Revealing cryptic bat diversity: three new *Murina* and redescription of *M. tubinaris* from Southeast Asia

GABOR CSORBA,* NGUYEN TRUONG SON, ITH SAVENG, AND NEIL M. FUREY

Department of Zoology, Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary (GC)
Institute of Ecology and Biological Resources, 18 Hoang Quoc Viet Road, Cau Giay District, Hanoi, Vietnam (NTS)
Centre for Biodiversity Conservation, Room 415, Department of Biology, Faculty of Science, Royal University of Phnom Penh, Confederation of Russia Boulevard, Phnom Penh, Cambodia (IS)
Fauna & Flora International, Cambodia Programme, No. 19, Street 360, Boeung Keng Kong 1, Phnom Penh, Cambodia, 12000 (NMF)
Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, United Kingdom (NMF)

* Correspondent: csorba@nhmus.hu

Based on a series of specimens collected in Cambodia and Vietnam, this paper describes 3 new species of tube-nosed bats belonging to the *Murina* ''*suilla*-group'' (Vespertilionidae: Murininae). We provide detailed accounts of their external and craniodental morphology, including a suite of standard measurements, and compare the new taxa with all other members of the group currently recognized in Southeast Asia. The 1st new species was previously included in *M. tubinaris* (Scully, 1881) but is considered distinct due to differences in external and craniodental features. This new species is widespread in continental Southeast Asia and relatively well represented in museum collections, whereas the other new species are known only from a few specimens collected at scattered localities. The new taxa are known only from forested areas, which highlights the incompleteness of existing knowledge and strong potential for further discoveries in the region.

Key words: Murininae, new species, taxonomy, tube-nosed bats

The Old World subfamily of vespertilionid bats, Murininae Miller, 1907, is rich in cryptic species. Relatively rare in museum collections and seldom abundant in the wild, the subfamily was regarded as including 19 species (Simmons 2005). Although our understanding of this morphologically challenging group has been constrained historically by lack of voucher material, increased survey effort using improved capture methods (particularly harp traps) has greatly expanded the quantity of specimens available. As a consequence, recent studies have added substantially to our existing knowledge, with 8 new species described from Southeast Asia (Csorba and Bates 2005; Csorba et al. 2007; Furey et al. 2009; Kruskop and Eger 2008; Kuo et al. 2006, 2009). The purpose of the present study is to present a morphological analysis of selected *Murina* within the ''*suilla*-group'' (sensu Corbet and Hill 1992) from the Indo-Malayan region.

Scully's tube-nosed bat, *M. tubinaris* (Scully, 1881), traditionally is considered a widely distributed species in the region (Corbet and Hill 1992; Francis 2008). The species originally was described from a single specimen collected in

Gilgit (Pakistan), with several more subsequently collected in the northwestern Himalayan region. We explore differences in external and craniodental morphology between these specimens and historical and recent material collected from a large and disjunct area spanning northeastern India to southern Indochina.

In 1999 a relatively large and dark-colored individual of *Murina* was collected at Kon Ka Kinh Nature Reserve in the Central Highlands of Vietnam. Initially identified as *M. tubinaris* (Hendrichsen et al. 2001), comparisons with specimens collected subsequently in the Annamite Mountains to the north reveal that these bats exhibit several features that clearly distinguish them from this species. More recently, 3 additional individuals of *Murina* with uniformly white ventral hairs were collected separately from isolated areas in Southeast Asia. This pelage character, combined with

craniodental features, distinguishes them from all other named forms. As a consequence, we also present descriptions of 2 additional taxa and compare them with all other morphologically similar species of *Murina* currently recognized in Southeast Asia.

MATERIALS AND METHODS

Bats were captured and handled in the field in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Age and reproductive status of *Murina* were assessed following Anthony (1988) and Racey (1988). External measurements were taken from dry skins and alcohol-preserved museum specimens to the nearest 0.1 mm. Craniodental measurements were taken to the nearest 0.01 mm using digital calipers and a stereomicroscope. Measurements include only those taken from nonjuveniles, as indicated by the presence of fully ossified metacarpal–phalangeal joints. A list of abbreviations for institutions and comparative material examined is given in Appendix I. Abbreviations and definitions for external measurements include FA: forearm length—from the extremity of the elbow to the extremity of the carpus with the wings folded; TAIL: tail length—from the tip of the tail to its base adjacent to the anus; HF: hind foot—from the tip of the longest digit, excluding the claw, to the extremity of the heel, behind the os calcis; TIBIA: tibia length—from the knee joint to the ankle; 5met, 4met, and 3met: length of the metacarpal of the 5th, 4th, and 3rd digits, respectively—taken from the extremity of the carpus to the distal extremity of each metacarpal; 3d1ph: length of the 1st phalanx of the 3rd digit; 3d2ph: length of the 2nd phalanx of the 3rd digit; EAR: ear length—from the lower border of the external auditory meatus where it joins with the body to the tip of the pinna; and TRAGUS: tragus length—from the lower posterior emargination to the tip of the tragus.

Abbreviations and definitions for craniodental measurements are STOTL: total length of skull—from the anterior rim of the alveolus of the 1st upper incisor to the most projecting point of the occipital region; CCL: condylo-canine length—from the exoccipital condyle to the most anterior part of the canine; CCW: width across the upper canines—greatest width across the outer borders of the upper canines; M3M3W: width across the upper molars—greatest width across the outer crowns of the last upper molars; ZYW: zygomatic width—greatest width of the skull across the zygomatic arches; MAW: mastoid width—greatest distance across the mastoid region; IOW: interorbital width—least width of the interorbital constriction; BCW: braincase width—greatest width of the braincase; BCH: braincase height—from the basisphenoid at the level of the hamular processes to the highest part of the skull, including the sagittal crest (if present); CM3L: maxillary toothrow length—from the front of the upper canine to the back of the crown of the third molar; CP4L: upper canine–premolar length—from the front of the upper canine to the back of the crown of the posteriormost premolar; ML: mandible length—from the anterior rim of the alveolus of

the 1st lower incisor to the most posterior part of the condyle; cm3L: mandibular toothrow length—from the front of the lower canine to the back of the crown of the 3rd lower molar (m3); cp4L: lower canine–premolar length—from the front of the lower canine to the back of the crown of the posteriormost premolar; and CPH: least height of the coronoid process—from the tip of the coronoid process to the apex of the indentation on the inferior surface of the ramus adjacent to the angular process.

Absolute height was used in all height comparisons for individual teeth (e.g., C versus P4). Height comparisons of hypoconids relative to entoconids were standardized by ensuring that the ramus of the mandible overlapped in the lateral view in each instance.

RESULTS

Vespertilionidae Gray, 1821
Murininae Miller, 1907
Murina Gray, 1842
Redescription of *Murina tubinaris* (Scully, 1881)

Harpiocephalus tubinaris Scully, 1881:200
Murina tubinaris: Miller 1907:230 (First use of current name combination)
Murina [*huttoni*] *tubinaris*: Ellermann and Morrison-Scott 1951:186

Holotype.—The type specimen of *M. tubinaris* cannot be found but was reportedly housed in the collection of the Indian Museum, Kolkata.

Type locality.—Pakistan, Northern Areas, Gilgit.

Diagnosis.—Pelage is superficially light gray with brown on the dorsal surface and whitish with dark bases on the ventral surface. The plagiopatagium is attached to the proximal phalanx of the outer toe. The zygoma is weak, and the basal area of P4 is larger than that of C, whereas the basal area of P2 is less than one-half that of P4. The mesostyles of M1 and M2 are reduced in bulk but retain distinct cusps.

Description.—This is a small species of *Murina* (Table 1). The nostrils are tubular and highly protuberant, as is typical of the genus. On the dorsal surface the lower portion of individual hairs is medium brown. This is succeeded by a short, light gray portion that progresses to light brown before terminating in a darker brown tip (Figs. 1a and 2a). The upper surfaces of the hind limbs, feet, and uropatagium are evenly covered in long, light brown hairs that extend onto the wing membrane next to the tibia. Ventrally, individual hairs are medium brown basally (although slightly darker than the basal portion of the dorsal hairs), whereas the upper portion is off-white (Fig. 2b). The ventral surface of the uropatagium is covered in short, uniformly white hairs that extend onto the plagiopatagium next to the body. The plagiopatagium is attached to the proximal phalanx of the outer toe.

The skull is small (Table 1). In lateral view a shallow concavity is present over the orbits (Fig. 3a) and the midportion of the braincase exceeds the frontal region in

height. A sagittal crest is not present, and the lambdoidal crests are relatively weak. The rostrum is not inflated. The depth of the narial emargination is equal to its width, and the outline of the emargination is smoothly concave in dorsal view. The zygoma is very delicate and lacks a dorsal process, and its upper and lower surfaces in the midportion are parallel. The palate is concave and narrows toward the canines, whereas the pterygoid plates are convergent posteriorly. The posterior border of the palatal emargination extends to the middle of the upper canine, and a poorly defined medial process is present in the posterior palatal region. The basioccipital pits are well defined and separated by a relatively broad medial ridge.

The maxillary toothrows are convergent anteriorly (C1C1W/M3M3W: $\bar{X}$ = 0.71, range = 0.68–0.72, SD = 0.02, n = 5). The 1^2 is strongly bifid and situated anterior to the 1^3, such that it is readily visible in lateral view (Fig. 3a). The 1^2 and 1^3 are equal in height, and the 1st comprises only about one-half of the basal area of the 2nd upper incisor (Fig. 3b). The 2nd upper incisor is not in contact with the upper canine. The basal area of C is exceeded by that of the posteriormost premolar, and its width exceeds its length, such that the tooth appears more elliptical than round in the occlusal view. C exceeds P4 in height and has a distinct cingular cusp on the lingual side. P2 is compressed with a basal area less than one-half that of P4 and a height approximately one-half that of P4. The mesostyle of M1 is reduced but retains a distinct cusp, and the medial portion of the labial face is very slightly convex. On M2 the mesostyle is reduced further in bulk such that the medial portion of its labial face is smoothly concave. The metacones of M1 and M2 exceed their respective paracones in height.

The mandible is delicate, and the lower incisors are tricuspid and overlap laterally (Fig. 3). The lower canine exceeds the posterior premolar in height and basal area. It has a well-developed inner cingulum with the anteriormost portion in contact with the posterior face of i3. The basal area of p2 is approximately one-half that of p4, and the height of p2 is more than two-thirds that of p4. The talonids of m1 and m2 equal their respective trigonids in crown area, and the hypoconids and entoconids of these teeth are of equal height. The postcristid terminates posterior to the entoconid.

Comparisons with other taxa.—On the basis of its dentition, *M. tubinaris* belongs to the ''*suilla*-group'' (Corbet and Hill 1992), which includes *M. aurata*, *M. eleryi*, *M. gracilis*, *M. harpioloides*, *M. leucogaster*, *M. recondita*, *M. silvatica*, *M. suilla*, and *M. ussuriensis*. The maxillary toothrows are convergent anteriorly; the 1st upper incisors lie anterior to the 2nd upper incisors; the basal area of the anterior upper premolar is one-half or less that of the posteriormost upper premolar; and the basal area of the upper canine is exceeded by that of the posteriormost upper premolar. These features distinguish *M. tubinaris* from all members of the ''*cyclotis*-group,'' which in mainland Southeast Asia includes *M. aenea*, *M. cyclotis*, *M. harrisoni*, *M. huttoni*, and *M. tiensa*.

In addition to its plagiopatagium being attached to the base of the 1st toe and having a very delicate zygoma, similar-sized species in the ''*suilla*-group'' (Table 2) are distinguished individually from *M. tubinaris* by several other characteristics. *M. aurata* differs markedly in dorsal pelage in possessing yellowish brown to reddish yellow underhair with scattered metallically glossy golden overhairs (Maeda 1980). Dentally, *M. tubinaris* can be separated from *M. aurata* by the height of its upper and lower canines, which exceeds that of their posteriormost premolars, whereas in *M. aurata* C is less than or equal to P4 and c is not larger than p4 (Maeda 1980). *M. eleryi* similarly differs from *M. tubinaris* externally in possessing ''copper-reddish dorsal hair mottled with underlying dark brown and overlain by individual shiny golden hairs'' (Furey et al. 2009:227). Cranially, dentition in *M. tubinaris* is also typically larger and the rostrum more robust in lateral and dorsal views. In relation to *M. harpioloides*, *M. tubinaris* is distinguished readily by the same external features that separate it from *M. aurata* (Kruskop and Eger 2008).

In contrast to *M. tubinaris*, the dorsal pelage of the recently described *M. gracilis* is ''dark brown mottled with yellowish brown'' with ''shiny golden individual hairs scattered on the back'' (Kuo et al. 2009:985). In the dentition of *M. tubinaris* the basal area of I2 is equal to or greater than one-half that of I3 (versus less than one-half in *M. gracilis*), and the labial face of M2 is smoothly concave (versus slightly convex medially in *M. gracilis*). The Taiwanese species *M. recondita* also is separated easily externally by its dorsal pelage, which is ''medium brown or yellowish brown scattered with bright yellow and small amount of shiny golden [hairs]'' (Kuo et al. 2009:987), as opposed to light gray brown and absence of conspicuous guard hairs in *M. tubinaris*. The dentition of *M. recondita* is less robust, and its upper incisors and M2 are similar to those of *M. gracilis*.

Murina suilla is distinguished by pelage coloration, which is reddish brown dorsally (versus light gray brown in *M. tubinaris*) and uniformly white medially on the ventral side (versus dark bases in *M. tubinaris*). *M. suilla* differs cranially in possessing a deeper orbital concavity in the lateral view, shallower basioccipital pits, and I2 comprising one-third the basal area of I3 (versus greater than one-half in *M. tubinaris*). The pelages of *M. ussuriensis* and *M. silvatica* differ in being reddish brown dorsally with a dense covering of long hairs on the upper surface of the uropatagium (Kruskop 2005; Maeda 1980; Yoshiyuki 1983, 1989). In the upper dentition the canine is more robust in *M. ussuriensis* and *M. silvatica* than in *M. tubinaris*.

Taxonomic remarks and distribution.—Since its description *M. tubinaris* has been subject to considerable misinterpretation. Scully (1881:200) provided a general description with relatively few diagnostic characters and compared *M. tubinaris* only with *M. suilla*, noting for the former that the ''wings [are] from the side of the proximal phalanx of the outer toe'' (i.e., plagiopatagium is attached to the base of the toe as opposed to close to the claw). Although recent works indicate that the insertion point of the plagiopatagium can be effective in externally distinguishing otherwise similar *Murina* species (Csorba and Bates 2005; Kuo et al. 2009), this feature

TABLE 1.—Selected external and craniodental measurements (mm) of *Murina tubinaris* (Scully, 1881), *M. cineracea* sp. nov., *M. beelzebub* sp. nov., and *M. walstoni* sp. nov. Values are given as mean ($\bar{X}$), *SD* (if $n \geq 5$), and minimum–maximum (Min-max) *n*. Abbreviations and definitions for measurements are given in the text.

| Character | *M. tubinaris* (Scully, 1881) | *M. cineracea* sp. nov. | | *M. beelzebub* sp. nov. | *M. walstoni* sp. nov. |
		♂♂	♀♀		
FA					
$\bar{X} \pm SD$	32.2 ± —	29.0 ± 1.2	32.0 ± 1.3	35.2 ± —	33.0 ± —
Min-max	31.0–32.9	27.5–31.0	29.8–33.8	33.7–36.3	31.5–33.7
n	4	13	14	4	3
STOTL					
$\bar{X} \pm SD$	15.25 ± 0.28	15.22 ± 0.32	15.58 ± 0.38	16.69 ± —	15.77 ± —
Min-max	14.92–15.74	14.75–15.67	14.92–16.35	16.54–16.77	15.32–16.02
n	6	14	18	4	3
CCL					
$\bar{X} \pm SD$	13.48 ± 0.36	13.46 ± 0.24	13.88 ± 0.32	14.72 ± —	13.92 ± —
Min-max	13.08–13.89	12.95–13.90	12.98–14.30	14.53–14.99	13.76–14.09
n	5	14	16	4	3
C1C1W					
$\bar{X} \pm SD$	3.66 ± 0.08	3.65 ± 0.13	3.74 ± 0.13	3.89 ± —	3.99 ± —
Min-max	3.59–3.78	3.46–3.92	3.40–3.96	3.82–3.95	3.92–4.02
n	5	16	20	4	3
M3M3W					
$\bar{X} \pm SD$	5.17 ± 0.17	5.17 ± 0.18	5.21 ± 0.18	5.50 ± —	5.48 ± —
Min-max	4.97–5.32	4.91–5.55	4.90–5.60	5.25–5.75	5.36–5.55
n	5	16	20	4	3
ZYW					
$\bar{X} \pm SD$	8.43 ± —	8.53 ± 0.24	8.78 ± 0.27	9.25 ± —	9.24 ± —
Min-max	8.07–8.66	8.22–8.92	8.41–9.25	8.98–9.36	9.13–9.40
n	4	13	16	4	3
MAW					
$\bar{X} \pm SD$	7.39 ± 0.09	7.48 ± 0.19	7.50 ± 0.15	7.89 ± —	7.87 ± —
Min-max	7.27–7.51	7.19–7.76	7.23–7.82	7.65–8.08	7.76–8.07
n	5	13	20	4	3
IOW					
$\bar{X} \pm SD$	4.38 ± 0.09	4.29 ± 0.15	4.29 ± 0.14	4.65 ± —	4.16 ± —
Min-max	4.28–4.51	4.07–4.62	4.02–4.50	4.46–4.74	4.09–4.24
n	6	16	20	4	3
BCW					
$\bar{X} \pm SD$	7.19 ± 0.12	7.36 ± 0.25	7.34 ± 0.26	7.90 ± —	7.50 ± —
Min-max	7.01–7.30	6.96–7.92	6.68–7.66	7.67–8.05	7.43–7.56
n	5	13	15	4	3
BCH					
$\bar{X} \pm SD$	5.60 ± —	6.05 ± 0.12	6.04 ± 0.15	6.37 ± —	6.15 ± —
Min-max	5.55–5.86	5.71–6.18	5.77–6.34	6.28–6.44	6.04–6.34
n	4	13	15	4	3
CM3L					
$\bar{X} \pm SD$	5.03 ± 0.12	5.02 ± 0.13	5.13 ± 0.16	5.47 ± —	5.46 ± —
Min-max	4.88–5.19	4.84–5.31	4.81–5.36	5.41–5.54	5.36–5.54
n	6	17	21	4	3
CP4L					
$\bar{X} \pm SD$	2.34 ± 0.07	2.33 ± 0.08	2.39 ± 0.08	2.45 ± —	2.45 ± —
Min-max	2.20–2.40	2.23–2.50	2.21–2.54	2.34–2.52	2.41–2.48
n	6	16	16	4	3
ML					
$\bar{X} \pm SD$	10.24 ± 0.24	10.07 ± 0.25	10.41 ± 0.30	11.07 ± —	10.93 ± —
Min-max	10.07–10.62	9.75–10.46	9.90–10.92	10.90–11.34	10.65–11.18
n	6	17	21	4	3

TABLE 1.—Continued.

Character	M. tubinaris (Scully, 1881)	M. cineracea sp. nov.		M. beelzebub sp. nov.	M. walstoni sp. nov.
		♂♂	♀♀		
cm3L					
$\bar{X} \pm SD$	5.51 ± 0.12	5.42 ± 0.14	5.54 ± 0.17	5.92 ± —	5.93 ± —
Min-max	5.37–5.69	5.15–5.72	5.18–5.78	5.81–6.00	5.86–5.98
n	6	17	21	4	3
cp4L					
$\bar{X} \pm SD$	2.10 ± 0.09	2.10 ± 0.09	2.21 ± 0.09	2.23 ± —	2.27 ± —
Min-max	1.97–2.19	1.90–2.24	2.02–2.38	2.18–2.36	2.24–2.32
n	5	15	16	4	3
CPH					
$\bar{X} \pm SD$	3.22 ± —	3.34 ± 0.17	3.56 ± 0.24	3.75 ± —	3.70 ± —
Min-max	3.04–3.39	3.04–3.60	3.20–4.02	3.72–3.77	3.53–3.81
n	4	16	20	4	3

previously was attributed exclusively to *Harpiola* within the Murininae (Corbet and Hill 1992; Koopman 1994; Tate 1941). Consequently, numerous authors, beginning with Wroughton (1916) and Osgood (1932), referred all similarly colored and small-bodied *Murina* in mainland Southeast Asia to *M. tubinaris*. Furthermore, some authors suggested that *M. tubinaris* might be conspecific with *M. huttoni* (Ellermann and Morrison-Scott 1951; Tate 1941), which was rejected by Hill (1964), or with *M. suilla* (Koopman 1994; Koopman and Danforth 1989). As a result, *M. tubinaris* has been assumed to occupy a huge area ranging from the mountains of northern Pakistan to the tropical forests of South Vietnam (Corbet and Hill 1992; Francis 2008).
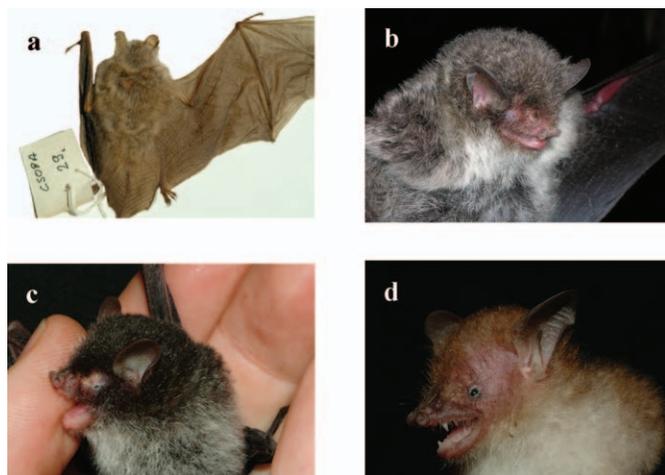

FIG. 1.—a) Dry skin of *Murina tubinaris* (Northwest Frontier Province, Pakistan, HNHM.99.14.6), dorsal view; and living specimens of b) *M. cineracea* (Kim Hy, Vietnam, NF.250407.1); c) *M. beelzebub* (paratype, HNHM.2007.50.7); and d) *M. walstoni* (holotype, HNHM.2010.20.1).
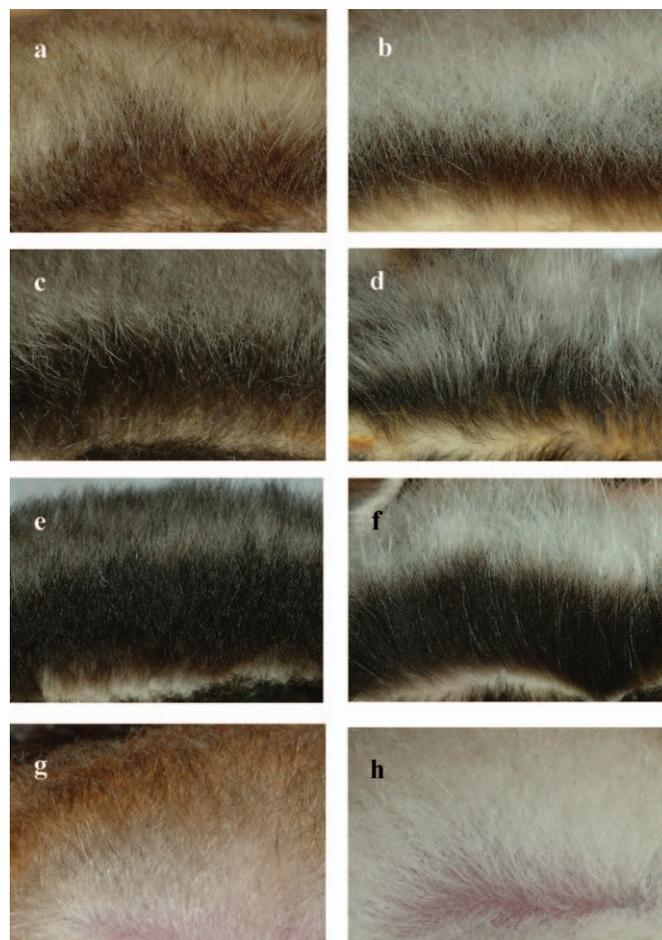

FIG. 2.—Detailed view of a) dorsal and b) ventral pelage of *Murina tubinaris* (Northwest Frontier Province, Pakistan, HNHM.99.14.6); c) dorsal and d) ventral pelage of *M. cineracea* (paratype, HNHM.2001.81.36); e) dorsal and f) ventral pelage of *M. beelzebub* (holotype, HNHM.2007.50.24); and g) dorsal and h) ventral pelage of *M. walstoni* (holotype, HNHM 2010.20.1).
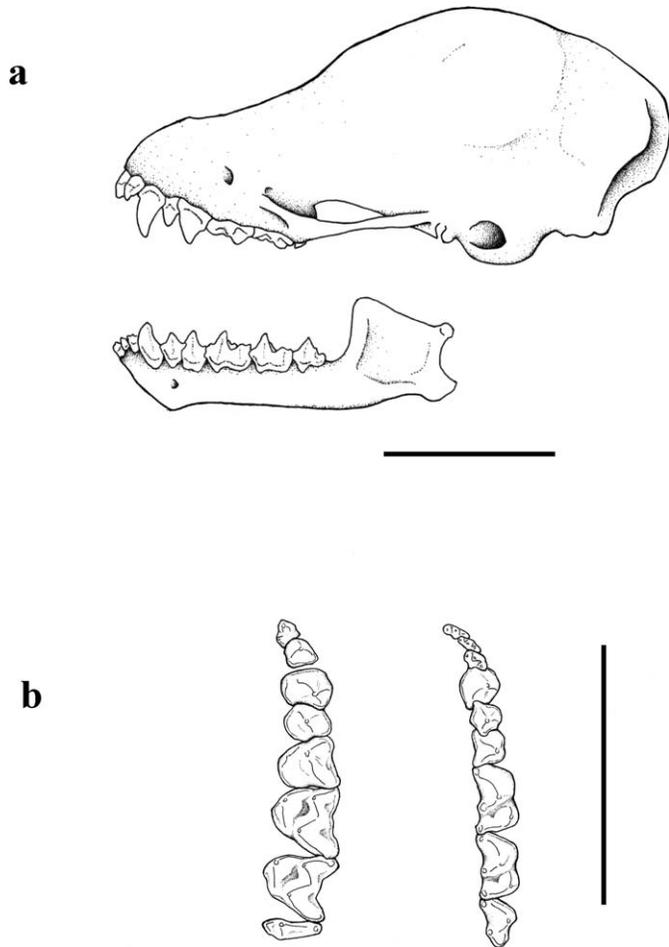
Fig. 3.—Skull and dentition of *Murina tubinaris* (Northwest Frontier Province, Pakistan, HNHM.99.14.7): a) lateral view of the skull and mandible; and b) occlusal view of the left upper (left) and right lower (right) dentition. Scale = 5 mm.

Although the type specimen of *M. tubinaris* cannot be found, all other specimens from the area of the type locality (see Appendix I) in the collections of the Natural History Museum (London), Museum d'histoire naturelle (Geneva), and the Hungarian Natural History Museum (Budapest) agree with Scully's original description and exhibit the distinguishing characters described above. All specimens examined from other regions (eastward from West Bengal and Arunachal Pradesh in India through Myanmar, Thailand, Laos, and Vietnam), and hitherto referred to as *M. tubinaris*, do not agree with the original description and consequently represent a different species. On this basis, *M. tubinaris* presently is known only from an isolated region in the westernmost Himalayas where no other member of the Murininae is known to occur. Although Roberts (1977) recorded *M. huttoni* from Gilgit and Miranjani, he recognized only a single species of the genus in Pakistan and considered *Harpiocephalus tubinaris* a junior synonym of *M. huttoni*. The specimen BM[NH] 65.1023 of *M. huttoni* he collected from Nathia Gali actually represents *M. tubinaris* and led to the erroneous

mapping of *M. huttoni* in the area by Bates and Harrison (1997).

Murina cineracea Csorba and Furey, new species

Murina tubinaris: Wroughton 1916:765 (part); Ellermann and Morrison-Scott 1951:186 (part); Corbet and Hill 1992:151 (part); Koopman 1994:132 (part); Bates et al. 2000:56; Bumrungsri et al. 2006:337; Francis et al. 1999:233; Francis 2008:253; Furey et al. 2009:236.

Holotype.—HNHM 2005.81.35 (collector's number: CSOCA 35), adult male, in alcohol skull removed, collected by G. Csorba and S. H. Hout on 12 July 2005. Measurements (in mm) are as follows: FA = 28.3; TAIL = 35.8; HF = 7.9; TIBIA = 16.7; 5met, 4met, and 3met = 27.2, 26.7, and 27.6, respectively; 3d1ph = 13.9; 3d2ph = 12.4; EAR = 13.2; TRAGUS = 6.9; STOTL = 15.64; CCL = 13.74; C1C1W = 3.78; M3M3W = 5.4; ZYW = 8.92; MAW = 7.63; IOW = 4.38; BCW = 7.32; BCH = 6.18; CM3L = 5.17; CP4L = 2.31; ML = 10.35; cm3L = 5.53; cp4L = 2.11; CPH = 3.53; mass = 5.0 g.

Type locality.—Cambodia, Mondulkiri Province, Seima Biodiversity Conservation Area, near the road between Seima and O'Rang, 12°15′44″N, 107°03′49″E, elevation 360 m.

Paratypes.—HNHM 2005.81.36 (CSOCA 36), adult female, skin, skull, postcranial skeleton, collected by G. Csorba and S. H. Hout on 12 July 2005, GenBank accession number for ND1 is FJ743889 and for 12s rRNA is FJ743911; HNHM 2005.81.49 (CSOCA 49), adult male, in alcohol, skull removed, collected by G. Csorba and S. H. Hout on 14 July 2005; HNHM 2005.81.50 (CSOCA 50), adult female, skin, skull, collected by G. Csorba and S. H. Hout on 14 July 2005; HNHM 2005.81.51 (CSOCA 51), adult female, in alcohol, collected by G. Csorba and S. H. Hout on 14 July 2005; HNHM 2005.81.52 (CSOCA 52), adult female, in alcohol, skull removed, collected by G. Csorba and S. H. Hout on 14 July 2005; HNHM 2005.81.53 (CSOCA 53), adult male, in alcohol, skull removed, collected by G. Csorba and S. H. Hout on 14 July 2005; HNHM 2006.34.40 (CSOCA 104) adult male, in alcohol, skull removed, collected by G. Csorba, G. Ronkay, and L. Duval on 28 January 2006. All paratypes were collected from the type locality.

Referred material.—INDIA: BM(NH) 16.3.25.26 (West Bengal, Darjeeling), 36.3.24.1, 36.3.24.2, 36.3.24.3, 36.3.24.4 (Arunachal Pradesh, Lohit Valley). LAOS: MHNG 1926.035 (Phongsaly Province, Naten). MYANMAR: BM(NH) 16.3.26.5, 16.3.26.7, 16.3.26.8, 16.3.26.85, 16.3.26.86, 16.3.26.87, 16.3.26.88, HNHM 2000.20.1. (Chin Hills), BM(NH) 50.485, 50.486 (Nam Tamai Valley), HZM 2.3596 (Kachin State). THAILAND: BM(NH) 82.163 (Doi Intanon), SMF 75355, 75356 (Doi Ang Khang). VIETNAM: HNHM 2000.84.4., 2000.84.7. (Thanh Hoa Province, Ben En National Park); HZM 1.31524, 1.31780 (Nghe An Province, Pu Mat National Park); IEBR QHB005 (Nghe An Province, Pu Huong Nature Reserve), NF.071206.2, 250407.1 (Bac Kan Province, Kim Hy Nature Reserve); collector's number (retained by Vu Dinh Thong of IEBR) T.12 (Thai Nguyen Province, Than Sa-Phuong Hoang Tourism

TABLE 2.—Selected external and craniodental measurements (mm) of species within the *Murina* ''*suilla*-group''. Values are given as mean ($\bar{X}$), SD (if $n \geq 5$), and minimum–maximum (Min-max) n. Abbreviations and definitions for measurements are given in the text.

Character	M. aurata	M. eleryi	M. ussuriensis[a]	M. silvatica	M. gracilis	M. recondita	M. suilla	M. florium
FA								
$\bar{X} \pm SD$	29.0 ± —	29.2 ± 1.2	—	—	30.0 ± 1.1	29.6 ± 1.1	30.6 ± 1.3	34.5 ± 1.5
Min-max	28.5–30.0	27.7–31.3			28.5–31.7	28.0–31.2	28.7–33.6	32.2–36.5
n	4	11			6	10	17	9
STOTL								
$\bar{X} \pm SD$	13.99 ± —	14.55 ± 0.34	15.49 ± —	14.80 ± —	14.98 ± 0.31	14.87 ± 0.26	14.58 ± 0.33	16.56 ± 0.50
Min-max	13.99	13.79–14.98	14.98–15.73	14.53–15.06	14.54–15.44	14.38–15.37	13.73–15.10	15.65–17.14
n	1	11	4	2	6	14	18	10
CCL								
$\bar{X} \pm SD$	12.00 ± —	12.53 ± 0.27	13.48 ± —	—	—	—	12.67 ± 0.34	14.58 ± 0.41
Min-max	11.70–12.28	12.14–12.99	13.11–13.98				12.07–13.23	13.81–15.05
n	3	9	10				16	9
MAW								
$\bar{X} \pm SD$	7.12 ± —	7.22 ± 0.19	7.36 ± —	7.16 ± —	7.34 ± 0.16	7.29 ± 0.12	7.35 ± 0.12	8.11 ± 0.18
Min-max	6.90–7.34	7.01–7.60	7.10–7.67	7.03–7.28	7.11–7.56	7.16–7.53	7.14–7.57	7.83–8.44
n	2	11	10	2	6	14	17	9
IOW								
$\bar{X} \pm SD$	4.04 ± 0.16	4.22 ± 0.11	4.33 ± —	4.00 ± —	4.22 ± 0.07	4.18 ± 0.09	4.08 ± 0.11	4.50 ± 0.14
Min-max	3.77–4.22	4.01–4.46	4.12–4.6010	3.99–4.00	4.14–4.35	4.03–4.34	3.85–4.30	4.27–4.67
n	5	11		2	6	15	19	13
BCH								
$\bar{X} \pm SD$	5.61 ± —	5.62 ± 0.12	5.75 ± —	5.54 ± —	5.89 ± 0.15	5.71 ± 0.15	5.96 ± 0.19	6.37 ± 0.20
Min-max	5.39–5.83	5.44–5.78	5.62–5.88	5.43–5.64	5.75–6.14	5.49–5.91	5.67–6.33	6.19–6.74
n	2	11	2	2	6	14	17	9
CM3L								
$\bar{X} \pm SD$	4.49 ± 0.07	4.64 ± 0.09	4.91 ± —	4.98 ± —	4.88 ± 0.17	4.86 ± 0.10	4.90 ± 0.13	5.55 ± 0.14
Min-max	4.37–4.57	4.50–4.82	4.73–5.16	4.79–5.16	4.68–5.08	4.70–5.07	4.54–5.08	5.27–5.70
n	5	9	10	2	6	15	19	14
ML								
$\bar{X} \pm SD$	9.17 ± 0.10	9.52 ± 0.20	10.21 ± —	9.95 ± —	9.80 ± 0.27	9.78 ± 0.29	9.82 ± 0.36	11.32 ± 0.27
Min-max	9.07–9.28	9.29–9.97	9.78–10.64	9.54–10.36	9.34–10.09	9.41–10.25	9.05–10.53	10.71–11.65
n	5	11	10	2	6	15	18	14
cm3L								
$\bar{X} \pm SD$	4.79 ± 0.15	5.15 ± 0.13	5.36 ± —	5.42 ± —	5.36 ± 0.14	5.31 ± 0.11	5.32 ± 0.12	6.07 ± 0.15
Min-max	4.58–4.90	4.89–5.33	5.19–5.55	5.34–5.50	5.17–5.52	5.10–5.51	5.06–5.52	5.75–6.24
n	5	11	10	2	6	15	18	14
CPH								
$\bar{X} \pm SD$	2.80 ± 0.15	2.98 ± 0.14	3.70 ± —	3.33 ± —	2.90 ± 0.11	3.04 ± 0.16	3.30 ± 0.14	3.87 ± 0.14
Min-max	2.54–2.93	2.80–3.23	3.50–3.93	3.18–3.48	2.73–3.04	2.76–3.23	3.05–3.61	3.65–4.09
n	5	11	10	2	6	15	18	12

[a] With the exception of STOTL and BCH, measurements pool data from Kruskop (2005) for *M. ussuriensis ussuriensis* and *M. u. katerinae*.

Area), T.32 (Kon Tum Province, Chu Mom Ray National Park), T.210708.1 (Bac Kan Province, Phuong Vien), T.251107.5 (Son La Province, Muong Do), T.290708.8 (Phu To Province, Xuan Son National Park), T.250607.1 (Bac Kan Province, Phuong Vien), T.83 (Bac Kan Province, Kim Hy Nature Reserve), T.112 (Thua Thien-Hue Province, Bach Ma National Park), VN01-C4 (Ha Tinh Province, Huong Son Forest Enterprise).

Etymology.—The name *cineracea* (= ash gray) refers to the color of the dorsal pelage.

Diagnosis.—The dorsal pelage is superficially ashy gray, and the ventral fur is dark gray at the base and white distally.

The plagiopatagium is attached to the base of the claw of the outer toe. The basal area of P4 is larger than that of C, whereas the basal area of P2 is about one-half that of P4. The mesostyles of M1 and M2 are reduced in bulk, and both teeth retain distinct cusps.

Description.—This is a small species of *Murina* (Table 1). On the dorsal surface the lower portion of individual hairs is dark brown, whereas the upper portion is light gray and terminates in a distinctly darker tip (Figs. 1b and 2c). Darkening of hair tips is more evident on the nape and head, with an overall impression of dark grayish brown and darker brown toward the head. The upper surface of the hind limbs,
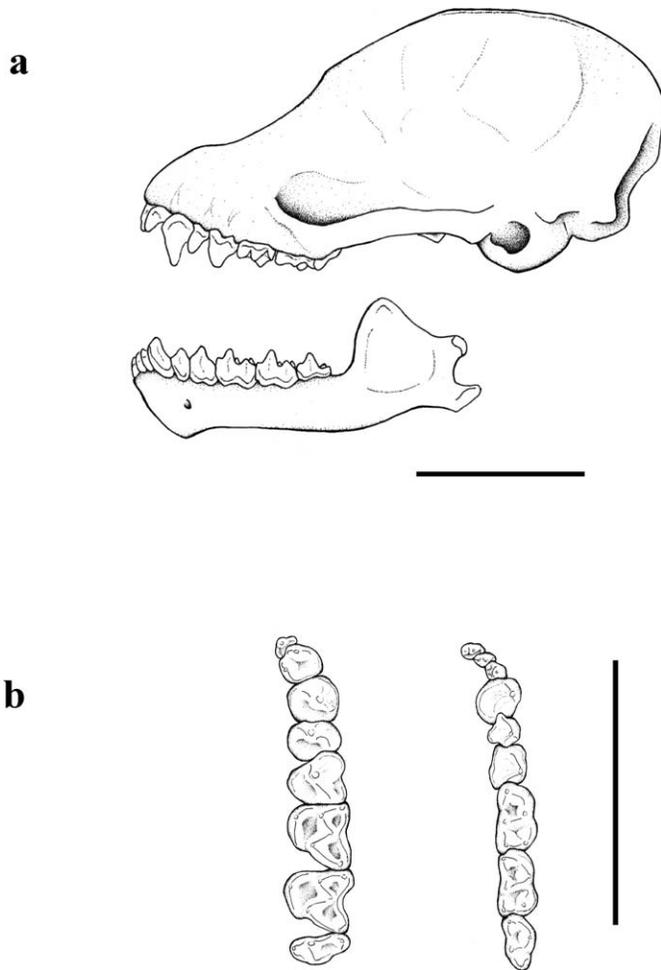
a

b

Fig. 4.—Skull and dentition of *Murina cineracea* (holotype, HNHM.2005.81.35.): a) lateral view of the skull and mandible; and b) occlusal view of the left upper (left) and right lower (right) dentition. Scale = 5 mm.

feet, and uropatagium are covered sparsely in short, uniformly dark brown hairs. On the ventral surface of the body hairs are dark brown basally, whereas the upper portion is white (Fig. 2d). The ventral surface of the uropatagium is covered in relatively short uniformly white hairs, which are also present on the plagiopatagium adjacent to the body. The ear is evenly rounded and without an emargination. The plagiopatagium is attached to the base of the claw on the outer toe.

In the lateral view of the skull a shallow concavity is present over the orbits (Fig. 4a). This ascends relatively abruptly toward the rear of the rostrum because of inflation of the frontal compartments forming the anterior portion of the braincase. Because the midportion of the braincase exceeds the frontal region in height, the braincase is domed. A weak sagittal crest is always present. The lambdoidal crests are comparatively distinct, and the rostrum is not inflated. The depth of the narial emargination is variable but typically exceeds its width, and its dorsal outline varies from smoothly concave to squarish. The zygoma often possesses a slight dorsal process. The palate is concave and narrows toward the canines. The posterior border of the palatal emargination

extends to the middle of the upper canine, and a medial process is present in the posterior palatal region. The basioccipital pits are well defined and vary slightly in their lateral extent, such that the intervening medial ridge is of variable width.

The maxillary toothrows are convergent anteriorly (C1C1W/M3M3W: $\bar{X}$ = 0.71, range = 0.62–0.77, SD = 0.03, n = 36). I2 is scarcely visible in the lateral view (Fig. 4a), is slightly exceeded in height by I3, and comprises no more than one-third of the latter's basal area (Fig. 4b). I3 is close to and sometimes in contact with C. The basal area of C is less than that of P4, and its length is equivalent to its width, such that the tooth has a circular outline in the occlusal view. C exceeds P4 in height. P2 is strongly compressed and typically possesses a small cusp on the anterior inner cingulum. Its basal area and height are approximately one-half or slightly less than that of P4. The mesostyles of M1 and M2 are reduced, and the adjacent medial portion on the labial face of these teeth is essentially flat or slightly convex. The metacones of M1 and M2 exceed their respective paracones in height.

The lower canine (c) slightly exceeds p4 in height and is equal or greater in basal area (Fig. 4). The lower premolar p2 has less than one-half the basal area of p4 and attains more than two-thirds its height. The talonids of m1 and m2 equal their respective trigonids in crown area, and the entoconids of these teeth exceed their hypoconids in height. The postcristid connects the hypoconid with the very tip of the entoconid.

Comparisons with other taxa.—On the basis of its dentition, *M. cineracea* belongs to the ''*suilla*-group'' and therefore is distinguished readily from all members of the ''*cyclotis*-group.'' The following features separate *M. cineracea* from similar-sized species in the ''*suilla*-group.'' *M. tubinaris*, the species in which *M. cineracea* formerly was included, differs in several important external and craniodental features. First, the plagiopatagium in *M. tubinaris* is attached to the proximal phalanx of the outer toe, whereas in *M. cineracea* it is attached to the base of the 1st claw. Second, the dorsal pelage of *M. cineracea* is a darker grayish brown with darker brown on the nape and head, whereas *M. tubinaris* is light gray– nicotine brown throughout (Figs. 1 and 2). Cranially, the zygoma is much weaker in *M. tubinaris* and lacks a dorsal process, and I2 is equal in height to I3 and comprises one-half or more of its basal area (whereas in *M. cineracea* I2 is exceeded by I3 in height and comprises no more than one-third of its basal area; Figs. 3 and 4). In addition, C has a distinct cingular cusp and is elliptical in occlusal outline in *M. tubinaris* (versus round and lacking a cingular cusp in *M. cineracea*), and this tooth and I3 are much more robust in *M. cineracea*. Finally, the anterior region of the mandible is more robust in *M. cineracea*, and the entoconids of m1 and m2 exceed their respective hypoconids in height (whereas in *M. tubinaris* these are of equal height).

Murina cineracea is distinguished easily from *M. aurata*, *M. harpioloides*, *M. gracilis*, *M. recondita*, and *M. eleryi* by its dorsal pelage, which lacks conspicuous golden guard hairs and any suggestion of yellow or reddish hues in the underhair. Dentally, *M. cineracea* is distinguished from *aurata* and *harpioloides* by the height of C, which exceeds that of P4,

whereas in the latter 2 species C is equal to or less in height than P4. Compared with *M. gracilis* and *M. recondita*, upper and lower dentition in *M. cineracea* is larger (particularly the incisors, canines, and premolars). The entoconids of m1 and m2 exceed their hypoconids in height in *M. cineracea*, whereas these are equal in *M. gracilis* and *M. recondita*. Compared with *M. eleryi*, dentition in *M. cineracea* is also more robust (particularly I3 and P2), and its zygoma is much better developed. *M. suilla* is distinguished readily by its reddish brown dorsal pelage (versus dark grayish brown in *M. cineracea*) and uniformly white medial ventral hairs (which have dark bases in *M. cineracea*). Cranially, the zygoma and dentition are also more robust in *M. cineracea*, and C has a circular outline in the occlusal view, whereas it is elliptical in *M. suilla*. The closely related *M. ussuriensis* and *M. silvatica* similarly differ in their reddish brown dorsal pelage and dense covering of hairs on the upper surface of the uropatagium (which is sparsely covered with short dark brown hairs in *M. cineracea*). In addition, I2 comprises one-half or more of the basal area of I3 in the former 2 species but never more than one-third in *M. cineracea*.

With respect to other members of the ''*suilla*-group'' in Southeast Asia, *M. leucogaster* and *M. hilgendorfi* are larger externally and cranially (Bates and Harrison 1997; Hendrichsen et al. 2001; Yoshiyuki 1989), and *leucogaster* further differs in possessing uniformly pale ventral hairs. The exclusively Sundaic and Australasian species *M. florium* also averages larger and is more robust cranially (Tables 1 and 2). Compared with the 2 Japanese species, *M. ryukyuana* and *M. tenebrosa*, *M. cineracea* is smaller in all respects and differs markedly with gray fur (Maeda 2000; Maeda and Matsumura 1998; Maeda et al. 2002; Yoshiyuki 1989).

Distribution and ecological notes.—The type series was collected using four-bank harp traps set on forest trails in evergreen forest mixed with deciduous forest at an elevation of 360 m. Seima Biodiversity Conservation Area is located in the low-lying eastern plains of Cambodia and covers an area of 303,400 ha. The site supports a high diversity of forest types, including evergreen forests, mixed deciduous formations, and dry dipterocarp forests (Pollard 2007). Within its known range *M. cineracea* appears to be associated with mountainous areas. In the eastern part of the Indian Subcontinent it is found in forests on mountain slopes, whereas in northern Myanmar it has been found at altitudes from 615 to 1,230 m (Csorba et al. 2008; Hill 1962). The type locality is a low-lying hilly area on the southernmost fringe of the Annamite Mountain range. Despite its extensive distribution, the natural history of *M. cineracea* is poorly known, although comparative sampling in limestone forests of differing integrity in North Vietnam indicates that the species is tolerant of disturbed forest habitats (Furey et al. 2010).

Murina beelzebub Son, Furey, and Csorba, new species

Murina tubinaris: Hendrichsen et al. 2001:103 (part)

Holotype.—HNHM.2007.50.24, adult male, in alcohol, skull removed, collected by Nguyen Truong Son, Pham Duc Tien, and G. Csorba on 10 November 2007. Measurements (in mm) are as follows: FA = 33.7; TAIL = 40.6; HF = 7.7; TIBIA = 19.4; 5met, 4met, and 3met = 30.2, 30.3, and 31.8, respectively; 3d1ph = 15.1; 3d2ph = 13.7; EAR = 13.8; TRAGUS = 7.9; STOTL = 16.54; CCL = 14.57; C1C1W = 3.82; M^3M^3W = 5.25; ZYW = 8.98; MAW = 7.78; IOW = 4.46; BCW = 7.32; BCH = 7.67; CM3L = 5.41; CP4L = 2.45; ML = 10.91; cm3L = 5.81; cp4L = 2.20; CPH = 3.72; mass = 5.3 g.

Type locality.—Vietnam, Quang Tri Province, Huong Hoa District, Bac Huong Hoa Nature Reserve, centered at 16°56′15″N, 106°34′52″E, elevation 400 m.

Paratypes.—HNHM.2007.50.6, adult female, in alcohol, skull removed; HNHM.2007.50.7, adult female, in alcohol, skull removed. Both collected by Nguyen Truong Son, Pham Duc Tien, and G. Csorba on 7 November 2007 at the type locality.

Referred material.—VIETNAM: HZM 3.32053, Gia Lai Province, Kon Ka Kinh Nature Reserve, bounding coordinates 14°09′–14°30′N, 108°16′–108°28′E.

Etymology.—Beelzebub commonly appears as a high-ranking personality of the underworld in Christian texts; one of the presumed original meanings of the name is ''Lord of the Flies.'' The specific epithet (a noun in apposition) was chosen to reflect the dark ''diabolic'' coloration and the fierce protective behavior of the species experienced in the field, and also in reference to the insectivorous diet of tube-nosed bats.

Diagnosis.—On the dorsal surface the fur is very dark, almost black, whereas the tips of the hairs on the belly are white with dark bases. The plagiopatagium is attached to the base of the claw of the outer toe. The basal area of P4 is larger than that of C, whereas the basal area of P2 is about one-half that of P4. The mesostyles of M1 and M2 are reduced greatly but retain weak cusps.

Description.—This is a medium-sized species of *Murina* (Table 1). On the dorsal surface the proximal four-fifths of individual hairs is very dark brown (almost black), whereas the remaining distal portion is initially light gray and terminates in a distinctly darker tip (Figs. 1c and 2e). Longer silver guard hairs are scattered over all of the dorsum. The upper surface of the hind limbs, feet, and uropatagium are densely covered in long, uniformly dark brown hairs. Ventrally, hairs are very dark brown (almost black) for the proximal two-thirds, whereas the remaining upper portion is white (Fig. 2f). The ventral surface of the uropatagium is covered in uniformly white hairs, some of which are also present on the plagiopatagium adjacent to the body. The ear has a slight emargination along its posterior border, and the plagiopatagium is attached to the base of the claw on the outer toe.

In the lateral view of the skull a shallow concavity is present over the orbits (Fig. 5a). This ascends relatively evenly over the frontal compartments of the braincase. The sagittal crest is absent, and the lambdoidal crests are relatively well defined. The rostrum is slightly elongated but is not inflated. The depth of the narial emargination exceeds its width. The zygoma is strong and possesses a slight dorsal process. A medial process is present in the posterior palatal region. The medial ridge
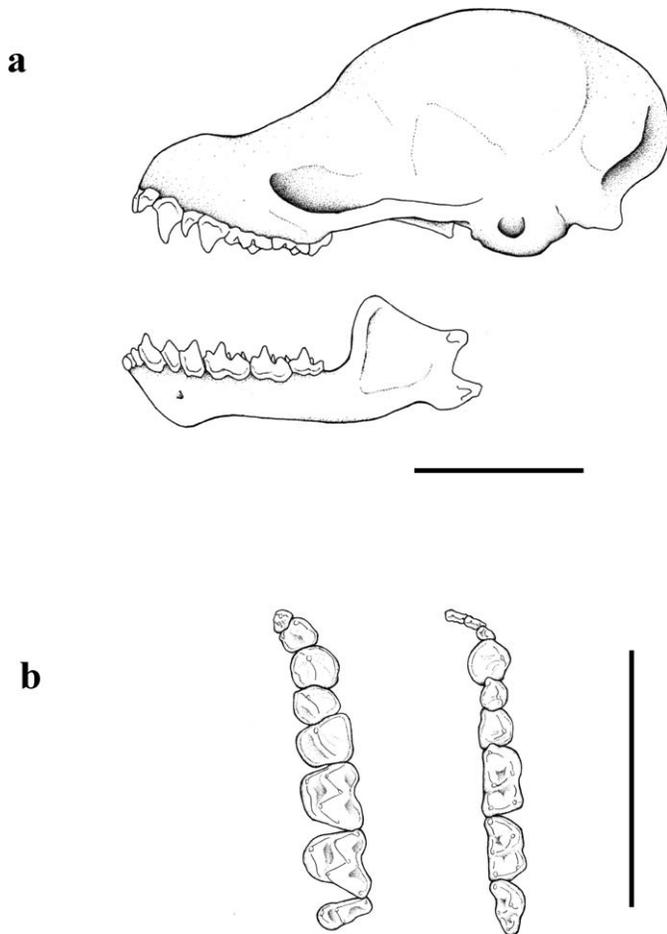
a

b

Fig. 5.—Skull and dentition of *Murina beelzebub* (holotype, HNHM.2007.50.24.): a) lateral view of the skull and mandible; and b) occlusal view of the left upper (left) and right lower (right) dentition. Scale = 5 mm.

separating the basioccipital pits is relatively narrow, and the anterior borders of the pits are weakly defined.

The upper toothrows are convergent anteriorly (C1C1W/ M3M3W: $\overline{X} = 0.71$, range = 0.69–0.73, $n = 4$). I2 is only partly obscured in the lateral view (Fig. 5a), matches I3 in height or is only slightly shorter, and comprises one-third of the basal area of I3 (Fig. 5b). I3 is not in contact with C, although its margins overlap. The basal area of C is less than that of P4, whereas its height is greater. In the occlusal view C is round in outline. P2 is compressed strongly and possesses a small cusp on the anterior inner cingulum. Its basal area and height are approximately one-half or slightly less than that of P4. The mesostyles of M1 and M2 are greatly reduced, such that the cusp is scarcely apparent and the medial region on the labial face of these teeth is flat.

The lower canine (c) slightly exceeds p4 in height and is equal or greater in basal area (Fig. 5). The lower premolar p2 has less than one-half the basal area of p4 and attains more than two-thirds its height. The talonids of m1 and m2 equal their trigonids in crown area, and the entoconids of these teeth distinctly exceed their hypoconids in height. The postcristid connects the hypoconid with the tip of the entoconid.

Comparisons with other taxa.—As a member of the ''*suilla*-group'' *M. beelzebub* is readily separable from all members of the ''*cyclotis*-group.'' The following features distinguish it from other species in the ''*suilla*-group'' in Southeast Asia. With the exception of *M. cineracea*, *M. beelzebub* easily is distinguished externally from all of the smaller-bodied species in the group (*M. aurata*, *M. harpioloides*, *M. gracilis*, *M. recondita*, *M. eleryi*, *M. suilla*, *M. ussuriensis*, and *M. silvatica*) by its dorsal pelage, which lacks conspicuous golden guard hairs and any suggestion of yellow, brown, or reddish hues in the underhair. The latter species and *M. tubinaris* are also somewhat smaller than *M. beelzebub*, with no overlap in forearm and little or no overlap in most craniodental measurements (Kruskop and Eger 2008; Tables 1 and 2). The pelage of *M. cineracea* is similar but visibly lighter due to the predominance of gray (as opposed to the blackish appearance of *M. beelzebub*; Fig. 1). *M. cineracea* is similar to *M. beelzebub* cranially and dentally but distinctly smaller with no overlap in several measurements (e.g. STOTL, CCL, CM3L, and cm3L; Table 1). In addition, a poorly developed sagittal crest is present in *M. cineracea* but not in *M. beelzebub*.

Compared with *M. beelzebub*, *M. leucogaster* and *M. hilgendorfi* are distinctly larger and differ markedly in fur coloration (Bates and Harrison 1997; Hendrichsen et al. 2001; Yoshiyuki 1989). In *M. florium* I1 is exceeded in height by I2 (in *M. beelzebub* these are equal in height), and the mesostyles of M1 and M2 are developed (versus greatly reduced in *M. beelzebub*). Compared with *M. ryukyuana* and *M. tenebrosa*, *M. beelzebub* is similar in size and has different fur coloration, with the others being predominantly brownish both dorsally and ventrally (Maeda 2000; Maeda and Matsumura 1998; Maeda et al. 2002; Yoshiyuki 1989).

Distribution and ecological notes.—At Bac Huong Hoa Nature Reserve the type series was collected in harp traps set on forest trails near a stream in disturbed secondary forest at an elevation of 400 m. The nature reserve encompasses an area of 25,200 ha and is predominantly low in elevation, although terrain is hilly and slopes are steep. More than 80% of the site consists of natural forests, which include lowland and midmontane evergreen forests, broadleaf forests over limestone karst, and bamboo forests. Detailed descriptions of vegetation at Bac Huong Hoa are provided by Mahood and Tran Van Hung (2008). At Kon Ka Kinh Nature Reserve *M. beelzebub* was collected on a ridge top in primary montane forest at an elevation of 1,600 m. Kon Ka Kinh encompasses an area of 41,780 ha, and elevations at the reserve range from 570 to 1,748 m. The site includes a mixture of montane vegetation with evergreen forests and agricultural lands at lower elevations (Tordoff et al. 2004).

Murina walstoni Furey, Csorba, and Son, new species

Holotype.—HNHM 2010.20.1, adult male, in alcohol, skull removed, collected by S. Phauk, S. Ith, and G. Csorba on 1 March 2010. Measurements (in mm) are as follows: FA =
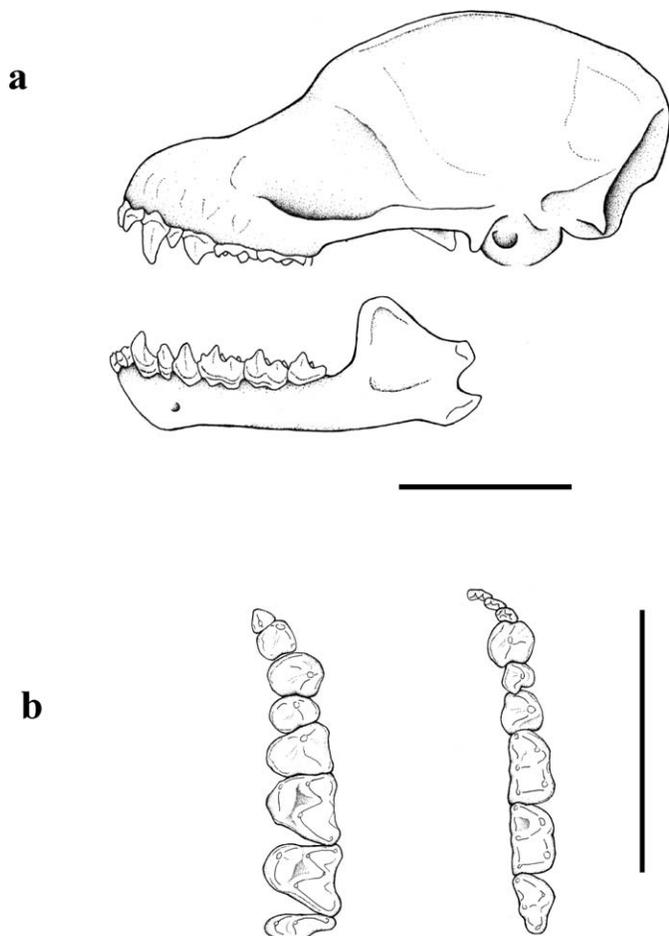
FIG. 6.—Skull and dentition of *Murina walstoni* (holotype, HNHM.2010.20.1.): a) lateral view of the skull and mandible; and b) occlusal view of the left upper (left) and right lower (right) dentition. Scale = 5 mm.

33.7; TAIL = 33.6; HF = 7.1; TIBIA = 15.4; 5met, 4met, and 3met = 30.8, 30.8, and 31.6, respectively; 3d1ph = 14.1; 3d2ph = 10.8; EAR = 13.0; TRAGUS = 6.6; STOTL = 16.02; CCL = 13.92; C1C1W = 3.92; M3M3W = 5.36; ZYW = 9.13; MAW = 7.78; IOW = 4.16; BCW = 7.51; BCH = 6.04; CM3L = 5.36; CP4L = 2.41; ML = 10.95; cm3L = 5.86; cp4L = 2.25; CPH = 3.76; mass = 5.0 g.

Type locality.—Cambodia, Ratanakiri Province, Veun Sai District, Veun Sai Protected Forest, 14°01′49″N, 106°45′06″E, elevation 110 m.

Referred material.—VIETNAM: HNHM 2008.23.15., Dak Lak Province, Yok Don National Park. CAMBODIA: HNHM 2010.4.1, Koh Kong Province, Botum Sakor National Park.

Etymology.—Named after Joe Walston in recognition of his contribution to bat research and biodiversity conservation in Vietnam and Cambodia.

Diagnosis.—On the dorsal surface the fur is warm brown, and on the ventral surface it is pure white. The plagiopatagium is attached to the base of the claw of the outer toe. The sagittal crest is prominent. I2 is exceeded in height by I3. The basal area of P4 is larger than that of C, whereas the basal area of P2

is about one-half that of P4. The mesostyles of M1 and M2 are developed.

Description.—This is a relatively small species of *Murina* (Table 1). On the dorsal surface the basal one-half of individual hairs is white, whereas the distal portion progressively darkens to a warm brown (Figs. 1d and 2g). The upper surface of the hind limbs, feet, and uropatagium are sparsely covered in similarly colored hairs. Ventrally, hairs are uniformly white (Fig. 2h). The ventral surface of the proximal region of the uropatagium is covered with white hairs, which extend onto the plagiopatagium adjacent to the body. The ear has a very distinct, almost rectangular emargination along its posterior border. The plagiopatagium is attached to the base of the claw on the outer toe.

In the lateral view of the skull a concavity is present over the orbits (Fig. 6a). The rear of the rostrum ascends relatively evenly over the frontal compartments of the braincase. A sagittal crest is present, which is equally or better defined than the lambdoidal crests. The rostrum is not inflated. The depth of the narial emargination is approximately equal to its width. The zygoma is strong and sometimes possesses a slight dorsal process. A well-defined medial process is present in the posterior palatal region, and the basioccipital pits are deep, reasonably well defined, and separated by a broad medial ridge.

The upper toothrows are convergent anteriorly (C1C1W/ M3M3W: $\overline{X}$ = 0.73, range = 0.72–0.73, n = 3). I2 is just visible in lateral view (Fig. 6a), is exceeded in height by I3, and comprises one-third of its basal area (Fig. 6b). I3 is not in contact with C, although its lateral margins sometime overlap in the occlusal and lateral views. The basal area of C is exceeded by that of P4, whereas its height is greater. In the occlusal view C is slightly oblong in outline, with the width exceeding the length. P2 is compressed strongly and has a basal area slightly less than one-half and a height approximately one-half those of P4. The mesostyles of M1 and M2 are developed and equal to or exceed their respective paracones in height. The labial slopes of the mesostyles extend to the cingulum, but the adjacent medial faces of M1 and M2 are flat or only slightly convex.

The lower canine (c) exceeds p4 in height and basal area (Fig. 6). The basal area of p2 varies from one-half to less than that of p4 and attains more than two-thirds its height. The talonids of m1 and m2 exceed their trigonids in crown area, and their entoconids are equal to or slightly higher than their respective hypoconids. The postcristid connects the hypoconid with the very tip of the entoconid.

Comparisons with other taxa.—As a member of the ''*suilla*-group'' *M. walstoni* is separated readily from all members of the ''*cyclotis*-group.'' The following features distinguish it from other species in the ''*suilla*-group'' in Southeast Asia. The uniformly white ventral hairs of *M. walstoni* separate it from all other small-bodied taxa within the group, with the exception of *M. suilla*. *M. walstoni* differs in that the basal portion of dorsal hairs is white, whereas these are dark in *M. suilla*. Cranially, *M. walstoni* is also larger in many measurements (Tables 1 and 2), and its upper and lower dentition is much more robust. In

addition, the sagittal crest is well defined in *M. walstoni* (versus very weak in *M. suilla*), and the basal area of P2 is one-half or less than that of P4 (in *M. suilla* is approximately one-third). *M. aurata*, *M. harpioloides*, *M. recondita*, *M. gracilis*, *M. silvatica*, *M. ussuriensis*, *M. eleryi*, and *M. tubinaris* also are distinctly smaller in most cranial and dental dimensions (Kruskop and Eger 2008; Tables 1 and 2).

Murina cineracea is in the same size class as *M. walstoni* craniodentally but has reduced mesostyles and indistinct metaconules on M1 and M2. Aside from its very different coloration, having black dorsal fur and white ventral fur (Fig. 1), *M. beelzebub* is typically larger in every respect than *M. walstoni* (Table 1). *M. ryukyuana* is also differently colored (brown) and distinctly larger, particularly in its dentition (Maeda 2000; Maeda and Matsumura 1998; Maeda et al. 2002), whereas *M. tenebrosa* is distinguished similarly by brown fur and slightly larger size (Yoshiyuki 1989). *M. florium* is similar to *M. walstoni* in size and dentition but is again differently colored (with ventral hairs having dark bases) and has a less globose skull. Finally, *M. leucogaster and M. hilgendorfi* are much larger than *M. walstoni* externally and cranially (Bates and Harrison 1997; Hendrichsen et al. 2001; Yoshiyuki 1989).

Distribution and ecological notes.—The holotype was caught 1 h after sunset in a harp trap set on a dry streambed in semievergreen forest. The Veun Sai Protected Forests encompass approximately 55,000 ha within the Veun Sai (Ratanakiri Province) and Siem Pang (Steung Treng Province) districts of northeastern Cambodia. Habitats at the site largely comprise lowland evergreen and semievergreen forest at elevations between 100 and 400 m, with more northerly areas mountainous and southern parts characterized by grasslands. The latter often are associated with dry deciduous dipterocarp forests. Areas of mixed deciduous forest dominated by *Lagerstoemia* also occur at the site, often in disturbed areas (B. Rawson, Conservation International, pers. comm.). The specimen from Botum Sakor National Park (Cambodia) was caught in a harp trap in an area of heavily disturbed lowland forest. Botum Sakor covers an area of 183,408 ha, the majority of which comprises gently sloping lowlands and flood plains. Vegetation at the site includes lowland evergreen forest, *Melaleuca* woodland, grassland, mangrove forest, and swamp forest with patches of palm (Royan et al. 2010). The specimen from Yok Don National Park (Vietnam) was similarly caught in a harp trap in deciduous forest at an elevation of 180 m near the Thac Phat-Buddha waterfall. Yok Don encompasses an area of 115,545 ha and an elevation range of 200–482 m. Vegetation at the site is dominated by a mosaic of deciduous forest and semievergreen (mixed deciduous) forest, with smaller areas of evergreen forest, particularly on hills and along watercourses (Tordoff et al. 2004).

DISCUSSION

The existence of cryptic diversity within *Murina* is demonstrated by the large number of new species described

in recent years, and species richness within the genus is likely greater than currently recognized. Species identification typically requires evaluation of morphological characters and availability of properly identified comparative material in museum collections. Because accessing such institutions can pose difficulties and morphological evaluations require particular expertise, molecular analysis can help to address these issues and likely will facilitate future recognition of undescribed taxa and improved understanding of biogeographical patterns. For instance, DNA bar coding, developed as a tool for rapid identification, has proved effective in differentiating morphologically distinct species of *Murina* (Francis et al. 2010). Despite this, the neighbor-joining tree in Francis et al. (2010) includes several distinct lineages that could not be assigned appropriate names, and some of these could represent species described in the present study. Judging from the region sampled, it also seems likely that *M. cineracea* represents the *M. tubinaris* lineage depicted in Francis et al. (2010).

The disparity between traditionally accepted species groups (''*suilla*'' and ''*cyclotis*'') within *Murina* and results of preliminary molecular study (Francis et al. 2010) is also notable. This suggests that the morphological characteristics used to differentiate the 2 groups (relative size of canines and premolars and position of upper incisors) have appeared several times in both groups as a result of convergent evolution and that traditional classifications do not reflect real phylogenetic relationships as a consequence. To assist future taxonomic and systematic research on Murininae detailed morphological descriptions, as in the present paper, of currently named forms are required to facilitate correct identification of existing material in collections. In addition, DNA samples should be taken from all voucher specimens originating from Southeast Asia, a renowned biodiversity hot spot.

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APPENDIX I

Institutional abbreviations.

Specimens included in this study are held in the collections of BAT: Bat Association of Taiwan, Taipei, Taiwan; BM(NH): The Natural History Museum, London, United Kingdom, formerly British Museum (Natural History); CBC: Center for Biodiversity Conservation, Phnom Penh, Cambodia; ESRI: Endemic Species Research Institute, Nantou, Taiwan; HNHM: Hungarian Natural History Museum, Budapest, Hungary; HZM: Harrison Institute, Sevenoaks, Great Britain, formerly Harrison Zoological Museum; IEBR: Institute of Ecology and Biological Resources, Hanoi, Vietnam; MHNG: Museum d'histoire naturelle, Geneva, Switzerland; MNHN: Museum National d'Histoire Naturelle, Paris, France; MZB: Museum Zoologicum Bogoriense, Bogor, Indonesia; NF: Kim Hy Nature Reserve Collection, Vietnam; NMNS: National Museum of Natural Science, Taichung, Taiwan; PSU: Prince Songkhla University, Hat Yai, Thailand; RMNH: National Museum of Natural History, Leiden, Netherlands, formerly Rijksmuseum van Natuurlijke Historie; SMF: Senckenberg Museum, Frankfurt, Germany; ZMA: Zoölogisch Museum, Amsterdam, Netherlands; ZMMU: Zoological Museum of Moscow State University, Moscow, Russia; and ZMNTU: Zoological Museum of the National Taiwan University, Taipei, Taiwan.

Comparative material examined.

Murina aurata.—CHINA (Sichuan)—MNHN 1870-590 (holotype), MNHN 1870-590a (paratype); INDIA (Sikkim)—BM(NH) 15.9.1.37, BM(NH) 91.10.7.58; NEPAL (Dhaulagiri)—BM(NH) 75.301; THAILAND (Chiang Mai)—BM(NH) 82.162.

Murina eleryi.—VIETNAM—HNHM 2007.51.1. (holotype), HNHM 2007.28.2., BM(NH) 2008.25, HZM 1.39006, NF 170906.3, NF 240507.1, NF 230707.1 (paratypes), IEBR T.241107.1, NF 250506.1, NF 030707.1, NF 240707.2.

Murina florium.—INDONESIA (Flores)—BM(NH) 63.12.26.14 (holotype), (Ambon) RMNH 28120, RMNH 30074, RMNH 30075, (Bacan) RMNH 33381, (Buru) BM(NH) 23.1.2.27 (holotype, subsp. *toxopei*), (Ceram) BM(NH) 10.3.4.24 (holotype, subsp. *lanosa*), RMNH 35769, BM(NH) 7.1.1.482, (Goram) BM(NH) 10.3.4.15, BM(NH) 10.3.4.115, (Sulawesi) MZB 22876, MZB 22877, MZB 22878, RMNH 33374, RMNH 34894; PAPUA NEW GUINEA (Admiralty I)—BM(NH) 14.4.1.33.

Murina gracilis.—TAIWAN—ZMNTU 1996.10.3 (holotype), ZMNTU 1995.10.1, ZMNTU 2003.8.2, ZMNTU 2004.3.1, BAT 060001, HNHM 2005.1.1. (paratypes).

Murina silvatica.—JAPAN—HNHM 2001.38.1., HNHM 2002.41.1.

Murina suilla.—INDONESIA (Java)—RMNH 35772 (holotype), HNHM 2000.13.2. (topotype), BM(NH) 79.11.15.15, BM(NH) 79.11.15.16, RMNH 15225, RMNH 15226, RMNH 15227, RMNH 15228, RMNH 15231, RMNH 15233, RMNH 15236, RMNH 15237, BM(NH) 9.1.5.354 (holotype, subsp. *balstoni*), BM(NH) 7.1.1.479, (Sumatra) BM(NH) 21.1.2.28 (holotype, subsp. *canescens*), ZMA 17352 (paratype, subsp. *canescens*); MALAYSIA – (Sabah) BM(NH) 84.2013, BM(NH) 84.2014, BM(NH) 84.2015, BM(NH) 84.2016, BM(NH) 84.2017, BM(NH) 84.2018.

Murina recondita.—TAIWAN—ZMNTU 2003.8.1 (holotype), HNHM 2005.1.2., HNHM 2005.36.1., HNHM 2005.36.2., NMNS 4856, NMNS 5133, NMNS 5161, NMNS 6010, ZMNTU 1998.7.4, ZMNTU 1.41, ZMNTU 11424, ZMNTU 2001.12.1, ZMNTU KHC040, ESRI A0015, BAT 060002 (paratypes).

Murina tubinaris.—PAKISTAN (Nathia Gali)—BM(NH) 65.1023, (Kaghan Valley) HNHM 99.14.6., HNHM 99.14.7., BM(NH) 1999.151; ''KASHMIR''—BM(NH) 3.9.29.2; INDIA (Himachal Pradesh)—MHNG 1926.060.

Murina ussuriensis.—RUSSIA—ZMMU 96368 (paralectotype), ZMMU 42508, ZMMU 50955, ZMMU S-181388.