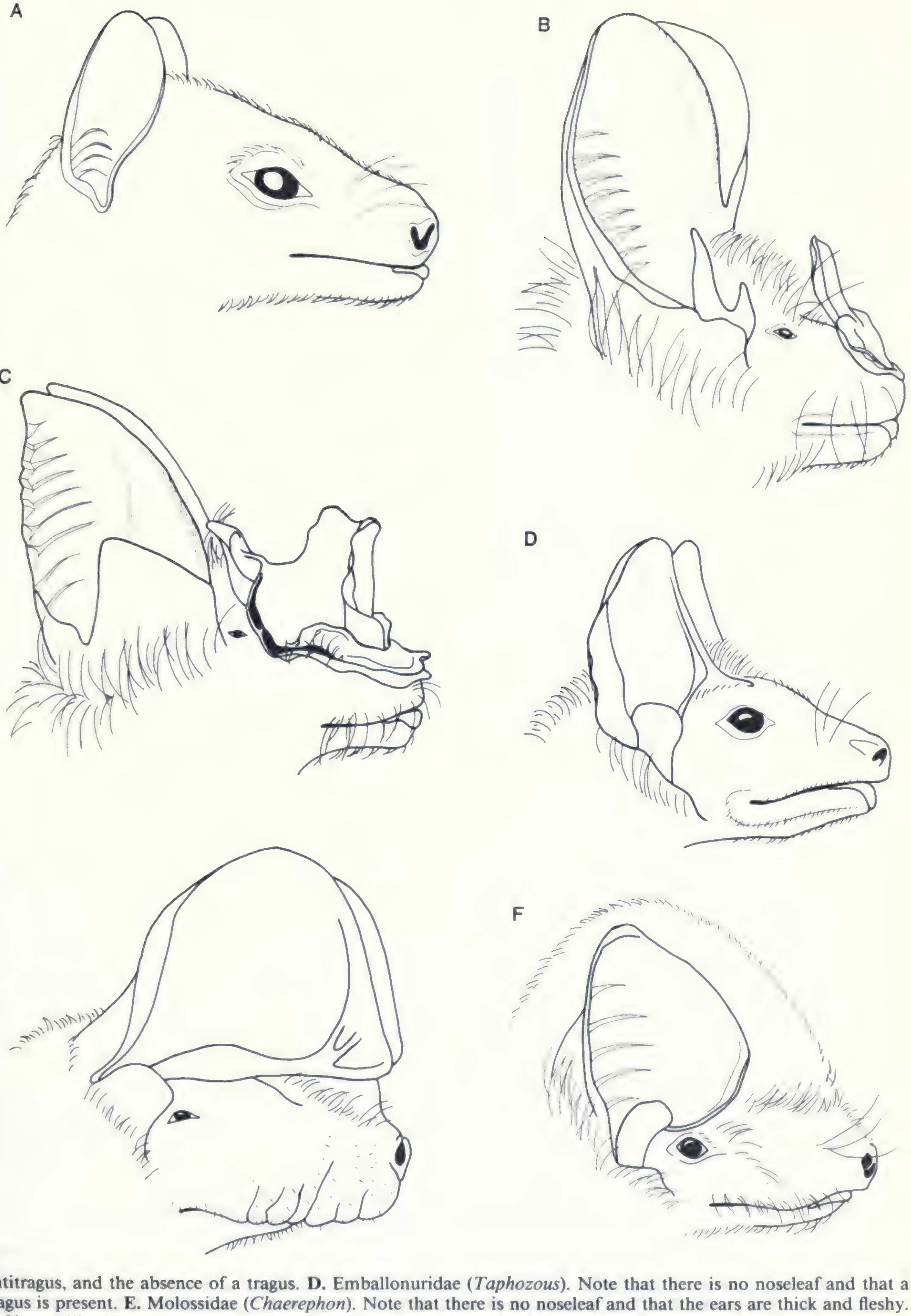
FIG. 8. Heads of representatives of Philippine bat families (not to same scale). **A.** Pteropodidae (*Rousettus*). Note that the ear margin is continuous, neither tragus nor noseleaf is present, the eyes are large, and the face is dog-like. **B.** Megadermatidae (*Megaderma*). Note that a noseleaf is present, the tragus is forked, and the large ears are connected across the top of the forehead. **C.** Rhinolophidae (*Rhinolophus*). Note the elaborate noseleaf, the well-developed



antitragus, and the absence of a tragus. **D.** Emballonuridae (*Taphozous*). Note that there is no noseleaf and that a tragus is present. **E.** Molossidae (*Chaerephon*). Note that there is no noseleaf and that the ears are thick and fleshy. **F.** Vespertilionidae (*Miniopterus*). Note that there is no noseleaf and that a tragus is present.

folds of skin in the nasal region (also associated with the use of echolocation) that are present in two other families of bats in the Philippines (Megadermatidae and Rhinolophidae). The external portion of the ear is simple and of moderate size, and the margin of the ear forms a continuous ring. Fruit bats do not have a tragus or antitragus (figs. 3A, 8A). All but three species (*Dobsonia chapmani, Eonycteris robusta,* and *E. spelaea*) have a claw on the second digit (fig. 2), along the leading edge of the wing; bats belonging to other families lack this claw. Many species have no tail, and in none does the tail comprise more than 20% of the body length. Their size varies greatly, with forearm lengths ranging from 40 to 215 mm, and weight from about 16 g (*Alionycteris paucidentata*) to at least 1,200 g (*Acerodon jubatus*; table 1).

Most species show substantial sexual dimorphism; males are larger than females and often have broader, more heavily muscled heads. Males of many species possess a ruff of fur (often colored yellow or rusty red) around the neck and on the shoulders that is lacking or poorly developed in females. Subadults of both sexes resemble adult females. Parous adult females of all species have a pair of axillary nipples that are large and prominent; males and subadult females have very small but visible nipples.

The skulls of all pteropodids are characterized by the presence of prominent postorbital processes, and all but a few species have postorbital foramina (figs. 19–32). The dental formula is variable. Most species have broad, blunt, rounded molariform teeth, but the nectarivorous species have greatly reduced premolars and molars. All species have long, prominent canines. In many species, males have longer canines than do females and often have more strongly developed cranial crests.

As the English name for the family implies, most fruit bats feed on fruit, but three species (*Eonycteris robusta, E. spelaea,* and *Macroglossus minimus*) feed primarily on nectar and pollen. Fruit bats often are abundant, being uncommon only in upper montane and mossy forest (Heaney and Rickart, 1990; Heaney et al., 1989). In forested areas, small to medium-sized species roost in hollow trees and in foliage, either alone or in groups; the large flying foxes roost in exposed treetops. Several species roost in caves, often forming colonies in the hundreds or thousands.

Andersen (1912) provided descriptions of most species of pteropodids found in the Philippines. Additional descriptions may be found in Bergmans (1975, 1978), Francis (1989), Heaney and Peterson (1984), Klingener and Creighton (1984), Kock (1969a,b,c), Musser et al. (1982), Peterson and Fenton (1970), Rookmaaker and Bergmans (1981), and Yoshiyuki (1979).

Key to Pteropodidae

1. Claw on thumb but not on second digit 2
1′. Claws on both thumb and second digit (fig. 2) 4
2. Wings attach to body along midline of back; two upper incisors and two minute lower incisors; forearm 123–131 mm; skull as in Figure 21 .... *Dobsonia chapmani*
2′. Wings attach along sides of body; four upper and four lower incisors, all very small; forearm 67–82 mm .... (*Eonycteris*) 3
3. Pair of prominent 2–6-mm-long kidney-shaped glands lateral to anus; tail 12–20 mm; forearm 67–80 mm; skull as in Figure 23 .... *Eonycteris spelaea*
3′. No glands near anus; tail 20–28 mm; forearm 67–82 mm; skull as in Figure 22 .... *Eonycteris robusta*
4. Forearm 94–215 mm; tail absent; four upper and four lower incisors 5
4′. Forearm 41–92 mm; tail present or absent; number of incisors varies between species 13
5. Wings with prominent pale blotches, particularly along thumb and anterior edge of wing adjacent to first and second digit, especially at wing tips; forearm 135–141 mm ..... *Pteropus leucopterus*
5′. Wings dark brown without prominent pale blotches; forearm 94–215 mm 6
6. Pelage on dorsal surface of lower back pale brown or gray 7
6′. Pelage on dorsal surface of lower back dark brown or black, sometimes with yellow flecks 8
7. Forearm 132–165 mm; condylobasal length 65–70 mm; three cusps on second and third upper molariform teeth, including a well-developed anterolingual cusp .... *Acerodon leucotis*
7′. Forearm 94–113 mm; condylobasal length 46–52 mm; two cusps on second and third upper molariform teeth (no anterolingual cusps); skull as in Figure 30 .... *Pteropus pumilus*

TABLE 1. Measurement ranges of adult Philippine Pteropodidae. Ranges represent at least 10 individuals, except when sample sizes are given in parentheses. Measurements, as defined in text, were taken from Philippine specimens.

Species	CBL	C¹-last M	Total Length	Tail	Ear	Forearm	Weight
Acerodon jubatus	72.5–85.5	29.0–36.0	255–310	0	31–41	165–215	900–1,250
Acerodon leucotis	65.0–70.0	25.5–28.0	220–250	0	29–32	132–165	—
Acerodon lucifer	71.0–73.5	29.0–31.0	—	0	—	167–170	—
Alionycteris paucidentata	21.0–22.0	6.8–7.3	(5) 64–70	(5) 0	(5) 11–12	(5) 45–50	14–18
Cynopterus brachyotis	26.0–29.5	8.3–10.0	88–110	3–15	14–20	58–68	26–41
Dobsonia chapmani	48.5–53.5	19.0–21.0	218–221	23–26	25–27	123–131	—
Dyacopterus spadiceus	(2) 41.3–42.2	(2) 14.4–15.3	(1) 171	(1) 29	(1) 22	(1) 92	—
Eonycteris robusta	33.9–37.9	11.6–14.0	127–155	20–28	19–23	67–82	75–80
Eonycteris spelaea	31.3–35.6	10.8–13.1	121–145	12–20	18–23	67–80	48–90
Haplonycteris fischeri	22.0–25.4	7.6–9.2	65–80	0	11–16	46–53	16–21
Harpyionycteris whiteheadi	39.7–43.3	15.4–16.6	130–156	0	19–25	80–91	99–122
Macroglossus minimus	24.7–26.5	7.6–9.6	65–81	0	12–18	41–45	15–20
Megaerops wetmorei	21.7–22.9	7.1–7.7	70–76	0–6	12–15	45–52	17–20
Nyctimene rabori	33.4–35.3	11.2–12.1	131–149	20–30	17–24	71–79	61–74
Otopteropus cartilagonodus	20.8–23.0	7.0–8.0	70–76	0	12–14	43–50	15–17
Ptenochirus jagori	32.5–37.2	11.0–13.3	120–145	6–18	18–25	76–90	62–97
Ptenochirus minor	27.2–31.7	9.5–11.0	98–125	4–12	13–22	60–78	31–62
Pteropus dasymallus	57.6–64.2	22.3–24.6	220–230	0	(1) 25	(3) 133–152	(3) 380–490
Pteropus hypomelanus	56.0–65.5	21.4–24.6	210–240	0	28–32	136–149	425–450
Pteropus leucopterus	56.5–63.0	16.5–22.0	205–240	0	26–28	135–141	340
Pteropus pumilus	46.0–51.5	16.5–19.5	155–180	0	20–28	94–113	145–200
Pteropus speciosus	53.9–61.5	20.3–22.9	190–215	0	24–30	118–133	—
Pteropus vampyrus	68.8–79.0	26.0–31.5	270–320	0	35–45	179–204	725–810
Rousettus amplexicaudatus	34.0–38.8	12.1–14.4	128–154	13–24	18–24	80–92	64–106

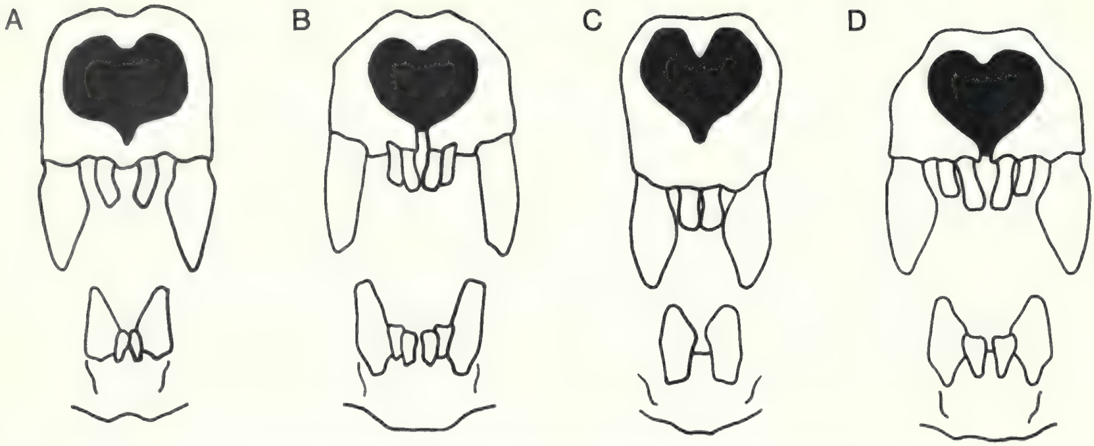


FIG. 9. Frontal views of fruit bat skulls, showing incisors and canines (not to same scale). **A,** *Otopteropus cartilagonodus* (*Alionycteris paucidentata* and *Haplonycteris fischeri* have an equal number of incisors); **B,** *Cynopterus brachyotis*; **C,** *Nyctimene rabori*; **D,** *Ptenochirus minor* (*Ptenochirus jagori* incisors are very similar).

8. Forearm 165–215 mm; condylobasal length 68–86 mm; fur on upper back sometimes completely black 9
8′. Forearm 118–152 mm; condylobasal length 54–66 mm; fur on upper back never completely black, usually golden 11
9. Dorsal pelage may be completely dark brown or black; if upper back is golden, the posterior margin of the golden area forms a sharply defined transverse line with the dark brown lower back; tips of ears nearly pointed; two cusps on second and third upper molariform teeth (no anterolingual cusps); condylobasal length 68–79 mm; forearm 179–204 mm; skull as in Figure 31 .... *Pteropus vampyrus*
9′. Dorsal pelage never completely dark brown or black; a golden patch on top of head, extending anterior to line between ears, is always present; the golden dorsal pelage never forms a transverse line along the edge of the dark brown of the lower back; tips of ears bluntly rounded; three cusps on second and third upper molariform teeth, including a well-developed anterolingual cusp; forearm 165–215 mm; condylobasal length 71–86 mm 10
10. Forearm 167–170 mm; condylobasal length 71–74 mm (occurs only on Panay Island; see Notes) .... *Acerodon lucifer*
10′. Forearm 165–215 mm; condylobasal length 72–86 mm; skull as in Figure 19 ... *Acerodon jubatus*
11. Forearm 118–133 mm; condylobasal length 53–62 mm (occurs only from Zamboanga to Sulu) .. .. *Pteropus speciosus*
11′. Forearm 133–152 mm; condylobasal length 56–66 mm 12
12. Lower legs heavily furred nearly to ankle; forearm 133–152 mm (see Notes) .... *Pteropus dasymallus*
12′. Lower legs nearly naked; forearm 136–149 mm; skull as in Figure 29 ... *Pteropus hypomelanus*
13. Tail absent 14
13′. Tail present (fig. 7A; it may be small, so look carefully) 19
14. Two small lumps of soft white tissue on each ear, at anterior and posterior margins; forearm 43–50 mm .... *Otopteropus cartilagonodus*
14′. No lumps of soft white tissue at margins of ears; forearm 41–91 mm 15
15. Forearm 80–91 mm; well-developed secondary cusps on canines (one on upper canines, two on lower canines); six cusps on last two upper and lower molariform teeth; dorsal surface of hind feet thickly furred; skull as in Figure 25 .... *Harpyionycteris whiteheadi*
15′. Forearm 41–53 mm; canines do not have well-developed secondary cusps; two or three cusps on molariform teeth; dorsal surface of hind feet may or may not be thickly furred 16
16. Muzzle long and slender (fig. 10A); nostrils are not tubular and do not project beyond rest of muzzle; wing membrane attaches on top of foot, above gap between third and fourth toes from outside (fig.

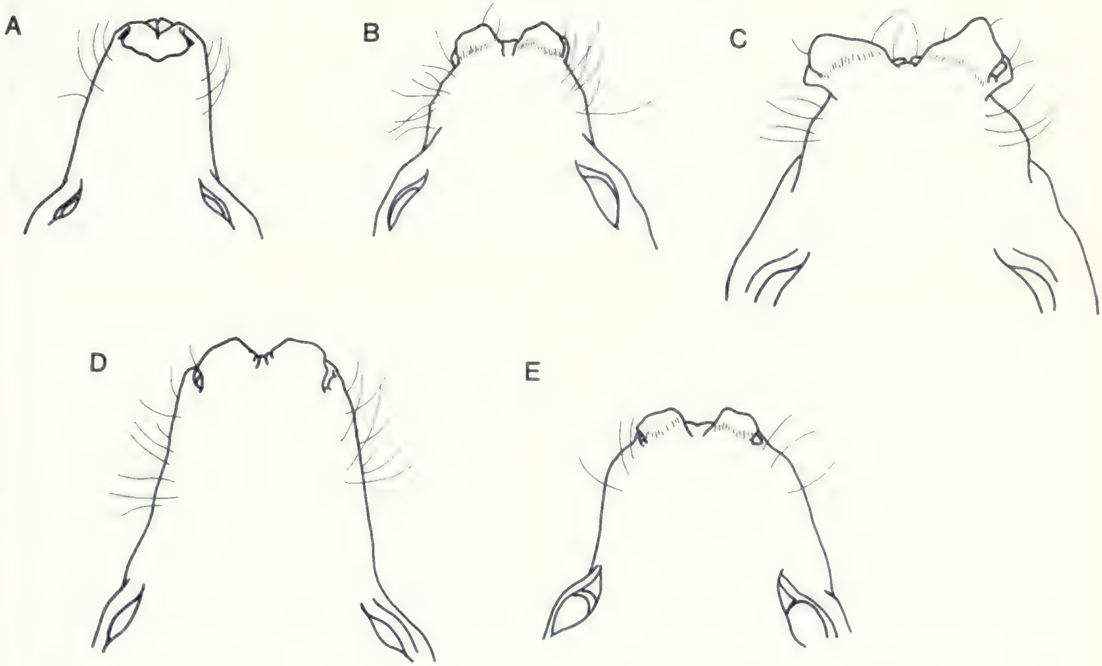


FIG. 10. Dorsal views of fruit bat muzzles (not to same scale). **A,** *Macroglossus*; **B,** *Haplonycteris*; **C,** *Nyctimene*; **D,** *Rousettus*; **E,** *Cynopterus*.

11A); teeth, except canines, greatly reduced; forearm 41–45 mm; skull as in Figure 26 .... *Macroglossus minimus*

16′. Muzzle short and broad; nostrils tubular (as in fig. 10B); wing membrane attaches on side of foot (on or above outermost toe; fig. 11C); teeth robust; forearm 43–53 mm 17

17. Four upper and two lower incisors (fig. 9D); forearm 45–52 mm .... *Megaerops wetmorei*

17′. Two upper and two lower incisors (as in fig. 9A); forearm 43–53 mm 18

18. Band of pale fur along dorsal surface of forearm; interfemoral membrane present; forearm 46–53 mm; skull as in Figure 24 .... *Haplonycteris fischeri*

18′. No band of pale fur along dorsal surface of forearm; no interfemoral membrane; forearm 45–50 mm .... *Alionycteris paucidentata*

19. Ears and skin on dorsal surface of bones of wings with prominent pale yellow spots; dark stripe along most of dorsal midline; two upper and no lower incisors (fig. 9C); nostrils elongated into tubes about 2–3 mm long (fig. 10C); forearm 71–79 mm; skull as in Figure 27 ...... *Nyctimene rabori*

19′. Ears and wings without yellow spots; no stripe along dorsal midline; four upper incisors and at least two lower incisors; nostrils not elongated into tubes (although when viewed from above they may appear slightly tubular); forearm 45–92 mm 20

20. Muzzle moderately long and tapered (fig. 10D); anterior surface of upper canines with vertical groove (not always prominent); wing membrane terminates above gap between outermost toe and second toe from outside (fig. 11B); forearm 80–92 mm; skull as in Figure 32 .... *Rousettus amplexicaudatus*

20′. Muzzle short and broad (fig. 10E); anterior surface of upper canines smooth, not grooved; wing membrane terminates either on outermost toe (fig. 11C) or above gap between outermost toe and second toe from outside (fig. 11B); forearm 45–92 mm 21

21. Four upper and two lower incisors (outer pair of upper incisors much smaller than inner pair; fig. 9D) 22

21′. Four upper and four lower incisors (fig. 9B) 23

22. Forearm 76–90 mm; skull as in Figure 28 .... *Ptenochirus jagori*

22′. Forearm 60–78 mm (Greater Mindanao only) .... *Ptenochirus minor*
22″. Forearm 45–52 mm .... *Megaerops wetmorei*
23. Anterior edges of ears pale; wing membrane terminates on side of foot, on outermost toe (fig. 11C); cheek teeth moderate in size; forearm 58–68 mm; skull as in Figure 20; (see Notes) .... *Cynopterus brachyotis*
23′. No pale rims to ears; wing membrane terminates above gap between first and second toe from outside (fig. 11B); cheek teeth greatly enlarged, squarish in outline with large cusps and ridges; forearm about 92 mm .... *Dyacopterus spadiceus*

Family Emballonuridae: Sheath-Tailed Bats

Sheath-tailed bats are small to moderate-sized bats (forearm 44–71 mm; table 2). They are the only bats in the Philippines in which the tail perforates the dorsal surface of the interfemoral membrane (fig. 7F), so that the basal portion (usually about half) of the tail is enclosed within the membrane and the distal portion is free, lying on the dorsal surface of the membrane. The eyes are small to moderate in size, and the ears are simple and of moderate size (fig. 8D). A tragus is always present. The muzzle is rather pointed, with the nostrils at the tip; it does not have a noseleaf.

The skulls of emballonurids have postorbital processes that are very well developed (figs. 33–35); these processes are absent in vespertilionids, which are superficially the most similar to emballonurids. Emballonurid premaxillaries are small and delicate; they do not fuse to each other at the anterior midline and are attached to the maxillaries by flexible connective tissue. The anterior edge of the palate has a deep emargination.

All of the sheath-tailed bats in the Philippines feed on insects. Common roosting sites are caves, hollow trees, and attics of buildings; they usually aggregate in moderate to large groups (ten to several hundred).

Key to Emballonuridae

1. Two distinct pairs of upper incisors; forearm 44–49 mm; skull as in Figure 33 .... *Emballonura alecto*
1′. One pair of upper incisors; forearm 61–71 mm 2
2. Forearm 61–65 mm; dorsal pelage pale brown to sandy at tips, very pale at bases; skull as in Figure 35 .... *Taphozous melanopogon*
2′. Forearm 66–71 mm; dorsal pelage very dark brown, usually with flecks of white; dark hairs do not have pale bases; skull as in Figure 34 .... *Saccolaimus saccolaimus*

Family Megadermatidae: False Vampire Bats

This is the least diverse of bat families in the Philippines, with only a single species present, *Megaderma spasma* (fig. 8B). *M. spasma* is a medium-sized bat (forearm 57–63 mm; table 2) easily recognized by its large ears that meet across the top of the forehead, erect, simple noseleaf, and lack of tail (although the interfemoral membrane is well developed).

The skull of *Megaderma spasma* is of moderate size and its stoutly constructed (fig. 36). The premaxillaries are absent, so there are no upper incisors, and the anterior edge of the palate has a deep emargination. The postorbital processes are very poorly developed. The upper canines have a large secondary cusp.

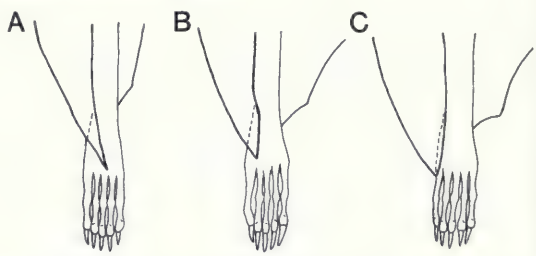


FIG. 11. Posterior attachment of wing membrane on left foot. **A,** *Macroglossus*; **B,** *Rousettus*; **C,** *Ptenochirus/Haplonycteris.*

TABLE 2. Measurement ranges of at least 10 individuals of adult Philippine Emballonuridae and Megadermatidae. Measurements, as defined in text, were taken from Philippine specimens.

Species	CBL	CCL	C'-last M	Total Length	Tail	Hind Foot	Ear	Fore-arm	Weight
Emballonura alecto	13.3–14.2	12.5–13.4	5.0–5.8	56–69	9–12	7–10	12–16	44–49	4–6.5
Saccolaimus saccolaimus	20.9–23.3	–	8.8–9.9	103–117	20–28	15–19	16–20	66–71	28–36
Taphozous melanopogon	19.6–20.6	–	8.1–8.8	100–111	20–25	11–15	20–24	61–65	20–29
Megaderma spasma	–	21.2–23.6	8.7–9.4	70–89	0	18–22	36–43	57–63	21–27

Megaderma spasma feeds primarily on large insects (especially cicadas and katydids) and occasionally on small vertebrates such as lizards, frogs, and small birds (D. Balete, pers. comm.). It has been found roosting in caves and in hollow trees, singly and in small groups.

Because only a single species is present, no key to the family is necessary.

Family Rhinolophidae: Horseshoe and Leaf-Nosed Bats

The family Rhinolophidae is composed of about ten genera and over 100 species; it is represented in the Philippines by three genera (*Coelops, Hipposideros,* and *Rhinolophus*) and at least 17 species (see Notes). All rhinolophids have a noseleaf, a structure consisting of elaborate folds of skin in the nasal region. The shape of the noseleaf varies among species and is an important character for identification (fig. 12). In members of the genus *Rhinolophus,* the posterior noseleaf is long and pointed (fig. 12A) and the anterior noseleaf is horseshoe-shaped. Between the anterior and posterior noseleaves lies the sella, an anterior-facing structure that is connected to the posterior noseleaf by the connecting process. In some species, supplementary leaflets are present lateral and ventral to the posterior noseleaf (fig. 12A). In *Coelops* and *Hipposideros,* the posterior noseleaf is low and rounded (fig. 12B) and may be divided into pockets by vertical septa. The intermediate noseleaf is a cushion-like structure. Supplementary leaflets are sometimes present lateral and ventral to the anterior noseleaf (not shown in fig. 12B, but see fig. 12A). Between the nostrils is the internarial septum. Rhinolophids lack a tragus, but many species, especially those belonging to the genus *Rhinolophus,* possess a well-developed antitragus, a flap of skin on the lower posterior margin of the ear (fig. 12). Most rhinolophids are small (forearm 34–60 mm), but a few are medium-sized (forearm up to 90 mm; table 3).

The skulls of most rhinolophids are delicate and slender, although some, especially those of the larger *Hipposideros,* are fairly stout. Postorbital processes are absent. Premaxillary bones are present but are small and connected to the skull by cartilaginous articulations, and so are movable in live or freshly killed animals. Incisors are present but are moderate to very small. The lower incisors are trilobed, although this is often inconspicuous. Many species have a strongly expanded nasal region (which supports the noseleaf structures), giving the skull a strongly sinuous dorsal profile in lateral view (figs. 37–46).

Rhinolophids are insectivorous. Some species roost in caves, in numbers ranging from a few to several hundred. Other species roost in hollow trees, hollow fallen logs, and other sites in forest. Although rhinolophids usually comprise a small proportion of captures in mist nets, at times a single species may be the most common bat species netted at a given site.

For further descriptions of members of the genus *Hipposideros,* see Hill (1963a) and Jenkins and Hill (1981). For *Rhinolophus,* see Andersen (1905a,b,c,d).

Key to Rhinolophidae

1. Posterior noseleaf pointed (fig. 12A); six pairs of lower cheek teeth .... (*Rhinolophus*) 2
1′. Posterior noseleaf low and flattened (fig. 12B); five pairs of lower cheek teeth 8
2. Forearm 68–73 mm .... *Rhinolophus rufus*
2′. Forearm 38–57 mm 3
3. Dorsal tip of connecting process sharply pointed (fig. 13A); forearm 47–49 mm .... *Rhinolophus acuminatus*

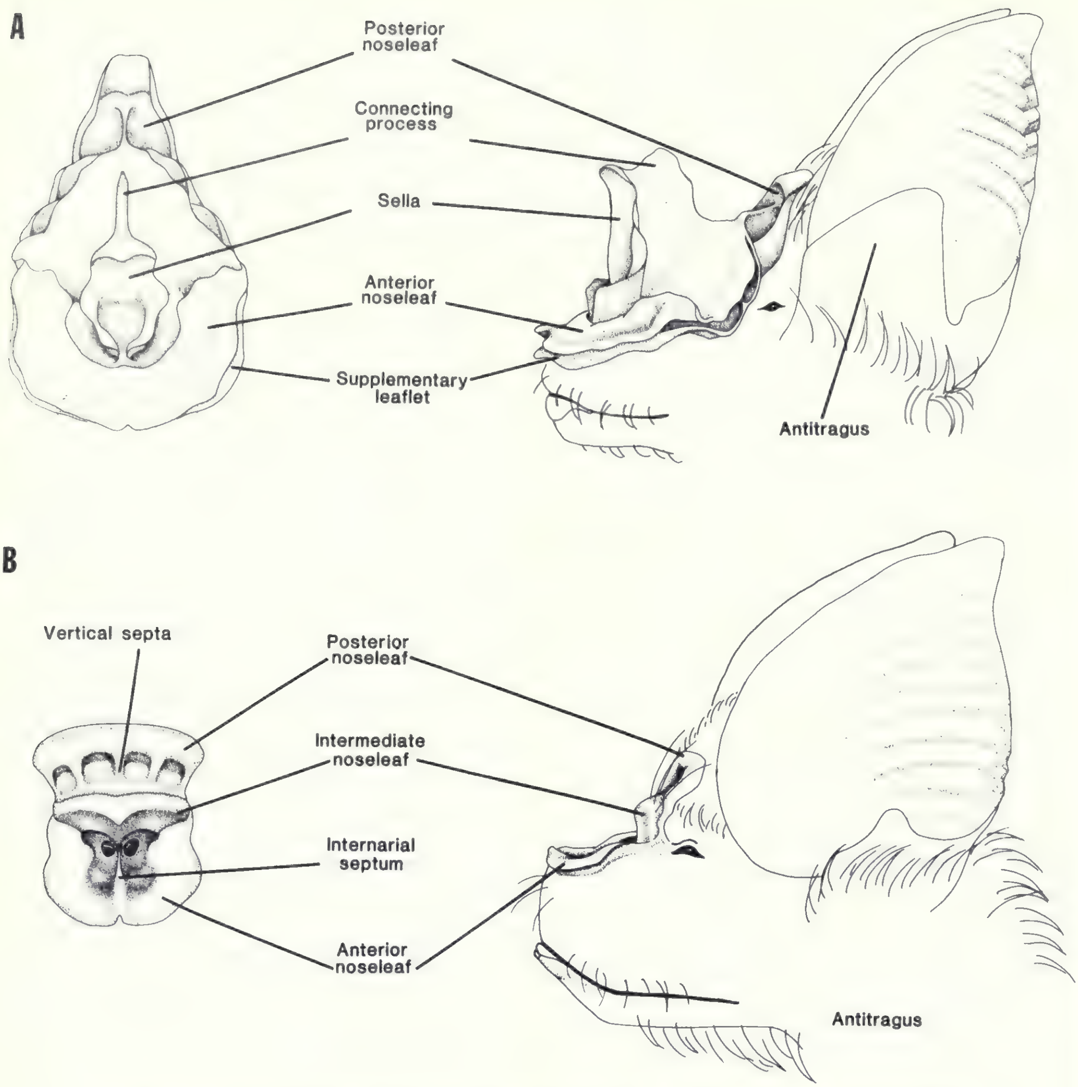


FIG. 12. Noseleaves of *Rhinolophus* and *Hipposideros*. **A,** *Rhinolophus*; **B,** *Hipposideros*.

3′. Dorsal tip of connecting process not pointed (figs. 13B,C); forearm 38–57 mm 4
4. Antitragus nearly triangular (as in fig. 12A); cup at base of sella (immediately above nostrils) 8–10 mm wide, almost as wide as anterior noseleaf; forearm 51–57 mm; skull as in Figure 45 .... *Rhinolophus philippinensis*
4′. Antitragus most nearly rectangular; cup at base of sella 2–4 mm wide, no more than half as wide as anterior noseleaf; forearm 38–56 mm 5
5. Connecting process attaches below tip of sella (fig. 13B) 6
5′. Connecting process attaches at tip of sella (fig. 13C) 7
6. Ears 25–26 mm; sella 3–4 mm wide; forearm 43–44 mm; skull as in Figure 44 (see Notes) .... *Rhinolophus macrotis*
6′. Ears 17–21 mm; sella 1–2 mm wide; forearm 38–44 mm; skull as in Figure 46 .... *Rhinolophus virgo*
7. Forearm 43–46 mm; condylocanine length 16.2–17.4 mm; maxillary toothrow 6.7–7.5 mm; skull as in Figure 42 (see Notes) .... *Rhinolophus arcuatus*-s

TABLE 3. Measurement ranges of adult Philippine Rhinolophidae. Ranges represent at least 10 individuals, except when sample sizes are given in parentheses. Measurements, as defined in text, were taken from Philippine specimens unless otherwise indicated.

Species	CBL	CCL	C^1-last M	Total Length	Tail	Hind Foot	Ear	Forearm	Weight
*Coelops hirsuta**	(1) 13.0	—	(1) 4.8	(1) 40	(1) 7	(1) 65	—	(1) 34	—
Hipposideros ater	13.9–14.9	12.9–14.1	4.5–5.5	71–81	27–36	7–10	17–20	38–43	5–7
Hipposideros bicolor	(1) 16.2	(1) 15.2	(1) 5.8	—	(1) 31	(1) 8	(1) 20	(1) 42	—
Hipposideros bicolor†	(5) 16.1–17.7	—	(9) 5.6–6.2	74–85	25–32	8–9	18–20	41–47	(9) 7–10
Hipposideros cervinus	(1) 15.5	(1) 14.9	(1) 5.3	—	—	—	—	—	—
Hipposideros cervinus†‡	(7) 15.6–17.3	—	5.8–6.5	77–81	(7) 24–32	(7) 8–9	(7) 11–16	44–50	(1) 7.5
*Hipposideros coronatus**	—	—	(1) 7.0	(1) 100	(1) 34	(1) 10	(1) 15	(1) 47	—
Hipposideros diadema (males)	26.1–29.9	24.9–28.2	10.5–12.0	140–151	44–50	16–21	30–35	79–89	34–84
Hipposideros diadema (females)	26.5–28.2	24.7–26.6	9.5–10.9	135–147	39–51	17–21	28–32	77–86	33–66
Hipposideros obscurus	15.4–17.2	14.7–16.7	5.8–6.7	71–79	18–24	10–12	18–22	42–48	7–12
Hipposideros pygmaeus	12.0–13.3	11.1–12.5	4.3–4.8	60–73	21–27	6–8	11–15	37–40	(3) 3–4
Rhinolophus acuminatus	19.5–20.5	(1) 18.3	7.4–8.1	(1) 85	(1) 25	(5) 11–13	(4) 16–20	(5) 47–49	(3) 10–14
Rhinolophus arcuatus-s§	17.4–19.0	16.2–17.4	6.7–7.5	68–73	16–23	9–12	19–22	43–45.5	7–9.5
Rhinolophus arcuatus-l§	19.3–20.9	17.9–19.0	7.7–8.1	73–81	18–26	11–12	22–25	47–50	8.5–10
Rhinolophus inops	21.6–22.9	19.9–21.0	8.3–9.2	78–90	20–27	12–15	22–28	49–55	11–16
Rhinolophus macrotis	(3) 17.5–18.6	(4) 15.6–17.5	(8) 5.8–6.8	(2) 71–72	(2) 23–25	(2) 8–9	(2) 25–26	(2) 43–44	(1) 6
Rhinolophus philippinensis	(3) 21.7–22.2	(3) 19.9–20.3	(4) 7.9–8.2	(6) 89–94	(6) 29–33	(6) 10–12	(6) 28–36	(6) 51–57	(2) 11
Rhinolophus rufus	(6) 27.3–29.9	(6) 25.3–26.4	(6) 11.0–12.2	(8) 110–130	(7) 30–33	(7) 17–21	(8) 33–37	(8) 68–73	(8) 26–34
Rhinolophus subrufus	(6) 22.3–24.0	(1) 21.8	9.0–9.5	(8) 80–90	(9) 20–23	12–15	24–27	(9) 51–56	—
Rhinolophus virgo	15.5–16.7	14.2–15.2	5.7–6.4	62–73	18–26	7–10	17–21	38–44	(6) 5–7

* Measurements from Taylor, 1934.
† Borneo.
‡ Sulawesi.
§ See Notes section for explanation.

7′. Forearm 47–50 mm; condylocanine length 17.9–19.0 mm; maxillary toothrow 7.7–8.1 mm; skull as in Figure 41 (see Notes) ... *Rhinolophus arcuatus*-l

7″. Forearm 49–55 mm; condylocanine length 19.9–21.0 mm; maxillary toothrow 8.3–9.2 mm; skull as in Figure 43 (see Notes) ... *Rhinolophus inops*

7‴. Forearm 51–56 mm; condylocanine length about 21.8 mm; maxillary toothrow 9.0–9.5 mm (see Notes) ... *Rhinolophus subrufus*

8. Tail absent; anterior noseleaf bilobed with two lateral leaflets underneath that project downward; no ridges on ears; well-developed secondary cusps on upper canines; forearm about 34 mm ... *Coelops hirsuta*

8′. Tail present, greater than 15 mm; anterior noseleaf undivided, without leaflets that project downward; ridges on ears; only one cusp on upper canines; forearm 37–89 mm ... (*Hipposideros*) 9

9. Forearm 77–89 mm; cream-colored patch of fur anterior to leading edge of wing; skull as in Figure 38 ... *Hipposideros diadema*

9′. Forearm 37–50 mm ... 10

10. Two pairs of supplementary leaflets (see fig. 12A) lateral to anterior noseleaf ... 11

10′. No supplementary leaflets lateral to anterior noseleaf ... 12

11. Inner pair of lateral leaflets meet under anterior noseleaf but outer pair do not; forearm 37–40 mm; skull as in Figure 40 ... *Hipposideros pygmaeus*

11′. Both pairs of lateral leaflets do not meet under anterior noseleaf; forearm 44–50 mm ... *Hipposideros cervinus*

12. No vertical septa in posterior noseleaf and tail >30 mm; forearm about 47 mm (see Notes) ... *Hipposideros coronatus*

12′. Vertical septa may or may not be present in posterior noseleaf; if they are absent, then tail 18–24 mm; forearm 38–48 mm ... 13

13. Anterior noseleaf 5.5–7.0 mm wide, intermediate noseleaf 5.0–6.0 mm wide, posterior noseleaf 6.0–8.0 mm wide; hind foot length 10–12 mm; forearm 42–48 mm; skull as in Figure 39 ... *Hipposideros obscurus*

13′. Anterior noseleaf 4.0–5.0 mm wide, intermediate noseleaf 3.5–4.0 mm wide, posterior noseleaf 4.5–5.5 mm wide; hind foot length 7–10 mm; forearm 38–43 mm ... 14

14. Internarial septum not swollen at base; forearm about 42 mm ... *Hipposideros bicolor*

14′. Internarial septum swollen at base; forearm 38–43 mm; skull as in Figure 37 ... *Hipposideros ater*

Family Vespertilionidae: Evening Bats

This is an exceptionally large and diverse family, with about 40 genera and 275 species worldwide and about 11 genera and 22 species in the Philippines. Vespertilionids are identified as having a long tail that is completely enclosed by the interfemoral membrane (except occasionally the extreme tip; fig. 7C), a simple face without a noseleaf (among species in the Philippines; fig. 8F), and a well-developed tragus. Most vespertilionids are small to medium-sized (forearm 22–55 mm; table 4) and have small eyes.

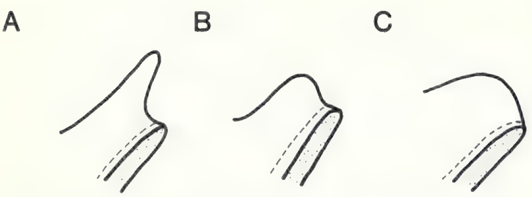


FIG. 13. Lateral views of connecting processes of some rhinolophids. **A,** *R. acuminatus*; **B,** *R. macrotis* (that of *R. virgo* is very similar); **C,** *R. subrufus*/*R. arcuatus*.

The skulls of vespertilionids are generally small, with a great variety of shapes and degrees of robustness (figs. 47–59). The braincase is high and domed in some genera (e.g., *Miniopterus, Myotis*; figs. 48–50, 52–55) and exceptionally low and flattened in others (e.g., *Tylonycteris*). They all lack postorbital processes. All species have a deep emargination at the anterior end of the palate, so that the incisors on either premaxillary are widely separated. The molariform teeth are generally typical of those of insectivorous bats, with broad crowns and sharp, shearing crests.

All of the vespertilionids in the Philippines are insectivorous. Roosting sites include caves, buildings, foliage, hollow trees, unfurled banana leaves,

TABLE 4. Measurement ranges of adult Philippine Vespertilionidae. Ranges represent at least 10 individuals, except when sample sizes are given in parentheses. Measurements, as defined in text, were taken from Philippine specimens unless otherwise indicated.

Species	CBL	CCL	C^1-last M	Total Length	Tail	Hind Foot	Ear	Forearm	Weight
*Glischropus tylopus**	(1) 11.4	10.7–11.6	4.3–4.5	70–90	33–40	6	10–11	26–30	—
Harpiocephalus harpia	(1) 20.6	(1) 19.7	(1) 6.9	(2) 121–125	(2) 46–51	(2) 13–14	(2) 18–19	(2) 51	19
Kerivoula hardwickii	(3) 12.6–12.7	(3) 11.9–12.4	(3) 5.1–5.4	(3) 77–88	(3) 38–47	(3) 8–10	(3) 14–15	(3) 34–35	(2) 4–5
Kerivoula pellucida	(1) 14.1	(1) 13.5	(1) 6.5	(1) 90	(1) 40	(1) 9	(1) 15	(1) 35	—
Kerivoula whiteheadi	(2) 11.8–12.1	(2) 11.3–11.4	(2) 5.2	(2) 66–72	(2) 31–37	(2) 7–8	(2) 12–14	(2) 30	—
Miniopterus australis	12.5–13.4	11.7–12.5	5.0–5.4	81–91	34–43	7–9	9–11	34–39	5–7
Miniopterus schreibersi	14.2–15.4	13.1–14.2	5.7–6.3	101–112	46–57	8–10	11–13	42–46	8–14
Miniopterus tristis	18.2–19.0	16.7–17.5	7.5–8.1	115–134	50–61	10–12	15–17	51–55	16–22
Murina cyclotis	(4) 16.6–17.5	(4) 15.8–16.8	(4) 5.9–6.3	(4) 90–101	(4) 38–42	(4) 9–12	(4) 14–17	(4) 36–39	(4) 9–11
Myotis horsfieldii	13.5–14.2	12.6–13.2	5.3–5.7	83–95	30–41	10–12	12–16	35–38	5–6.5
Myotis macrotarsus	16.3–17.4	14.9–16.0	6.7–7.1	98–114	39–49	15–17	16–19	44–49	10–15
Myotis muricola	11.8–12.6	10.9–11.7	4.5–5.0	69–79	30–38	6–8	11–14	30–34	3–4
Myotis rufopictus	(4) 17.1–19.2	(4) 16.1–17.9	(4) 7.1–8.5	(1) 115	(1) 48	(1) 14	(1) 20	(2) 52–53	(1) 17
Philetor brachypterus	(7) 14.0–14.6	(7) 12.5–13.7	(7) 4.4–5.0	(7) 90–99	(7) 31–39	(7) 9–11	(7) 13–15	(7) 34–39	(7) 11–13
*Phoniscus jagorii**,†	(1) 15.4	—	(2) 6.6–7.2	(2) 89–94	(2) 40–42	(2) 8–9	(1) 17	(1) 39	—
Pipistrellus javanicus	12.6–13.6	11.8–12.8	4.5–5.0	75–90	29–37	7–10	10–13	32–36	4–6
Pipistrellus petersi	(2) 14.6–14.8	(2) 14.0	(2) 5.7	—	—	—	—	(1) 38	—
*Pipistrellus stenopterus**,‡	(4) 15.1–15.9	(6) 14.9–15.3	(6) 5.7–6.1	(1) 92	(1) 36	(1) 11	(1) 13	(4) 38–40	12–16
Pipistrellus tenuis	(6) 11.2–11.7	(6) 10.6–11.0	(6) 3.9–4.2	(6) 68–76	(6) 26–31	(4) 6–7	(6) 11–12	(4) 30–32	3–4
Scotophilus kuhlii	17.4–18.7	16.4–17.8	6.1–6.9	110–131	40–52	10–13	12–16	47–53	17–22
Tylonycteris pachypus	9.7–10.3	9.1–9.7	3.1–3.5	(2) 60–62	(2) 24–25	—	(2) 7–8	22–25	1–2
Tylonycteris robustula	(4) 11.5–11.9	(4) 11.0–11.3	(4) 4.0–4.1	(2) 71–75	(2) 27	—	(2) 8–9	(3) 24–27	—

* Borneo.
† Bali.
‡ Malaya.

and bamboo internodes. Some species have been captured only within forest, whereas others are common in urban areas. Species that roost in caves and buildings often form large colonies, ranging from hundreds to tens of thousands.

Many vespertilionid species that occur in the Philippines are described in Hill (1983). Other useful descriptions can be found in Francis and Hill (1986), Heaney and Alcala (1986), Hill (1963b, 1965, 1966, 1971), Kock (1981), and Tate (1942).

Key to Vespertilionidae

1. Nostrils elongated into short tubes that open laterally (fig. 14A); long orange hairs on dorsal surface of interfemoral membrane and feet; tragus straight and pointed, at least half length of ear (fig. 15A) 2
1′. Nostrils not elongated into tubes (fig. 14B); hairs on interfemoral membrane very short and almost invisible; tragus shape and size varies between species 3
2. Forearm 36–39 mm; five well-developed pairs of upper cheek teeth; skull as in Figure 51 . . . . *Murina cyclotis*
2′. Forearm about 51 mm; fifth pair of upper cheek teeth minute or absent (see Notes) . . . . *Harpiocephalus harpia*
3. Posterior margin of ear has a pronounced concave inflection near tip and forms a large, rounded flap below inflection, producing funnel-shaped ears (fig. 15B); tragus straight and pointed, at least half length of ear 4
3′. No large, rounded flap on posterior margin of ear (figs. 15C,D); tragus shape and size varies between species 7
4. Longitudinal groove on anterior surface of upper canines; individual hairs of dorsal pelage with four bands of color (dark at base, then buff, then dark brown, tip buff or golden), producing a flecked or salt-and-pepper appearance; forearm about 39 mm . . . . *Phoniscus jagorii*
4′. Upper canines not grooved; hairs of dorsal pelage have two or three bands of color; forearm 30–35 mm . . . . (*Kerivoula*) 5
5. Bases of dorsal hairs pale; forearm about 35 mm . . . . *Kerivoula pellucida*
5′. Bases of dorsal hairs dark; forearm 30–35 mm 6
6. Anterior two pairs of upper and lower premolars narrow and elongate, oval in cross-section; forearm about 30 mm . . . . *Kerivoula whiteheadi*
6′. Anterior two pairs of upper and lower premolars approximately round in cross-section; forearm 34–35 mm; skull as in Figure 47 . . . . *Kerivoula hardwickii*
7. One pair of upper incisors, which are large and conical; dorsal pelage rusty orange; forearm 47–53 mm; skull as in Figure 59 . . . . *Scotophilus kuhlii*
7′. Two pairs of upper incisors; color of dorsal pelage varies between species; forearm 22–55 mm . . . 8
8. Tragus erect and tapering (fig. 15C) . . . . (*Myotis*) 9
8′. Tragus blunt (e.g., fig. 15D) 12
9. Wing membrane black except for reddish orange skin along digits; dorsal pelage reddish orange; forearm 52–53 mm; skull as in Figure 55 . . . . *Myotis rufopictus*
9′. Wings uniformly colored; dorsal pelage gray or brown 10
10. Posterior margin of wing membrane terminates on ankle (fig. 16A); hind foot 15–17 mm; forearm 44–49 mm; skull as in Figure 53 . . . . *Myotis macrotarsus*
10′. Posterior margin of wing membrane terminates on side of foot, below ankle (figs. 16B,C); hind foot 6–12 mm; forearm 30–38 mm 11
11. Posterior margin of wing membrane terminates on side of foot, at least 1 mm above base of outermost toe (fig. 16B); hind foot 10–12 mm; forearm 35–38 mm; skull as in Figure 52 . . . . *Myotis horsfieldii*
11′. Posterior margin of wing membrane terminates on side of foot at base of outermost toe (fig. 16C); hind foot 6–8 mm; forearm 30–34 mm; skull as in Figure 54 . . . . *Myotis muricola*
12. Pads present on feet and wrists (fig. 17); forearm 22–30 mm 13
12′. No pads on feet and wrists; forearm 30–55 mm 15
13. Pads on feet and wrists pink or white; dorsal fur dark at base; posterior margin of wing membrane

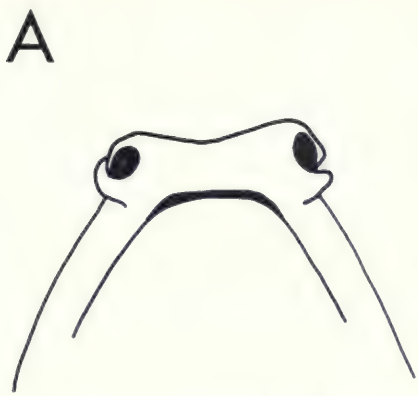


Fig. 14. Ventral views of muzzles of *Murina* (**A**) and *Myotis* (**B**).

terminates on side of foot, at base of outermost toe; five pairs of upper cheek teeth; forearm 26–30 mm .... *Glischropus tylopus*

13′. Pads on feet and wrists dark brown; dorsal fur not dark at base; posterior margin of wing membrane terminates on ankle or on side of foot, at least 1 mm above base of outermost toe; four pairs of upper cheek teeth; forearm 22–27 mm .... (*Tylonycteris*) 14

14. Lower third of posterior margin of ear distinctly thicker than rest of ear (fig. 18A); forearm 24–27 mm .... *Tylonycteris robustula*

14′. Lower third of posterior margin of ear not distinctly thicker than rest of ear (fig. 18B); forearm 22–25 mm .... *Tylonycteris pachypus*

15. Most distal bone of third digit of wing about three times length of adjoining phalanx .... (*Miniopterus*) 16

15′. Most distal bone of third digit of wing (fig. 2) not more than two times length of adjoining phalanx 17

16. Forearm 51–55 mm; tail 50–61 mm; skull as in Figure 50 .... *Miniopterus tristis*

16′. Forearm 42–46 mm; tail 46–57 mm; skull as in Figure 49 .... *Miniopterus schreibersi*

16″. Forearm 34–39 mm; tail 34–43 mm; skull as in Figure 48 .... *Miniopterus australis*

17. Posterior margin of wing membrane terminates on lower leg, at or above ankle; fifth digit of wing (see fig. 2) does not extend beyond midpoint between first and second joint of third digit 18

17′. Posterior margin of wing membrane terminates on side of foot, below ankle (as in figs. 16B,C); fifth digit of wing extends beyond midpoint between first and second joint of third digit 19

18. Inner upper incisors transversely elongate in cross-section, about three times as wide as outer upper incisors; outer secondary cusp on inner upper incisors is not as high but almost as wide as the main cusp; forearm 34–39 mm; skull as in Figure 56 .... *Philetor brachypterus*

18′. Inner upper incisors conical in shape, about two times as wide as outer upper incisors; outer

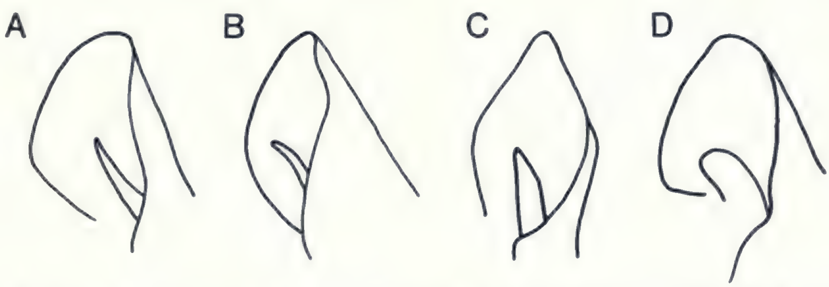


Fig. 15. Left external ears (pinnae) of some vespertilionids. **A,** *Murina/Harpiocephalus*; **B,** *Kerivoula/Phoniscus*; **C,** *Myotis*; **D,** *Pipistrellus*.

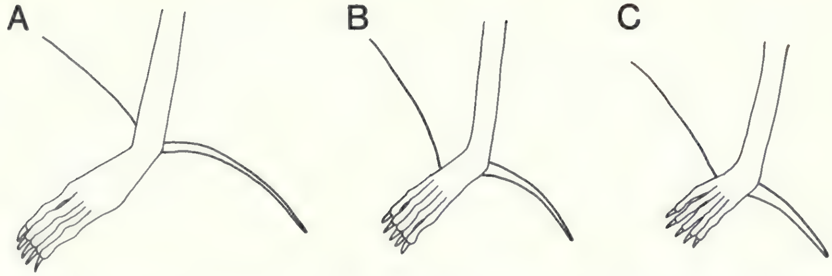


FIG. 16. Left hind feet of *Myotis* spp., showing attachment of wing membrane. **A,** *M. macrotarsus*; **B,** *M. horsfieldii*; **C,** *M. muricola.*

secondary cusp on inner upper incisors is much narrower than main cusp; forearm 38–40 mm . . . . *Pipistrellus stenopterus*

19. Forearm about 39 mm . . . . *Pipistrellus petersi*

19′. Forearm 32–36 mm; tail 29–34 mm; skull as in Figure 57 . . . . *Pipistrellus javanicus*

19″. Forearm 30–32 mm; tail 26–31 mm; skull as in Figure 58 . . . . *Pipistrellus tenuis*

Family Molossidae: Free-Tailed Bats

This family of at least 80 species is represented in the Philippines by only four species. As the English name for the family implies, molossid bats are the only bats with long tails that project well beyond the posterior edge of the interfemoral membrane (fig. 7E). The wings tend to be unusually long and narrow for the size of the bats. There is no noseleaf; the lips are often wrinkled and thick and the upper lip thickly sprinkled with short, bristly hairs (fig. 8E). The eyes are moderate to small. The external ear is moderately small, with the tragus small and the antitragus well developed. Philippine molossids are of moderate to large size, with forearms ranging from 40 to 90 mm (table 5). Two of the species in the Philippines (both *Cheiromeles*) have only scattered hairs over most of their bodies, leading to their common name, "naked bats."

The skulls of molossids are characterized by moderately sturdy construction, lack of postorbital processes, and broad, strong molars (fig. 60). Among Philippine molossids, the anterior edge of the palate is continuous, so that the upper pairs of incisors are separated by no more than a narrow gap. The jaws are powerful, and the large masseteric muscles on the head attach to a moderate to high sagittal crest.

These bats are strong, fast fliers that feed primarily on beetles and other large insects. *Chaerephon plicata,* which roosts in caves and occasion-

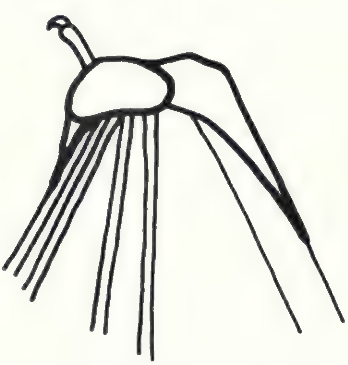


FIG. 17. Pad on right wrist of *Glischropus.*

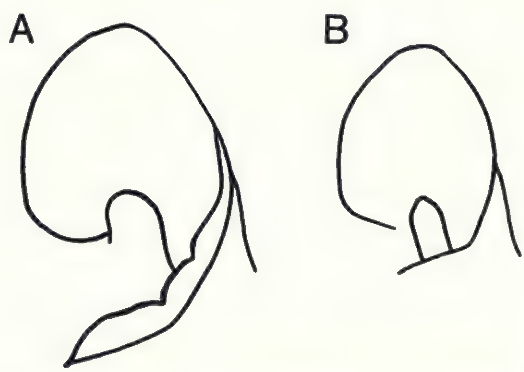


FIG. 18. Left ears of *Tylonycteris.* **A,** *T. robustula*; **B,** *T. pachypus.*

ally in buildings, probably once formed the largest colonies of bats in the Philippines, exceeding 100,000 individuals, according to early descriptions, but most colonies are now much reduced in size or entirely destroyed. *Cheiromeles parvidens* and *C. torquatus* are known to roost in hollow coconut palms, hollow trees, and occasionally in caves, and *Mops sarasinorum* in hollow trees, where they form colonies of four to hundreds of individuals.

The systematics of bats of this family has been reviewed by Freeman (1981).

Key to Molossidae

1. Body furred; upper lip wrinkled; forearm 39–45 mm; ears joined together over top of head by narrow band of skin 2
1′. Body almost naked; upper lip not wrinkled; forearm 73–90 mm; ears separate, not joined across top of head .... (*Cheiromeles*) 3
2. Five upper cheek teeth, including a small anterior premolar that is very much smaller than the other cheek teeth (fig. 60); condylocanine length 14.9–15.5 mm; forearm 40–43 mm; skull as in Figure 60 .... *Chaerephon plicata*
2′. Four upper cheek teeth; condylocanine length 17.3–17.8 mm; forearm 39–45 mm .... *Mops sarasinorum*
3. Forearm 73–78 mm (occurs throughout the Philippines except Palawan) .... *Cheiromeles parvidens*
3′. Forearm 80–90 mm (occurs only in Palawan region) .... *Cheiromeles torquatus*

Notes

The following brief comments on the status of several species of Philippine bats are intended to make users of the key aware of potential taxonomic problems and of recent records of bats that are referred to in the text.

Acerodon lucifer

This species is known only from the type series collected on Panay Island in 1888. Based on current knowledge, it differs from most *Acerodon jubatus* only on the basis of smaller size, but it overlaps with some populations for all measurements. It is possible that careful study will show it to have defining characters that are not yet recognized, or, alternatively, to be a geographic variant of the widespread *A. jubatus*.

Cynopterus brachyotis

Philippine representatives of the genus *Cynopterus* have until recently been referred to *C. brachyotis*, which is widespread in Southeast Asia. Based primarily on morphometric analyses, however, Kitchener and Maharadatunkamsi (1990) split what had been known as *Cynopterus brachyotis* into several species, allocating Philippine specimens to *C. luzoniensis* based on a single sample from Negros Island. We have not yet been able to examine enough material to evaluate their proposed changes and have therefore followed the older terminology, while recognizing that further study may support the proposed revision.

Pteropus dasymallus

This species has been reported previously only from Japan, Taiwan, and adjacent and intervening islands. We have recently identified several specimens in FMNH, PNM, and USNM from the Babuyan and Batanes islands, which lie between northern Luzon and Taiwan, as representing this species. Details will be published elsewhere. The species is very similar to *P. hypomelanus*, differing most visibly in that the pelage is longer and denser, and the dorsal surface of the hind leg is thickly furred nearly to the ankle (rather than being nearly naked).

Hipposideros coronatus

No specimens of this moderately large horseshoe bat have been reported since the species was described in 1871 (Peters, 1871). Our placement

TABLE 5. Measurement ranges of adult Philippine Molossidae. Ranges represent at least 10 individuals, except when sample sizes are given in parentheses. Measurements, as defined in text, were taken from Philippine specimens unless otherwise indicated.

Species	CBL	CCL	C^1-last M	Total Length	Tail	Hind Foot	Ear	Forearm	Weight
Chaerephon plicata	15.7–16.3	14.9–15.5	6.1–6.5	95–101	28–34	10–12	16–20	40–43	—
*Cheiromeles parvidens**	(1) 29.1	(2) 27.5–28.2	(2) 10.5–10.6	(4) 170–185	(4) 54–58	—	(4) 19–20	(4) 73–78	—
Cheiromeles torquatus†‡	(1) 29.9	(1) 28.4	(1) 11.5	(1) 261	(1) 59	(1) 26	(1) 29	80–90	—
*Mops sarasinorum**	(7) 18.2–18.7	(7) 17.3–17.8	(7) 7.1–7.3	90–109	30–36	11–13	18–22	39–45	—

* External measurements from Taylor, 1934.
† External measurements taken from Bornean specimens.
‡ Forearm (of Thai bats) from Lekagul and McNeely, 1977.

of the species in the key is based solely on the original description and the comments of Taylor (1934).

Rhinolophus anderseni

This species is known only from the holotype, which we have been unable to examine. As noted under the following species, it is possible that recently taken specimens may be referred to this species, but this remains uncertain.

Rhinolophus arcuatus

Heaney et al. (1991) recently noted that bats previously identified as belonging to this species appear to fall into two morphotypes: one is slightly smaller with a narrower anterior noseleaf and is typically found in lowland caves or disturbed habitats, and the other is slightly larger with a proportionately wider anterior noseleaf and is usually found in primary upland forest. We designate these in the key as "*R. arcuatus*-s" and "*R. arcuatus*-l", respectively. J. Hill (in litt.) has suggested that one of these may be *R. anderseni,* but we have not examined the relevant holotypes and so remain uncertain of the appropriate use of names. More specimens, especially of the larger upland form, are badly needed.

Rhinolophus inops and *R. subrufus*

Our studies of specimens currently in collections have indicated that Philippine bats in this species group may be broken into at least two morphs, based on size; these are very similar in morphology of the noseleaf and skull. In this key, we refer the range of smaller bats to *R. inops* and that of the larger ones to *R. subrufus.* However, we note that there are several unresolved problems with these bats.

First, the noseleaf of the holotype of *R. inops* has a distinctly shaped sella: the tip is modified into a downward-projecting triangular pouch (Andersen, 1905c). This modified sella is not found in any other specimen that has been referred to *R. inops* or in any other species in the genus; it may represent an aberration found in only one individual or it may be a diagnostic character for a species still known only from the holotype, with the other specimens referred to *R. inops* actually representing an undescribed species.

Second, the definition of *R. inops* is complicated by the variation in size among specimens that we have assigned to *R. inops*; available specimens from Negros are consistently smaller than those from Leyte and Biliran, whereas those from Catanduanes are intermediate (specimens from elsewhere are inadequate for comparison). It is possible that each morph represents a distinct species. Additional specimens and further study will be needed to clarify the status of all of these bats.

Rhinolophus macrotis

The Philippine form of *R. macrotis* was first described as a distinct species, *R. hirsutus* (Andersen, 1905b), but was later subsumed under *R. macrotis* (Tate, 1943). We have examined the holotypes and referred specimens of both taxa and find that they differ in overall size, in proportionate tail length, and in the size and shape of noseleaf structures, particularly the sella. We suspect that the Philippine population is morphologically distinct and genetically independent and will eventually be shown to be a distinct species, but we refrain from making this change because we have not conducted comprehensive studies.

Harpiocephalus harpia

Three specimens of this large and striking vespertilionid have been taken recently, one on Leyte (Rickart et al., in prep.), one on Luzon (Heaney et al., in prep.), and one on Negros (Utzurrum, pers. comm.). Further details will be published elsewhere.

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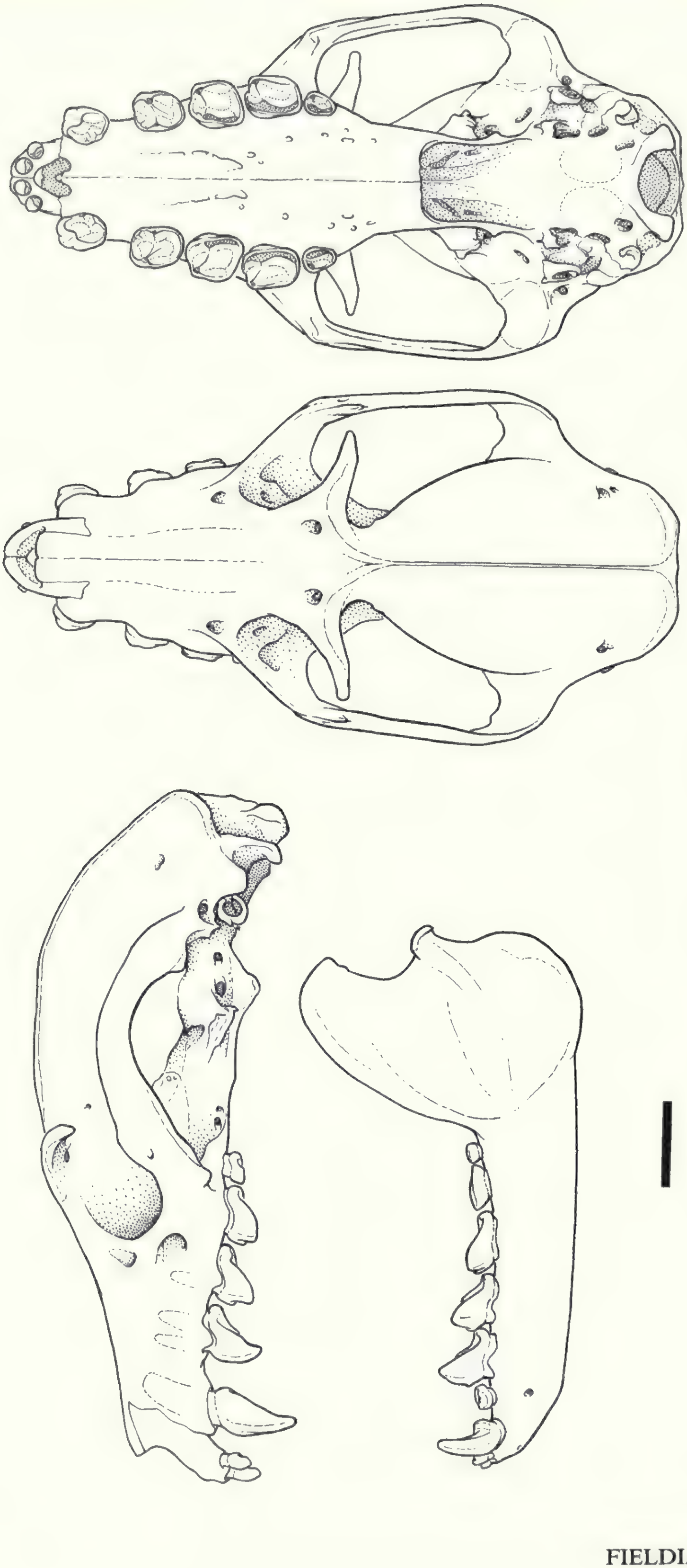

FIG. 19. Skull of *Acerodon jubatus* (USNM 74321). Scale = 10 mm.

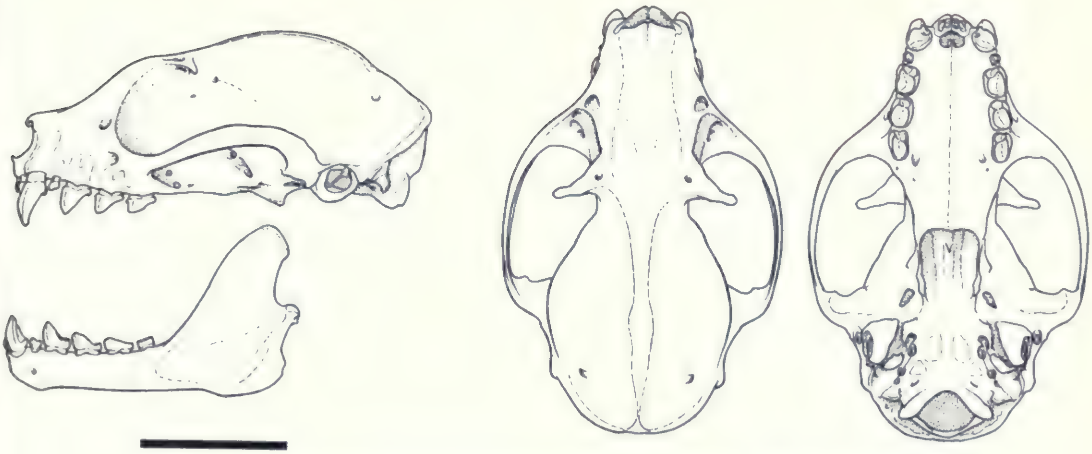

FIG. 20. Skull of *Cynopterus brachyotis* (UMMZ 156664). Scale = 10 mm.

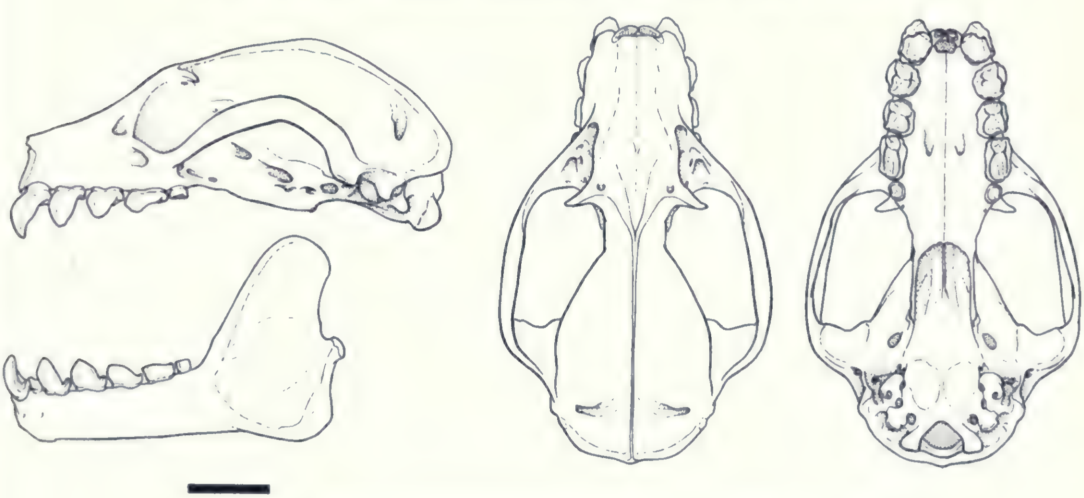

FIG. 21. Skull of *Dobsonia chapmani* (DMNH 5131). Scale = 10 mm.

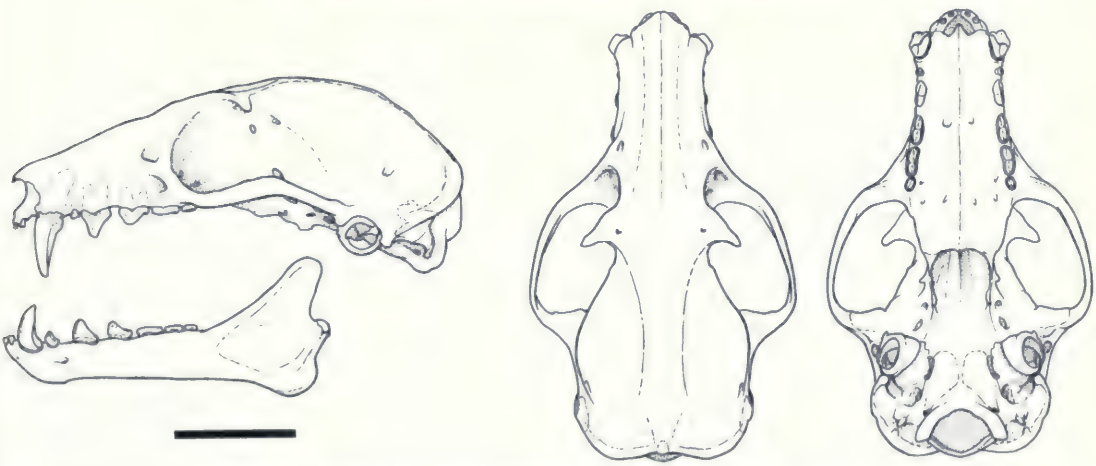

FIG. 22. Skull of *Eonycteris robusta* (UMMZ 162221). Scale = 10 mm.

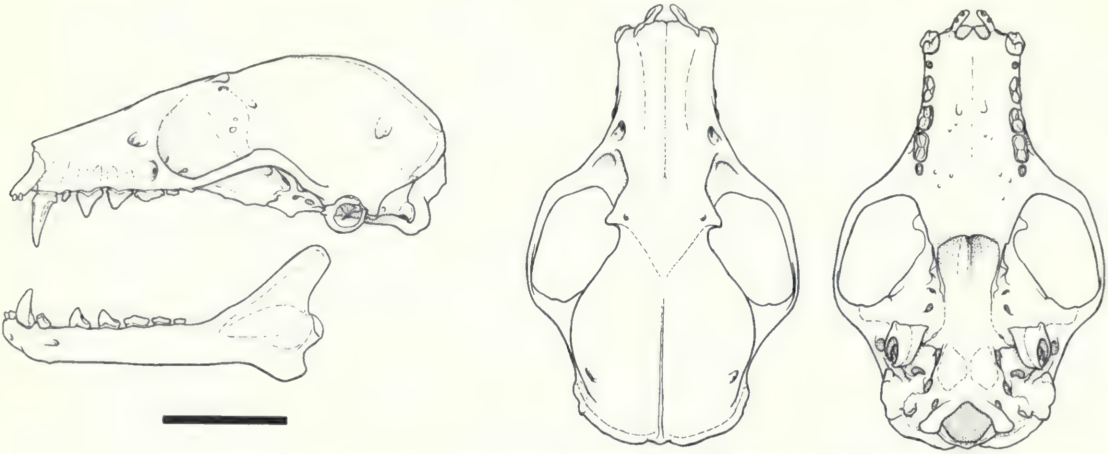

Fig. 23. Skull of *Eonycteris spelaea* (UMMZ 158482). Scale = 10 mm.

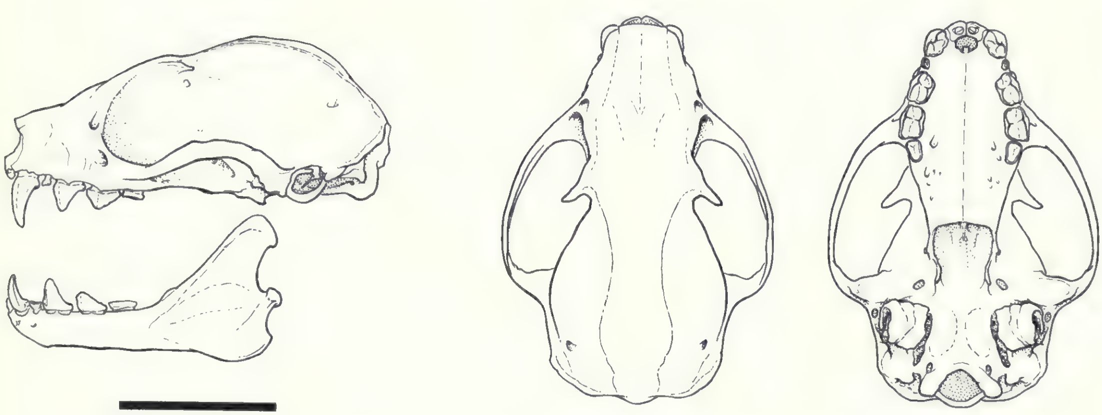

Fig. 24. Skull of *Haplonycteris fischeri* (UMMZ 157047). Scale = 10 mm.

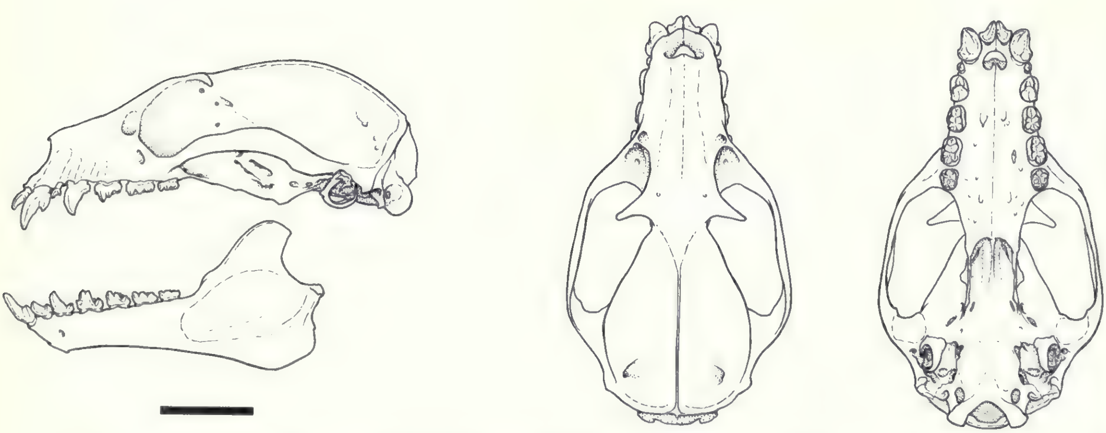

Fig. 25. Skull of *Harpyionycteris whiteheadi* (UMMZ 158838). Scale = 10 mm.

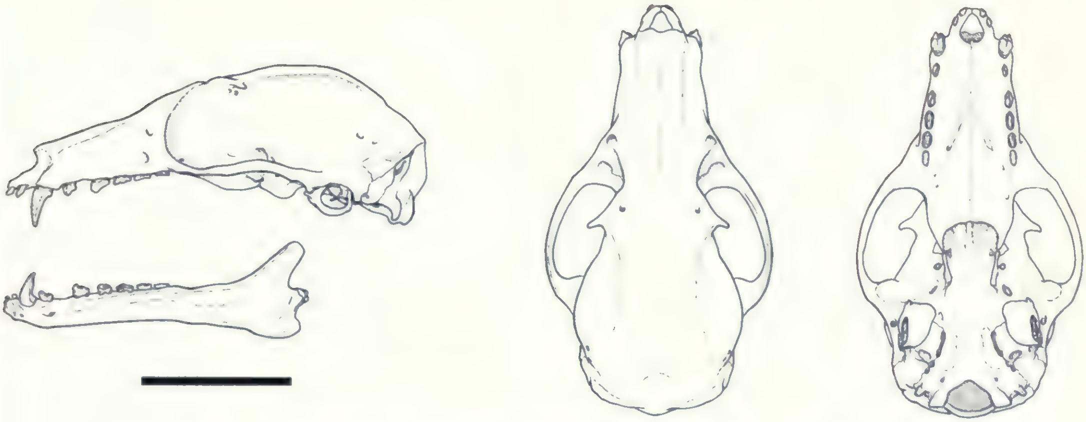

FIG. 26. Skull of *Macroglossus minimus* (UMMZ 158725). Scale = 10 mm.

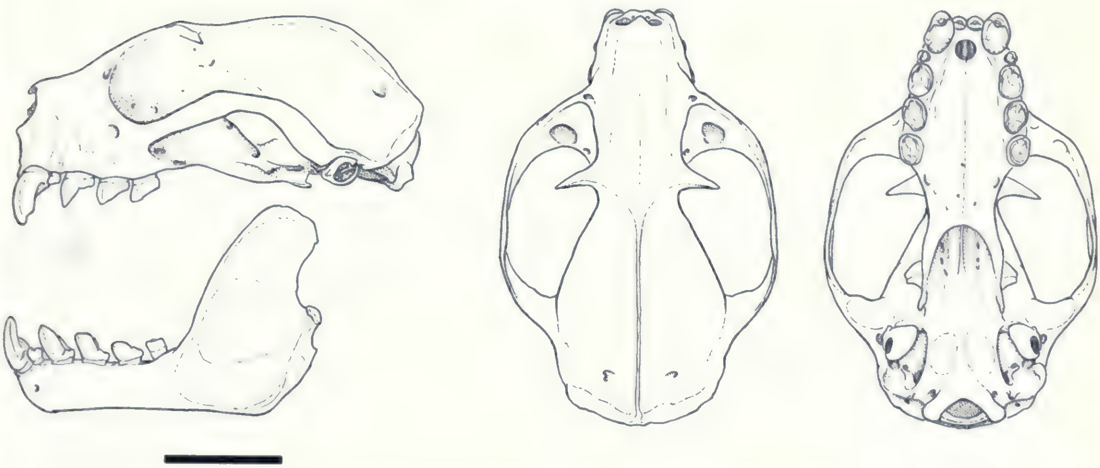

FIG. 27. Skull of *Nyctimene rabori* (USNM 458281). Scale = 10 mm.

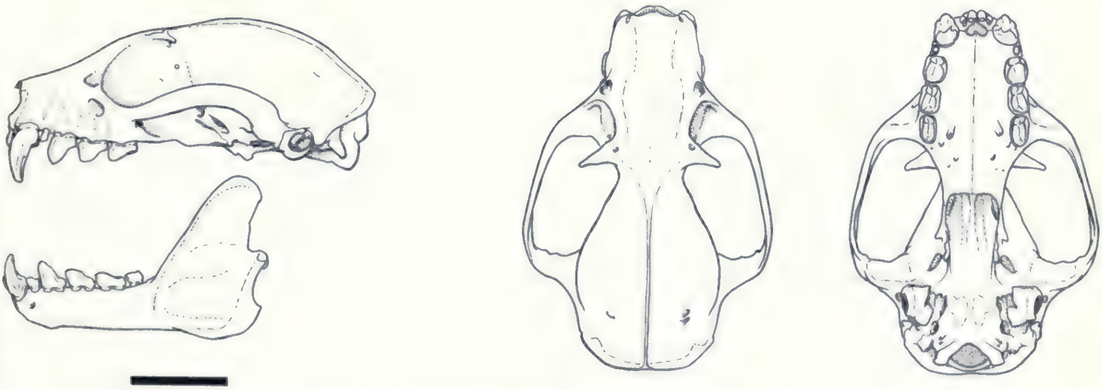

FIG. 28. Skull of *Ptenochirus jagori* (UMMZ 158513). Scale = 10 mm.

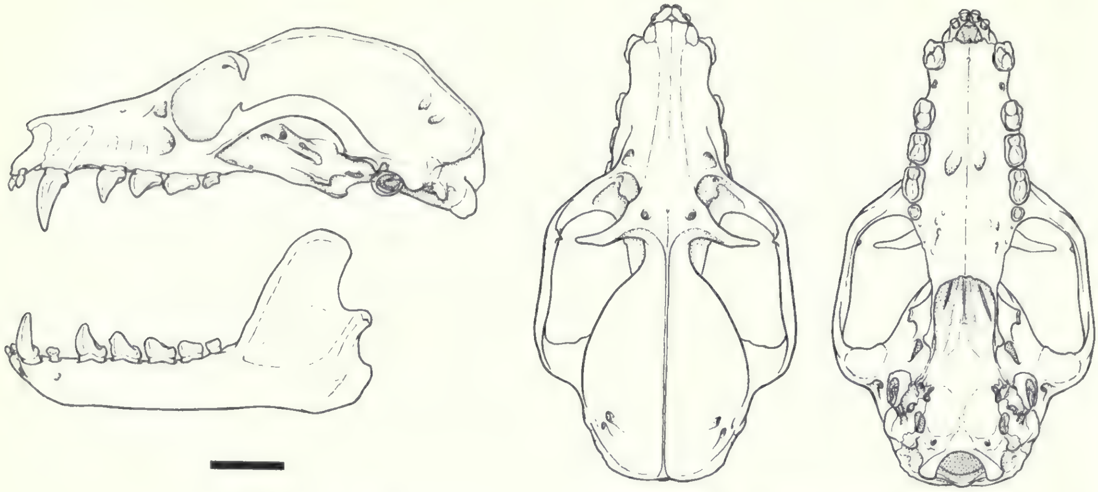

FIG. 29. Skull of *Pteropus hypomelanus* (USNM 105443). Scale = 10 mm.

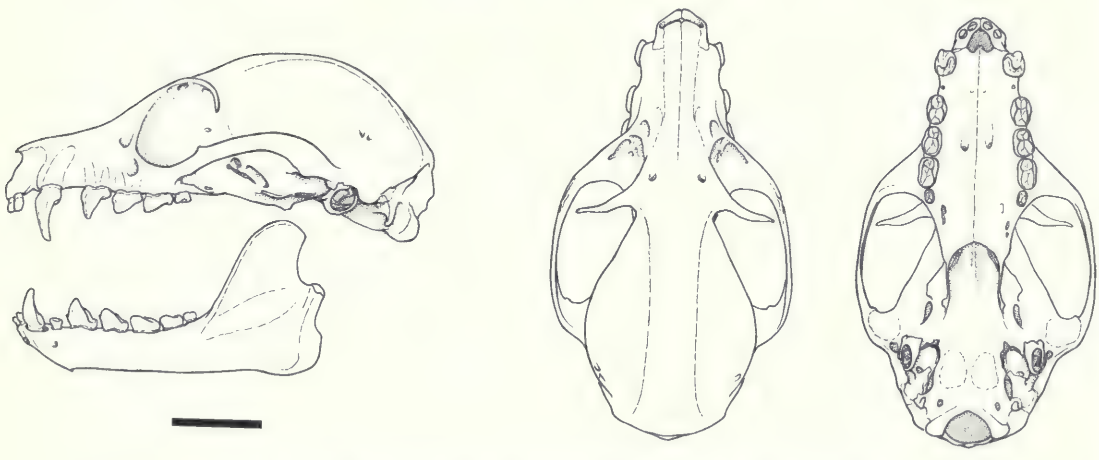

FIG. 30. Skull of *Pteropus pumilus* (UMMZ 158517). Scale = 10 mm.

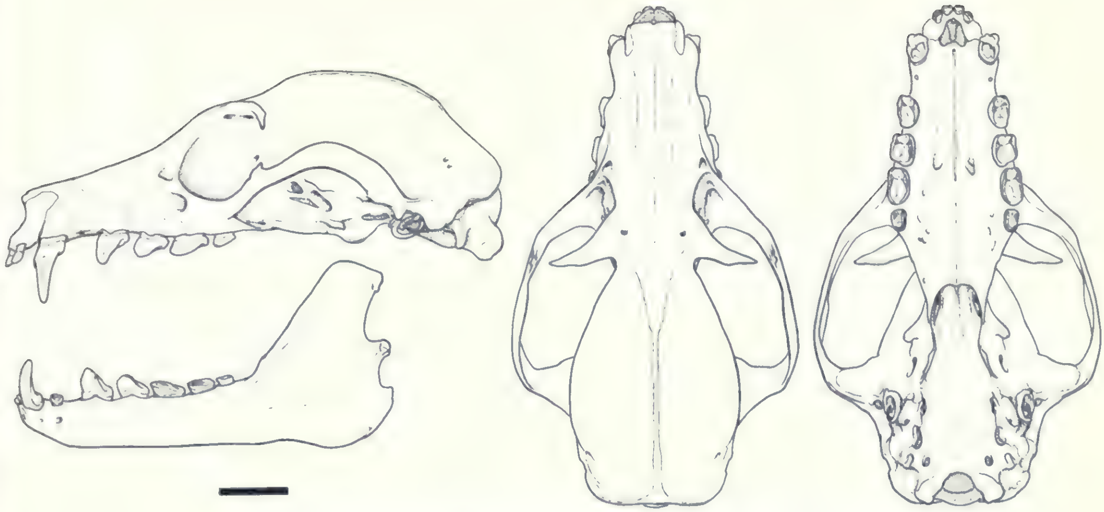

FIG. 31. Skull of *Pteropus vampyrus* (UMMZ 158849). Scale = 10 mm.

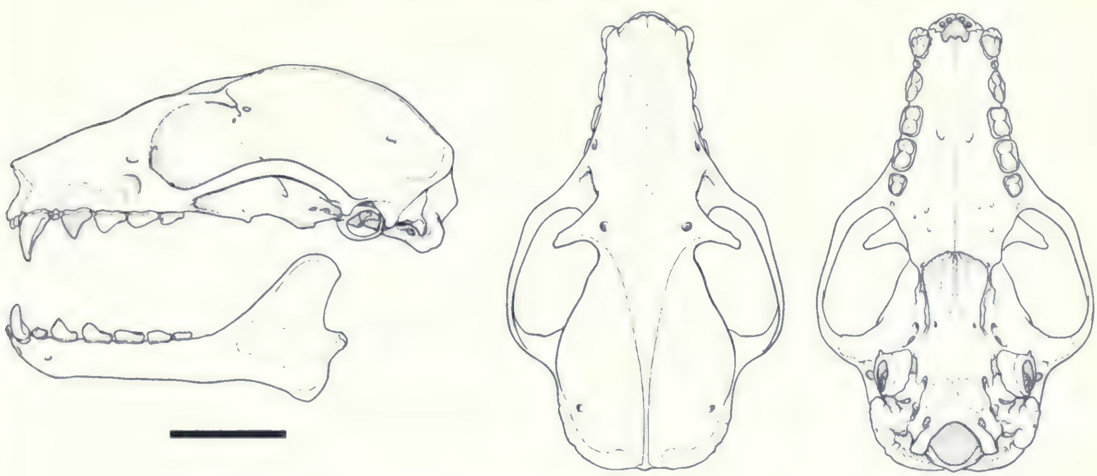

FIG. 32. Skull of *Rousettus amplexicaudatus* (UMMZ 162304). Scale = 10 mm.

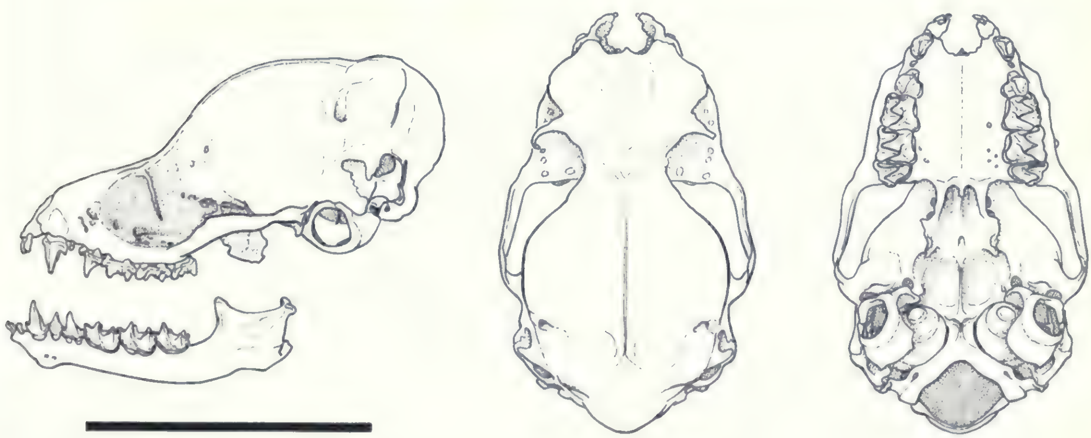

FIG. 33. Skull of *Emballonura alecto* (USNM 458536). Scale = 10 mm.

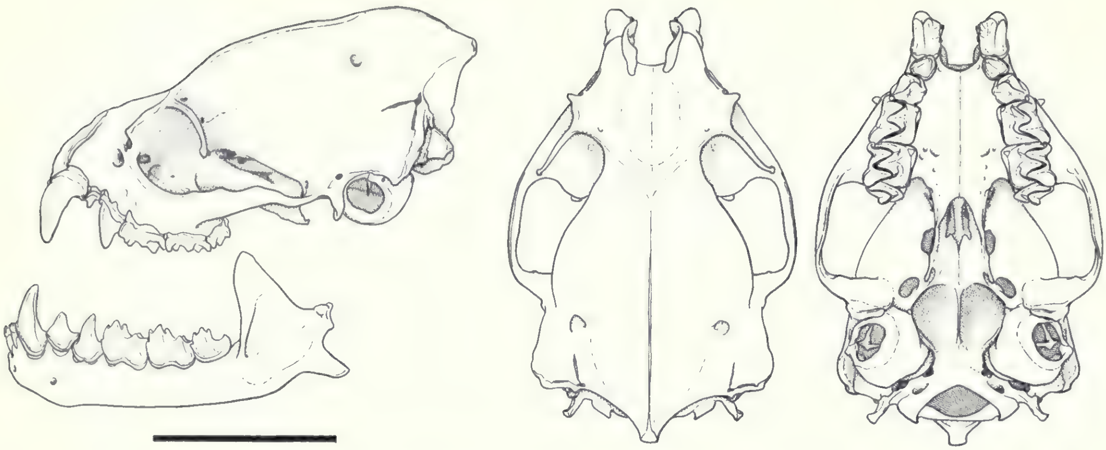

FIG. 34. Skull of *Saccolaimus saccolaimus* (USNM 458555). Scale = 10 mm.

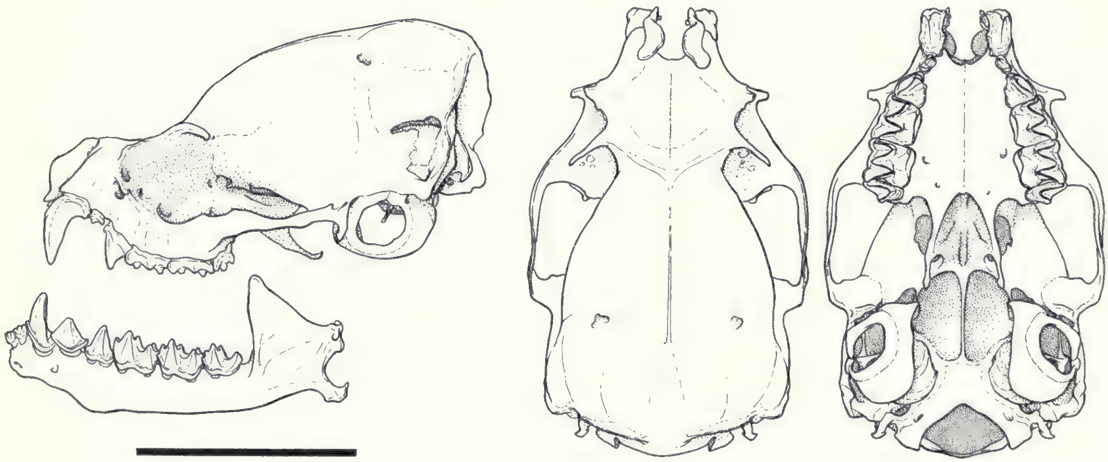

FIG. 35. Skull of *Taphozous melanopogon* (USNM 458571). Scale = 10 mm.

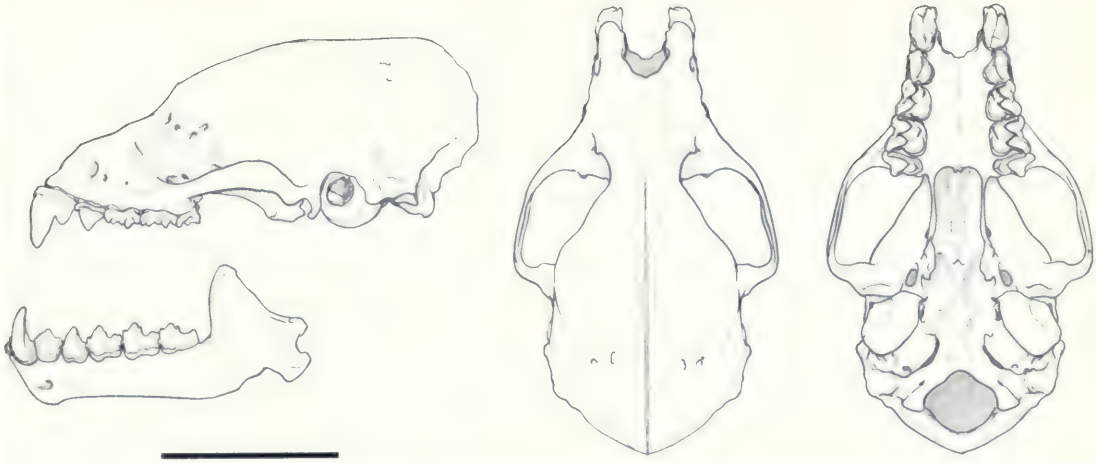

FIG. 36. Skull of *Megaderma spasma* (UMMZ 160295). Scale = 10 mm.

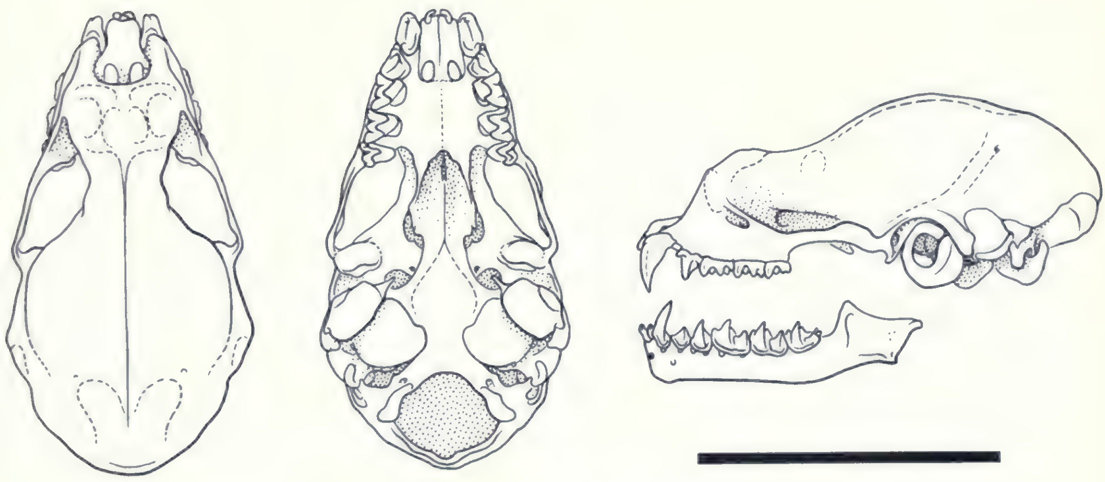

FIG. 37. Skull of *Hipposideros ater* (ROM 40735). Scale = 10 mm.

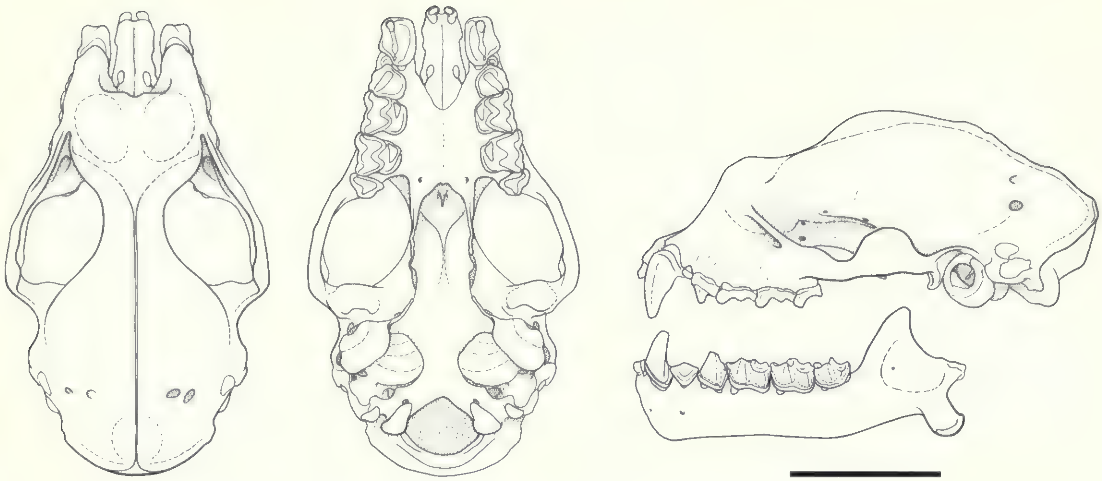

FIG. 38. Skull of *Hipposideros diadema* (UMMZ 160296). Scale = 10 mm.

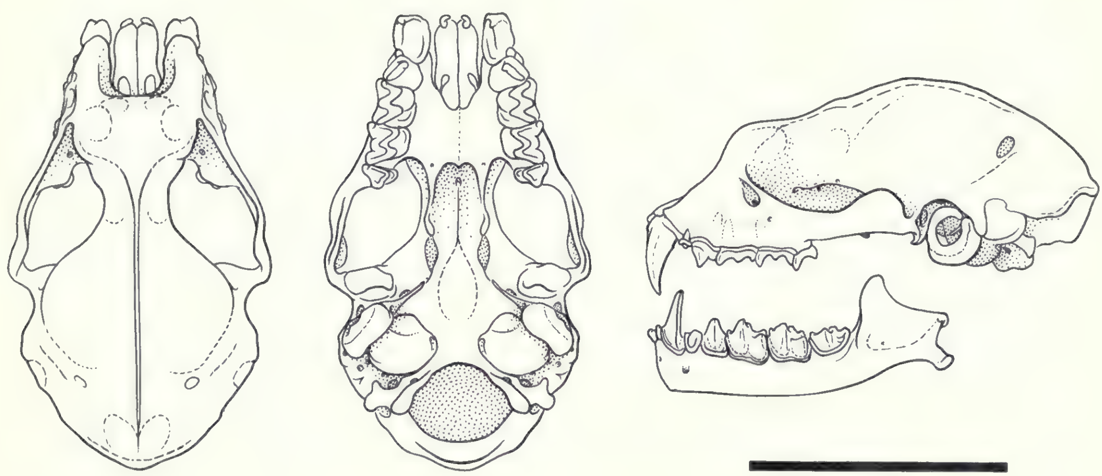

FIG. 39. Skull of *Hipposideros obscurus* (SU 787). Scale = 10 mm.

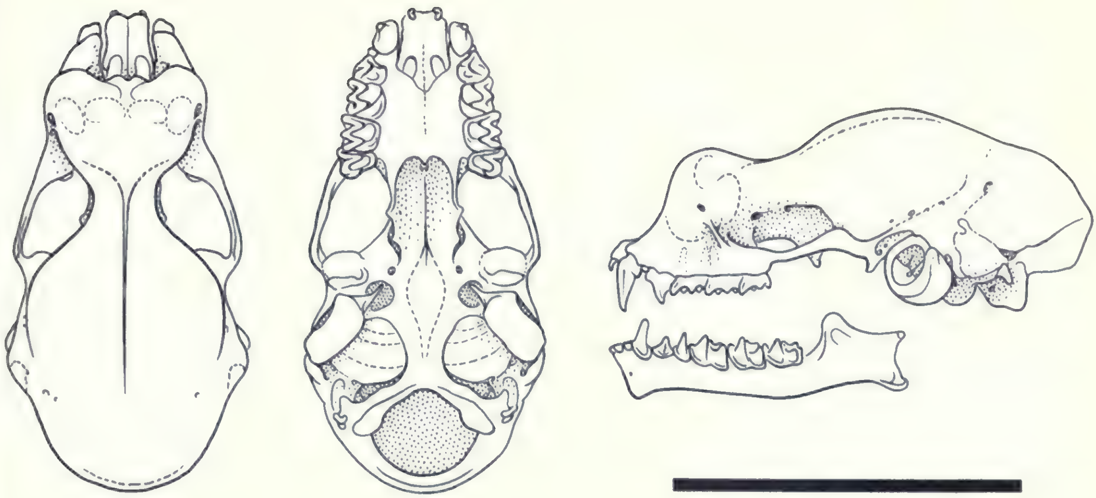

FIG. 40. Skull of *Hipposideros pygmaeus* (UMMZ 156872). Scale = 10 mm.

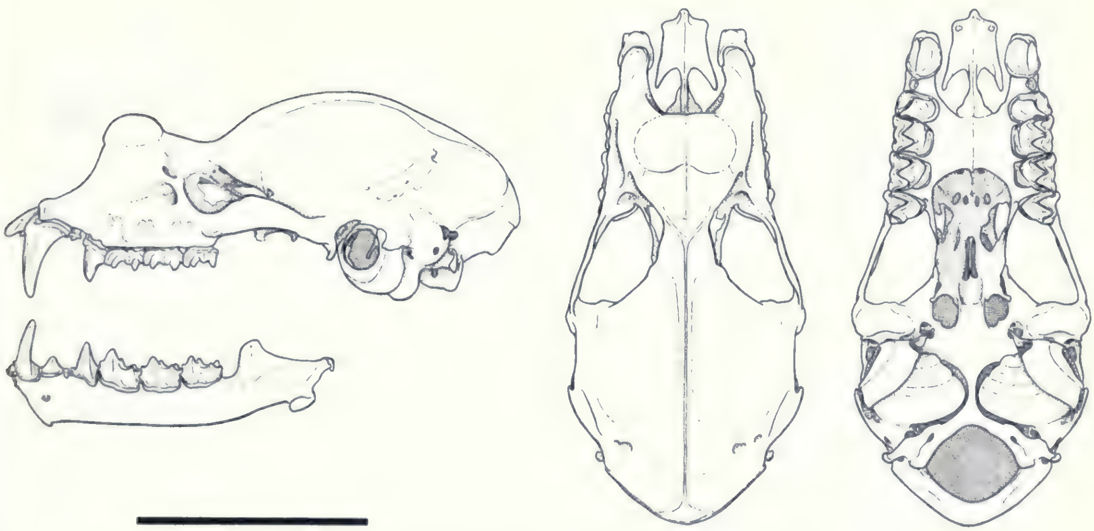

FIG. 41. Skull of *Rhinolophus arcuatus*-I (UMMZ 158526). Scale = 10 mm.

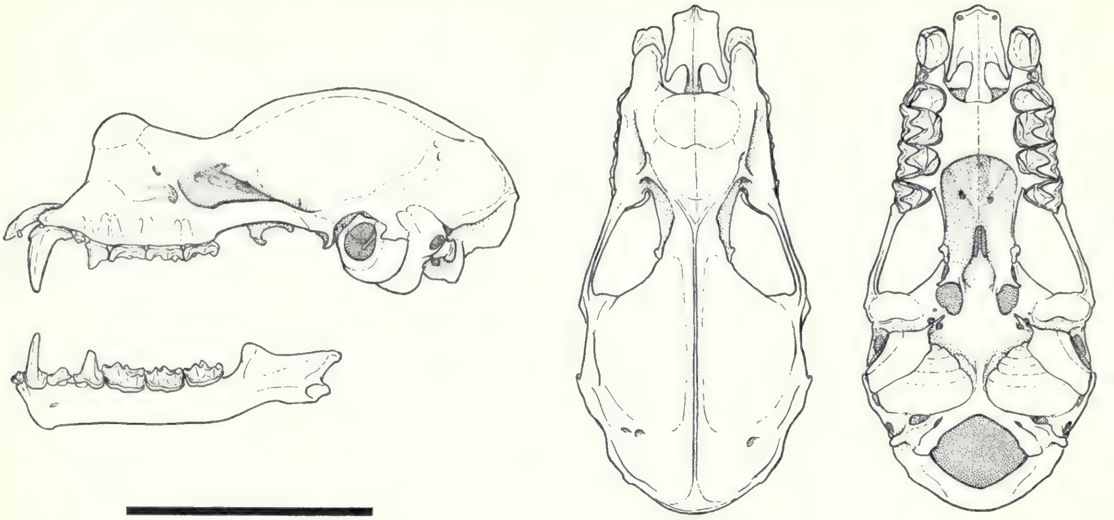

FIG. 42. Skull of *Rhinolophus arcuatus*-s (UMMZ 157106). Scale = 10 mm.

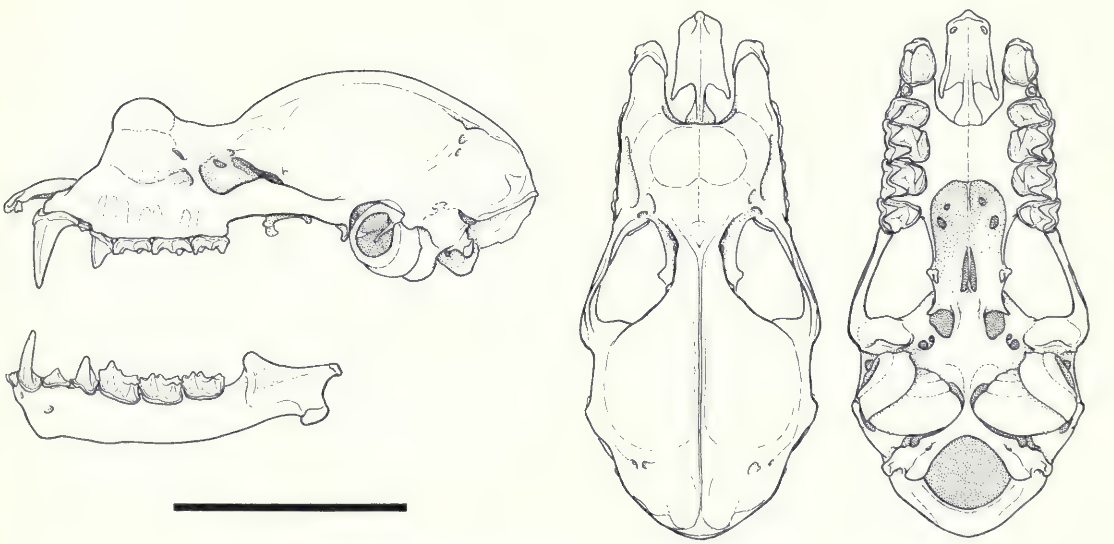

FIG. 43. Skull of *Rhinolophus inops* (USNM 459495). Scale = 10 mm.

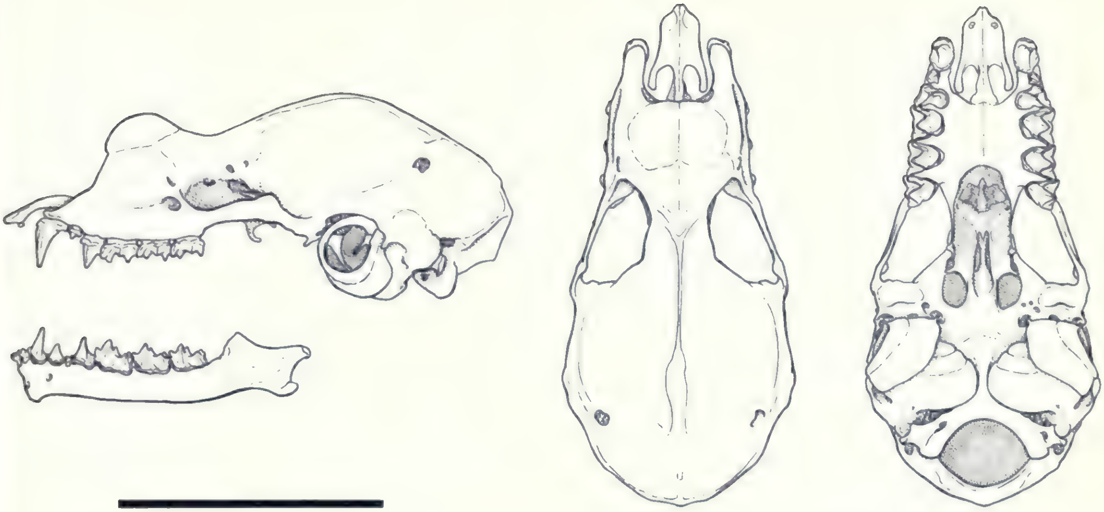

FIG. 44. Skull of *Rhinolophus macrotis* (UMMZ 160328). Scale = 10 mm.

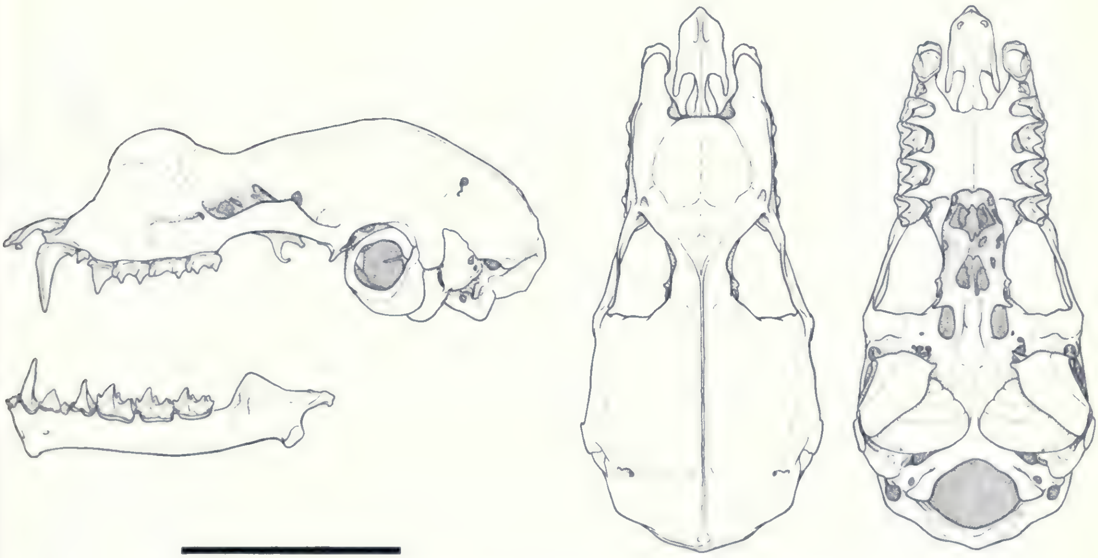

FIG. 45. Skull of *Rhinolophus philippinensis* (UMMZ 459497). Scale = 10 mm.

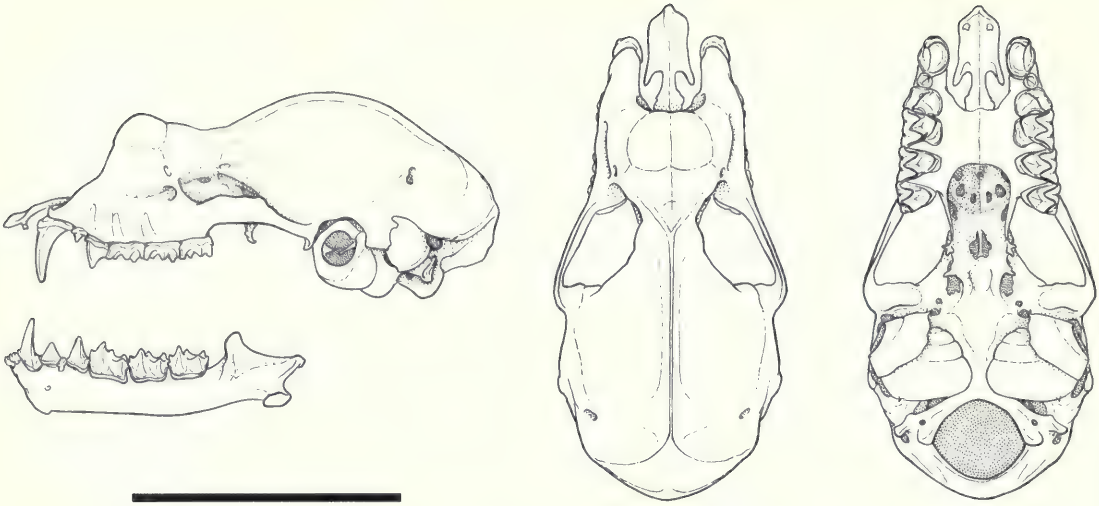

FIG. 46. Skull of *Rhinolophus virgo* (USNM 459454). Scale = 10 mm.

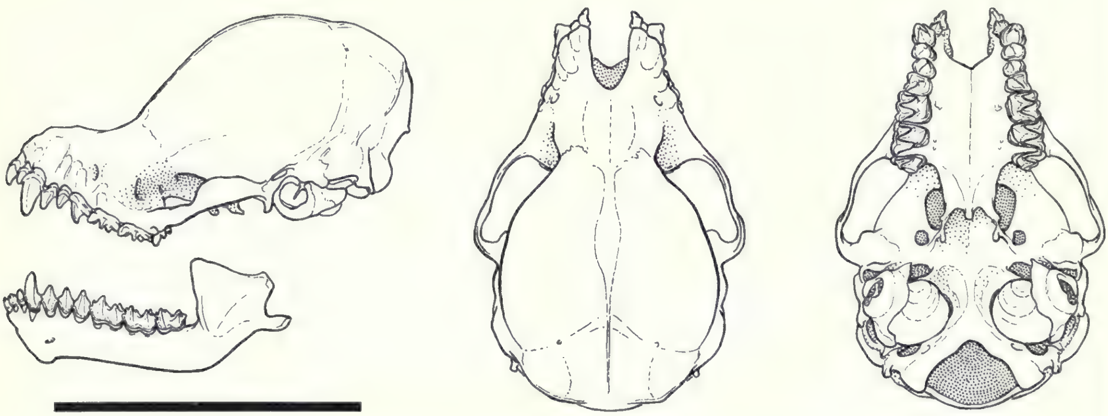

FIG. 47. Skull of *Kerivoula hardwickii* (USNM 459511). Scale = 10 mm.

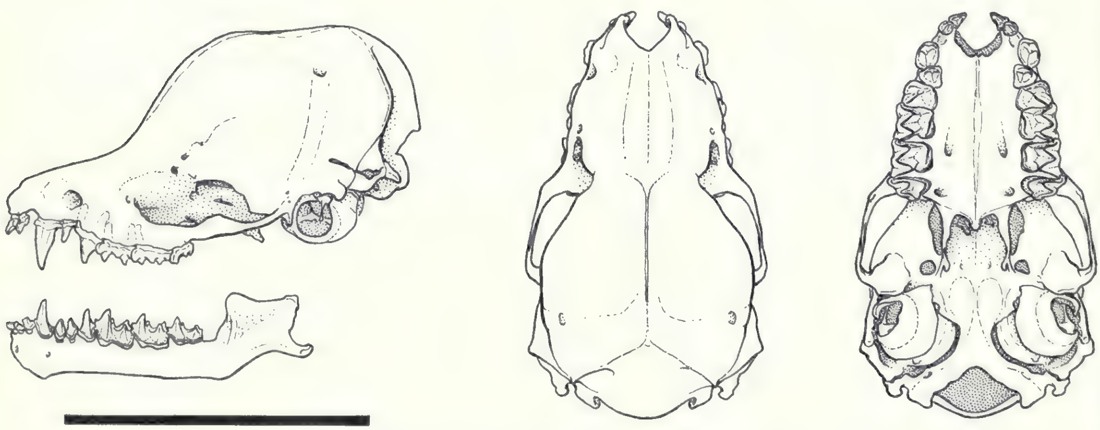

FIG. 48. Skull of *Miniopterus australis* (USNM 458658). Scale = 10 mm.

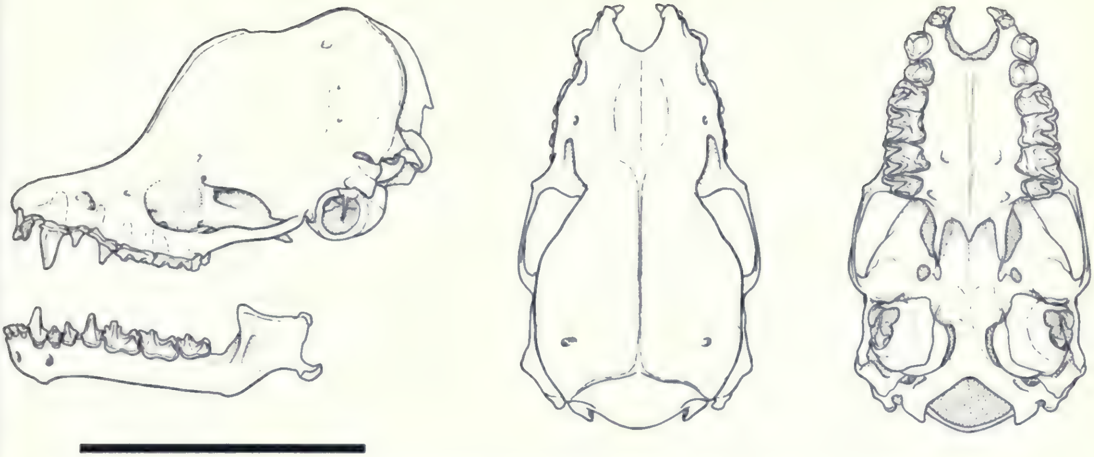

FIG. 49. Skull of *Miniopterus schreibersi* (UMMZ 157001). Scale = 10 mm.

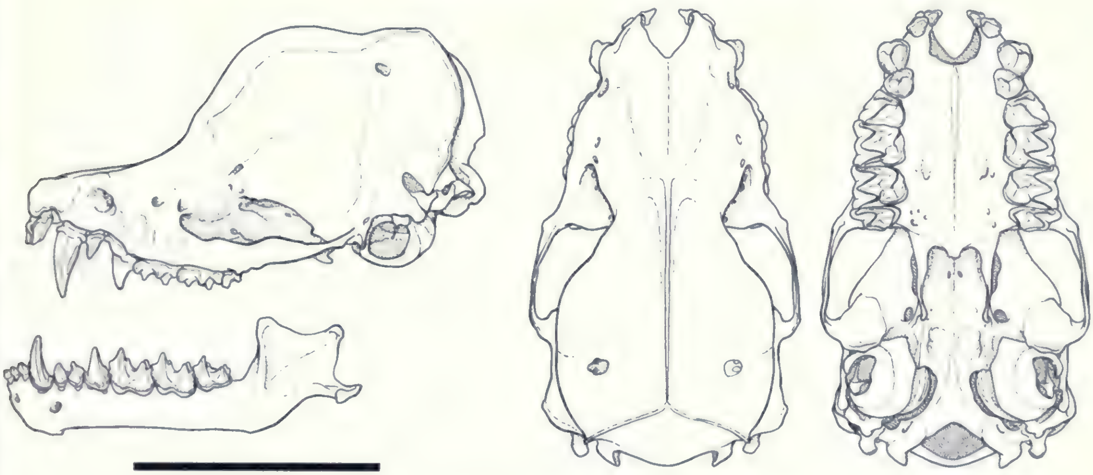

FIG. 50. Skull of *Miniopterus tristis* (USNM 458680). Scale = 10 mm.

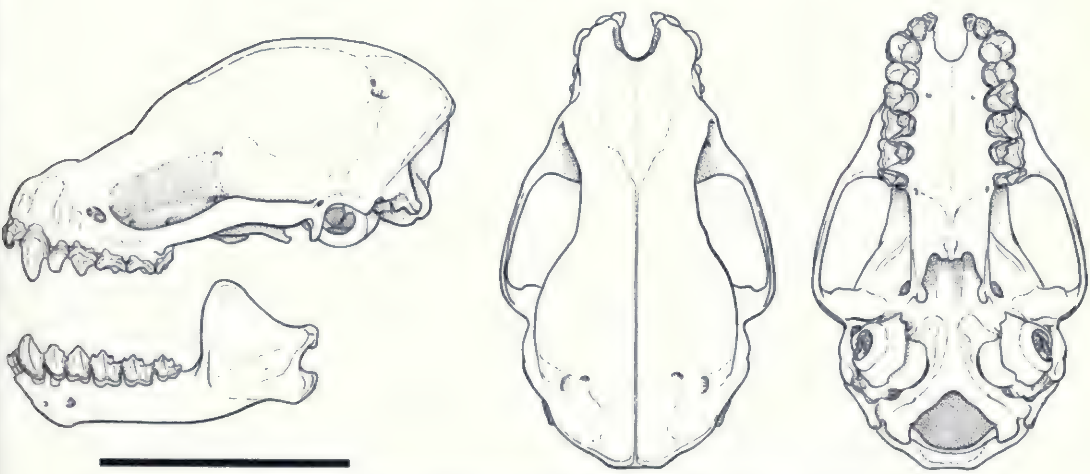

FIG. 51. Skull of *Murina cyclotis* (USNM 573776). Scale = 10 mm.

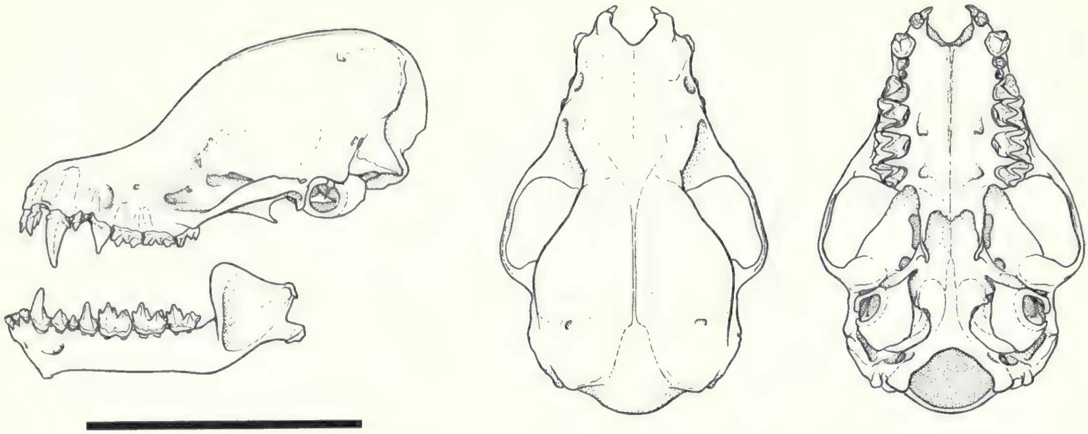

FIG. 52. Skull of *Myotis horsfieldii* (UMMZ 158872). Scale = 10 mm.

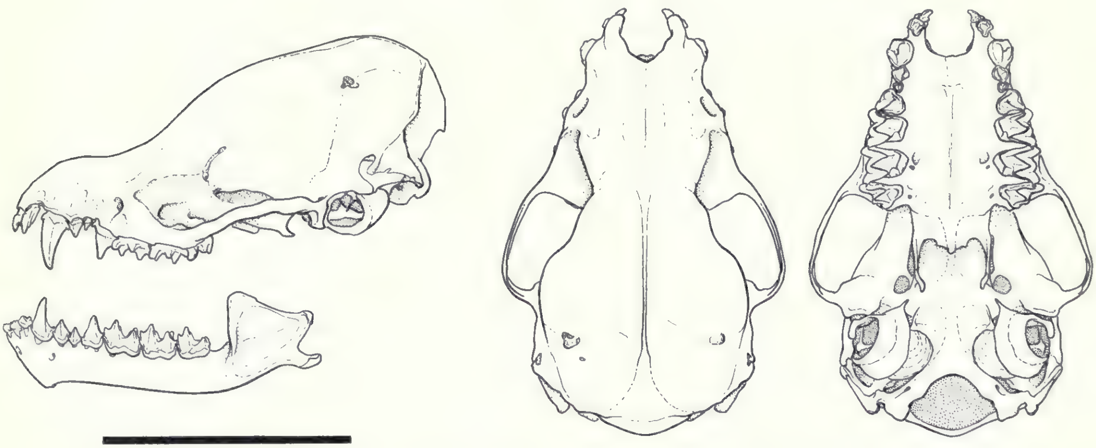

FIG. 53. Skull of *Myotis macrotarsus* (UMMZ 162364). Scale = 10 mm.

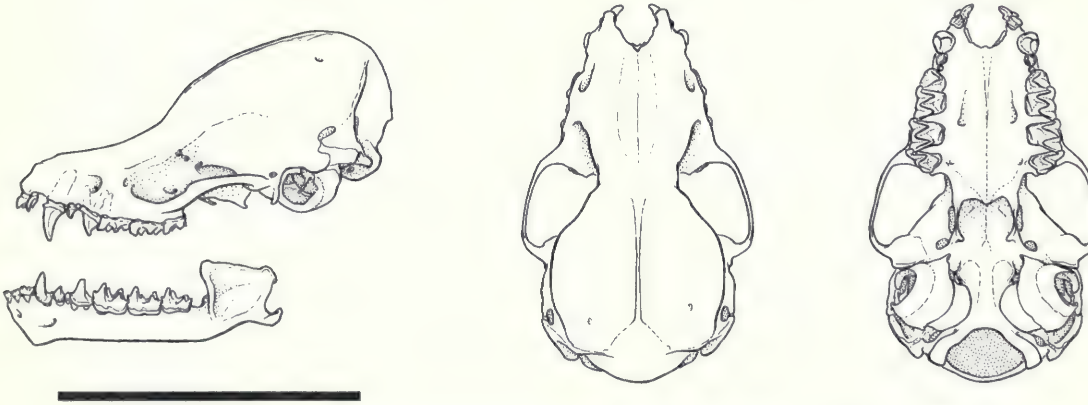

FIG. 54. Skull of *Myotis muricola* (UMMZ 158873). Scale = 10 mm.

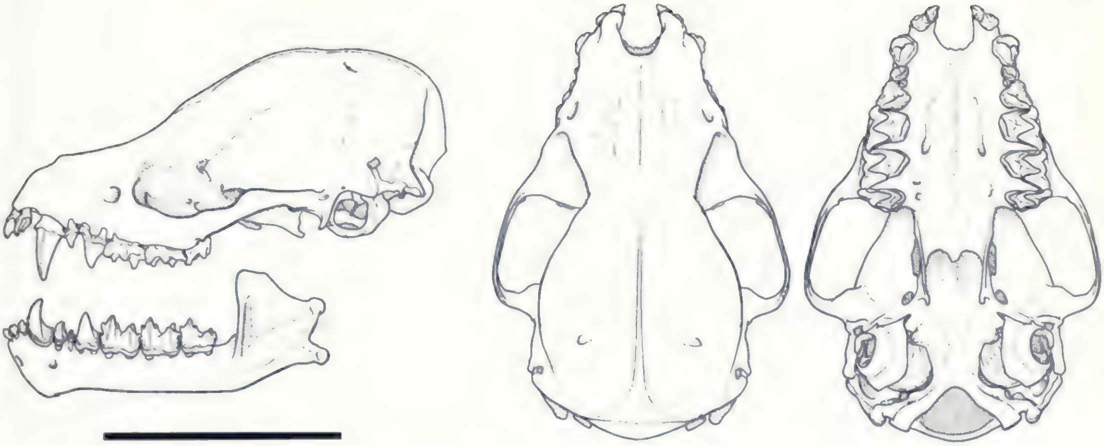

FIG. 55. Skull of *Myotis rufopictus* (UMMZ 158878). Scale = 10 mm.

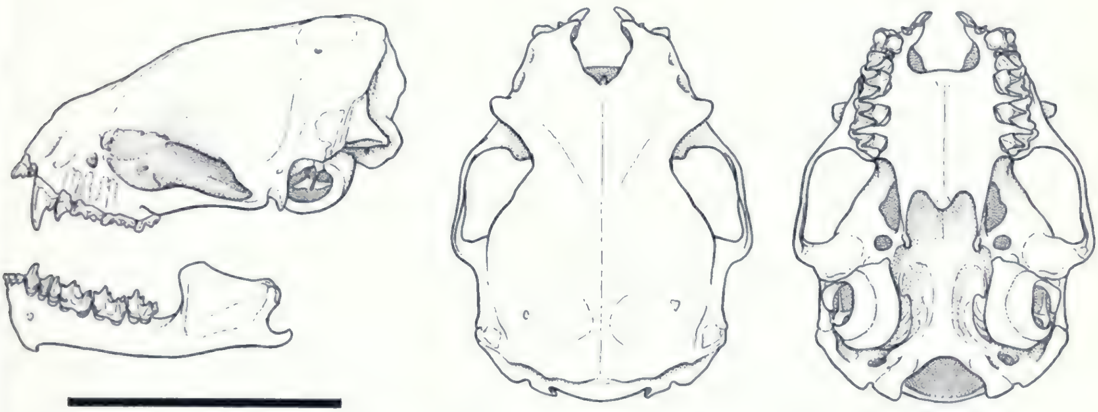

FIG. 56. Skull of *Philetor brachypterus* (USNM 573781). Scale = 10 mm.

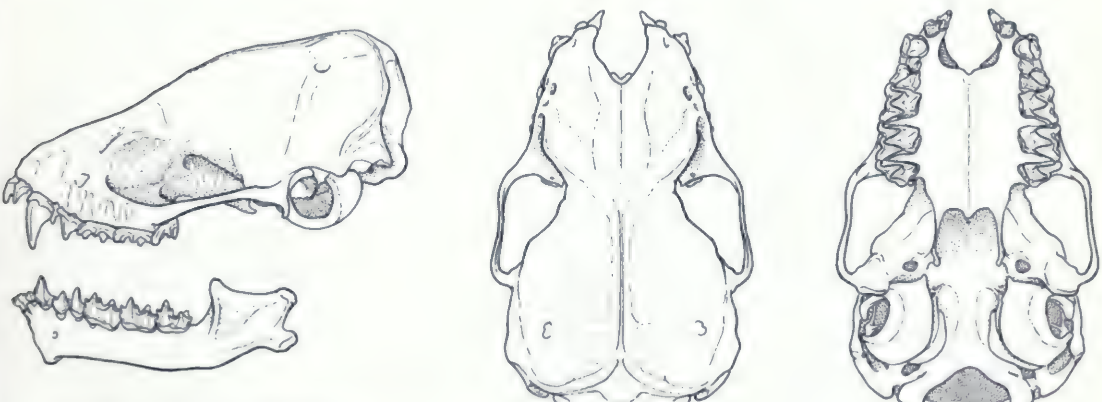

FIG. 57. Skull of *Pipistrellus javanicus* (USNM 459762). Scale = 10 mm.

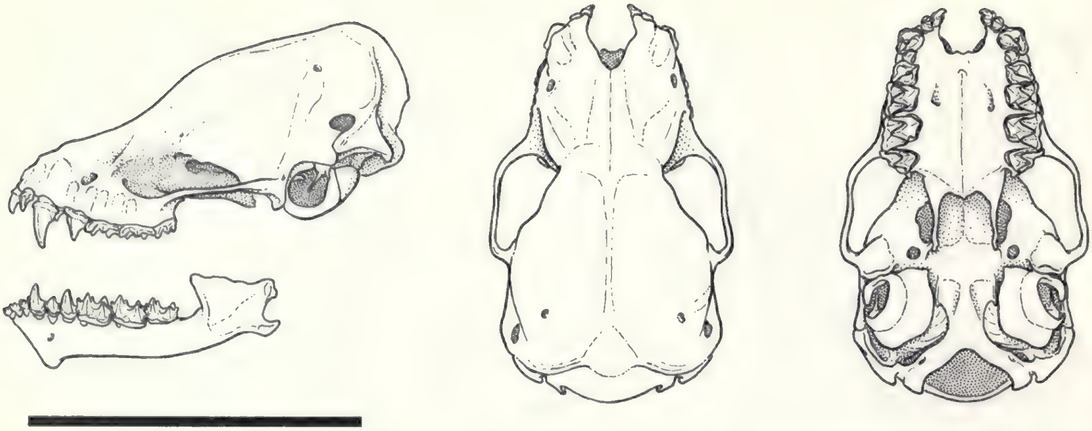

FIG. 58. Skull of *Pipistrellus tenuis* (USNM 160338). Scale = 10 mm.

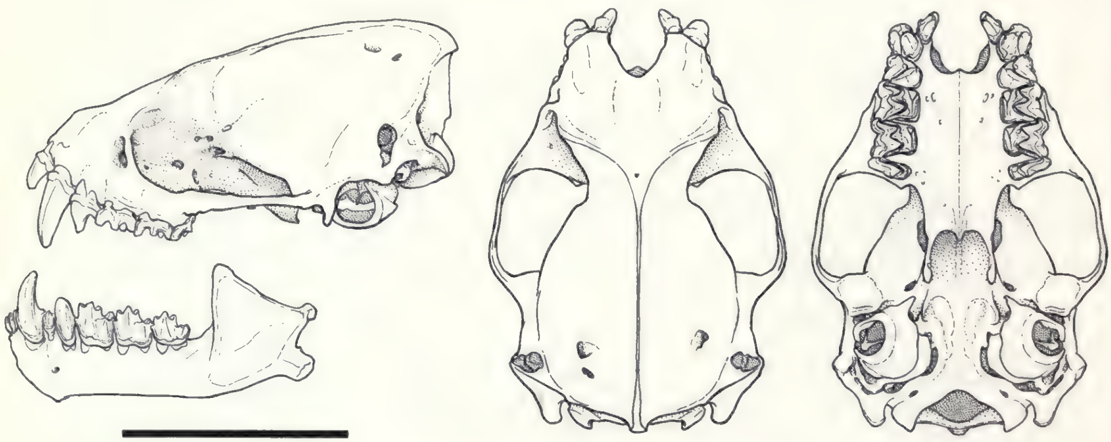

FIG. 59. Skull of *Scotophilus kuhlii* (USNM 458704). Scale = 10 mm.

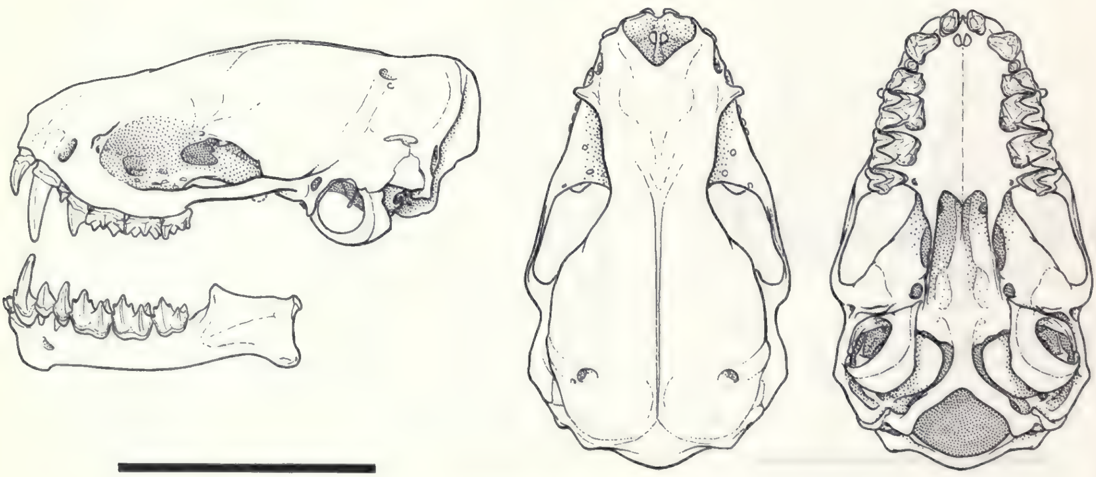

FIG. 60. Skull of *Chaerephon plicata* (USNM 304238). Scale = 10 mm.

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