

*Cynopterus sphinx*. By Jay F. Storz and Thomas H. Kunz

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*Cynopterus* Cuvier, 1824

*Cynopterus* Cuvier, 1824: 248. Type species *Pteropus marginatus* Geoffroy, 1810 (= *Vespertilio sphinx* Vahl, 1797).

**CONTEXT AND CONTENT.** Order Chiroptera, Family Pteropodidae, Subfamily Pteropodinae, Tribe Cynopterini, Subtribe Cynopterina, Genus *Cynopterus*. Five species are recognized: *C. brachyotis*, *C. horsfieldi*, *C. nusatenggara*, *C. sphinx*, and *C. titthaechileus* (Koopman, 1993). A key to the species is given in Lekagul and McNeely (1977).

*Cynopterus sphinx* (Vahl, 1797)

Short-nosed Fruit Bat

*Vespertilio sphinx* Vahl, 1797:123. Type locality "Tranquebar, Madras, India."

*Vespertilio fibulatus* Vahl, 1797:124. Type locality "Tranquebar, Madras, India."

*Pteropus pusillus* Geoffroy, 1803:49. Type locality "India."

*Pteropus marginatus* Geoffroy, 1810:97, pl. V. Type locality "Bengal."

*Pachysoma brevicaudatum* Temminck, 1837:92, pl. 35. Type locality "Calcutta, India" (not *P. brevicaudatum* Geoffroy, I., 1828).

*Cynopterus marginatus* var. (*Pachysoma scherzeri*) Zelebor, 1869: 13. Type locality "Car Nicobar, Nicobar Islands."

*Cynopterus marginatus* var. *elliotti* Gray, 1870:122. Type locality "Dharwar, India."

*Cynopterus brachysoma* Dobson, 1871:105. Type locality "Andaman Islands, Bay of Bengal."

*Cynopterus marginatus* var. *andamanensis* Dobson, 1873:201, pl. xiv, Fig. 5. Type locality "Andaman Islands, Bay of Bengal."

*Cynopterus angulatus* Miller, 1898:316. Type locality "Trong, Lower Siam" (= Trang, Thailand).

*Cynopterus pagensis* Miller, 1906:62. Type locality "North Pagi Island, Mentawai Islands."

*Cynopterus sphinx gangeticus* Andersen, 1910:623. Type locality "Lucknow, Uttar Pradesh, India."

*Cynopterus babi* Lyon, 1916:438. Type locality "Pulo Babi" (= Babi Island, western Sumatra).

*Cynopterus sphinx serasani* Paradiso, 1971:293. Type locality "Serasan Island, Natuna Islands, Indonesia."

**CONTEXT AND CONTENT.** Context same as for genus. Seven subspecies are recognized (Hill, 1983; Kitchener and Maharadatunkamsi, 1991):

*C. s. angulatus* Miller, 1898, see above.

*C. s. babi* Lyon, 1916, see above.

*C. s. gangeticus* Andersen, 1910, see above.

*C. s. pagensis* Miller, 1906, see above.

*C. s. scherzeri* Zelebor, 1869, see above.

*C. s. serasani* Paradiso, 1971, see above.

*C. s. sphinx* Vahl, 1797, see above.

**DIAGNOSIS.** *Cynopterus sphinx* (Fig. 1) is easily distinguished from *Pteropus* on the basis of its smaller size. The muzzle of *C. sphinx* also is shorter and broader relative to *Pteropus*. *C. sphinx* is intermediate in size between the slightly larger *Rousettus* and the slightly smaller *Megaerops* and is superficially similar to both. *C. sphinx* can be distinguished from members of both genera on the basis of dental formula: M2 is absent in *C. sphinx* and present in *Rousettus*, whereas I2 is present in *C. sphinx* and absent in *Megaerops* (Bates and Harrison, 1997; Lekagul and McNeely, 1977; Sinha, 1980). *C. sphinx*, *C. brachyotis*, and other pteropodid

species also can be distinguished on the basis of characteristic features of the humerus (Yoon and Uchida, 1989).

In areas of sympatry throughout the Indomalayan region, *C. sphinx* can be distinguished from congeneric species on the basis of forearm length and condylobasal length, respectively (measurements, in mm): 66–78, 29–35 (*C. sphinx*), <67, <29.5 (*C. brachyotis*), 64–89.5, 29–37 (*C. horsfieldi*), and 73–83, 34–37 (*C. titthaechileus*; Corbet and Hill, 1992). In areas of sympatry in southern India and Sri Lanka, *C. sphinx* can be distinguished from *C. brachyotis* on the basis of four characters (mean and range, in mm): length of forearm, 70.2 (64–79), 60.3 (57.3–63.3); condylobasal length, 30.9 (28.4–33.3), 27.6 (26.0–28.8); length of maxillary toothrow, 11.1 (10.2–12.2), 9.7 (8.9–10.7); and length of ear, 20.6 (17.5–24.0), 16.7 (14.5–18.0—Bates and Harrison, 1997). Also, the ears of *C. sphinx* are larger and are characterized by pale anterior and posterior borders; the ears of *C. brachyotis* are smaller and have more poorly developed borders (Bates and Harrison, 1997).



FIG. 1. Adult male *Cynopterus sphinx* in Kuttalam, India (photograph by J. F. Storz).

In a comprehensive morphometric analysis (Kitchener and Maharadatunkamsi, 1991), *C. sphinx* was compared to *C. brachyotis*, *C. nusatenggara*, and two morphologically close congeners, *C. minutus* and *C. luzoniensis*, which Hill (1983) and Koopman (1993) considered conspecific with *C. brachyotis*. These taxa make up the 'Cynopterus Section' of Andersen (1912). *C. sphinx* averaged larger than *C. brachyotis*, *C. nusatenggara*, *C. minutus*, and *C. luzoniensis* for almost all cranial, dentary, and dental characters as well as external characters and body mass. *C. sphinx* differs from *C. brachyotis* in that it averages larger in all measurements except length of P3 in females and least interorbital width in males. For example (mean and range, in mm), for females, greatest length of skull, 30.3 (28.1–32.9), 28.6 (27.0–29.7); length of mandibular toothrow, 11.0 (9.9–13.1), 10.2 (9.4–10.8); length of forearm, 65.7 (58.1–75.8), 61.7 (54.7–66.2); and for males, greatest length of skull, 30.4 (28.7–33.7), 29.0 (26.9–30.7); length of mandibular toothrow, 11.1 (10.1–12.8), 10.5 (9.8–11.4); and length of forearm, 65.1 (59.2–75.0), 61.8 (55.9–66.7). Additionally, bivariate plots of cranial and dental measurements illustrate that the orbitonasal length is longer relative to the width of M1 (Kitchener and Maharadatunkamsi, 1991, fig. 9) and the first digit is generally longer relative to the greatest length of skull and zygomatic breadth (Kitchener and Maharadatunkamsi, 1991, figs. 5 and 7, respectively). With regard to pelage, the dorsum of *C. sphinx* is a darker olive black compared with the cinnamon brown to brown fawn of *C. brachyotis*.

*C. sphinx* differs from *C. minutus* in that it averages larger in all measurements. For example (mean and range, in mm), for females, condylobasal length, 28.0 (25.7–30.5), 24.5 (23.0–25.6); length of second metacarpal, 29.1 (23.6–31.4), 26.2 (24.0–28.8); length of forearm, 65.7 (58.1–75.8), 57.5 (54.2–61.9); and for males, greatest length of skull, 30.4 (28.7–33.7), 27.2 (26.2–28.3); condylobasal length, 28.2 (26.1–31.1), 24.9 (23.3–26.1); length of palate, 15.7 (14.9–18.2), 13.7 (13.0–14.2); length of P3, 2.1 (2.0–2.4), 1.8 (1.6–1.9); and length of forearm, 65.1 (59.2–75.0), 57.3 (52.9–60.9). Additionally, bivariate plots of cranial and dental measurements illustrate that the width of braincase is greater relative to the width of M1 (Kitchener and Maharadatunkamsi, 1991, fig. 4). Compared with *C. minutus*, the canines of *C. sphinx* are also much more robust and the pelage on the dorsum is a darker olive black compared to brown fawn to buffy brown.

*C. sphinx* differs from *C. luzoniensis* in that it averages larger in all measurements except the length and width of P3, length of M1, and length of the first digit in females, and least interorbital width in males. For example (measurements expressed as mean and range, in mm), greatest length of skull (females), 30.3 (28.1–32.9), 28.6 (27.3–30.5); length of mandibular toothrow (females), 11.0 (9.9–13.1), 10.2 (9.4–11.2); length of forearm (females), 65.7 (58.1–75.8), 61.4 (57.2–68.9); greatest length of skull (males), 30.4 (28.7–33.7), 28.6 (27.2–30.0); length of mandibular toothrow (males), 11.1 (10.1–12.8), 10.4 (9.7–11.1); and length of forearm (males), 65.1 (59.2–75.0), 60.9 (56.0–65.9). Additionally, bivariate plots of cranial and dental measurements illustrate that the width of braincase is greater relative to M1, greatest length of skull is generally greater relative to the length of the first digit, and the zygomatic breadth is generally greater relative to orbitonasal length (Kitchener and Maharadatunkamsi, 1991, figs. 4, 5, and 6, respectively). The posterolabial corner of P3 is generally less squarish. Pelage on the dorsum is a darker gray brown to olive black compared with cinnamon fawn to gray brown.

*C. sphinx* differs from *C. nusatenggara* in averaging larger in all measurements except the width of P3 and the length of M1 in females. For example (mean and range, in mm), for females, greatest length of skull, 30.3 (28.1–32.9), 28.1 (26.0–29.9); length of mandibular toothrow, 11.0 (9.9–13.1), 9.9 (9.3–10.6); length of forearm, 65.7 (58.1–75.8), 59.9 (55.1–64.8); and for males, greatest length of skull, 30.4 (28.7–33.7), 28.3 (27.2–29.7); length of mandibular toothrow, 11.1 (10.1–12.8), 10.1 (9.3–10.6); and length of forearm, 65.1 (59.2–75.0), 59.3 (54.7–61.9). Additionally, bivariate plots of cranial and dental measurements illustrate that the width of braincase is greater relative to the width of M1 and greatest length of skull is greater relative to the length of the first digit (Kitchener and Maharadatunkamsi, 1991, figs. 4 and 5, respectively). The p4 posterolabial corner generally is much less squarish, P3 lingual and labial cusp commissure slopes slightly posteriorly, and P4 lingual and labial cusps are connected by a low ridge or distinct commissure. In terms of pelage and skin color, *C. sphinx*

differs from *C. nusatenggara* in having white ear margins, the pelage on the head is not markedly darker than that on dorsum, and the surface color of metacarpals and phalanges are markedly lighter and contrast with the patagial membrane.

Compared with *C. horsfieldi* and *C. tiitthaecheileus*, *C. sphinx* is generally smaller in size and the skull and rostrum are less robust (Corbet and Hill, 1992; Hill, 1983). *C. sphinx* can be distinguished from *C. horsfieldi* by its somewhat darker pelage. *C. sphinx* also has narrower and more oval molars and lacks the central cusp on the lower molars found in *C. horsfieldi* (Corbet and Hill, 1992; Lekagul and McNeely, 1977). *C. sphinx* exhibits high levels of variability in size and morphology across its range. In a discriminant function analysis of morphometric characters, specimens of *C. sphinx* from India and Thailand clustered separately, whereas specimens from Sulawesi and Java clustered more closely with specimens from other localities within the Malay Archipelago (Kitchener and Maharadatunkamsi, 1991). *C. sphinx* specimens from northern India tend to average larger than those from southern India and Sri Lanka (Andersen, 1912; Bates and Harrison, 1997).

**GENERAL CHARACTERS.** *Cynopterus sphinx* is a medium-sized fruit bat with an average wingspan of 380 mm (Bates and Harrison, 1997; Fig. 1). The tail is short (13–18 mm) and the terminal half projects beyond the interfemoral membrane. Both the first and second digits have distinct claws (Bates and Harrison, 1997; Lekagul and McNeely, 1977). The muzzle of *C. sphinx* is short and broad and is characterized by a deep emargination between the projecting nostrils (Bates and Harrison, 1997). External and cranial measurements (mean and range, in mm) of adult male ( $n = 13$ ) and female ( $n = 8$ ) *C. sphinx*, respectively, from the Indian state of Bengal are as follows: length of head and body, 99.2 (89–109), 99.1 (91–109); length of tail, 15.1 (13–17.5), 15.1 (14–19); length of ear, 20.7 (19–22), 20.9 (19–23); length of forearm, 71.2 (67–74.5), 72.5 (67.5–76); length of tibia, 27.2 (25–29), 28 (24.5–30.5); length of hind foot, 17.6 (16–20.5), 17 (14.5–18.5); greatest length of skull, 33.1 (32–34), 33.1 (31.7–34.5); condylobasal length, 31.9 (30.6–32.5), 31.9 (30.8–33.3); zygomatic breadth, 20.7 (19–22.3), 20.4 (18.8–21.6); cranial width, 14.2 (13.3–14.5), 14.2 (13.2–15); length of palate, 17.5 (16.4–18.2), 17.2 (16.5–18.1); maxillary width, 10 (9.2–10.6), 9.8 (9.4–10.5); interorbital width, 6.5 (5.8–7), 6.5 (6–7); length of maxillary toothrow, 11.3 (10–12), 10.8 (10.5–11); and length of mandibular toothrow, 12.4 (11.6–13), 12.2 (11.8–12.6—Das and Sinha, 1971).

External and cranial measurements (mean  $\pm 1$  SD and range, in mm) of adult male ( $n = 28$ ) and female ( $n = 18$ ) *C. sphinx*, respectively, from India, Thailand, Sumatra, Java, Borneo, Sulawesi, and several smaller islands in the Malay Archipelago are the following: length of forearm, 65.1  $\pm$  3.2 (59.2–75.0), 65.7  $\pm$  4.3 (58.1–75.8); length of first digit, 2.2  $\pm$  1.5 (8.4–23.8), 21.0  $\pm$  1.2 (18.3–23.3); length of second metacarpal, 29.3  $\pm$  1.8 (25.6–32.6), 29.1  $\pm$  1.9 (23.6–31.4); length of third metacarpal, 43.2  $\pm$  2.3 (38.1–48.2), 43.0  $\pm$  2.5 (36.8–47.6); length of second phalanx of the third digit, 28.6  $\pm$  1.5 (25.9–33.0), 43.0  $\pm$  2.5 (36.8–47.6); length of fourth metacarpal, 40.6  $\pm$  2.2 (34.9–45.0), 40.9  $\pm$  2.6 (35.9–45.9); length of fifth metacarpal, 41.8  $\pm$  2.2 (37.1–45.5), 42.2  $\pm$  2.7 (36.0–47.0); length of tibia, 24.1  $\pm$  1.7 (20.1–27.6), 24.7  $\pm$  1.1 (21.4–29.6); greatest length of skull, 30.4  $\pm$  1.1 (28.7–33.7), 30.3  $\pm$  1.2 (28.1–32.9); condylobasal length, 28.2  $\pm$  1.0 (26.1–31.1), 28.0  $\pm$  1.1 (25.7–30.5); length of palate, 15.7  $\pm$  0.7 (14.5–18.2), 15.6  $\pm$  0.7 (14.3–17.5); width of mesopterygoid fossa, 4.3  $\pm$  0.3 (3.7–5.0), 4.3  $\pm$  0.3 (3.9–5.0); orbitonasal length, 7.3  $\pm$  0.6 (6.2–8.7), 7.2  $\pm$  0.6 (6.2–8.6); least interorbital width, 6.1  $\pm$  0.4 (5.2–6.9), 6.1  $\pm$  0.3 (5.3–6.7); postorbital width, 6.5  $\pm$  0.4 (5.5–7.4), 6.8  $\pm$  0.5 (5.8–7.8); zygomatic breadth, 19.4  $\pm$  0.9 (17.7–21.3), 19.3  $\pm$  0.9 (17.3–20.7); width of braincase, 12.9  $\pm$  0.5 (12.2–14.0), 12.9  $\pm$  0.4 (12.3–13.7); dentary condyle to tip of dentary, 22.8  $\pm$  1.0 (21.1–25.5), 23.0  $\pm$  1.2 (20.9–26.9); outside C1–C1 breadth, 6.4  $\pm$  0.3 (5.9–7.2), 6.2  $\pm$  0.3 (5.6–7.1); outside P4–P4 breadth, 8.8  $\pm$  0.4 (8.1–9.3), 8.6  $\pm$  0.5 (7.8–9.9); outside M1–M1 breadth, 9.0  $\pm$  0.4 (8.4–10.0), 8.9  $\pm$  0.5 (7.9–10.1); length of maxillary toothrow, 9.9  $\pm$  0.5 (9.0–11.7), 9.8  $\pm$  0.6 (8.7–11.6); length of mandibular toothrow, 11.1  $\pm$  0.5 (10.1–12.8), 11.0  $\pm$  0 (9.9–13.1); length of P3, 2.1  $\pm$  0.1 (2.0–2.4), 2.1  $\pm$  0.1 (1.9–2.3); width of P3, 1.6  $\pm$  0.1 (1.4–1.8), 1.5  $\pm$  0.1 (1.4–1.7); length of M1, 2.1  $\pm$  0.2 (1.8–2.5), 2.0  $\pm$  0.2 (1.6–2.3); and width of M1, 1.4  $\pm$  0.1 (1.2–1.6), 1.4  $\pm$  1.1 (1.2–1.6); Kitchener and Maharadatunkamsi, 1991). Body masses (in g) were 38.5  $\pm$  6.4 (34.5–

53.0;  $n = 10$ ) for males and  $46.5 \pm 16.1$  (28.0–70.0;  $n = 5$ ) for females (Kitchener and Maharadatunkamsi, 1991).

External and cranial measurements (mean  $\pm 1$  *SD* and range, in mm) of adult *C. sphinx* (sexes pooled) from throughout the Indian subcontinent are as follows: length of head and body,  $98.8 \pm 9.4$  (76.0–113.0;  $n = 60$ ); length of tail,  $10.9 \pm 4.5$  (4.5–19.0;  $n = 60$ ); length of hind foot,  $15.6 \pm 1.2$  (12.6–18.0;  $n = 60$ ); length of forearm,  $70.2 \pm 3.5$  (64.0–79.0;  $n = 60$ ); wingspan,  $380.4 \pm 39.8$  (309.0–436.0;  $n = 8$ ); length of third metacarpal,  $47.0 \pm 2.4$  (43.2–53.4;  $n = 57$ ); length of fourth metacarpal,  $44.4 \pm 2.3$  (40.7–51.1;  $n = 56$ ); length of fifth metacarpal,  $45.4 \pm 2.5$  (41.1–52.1;  $n = 57$ ); length of ear,  $20.6 \pm 1.6$  (17.5–24.0;  $n = 57$ ); greatest length of skull,  $32.4 \pm 1.1$  (30.2–34.9;  $n = 56$ ); condylobasal length,  $30.9 \pm 1.2$  (28.4–33.3;  $n = 50$ ); zygomatic breadth,  $20.6 \pm 1.0$  (18.8–23.1;  $n = 56$ ); width of braincase,  $13.5 \pm 0.6$  (11.1–14.8;  $n = 59$ ); least interorbital width,  $6.5 \pm 0.5$  (5.4–7.7;  $n = 62$ ); length of maxillary toothrow,  $11.1 \pm 0.5$  (10.2–12.2;  $n = 58$ ); length of mandibular toothrow,  $12.3 \pm 0.8$  (10.3–13.5;  $n = 62$ ); and length of mandible,  $24.9 \pm 1.0$  (22.7–27.5;  $n = 65$ ; Bates and Harrison, 1997).

The rostrum of *C. sphinx* is short and broad, and the ventral profile is nearly straight (Fig. 2; Bates and Harrison, 1997; Kitchener and Maharadatunkamsi, 1991; Lekagul and McNeely, 1977). The zygomata are robust and the postorbital processes are well developed. The braincase is ovoid with a weak sagittal crest. In contrast to *Pteropus*, *Rousettus*, and *Eonycteris*, the basicranial axis forms an essentially straight line with the palate. The supraoccipital is vertical and its posterior projection is even with the lamboid crests. The tympanic bullae are not well developed. The basioccipital region is broad. The horizontal ramus of each dentary is short and robust. The coronoid process is broad and the angular process is rounded ventrally. The maxillaries are separate and premaxillaries are in contact anteriorly, but not fused (Bates and Harrison, 1997; Lekagul and McNeely, 1977). Kitchener and Maharadatunkamsi (1991) provide a detailed description of the skull of *C. nusatenggara* which differs principally in absolute size from that of *C. sphinx*.

The dental formula of *C. sphinx* is  $i\ 2/2$ ,  $c\ 1/1$ ,  $p\ 3/3$ ,  $m\ 1/2$ , total 30 (Bates and Harrison, 1997; Lekagul and McNeely, 1977). The I1 and I2 are small and peg-like; they are closely situated to one another and are separated from the canine by a large diastema (Fig. 2—Bates and Harrison, 1997; Lekagul and McNeely, 1977). The C1 is relatively broad and has a recurved tip when unworn; it lacks a groove on its inner anterior surface but has a secondary cusp on its inner side. The cingulum is well developed posterolaterally. The P1 is similar in size to the incisors. The P2 is equal in crown area to P4 and is morphologically similar to P4 and M1. In the mandibular dentition,  $i1$  is subequal in size to  $i2$  and  $p2$  is larger than P2. The principal cusp of  $p3$  is triangular and sharply pointed; it is subequal in height with the canine. The outer cusp of  $p4$  is lower than  $p3$  and has a well-developed inner ridge. The  $m1$  is subequal in size with  $p4$ ; its outer cusp is less developed. The  $m2$  is small and has a simple, hollowed-out crown (Bates and Harrison, 1997).

The pelage of the sexes differs principally in the color of the mantle. In specimens from throughout Southeast Asia, the mantle of adult females is cinnamon fawn to olive brown, and the mantle of adult males typically is a deeper color, frequently olive brown (Kitchener and Maharadatunkamsi, 1991). The remainder of the adult pelage is characterized as follows: head and neck—gray brown, or occasionally charcoal brown; chin and flanks—a lighter lemon cream color, occasionally yellow tan, olive brown, or pale lemon yellow; dorsum—fawn olive to charcoal brown but occasionally lighter near tail to tawny olive; venter—pale drab gray merging to deep olive buff near tail. The ventral surface of the plagiopatagium adjacent to the body and forearm is lightly haired, as are the dorsal and ventral surfaces of the uropatagium. The fur at the base of the ears is the same color as the mantle; the ears are otherwise naked. The skin of the ears, lips, feet, and patagia is a dark lilac gray, except for the lighter ear margins. Surfaces of the metacarpals and phalanges are a pale tan color in contrast to the slightly darker patagial membrane (Kitchener and Maharadatunkamsi, 1991). Similar sex differences in pelage color are apparent in specimens from the Indian subcontinent. In adult males, the chin, shoulders, and flanks are orange tinted, and the forehead and the nape of the neck are a darker, rich russet brown. In adult females, the mantle is usually tawny brown (Bates and Harrison, 1997).

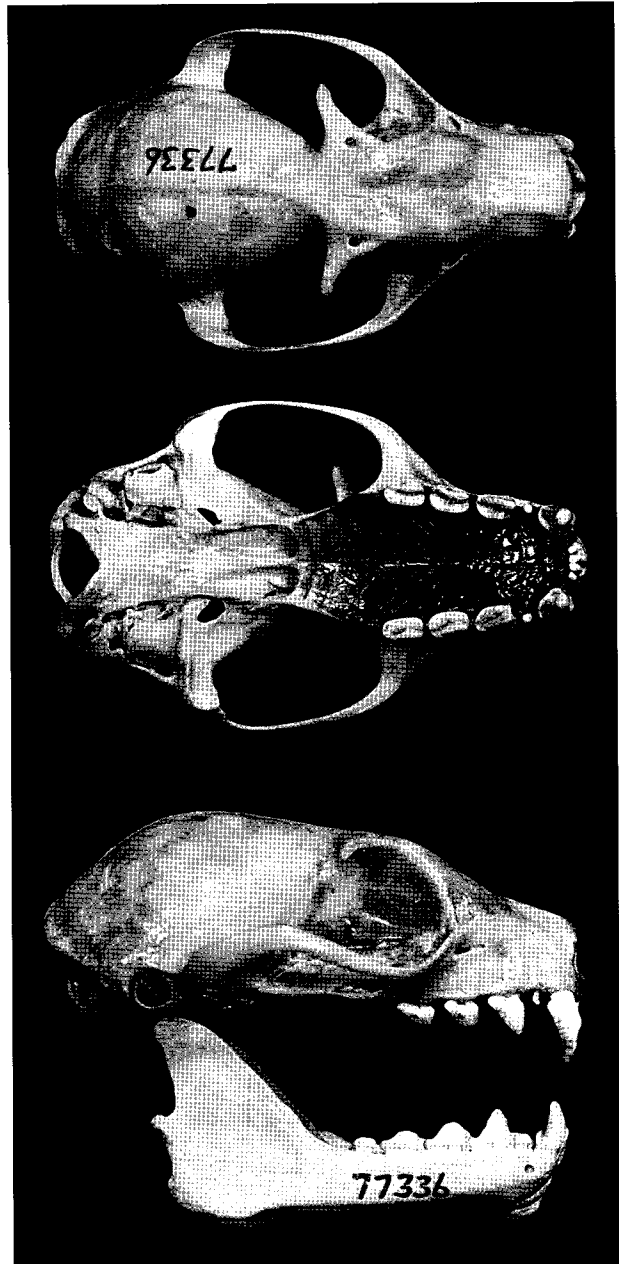


FIG. 2. Dorsal, ventral and lateral views of the cranium and lateral view of the mandible of an adult male *Cynopterus sphinx* from Jhabua, India (Royal Ontario Museum 77336). Greatest length of the skull is 35 mm.

The baculum of *C. sphinx* is characterized by its simple, unexpanded tip (Bates and Harrison, 1997). In the Krakatau Islands, the shape of the baculum is highly variable in adult *C. sphinx* and apparently is not related to age (Kitchener and Maharadatunkamsi, 1991).

In the Solomon Islands, there are no significant differences in the size of males and females (Goodwin, 1979). In Sri Lanka, the sexes are very similar in size, but females average slightly larger (Phillips, 1980).

**DISTRIBUTION.** *Cynopterus sphinx* ranges from Pakistan, India, and Sri Lanka to southern China, the Malay Peninsula, Sumatra, Java, Borneo, Sulawesi, Timor and smaller islands in the Malay Archipelago (Fig. 3—Bates and Harrison, 1997; Corbet and Hill, 1992; Kitchener and Maharadatunkamsi, 1991; Lekagul and McNeely, 1977). This bat has been recorded from as far east as Sind, Pakistan and as far north as Jammu and Kashmir in northern India (Bates and Harrison, 1997; Chakraborty, 1983; Roberts,

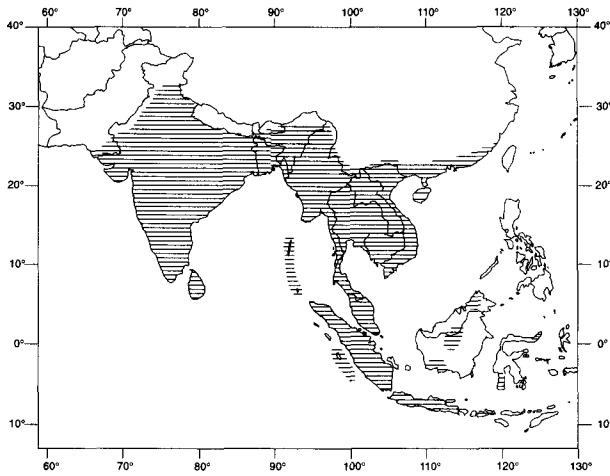


FIG. 3. Geographic distribution of *Cynoptyeris sphinx*.

1977). The subspecies have the following geographic distributions: *C. s. sphinx*—Sri Lanka, peninsular and northeastern India, Burma; *C. s. scherzeri*—Car Nicobar Island; *C. s. serasani*—Serasan Island, Natuna Island; *C. s. babi*—Babi Island; *C. s. gangeticus*—central and northwest India; *C. s. pagensis*—Mentawai Islands; and *C. s. angulatus*—northern Burma to southern China, Taiwan, Vietnam, Lankawi Island, peninsular Malaysia, Sumatra, Krakatau Islands, (possibly) Verlaten Island, Borneo, Sulawesi, and (possibly) Sangeang Island (Hill, 1983; Kitchener and Maharadatunkamsi, 1991).

**FORM AND FUNCTION.** In male *C. sphinx*, the testes are abdominal in position during periods of sexual quiescence and descend to an inguinal position and are markedly enlarged during periods of active spermatogenesis (Krishna and Dominic, 1984; Sandhu, 1988; Vamburkar, 1958). The penis is pendulous and is directed caudally; the glans is complex in structure; the corpora cavernosa are horseshoe-shaped in cross section and are enclosed in a common sheath; the baculum is a cartilaginous, curved plate and is restricted to the distal half of the glans. The caput and cauda epididymides are similar in size and shape. The caput epididymis is attached along the inner border of the testis and the cauda lies at the posteroventral side. The vasa deferentia pass forward along the inner margins of the testes and open into the collecting tubules of the paired seminal vesicles (Krishna and Dominic, 1984; Vamburkar, 1958). The unpaired prostate is a tubulo-alveolar gland and is located on the ventral side of the urethra. The lumina are lined by tall columnar secretory epithelial cells with basally located nuclei. The seminal vesicles are coiled vermiform structures and open separately into the urethra. Histological examination revealed the presence of secretory bodies in the lumina of the seminal vesicles (Mokkapati and Dominic, 1977). The Cowper's glands are large and open into the muscular urethra by a pair of short ducts. A urethral gland surrounding the lower part of the urethra also is present; ampullary glands are absent (Mokkapati and Dominic, 1977; Vamburkar, 1958). Holocrine cells and esterase-resistant esterase activity are present in the epididymis of *C. sphinx* (Mote and Nalavade, 1982).

The external genitalia of pregnant females is characterized by a glandular margin surrounding the vulvar orifice; the clitoridial pad is transversely divided and each portion shows further longitudinal division into smaller lobes (Khajuria, 1979). The uterus is bicornuate and opens into the vagina by independent cervical canals (Sandhu, 1984; Sandhu and Gopalakrishna, 1984). During pregnancy, nonspecific esterase activity in the corpus luteum is intense in thecal luteal cells and moderate in granulosa cells. During lactation, granular lysosomal activity is evident in the involuting corpus luteum (Mote, 1986). When female *C. sphinx* are sexually receptive, nonspecific esterase activity is very high in the epithelial cells of vaginal sebaceous glands and may play a role in mate attraction during the breeding season (Mote and Khumbar, 1986).

**ONTOGENY AND REPRODUCTION.** In peninsular India, *C. sphinx* is seasonally polyestrous, having two distinct reproductive periods per year. Parturition typically occurs in February–

March and again in June–July (Bhat and Sreenivasan, 1990; Brosset, 1962; Das and Sinha, 1971; Gopalakrishna, 1969; Krishna and Dominic, 1983a, 1983b; Moghe, 1956; Mote and Kumbhar, 1986; Mote and Nalavade, 1982; Ramakrishna, 1947; Sandhu, 1984, 1988; Sandhu and Gopalakrishna, 1984; Sreenivasan et al., 1974). Although a single instance of monozygotic twin embryos has been documented (Moghe, 1958), females normally give birth to single young (Sandhu, 1984). Females can produce a maximum of two young per year. After young are born in February–March, females undergo a postpartum estrus (Krishna and Dominic, 1983b; Ramakrishna, 1947; Sandhu, 1984; Sandhu and Gopalakrishna, 1984). Females are simultaneously pregnant and lactating until young from the February–March cohort are weaned. Although some degree of geographic variation in the timing of reproduction is apparent (Krishna and Dominic, 1983b; Sandhu and Gopalakrishna, 1984), collections of *C. sphinx* from sites throughout peninsular India are consistent with a seasonally bimodal reproductive cycle. In contrast, Phillips (1980) reported the occurrence of females in advanced stages of pregnancy during August and suggested that *C. sphinx* might breed intermittently throughout the year in Sri Lanka. Collections of *C. sphinx* spanning multiple breeding seasons in the same site in central India suggest little variation in the timing of reproductive activity between years (Sandhu, 1984, 1988).

In central India (Nagpur, Maharashtra—21°10'N, 79°12'E), mating occurs in October–November, and again during the postpartum estrus period in February–March (Sandhu, 1984, 1988; Sandhu and Gopalakrishna, 1984). The gestation period is 115–125 days for each of the two annual pregnancies (Gopalakrishna, 1969; Moghe, 1956; Sandhu, 1984). Females are anestrus from mid-July until the beginning of October (Sandhu, 1984; Sandhu and Gopalakrishna, 1984). Further north and east (Varanasi, Uttar Pradesh—25°20'N, 83°00'E), mating occurs in late October and again during the postpartum estrus period in March. Additionally, nulliparous females born in the previous June–July parturition period conceive their first young in late January. In contrast to the situation in Nagpur, the duration of the gestation period in Varanasi is seasonally variable. Pregnancies initiated in the postpartum estrus period in March–April last ca. 120 days, whereas pregnancies initiated in October and January last ca. 150 days (Krishna and Dominic, 1983b). Females are anestrus from August until October (Krishna and Dominic, 1983b). It is unknown whether parous females occasionally skip one of the two annual reproductive opportunities.

Male *C. sphinx* experience two seasonal periods of active spermatogenesis, although residual spermatozoa are retained in the epididymides year-round (Krishna and Dominic, 1984; Sandhu, 1988). In Nagpur, active spermatogenesis occurs in September–October (followed by a two month period of sexual quiescence) and January–March (followed by a six month period of sexual quiescence). Peaks in spermatogenic activity coincide with peaks in mass of the testes and epididymides (Sandhu, 1988). In Varanasi, active spermatogenesis occurs in October–November and mid-January–April. Peaks in spermatogenic activity occur in October and February and coincide with a reduction in the concentration of testicular lipids, a reduction in cholesterol concentration, and an increase in the total cholesterol content in the testes. The seasonally bimodal reproductive cycle of male *C. sphinx* also is reflected in changes in the mass and histological profile of the testes, epididymides, and accessory sex glands (Krishna and Dominic, 1984). In Varanasi, these histological data indicate that mating occurs in October–November and again in mid-January–April (Krishna and Dominic, 1984), which is consistent with data on the timing of conception and parturition in the same population (Krishna and Dominic, 1983b).

Females attain sexual maturity far earlier than males and the age at which both sexes first breed differs for members of each of the two biannual cohorts of offspring (Krishna and Dominic, 1983b; Sandhu, 1984, 1988). There also appears to be geographic variation in the pattern of recruitment of nulliparous females into the breeding population. In Nagpur, nulliparous females born in the parturition period in February–March first conceive at the beginning of the breeding season in late October when they are 7–8 months old. They give birth to their first young in February–March of the following calendar year when they are one year old. Females born in the June–July parturition period first conceive midway through the breeding season in November or early December when they are 5–6 months old. They give birth to their first young late in the Feb-

ruary–March parturition period when they are 8–9 months old. Thus, females born in the June–July parturition period participate in both of the two reproductive opportunities occurring within their first year, and primiparous females from each of the two biannual cohorts of offspring give birth in the same season (Sandhu, 1988). In Varanasi, females born in March become sexually mature in September when they are six months old, and first conceive in late October. They give birth to their first young in March of the following calendar year when they are one year old. The young conceived in the subsequent postpartum estrus period are born in July or early August. Females born in the June–August parturition period become sexually mature in December and first conceive in late January of the following calendar year. They give birth to their first young in late June or early July when they are one year old. Thus, in contrast to the situation in Nagpur, the reproductive cycles of nulliparous females born in the June–August parturition period are not synchronized with those of parous females and nulliparous females of the March cohort. In Nagpur, females of the June–August cohort can produce two young by the time they reach one year of age, whereas in Varanasi they produce only one. Primiparous females from each of the two biannual cohorts of offspring give birth in different seasons.

In Nagpur, males born in the February–March parturition period are first able to mate in September–October of the following calendar year, when they are 19–20 months old. Males born in the June–July parturition period are first able to mate in September–October of the following calendar year, when they are 15–16 months old (Sandhu, 1988). In Varanasi, by contrast, the presence of spermatozoa in the testes or epididymides of nearly all males collected between October and April suggests that males may attain sexual maturity within their first year (Krishna and Dominic, 1983a).

In Nagpur, all females attain a body mass of at least 50 g by the time they reach sexual maturity. Neonates weigh ca. 11 g and attain a body mass of ca. 35 g when they become semi-independent 45–50 days later. At this stage of growth they are able to move about freely in the roost and are no longer continually attached to their mother's nipple. Females continue to lactate for another 10–15 days after they are no longer continually carrying the young, and young probably continue to suckle occasionally during this time (Sandhu, 1984). In Varanasi, neonates weigh 13.5 g at birth (27% of average adult body mass). Young are weaned after one month, by which time they typically have achieved a body mass of ca. 25 g (51% of average adult body mass). Juveniles achieve fully adult dimensions at two months of age (Krishna and Dominic, 1983a, 1983b). The cheek teeth of young *C. sphinx* are fully erupted by the time they begin to forage (Khajuria, 1979). Juvenile males that have attained adult dimensions can be distinguished from sexually mature adults by their more grayish pelage and by mass of the testes during breeding periods (Krishna and Dominic, 1983a; Sandhu, 1988). Body mass is an unreliable indicator of sexual maturity (Sandhu, 1988).

Embryo implantation alternates between the two horns of the bicornuate uterus from one pregnancy to the next (Sandhu, 1984; Sandhu and Gopalakrishna, 1984). A large corpus luteum persists in the ovary for several days following parturition in February–March, and the graafian follicle is released from the contralateral ovary in the subsequent breeding cycle. After parturition in June–July, by contrast, the corpus luteum regresses within several days so that both ovaries have similar histological profiles during the anestrus period (mid-July until the beginning of October). Collection records from Nagpur indicate that over 70% of pregnant females carried their embryo in the right uterine horn following the September–October conception and this situation was reversed in the subsequent postpartum conceptions. This dextral dominance in the uterus also was evident among primigravid females as the majority of first-time breeders carried their embryos in the right uterine horn (Sandhu, 1984; Sandhu and Gopalakrishna, 1984). In the early stages of the pregnancy initiated during postpartum estrus, the contralateral uterine horn typically has not regressed to normal size and a placental scar is still present (Krishna and Dominic, 1983b; Sandhu and Gopalakrishna, 1984). This indicates that conception occurs shortly after postpartum estrus begins. In Varanasi, almost all lactating females had implanted embryos and a well-developed corpus luteum in the ipsilateral uterine horn by late April (Krishna and Dominic, 1983b).

**ECOLOGY.** *Cynopterus sphinx* is a relatively common and abundant species throughout its geographic range (Bates and Harrison, 1997; Mickleburgh et al., 1992; Prater, 1971). It is generally found at lower elevations but has been recorded in the foothills of the Himalayas in northern India at an elevation of 400 m (Bates and Harrison, 1997). Phillips (1980) reports that *C. sphinx* is a common species in Sri Lanka, especially in cultivated areas and is generally more abundant in drier regions of the island. In the Indian state of Rajasthan, *C. sphinx* is found primarily in forested regions where rainfall exceeds 600 mm/year (Advani, 1981, 1982a). Although not known to undergo seasonal migrations, strong dispersal capabilities are indicated by the recolonization rates of *C. sphinx* in the Krakatau Islands (Thornton et al., 1990; Tidemann et al., 1990). On the main island of Rakata, and on the more recently formed island of Anak Krakatau, populations of *C. sphinx* were established within 20–30 years of the cessation of major eruptive activity (Tidemann et al., 1990).

In western India (Pune), *C. sphinx* feeds on parts of at least 31 species of plants from 18 families. *C. sphinx* mainly feeds on the fruits of *Ficus racemosa* and *F. bengalensis*, as well as the leaves of *Cassia fistula* and *Moringa oleifera* and the flowers of *Parkia biglandulosa* and *Madhuca latifolia*. In this region, the various species of *Ficus* provide a reliable, year-round source of food for *C. sphinx*, as there is considerable overlap in the seasonal periods of fruit production (Bhat, 1994). In the North Indian state of Rajasthan, *C. sphinx* feeds on fruits of *Psidium guajava*, *Mangifera indica*, *Phoenix sylvestris*, *Anona squamosa*, and *Achras sapota* (Advani, 1982b). In the South Indian state of Tamil Nadu, *C. sphinx* feeds on *Atalantia monophylla* (Balasubramanian, 1989), the arils of the fruits of *Pithecellobium dulce* and the fleshy pericarp of *Terminalia catappa* and *Psidium guajava* (Marimuthu et al., 1998). In Sri Lanka, *C. sphinx* feeds on guava (*Psidium guajava*), soursop (*Anona muricata*), mango (*Mangifera indica*), and fruits and flowers of plantain (*Musa*; Phillips, 1980). *C. sphinx* appears to provide important pollination and seed dispersal services for many plant species (Bhat, 1994; Brosset, 1962; McCann, 1940) and apparently made important contributions to the revegetation of the Krakatau Islands (Whittaker and Jones, 1994). When chewing leaves, *C. sphinx* presses the pulp between the palate and tongue to extract leaf sap, and then discards the fibrous parts as pellets (Bhat, 1994). When *C. sphinx* feeds in the same fruiting trees as *Pteropus*, it typically occupies the lower branches, while *Pteropus* occupies the uppermost branches (Lekagul and McNeely, 1977).

**BEHAVIOR.** According to several anecdotal accounts, *C. sphinx* roosting groups contain 2–20 individuals, although usually no more than 10 (Advani, 1982b; Bhat and Kunz, 1995; Brosset, 1962; Goodwin, 1979; Sinha, 1981). Studies of composition of roosting groups in northern India (Varanasi—Krishna and Dominic, 1985), central India (Nagpur—Sandhu, 1984; Sandhu and Gopalakrishna, 1984), and southern India (Tirunelveli—Balasingh et al., 1993, 1995) provide somewhat conflicting accounts of the mode of *C. sphinx* social organization. It is unclear to what extent these discrepancies reflect geographic variation in behavior and demography, as different sampling methods were used in each of the different studies. The composition of *C. sphinx* roosting groups in central India (Sandhu, 1984; Sandhu and Gopalakrishna, 1984) indicates a highly female-biased adult sex ratio. Because male and female young are present in equal numbers prior to weaning, Sandhu (1984) attributed the disproportionate number of breeding females to a higher mortality rate for males. However, the composition of roosting groups may not necessarily provide an accurate demographic profile of the entire adult population. Indeed, demographic surveys based on mist-netting at feeding grounds in western India (Bhat and Sreenivasan, 1990; Sreenivasan et al., 1974) and collections of roosting groups in northern India (Krishna and Dominic, 1985) revealed adult sex ratios of ca. 1:1. In northern India, Krishna and Dominic (1985) reported that groups comprising 6–10 males and 10–15 females are formed from October to March and that males and females segregate to form unisexual groups from June to September. However, the age and reproductive status of group members were not specified. In southern India, adult males roost singly or in association with as many as 19 reproductive females and their dependent young during the breeding season (Balasingh et al., 1995).

*Cynopterus sphinx* is known to make use of several different types of day roosts, including aerial roots of banyan trees (*Ficus*



FIG. 4. Harem social group of *Cynoptyerus sphinx* roosting in the modified crown of a fruit cluster of the kitul palm, *Caryota urens*, in Pune, India (photograph by J. F. Storz).

*benghalensis*), tree hollows, and tree foliage (Advani, 1982b; Bhat, 1994; Brosset, 1962; Khajuria, 1979; Sandhu, 1984; Sinha, 1986). It occasionally roosts under the eaves of houses and buildings and less frequently in ruins and caves (Bates and Harrison, 1997; Bhat, 1994; Prater, 1971). *C. sphinx* is reported to construct foliage roosts called 'tents' (Balasingh et al., 1993, 1995; Bhat, 1994; Bhat and Kunz, 1995; Goodwin, 1979). Within the suborder Megachiroptera, tent-making behavior has been reported only in the genus *Cynoptyerus* (Kunz et al., 1994).

In Timor, *C. sphinx* constructs tents from large pinnate fronds of the Talipot palm (*Corypha umbraculifera*) by chewing veins of the large fan-shaped leaves, which causes the distal leaflets to collapse, thereby forming a flask-shaped enclosure. Groups of 3–8 *C. sphinx* typically will roost in a single palm leaf, although roosting groups as large as 20 have been observed. These shelters are built 2.4–6.0 m above the ground and typically are inhabited for no more than a few days. Thus, *C. sphinx* appears to move frequently among different foliage roosts. At higher altitudes where the Talipot palm does not grow, groups of *C. sphinx* can be found roosting in cavities of large fig trees (*Ficus*—Goodwin, 1979). In Sri Lanka, *C. sphinx* has been observed day roosting in altered palm leaves of the Talipot palm, the areca nut palm (*Areca catechu*), and the palmyra palm (*Borassus flabelliformis*; Phillips, 1980).

In western India, *C. sphinx* chew and sever the strings of dense flower or fruit clusters of the kitul palm (*Caryota urens*—Fig. 4). The tents typically are constructed by bats when the flower clusters are at an immature stage and the strings are thin and widely spaced (Bhat and Kunz, 1995). As the flowers and fruits mature, the strings supporting them become thicker and heavier and form a compact, bell-shaped roosting space. Bhat and Kunz (1995) reported groups of 8–23 bats roosting in a single, fully-formed kitul palm tent during their period of observation. Groups of *C. sphinx* will occupy these tent-roosts until the fruits drop and the tent withers. Bats do not use the newly altered flower clusters as diurnal roosts until a sufficient number of central strings have been severed and the cluster becomes dense enough to provide adequate shelter. The accumulation of chewed flower and fruit strings beneath these clusters suggests that tent-construction and tent-maintenance occurs at night (Bhat and Kunz, 1995). In this same area, single bats or small groups also roost in tents constructed from the fronds of various species of palms (*Borassus flabellifer*, *Coccothrinax argentea*, *Corypha umbraculifera*, *Livistona chinensis*, *Roystonea regia*, and *Sabal palmetto*) and tents constructed within the foliage of a variety of evergreen trees (Bhat, 1994).

In southern India, *C. sphinx* constructs tent-roosts by severing stems of the curtain creeper (*Vernonia scandens*) and stems and leaves of the ashoka tree (*Polyalthia longifolia*; Balasingh et al., 1993, 1995). Tents are constructed by single adult males. A tent constructed in *V. scandens* is completed in ca. 30 days, whereas one in *P. longifolia* is completed in ca. 50 days. Tent construction takes place mostly at night. Tents in both types of plants were occupied by a single adult male roosting in association with 2–19

adult females and their dependent young (Balasingh et al., 1995). The number of females in association with a particular male declines slightly following parturition. Male *C. sphinx* may construct tents and defend them against intrusions from other males for the purpose of gaining exclusive reproductive access to tent-roosting females (Balasingh et al., 1995).

*Cynoptyerus sphinx* is more agile on the wing than larger fruit bats and is able to feed on nectar, flowers, and fruit without landing (Bhat, 1994; Roberts, 1977). *C. sphinx* often removes fruits or leaves from food plants and then feeds in foliage roosts away from their diurnal roosting sites. These feeding roosts typically are located under a horizontal bough of a tree with an umbrella-like crown of leaves or beneath the fronds of fan palms. Typically *C. sphinx* selects feeding roosts within 20–100 m of the food plant and 10–30 m above the ground. Bats often shuttle between food plants and feeding roosts several times a night. Fruits which are too large to transport, such as mangoes, typically are eaten on the tree itself. Smaller fruits and flowers sometimes are consumed at the food plant as well (Bhat, 1994). Similarly, radiotracking studies reveal that *C. sphinx* continually shuttle between fruit trees and feeding roosts located in trees 10–30 m away. Over the course of five nights, three male *C. sphinx* travelled as far as 2.5 km from the day roost while foraging but spent <12 min in flight on any given night. The majority of their time was spent roosting in trees near their food plants (Marimuthu et al., 1998).

Audiograms recorded from *C. sphinx* indicated a sensitivity to ultrasound, although a capacity for echolocation has not been demonstrated in this species. *C. sphinx* is maximally sensitive to frequencies between 12 and 16 kHz (Neuweiler et al., 1984).

**GENETICS.** *Cynoptyerus sphinx* sampled from Java (Ando et al., 1980), Thailand (Harada et al., 1982), and India (Yong et al., 1973) have  $2n = 34$ . The autosomes of *C. sphinx* consist of 11 metacentric/submetacentric pairs, two subtelocentric pairs, and three small, acrocentric pairs ( $FN = 58$ ). One pair of the metacentric autosomes is characterized by a secondary constriction. The X chromosome is medium-sized and subtelocentric; the Y chromosome is small and acrocentric. Compared with the presumed ancestral karyotype of the family Pteropodidae, *C. sphinx* has relatively fewer subtelocentric autosomes, relatively more acrocentric autosomes, and an altered size ranking within the autosomal set (Ando et al., 1980). Though data are sparse, there appears to be very little karyotypic variation within the genus *Cynoptyerus* (Ando et al., 1980; Yong et al., 1973).

Schmitt et al. (1995) examined allozyme variability for seven species of *Cynoptyerus* within the Malay Archipelago. The genetic distances separating *Cynoptyerus* species are small relative to the divergence typically observed among congeneric mammals, which implies that this genus has undergone a rapid series of speciation events. The genetic distances among conspecific island populations are similar in magnitude to those reported for *C. brachyotis* in the Philippine Islands (Peterson and Heaney, 1993). The matrix of genetic distances indicate that the most closely related congener of *C. sphinx* is *C. brachyotis*, followed by *C. luzoniensis*.

The phylogeny of the epsilon-globin gene in *C. sphinx* has been interpreted as evidence for the monophyly of the Micro- and Megachiroptera relative to Primates (Bailey et al., 1992).

**REMARKS.** There is a great deal of uncertainty surrounding the taxonomic relationship between *C. sphinx* and *C. brachyotis* and the status of the many named forms within *C. sphinx* (Agrawal, 1973; Andersen and Kloss, 1915; Bates and Harrison, 1997; Corbet and Hill, 1992; Hill, 1983; Hill and Thonglongya, 1972; Phillips, 1934). Revisions of Andersen's (1912) classification of *C. sphinx* include placement of *C. major* Miller, 1906 as a subspecies of *C. sphinx* (Chasen, 1940) and placement of *C. pagensis* Miller, 1906 as a subspecies of *C. brachyotis*, following its removal from synonymy with *C. s. angulatus* (Chasen, 1940; Tate, 1942). The classification of Hill (1983) offered several substantial departures from previous treatments of *C. sphinx*: elevation of *tithaecheileus* to species status, following its removal as a subspecies of *C. sphinx*; placement of *angulatus*, *scherzeri*, *babi*, and *pagensis* as subspecies of *C. sphinx*, following their removal from *C. brachyotis* (cf. Chasen, 1940; Tate, 1942); placement of *major* as a subspecies of *C. tithaecheileus* following its removal from *C. sphinx* (cf. Chasen, 1940); and provisional recognition of *terminus* from Timor as representative of *tithaecheileus*, or possibly a distinct species, rather



than a subspecies of *C. sphinx*. According to Hill (1983), the large *C. s. gangeticus* from central and northwestern India and the slightly smaller *C. s. sphinx* from northeastern India and Burma merge into the characteristically smaller *C. s. angulatus* in Burma and Thailand. The range of this smaller form extends southward into the Malay Peninsula, Sumatra, and possibly as far east as Borneo. In Sri Lanka, Phillips (1934) distinguished between lowland and highland forms of *C. sphinx*, which he designated as *C. s. sphinx* and *C. s. ceylonensis*, respectively. In the mountains of Sri Lanka there is an intergradation of these two forms along an elevational gradient. The highland form (*ceylonensis*) is markedly smaller and darker in pelage (Phillips, 1934, 1980) and may be referable to *C. brachyotis* (Bates and Harrison, 1997).

The most frequently used English vernacular name for *C. sphinx* is the short-nosed fruit bat, but there are several local names applied to this bat, including Cotepkn vougha (Sinhalese) and Chamgadili (Hindi). The generic name *Cynopterus* is derived from the Greek word *kynos*, meaning "dog" and the Greek word *pteron*, meaning "wing" (Brown, 1954).

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