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Cynopterus horsfieldii.

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Cynopterus horsfieldii (Gray, 1843)

Horsfield's Fruit Bat

Cynopterus horsfieldii Gray, 1843:38. Type locality "Java," Indonesia.

Cynopterus marginatus: Blyth, 1852:345. Part, not *Pteropus marginatus* E. Geoffroy, 1810:97.

Pteropus [*Pachysoma*] *marginatus*: Wagner, 1853, 1855:609. Part, not *Pteropus marginatus* E. Geoffroy, 1810:97.

Pachysoma horsfieldii: Fitzinger, 1869:33. Name combination.

Cynopterus marginatus var. *horsfieldii*: Gray, 1870:123. Name combination.

Cynopterus princeps Miller, 1906:61. Type locality "Mojeia River, Nias Island, west Sumatra."

Niadias minor Lyon, 1908:665. Type locality "confluence of Gasip and Siak rivers, eastern Sumatra." Preoccupied by *Cynopterus* (*Cynonycteris*) *minor* Trouessart, 1878:206.

Cynopterus (*Niadius*) *harpax* Thomas and Wroughton, 1909:439. Type locality "Semangko Pass, Pahang boundary," Selangor–Pahang boundary, peninsular Malaysia, 3,000 feet (Andersen 1912a:633).

Cynopterus horsfieldi Anderson, 1912a:827. Name combination and unjustified emendation.

Cynopterus persimilis Andersen, 1912b:641. Type locality "Sarawak, Borneo."

CONTEXT AND CONTENT. Order Chiroptera, suborder Megachiroptera, family Pteropodidae, subfamily Pteropodinae, tribe Cynopterini, subtribe Cynopterina, genus *Cynopterus*. *Niadius* was synonymized with *Cynopterus* and the combined genus was divided in 2 sections (Anderson 1912a): the *Niadius* section with *C. harpax* and *C. horsfieldii*, and the *Cynopterus* section with *C. angulatus* (= *C. s. angulatus*), *C. brachyotis*, *C. sphinx*, and *C. s. titthaecheilus* (= *C. titthaecheilus*). *C. harpax* Thomas and Wroughton, 1909 was synonomized with *C. h. minor* by Hill (1961), who considered the type specimen to be morphologically indistinguishable from the Sumatran subspecies. *C. h. lyoni* Andersen, 1912a was considered the valid name and *C. h. minor* a homonym (Hill 1983). However, Koopman (1994) treated *C. h. lyoni* as a junior synonym of *C. h. harpax*. Four subspecies are recognized (Corbet and Hill 1992; Koopman 1994; Mickleburgh et al. 1992):

C. h. harpax Thomas and Wroughton, 1909:439; see above; *lyoni* (Anderson) and *minor* (Lyon) are synonyms.

C. h. horsfieldii (Gray, 1843):38; see above.

C. h. persimilis Andersen, 1912b:641; see above.

C. h. princeps Miller, 1906:61; see above.

DIAGNOSIS. *Cynopterus horsfieldii* (Fig. 1) is readily distinguished from *Pteropus* by its smaller size. *Aethalops alecto*, *Balionycteris maculata*, *Chironax melanocephalus*, and *Macroglossus* are all considerably smaller than *C. horsfieldii*. *Rousettus* has 5 cheek teeth in upper toothrow and is generally larger than *C. horsfieldii* (Lekagul and McNeely 1977; Payne et al. 1985). Among medium-sized members of Pteropodidae, *C. horsfieldii* can be differentiated as follows: *Megaerops* and *Penthetor lucasi* lack white ear margins and have 1 pair of lower incisors whereas *C. horsfieldii* has 2; *Megaerops* lacks a tail. *Eonycteris* has a longer, narrower rostrum than *C. horsfieldii* and lacks claw on 2nd digit. *Dyacopterus spadiceus* is slightly larger than *C. horsfieldii*, with a broader rostrum, deeper jaw, massive squared cheek teeth, and 2 upper premolars as compared to 3 in *C. horsfieldii* (Lekagul and McNeely 1977; Medway 1983; Payne et al. 1985).

Cynopterus horsfieldii is distinguished from all other congeners by having peglike cusps on the 3rd and 4th lower cheek teeth (p3, m1—Corbet and Hill 1992; Lekagul and McNeely 1977; Medway 1983; Payne et al. 1985). In peninsular Malaysia, *C. horsfieldii* is considerably larger than *C. brachyotis* and averages larger than *C. sphinx* in all characters except length of rostrum. Relative to *C. sphinx*, *C. horsfieldii* has a broader cranium, blunter rostrum, and more-robust cheek teeth (Campbell et al., in press).

GENERAL CHARACTERS. *Cynopterus horsfieldii* is a medium-sized fruit bat with large eyes and simple ears that lack a tragus. Skull (Fig. 2) is robust with a short, broad rostrum, and nostrils are subtubular. *C. horsfieldii* has 4 cheek teeth in each upper toothrow, 1 pair of upper and lower canines, and 2 pairs of upper and lower incisors. Well-developed surface cusps are on the 3rd lower premolar and 1st lower molar (Andersen 1912a; Lekagul and McNeely 1977; Medway 1983; Payne et al. 1985).

Pelage is short and dense (Andersen 1912a). Color in adults ranges from light or yellowish gray to dark or bright brown; juveniles are dull buff or gray. Breeding adults have a reddish brown or orange mantle (Lekagul and McNeely 1977; Medway 1983; Payne et al. 1985). Pelage around throat and shoulders of adult males is stiffer, brighter, and richer in color than that of females. In males, mantle may extend ventrally across chest (Andersen 1912a; Medway 1983; Payne et al. 1985). Color and area of mantle are the only consistently sexually dimorphic characters; males and

FIG. 1. Photograph of an adult male *Cynopterus horsfieldii* from Krau Wildlife Reserve in peninsular Malaysia. Used with permission of the photographer, T. Kingston.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Cynopterus horsfieldii* from Taman Negara, peninsular Malaysia (Department of Wildlife and National Parks, Kuala Lumpur, Malaysia, catalogue no. NP042). Greatest length of skull is 34.1 mm. Used with permission of the photographer, S. W. Murray.

females do not differ significantly in size (Campbell et al., in press). Margins of ears and membranes overlying metacarpals and phalanges are edged in white.

Mean external measurements (± *SD,* in g or mm, sexes combined unless noted) for *C. horsfieldii* in peninsular Malaysia are: body mass, 57.9 (4.8, *n* = 31—Campbell et al., in press); 55.6 (8.9, *n* = 7—Hodgkison et al. 2004a); 56.7 (6.1, *n* = 19 males), 59.7 (6.9, *n* = 26 females—Funakoshi and Zubaid 1997); length of forearm, 73.2 (1.79, *n* = 27—Campbell et al., in press); 74.2 (1.7, *n* = 14 males), 74.7 (1.9, *n* = 24 females—Hodgkison 2001); 74.3 (3.1, *n* = 19 males), 75.1 (2.3, *n* = 26 females—Funakoshi and Zubaid 1997); and length of tibia, 27.0 (1.2, *n* = 27—Campbell et al., in press). Lengths of ear and tail (range, in mm) are: 19–22 and 12–16, respectively (*n* = 8—Lim et al. 1999). Length of forearm (range, in mm, sexes combined) for *C. horsfieldii* in Indonesia is: 64.5–71 (*n* = 15, Java), 71.5–77.5 (*n* = 3, Sumatra), and 87.0–89.5 (*n* = 2, Nias Island—Andersen 1912a).

Mean cranial measurements (± *SD,* in mm, sexes combined) for *C. horsfieldii* in peninsular Malaysia are: total length of skull, 32.4 (0.76); maximum zygomatic breadth, 22.6 (0.85); maximum posterior skull width at mastoid, 14.4 (0.38); length of rostrum, 7.0 (0.32); length of palate, 17.0 (0.53); length from canine to M1, 10.7 (0.31); width of palate at M1, 9.7 (0.32); width of palate at P2, 8.6 (0.33); width of palate at canines, 6.9 (0.27); length of dentary, 24.8 (0.58); condylocanine length, 24.2 (0.59); length from condyle to p3, 18.7 (0.53); length from condyle to m1, 16.2 (0.48); length from condyle to m2, 13.5 (0.45); and height of coronoid process, 13.2 (0.51, *n* = 27—Campbell et al., in press).

Cranial measurements (ranges or individual measurements, in mm, sexes combined) for *C. horsfieldii* in Indonesia are: total length of skull, 30.5–33.3 (*n* = 16, Java), 33.5–35.8 (*n* = 3, Sumatra), 38.5, 39.3 (*n* = 2, Nias Island); condylobasal length, 29.5–31.5 (*n* = 16, Java), 31.8–34.0 (*n* = 3, Sumatra), 36.2, 37.2 (*n* = 2, Nias Island); length of rostrum (orbit to nares), 6.2–7.3 (*n* = 16, Java), 7.0–7.8 (*n* = 3, Sumatra), 8.7, 9.2 (*n* = 2, Nias Island); length from canine to M1, 10.5–11.5 (*n* = 16, Java), 11.0–12.0 (*n* = 3, Sumatra), 13.2, 13.5 (*n* = 2, Nias Island); total length of dentary, 23.0–25.3 (*n* = 16, Java), 25.5–26.8 (*n* = 3, Sumatra), 29.0, 30.5 (*n* = 2, Nias Island); length from canine to m2, 11.7–12.4 (*n* = 16, Java), 12.4–13.3 (*n* = 3, Sumatra), 14.4, 14.8 (*n* = 2, Nias Island); and height of coronoid process, 12–13.2 (*n* = 16, Java), 13.7–14.5 (*n* = 3, Sumatra), 16.8 (*n* = 2, Nias Island—Andersen 1912a).

Dental measurements (ranges or individual measurements, in mm, sexes combined) at crowns are: length and width of P3, 2.2–2.7 and 1.7–2.0 (*n* = 15, Java), 2.5–2.6 and 1.8–2.0 (*n* = 3, Sumatra), 2.8, 3.0 and 2.2, 2.3 (*n* = 2, Nias Island); length and width of M1, 2.3–2.7 and 1.6–1.9 (*n* = 15, Java), 2.6–2.8 and 1.8–1.9 (*n* = 3, Sumatra), 3.0, 3.1 and 2.0, 2.2 (*n* = 2, Nias Island); length and width of p1, 0.7–1.1 and 1.1–1.7 (*n* = 15, Java), 1.0–1.2 and 1.7 (*n* = 3, Sumatra), 1.2 and 1.7, 1.8 (*n* = 2, Nias Island); length and width of p3 (= p2), 2.0–2.5 and 1.7–2.0 (*n* = 15, Java), 2.2–2.5 and 1.8–2.0 (*n* = 3, Sumatra), 2.5, 2.8 and 2.3 (*n* = 2, Nias Island); length and width of p4 (= p3), 2.2–2.7 and 1.8–2.0 (*n* = 15, Java), 2.5–2.7 and 1.8–2.0 (*n* = 3, Sumatra), 2.8, 3.0 and 2.3 (*n* = 2, Nias Island); length and width of m1, 2.5–2.8 and 1.7–2.0 (*n* = 15, Java), 2.7–2.8 and 1.8 (*n* = 3, Sumatra), 2.9, 3.0 and 2.1, 2.2 (*n* = 2, Nias Island); and length and width of m2, 1.6–1.9 and 1.0–1.6 (*n* = 15, Java), 1.6–1.8 and 1.2–1.4 (*n* = 3, Sumatra), 1.8, 2.0 and 1.5, 1.7 (*n* = 2, Nias Island—Andersen 1912a).

DISTRIBUTION. *Cynopterus horsfieldii* (Fig. 3) occurs from ca. 9°N in southern Thailand, throughout peninsular Malaysia, on the Indonesian islands of Sumatra, Java, Bali, Lombok, and Sumbawa, and on the island of Borneo in Kalimantan (Indonesia), Sabah and Sarawak (Malaysia), and Brunei (Campbell et al. 2006b; Corbet and Hill 1992; Lekagul and McNeely 1977; Medway 1983; Mickleburgh et al. 1992; Schmitt et al. 1995; Simmons 2005). No recent records are available from Singapore (Teo and Rajathurai 1997).

Subspecies of *C. horsfieldii* have the following distributions: *C. h. harpax*, southern Thailand, peninsular Malaysia, and Sumatra; *C. h. horsfieldii*, Java to Sumbawa; *C. h. persimilis*, Borneo; *C. h. princeps*, Nias Island, Indonesia (Corbet and Hill 1992; Hill 1983; Koopman 1994; Lekagul and McNeely 1977; Medway 1983). No fossils are known.

FORM AND FUNCTION. Dental formula of *C. horsfieldii* is i 2/2, c 1/1, p 3/3, m 1/2, total 30 (Andersen 1912a). Premolars and molars are broad and subrectangular, with well defined surface cusps on p3 and m1 (Andersen 1912a; Koopman 1994).

Cynopterus horsfieldii has relatively short, broad wings (low aspect ratio) and a relatively high ratio of body mass to wing area (high wing loading—Campbell et al., in press; Hodgkison et al. 2004a; McKenzie et al. 1995). This unspecialized wing morphology

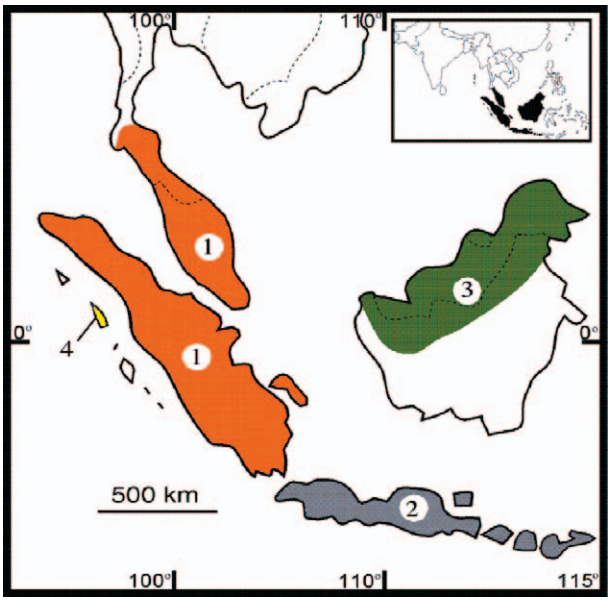

FIG. 3. Geographic distribution of *Cynopterus horsfieldii*, redrawn from Corbet and Hill (1992) with modifications according to Campbell et al. (in press) and Kitchener et al. (1990): 1, *C. h. harpax*, southern Thailand, peninsular Malaysia, and Sumatra; 2, *C. h. horsfieldii*, Java to Sumbawa; 3, *C. h. persimilis*, Borneo; 4, *C. h. princeps*, Nias Island. Inset map localizes the Malay peninsula and western Indonesia (black) in Asia.

indicates that *C. horsfieldii* is capable of slow flight in moderately cluttered airspace, but is ill-suited to foraging over long distances or maneuvering in dense vegetation (Campbell et al., in press; Norberg and Rayner 1987).

Mean brain mass of *C. horsfieldii* is 1,370 mg (n = 3, sexes combined—Bhatnagar et al. 1990). Pineal gland is deeply recessed and covered by cerebral hemispheres. Pineal volume is 0.4853 mm^3 and greatest width of pineal gland is 1,010 μm (Bhatnagar et al. 1986, 1990).

ONTOGENY AND REPRODUCTION. In peninsular Malaysia, *C. horsfieldii* is seasonally polyestrous and reproductively asynchronous, with pregnant females recorded throughout the year (Medway 1983). Two loosely synchronized peaks in birth occur per annum; during a 30-month study, peak numbers of lactating females were observed in February–March and July–August (Funakoshi and Zubaid 1997).

Concentrations (mg/g dry mass) of minerals and nitrogen in milk of *C. horsfieldii* are: iron, 0.173; calcium, 6.11; magnesium, 0.17; potassium, 7.9; sodium, 5.37; and nitrogen, 28.03 (n = 1—Studier et al. 1995). With the exception of sodium, concentrations of minerals in milk of *C. horsfieldii* are lower than those in milk of 2 other Old World fruit bats, *D. spadiceus* and *Megaerops ecaudatus* (Studier et al. 1995).

Based on mark–recapture data from peninsular Malaysia, average longevity for *C. horsfieldii* is at least 31 months (Hodgkison 2001).

ECOLOGY AND BEHAVIOR. *Cynopterus horsfieldii* is a habitat generalist, occurring in diverse lowland habitats, from primary rain forest to suburban parks (Hodgkison et al. 2004a; Lim 1966; Tan et al. 1999). Although relatively common, *C. horsfieldii* is typically less abundant than sympatric congeners, particularly *C. sphinx* and *C. brachyotis* (Campbell et al., in press; Francis 1994; Hodgkison et al. 2004b; Lim 1966; Zubaid 1993, 1994).

In peninsular Malaysia, *C. horsfieldii* is captured in both primary and disturbed lowland dipteropcarp forest (Campbell et al., in press; Fletcher 2001; Francis 1994, 1995; Funakoshi and Zubaid 1997; Hodgkison et al. 2004a; Zubaid 1993), limestone hill forest (Campbell et al., in press), fruit orchards (Campbell et al., in press; Lim 1966; Lim et al. 1999), and suburban gardens and parks (Campbell et al., in press; Tan et al. 1999). On the Indonesian island of Lombok, *C. horsfieldii* occurs in agricultural areas and secondary and primary rain forest (Kitchener et al. 1990).

Comparison of the relative abundance of *Cynopterus* species across adjacent habitat types in northern peninsula Malaysia indicates that estimated overlap in habitat use between *C. horsfieldii* and *C. sphinx* is relatively high (71.2%). However, *C. horsfieldii* is strongly associated with transitional habitat between forest and cultivated land, whereas *C. sphinx* is most abundant in highly disturbed habitats and suburban areas where *C. horsfieldii* is less common (Campbell et al., in press).

Within the forest, *C. horsfieldii* is captured in both understory and subcanopy (Francis 1994; Zubaid 1994), usually below 20 m (Hodgkison et al. 2004a), with a significant negative association between capture rate and density of vegetation (Hodgkison 2001). In lowland rain forest in central peninsular Malaysia, *C. horsfieldii* is a transient member of the fruit bat assemblage. Aseasonal shifts in abundance of *C. horsfieldii* are associated with exploitation of "big bang" food resources such as fruit of strangler figs (*Ficus*), *Elaeocarpus stipularils*, and *Payena lucida*, and flowers of *Parkia speciosa* (Hodgkison et al. 2004b). Data from the same site indicate that *C. horsfieldii* relies year-round on food resources in gardens and secondary habitats near the forest edge (Hodgkison 2001).

On Lombok Island, 11 pollen types were identified from stomachs and alimentary tracts of *C. horsfieldii* ($\bar{X} \pm SD$, 2.5 ± 1.12 pollen types/individual, n = 16) from various habitats (Kitchener et al. 1990). The pollen dietary niche breadth of *C. horsfieldii* was low relative to predominantly nectarivorous species such as *Eonycteris spelaea* and *Macroglossus minimus* and was intermediate to that of *C. brachyotis* (= *C. nusatenggara*, sensu Kitchener and Maharadatunkamsi 1991) and *C. titthaecheilus*. Pollen intake by *C. horsfieldii* was strongly influenced by the temporal and spatial availability of fruit: larger quantities of pollen were ingested during the dry season when fruit was less abundant and pollen dietary niche breadth was highest at sites where fruit was scarce. Across seasons and sites, *C. horsfieldii* exhibited high pollen dietary niche overlap with *C. brachyotis* and *C. titthaecheilus* (Kitchener et al. 1990).

When feeding in fruit trees, *C. horsfieldii* removes single fruits from parent tree to nearby day or feeding roosts (Funakoshi and Zubaid 1997; Hodgkison 2001). Germination rates for *Ficus* seeds ingested by *C. horsfieldii* are ca. twice that of controls (Fletcher 2001).

In secondary forest in peninsular Malaysia, mean home range sizes of adult *C. horsfieldii* were 5.8 ha ± 2.5 *SD* (n = 4 females) and 8.0 ha (n = 2 males—Funakoshi and Zubaid 1997). However, at another peninsular Malaysian site, individuals of *C. horsfieldii* that were captured while foraging in fruit orchards commuted up to 1.6 km to roosts in adjacent forest fragments (Fletcher 2001).

Cynopterus horsfieldii roosts in small groups in foliage, rock shelters, and limestone solution cavities on open cliff faces or near the mouths of caves (Campbell et al. 2006a; Funakoshi and Zubaid 1997; Lim 1966; Medway 1983; Payne et al. 1985; Tan et al. 1999). *C. horsfieldii* modifies foliage roosts in an opportunistic manner; individuals switch roosts frequently and do not exhibit detectable preferences for modified or unmodified roosts (Campbell et al. 2006a; Funakoshi and Zubaid 1997; Tan et al. 1999).

In a comparative study of the roosting ecology of *Cynopterus* species in northern peninsular Malaysia, estimated overlap in roost plant choice between *C. horsfieldii* and sympatric congeners ranged from 0.00% to 6.73% (Campbell et al. 2006a). All roosts of *C. horsfieldii* were located either in ecotonal habitat between cultivated land and secondary forest or <0.25 km inside the forest (Campbell et al. 2006a). Seventy-three percent (n = 35) of roosts of this species were in oblong leaves of wild and cultivated bananas (*Musa*). Ca. half of banana leaf roosts occupied by *C. horsfieldii* were modified into an inverted V-shaped structure by partial severing of midrib of leaf midway between base and tip. Height of roosts ($\bar{X} \pm SD$, in m) used by *C. horsfieldii* was significantly lower than that of roosts occupied by *C. sphinx* and *C. brachyotis* (2.94 ± 0.98, n = 26—Campbell et al. 2006a). Other plant species used as roosts by *C. horsfieldii* in peninsular Malaysia include palms in the genera *Arenga*, *Cocos*, *Corypha*, and *Nypa* and the epiphytic bird's nest fern *Asplenium nidas* (Campbell et al. 2006a; Funakoshi and Zubaid 1997; Lim 1966; Tan et al. 1999).

Mating system of *C. horsfieldii* is polygynous with a harem-based social structure that is maintained year-round (Campbell et al. 2006a; Tan et al. 1999). Harem groups contain 1 adult male and up to 5 adult females and their offspring (Campbell et al. 2006a; Tan et al. 1999). Individual composition of harem groups is

relatively labile and females may periodically roost singly without attendant males (Campbell et al. 2006a). Harem groups are found in both modified and unmodified roosts (Campbell et al. 2006a; Tan et al. 1999).

GENETICS. *Cynopterus horsfieldii* has 2n = 34 and FN = 58 (Yong et al. 1973). Autosomal chromosomes consist of 11 pairs of metacentrics or submetacentrics, 2 pairs of subacrocentrics, and 3 pairs of acrocentrics. X chromosome is a medium-sized subacrocentric and Y is a small acrocentric. Karyotype of *C. horsfieldii* is identical to those of *C. s. titthaecheilus* (= *C. titthaecheilus*), *C. brachyotis*, and *C. sphinx* (Andō et al. 1980; Ray-Chaudhuri et al. 1968; Yong et al. 1973).

Mean heterozygosity in *C. horsfieldii* from Java, Bali, Lombok, and Sumbawa was 0.032 compared with 0.028 for *C. sphinx*, 0.083 for *C. brachyotis*, and 0.052 for *C. nusatenggara* and *C. titthaecheilus*. *C. horsfieldii* had no relationship between genetic and geographic distance (Schmitt et al. 1995). In a phylogenetic supertree for Chiroptera *C. titthaecheileus* is sister to *C. horsfieldii* (Jones et al. 2002) in the *Cynopterus* clade. The mitochondrial lineage of *C. horsfieldii* is nested within the Malaysian *C. brachyotis* lineage (= *C. brachyotis* Forest). Sequence divergence between the 2 lineages is 4.2% (1,266 base pairs, partial cytochrome *b* and control region—Campbell et al. 2004) and 80% of all alleles for *C. horsfieldii* at 6 polymorphic nuclear microsatellite loci occur in *C. brachyotis* Forest (Campbell et al. 2006b). Populations of *C. horsfieldii* in peninsular Malaysia and southern Thailand are not geographically structured (Campbell et al. 2006b).

REMARKS. *Cynopterus* is from the Greek words *kynos* meaning dog and *pteron* meaning wing (Brown 1954). *Cynopterus horsfieldii* was named in honor of Dr. Thomas Horsfield (1773–1859), an American physician and naturalist who made extensive collections of plants and animals while working in Java for the Dutch East India Company (Bastin 1990). The type specimen of *C. horsfieldii* was among those presented to the British Museum by Horsfield on behalf of the Dutch East India Company (Gray 1843; Horsfield 1851). Alternate English vernacular names for *C. horsfieldii* include the larger dog-faced fruit bat (Medway 1983) and the peg-toothed short-nosed fruit bat (Lekagul and McNeely 1977). This paper is contribution 100 of the Lubee Foundation, Inc.

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