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Authors: Csorba, Gábor, Chou, Cheng-Han, Ruedi, Manuel, Görföl, Tamás, Motokawa, Masaharu, et al.

Source: Journal of Mammalogy, 95(4) : 663-678

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/13-MAMM-A-200

Journal of Mammalogy, 95(4):663–678, 2014

The reds and the yellows: a review of Asian *Chrysopteron* Jentink, 1910 (Chiroptera: Vespertilionidae: *Myotis*)

Gábor Csorba,* Cheng-Han Chou, Manuel Ruedi, Tamás Görföl, Masaharu Motokawa, Sigit Wiantoro, Vu Dinh Thong, Nguyen Truong Son, Liang-Kong Lin, and Neil Furey

Department of Zoology, Hungarian Natural History Museum, Baross 13, Budapest, H-1088, Hungary (GC, TG)
Department of Life Science, Tunghai University, Taichung City, Taiwan ROC No 181 Section 3, Taichung-kan Road, Taichung, 407-04, Taiwan, ROC (C-HC, L-KL)
Division of Zoology, Endemic Species Research Institute, Nantou County, Taiwan, ROC (C-HC)
Department of Mammalogy and Ornithology, Natural History Museum of Geneva, Route de Malagnou 1, Geneva, 1208, Switzerland (MR)
Institute for Veterinary Medical Research, Centre for Agricultural Research, Hungarian Academy of Sciences, Hungária krt. 21, Budapest, 1143, Hungary (TG)
Kyoto University Museum, Kyoto University, Yoshida Honmachi, Sakyo-ku, Kyoto, 606-8501, Japan (MM)
Indonesian Institute of Sciences, Jl Raya Jakarta—Bogor Km. 46, Cibinong, 16911, Indonesia (SW)
Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Cau Giay District, Hanoi, Vietnam (VDT, NTS)
Centre for Biodiversity Conservation, Royal University of Phnom Penh, Russian Federation Boulevard, Toul Kork, Phnom Penh, Cambodia (NF)

* *Correspondent: csorba@nhmus.hu*

Chrysopteron Jentink, 1910 is 1 of the 7 subgenera of *Myotis* Kaup, 1829 recognized by Tate that traditionally comprises Asian and African species characterized by conspicuously parti-colored wing membranes. Definition of *Myotis* subgenera has long challenged taxonomists and prior to the present study the systematic status of numerous forms within *Chrysopteron* remained unclear. Following examination of material (including available type specimens) in 21 European, North American, and Asian collections, and using morphological (external, cranial, and dental characters) and genetic data, we evaluate the validity of the *Chrysopteron* subgenus, revise the taxonomy of the named Asian forms, and review their distinguishing characters, distribution, and taxonomic history. We argue that *Chrysopteron* is an available name for a monophyletic "Ethiopian clade" recovered with high support in our analyses, which comprises species characterized by striking reddish or yellowish dorsal fur that strongly differentiates them from congeners. We also determine that *M. formosus* sensu lato contains several morphologically distinct forms, some of which occur in sympatry and some in widely separated localities. A morphological key is provided for all Asian species of *Chrysopteron* revealed by our study: *M. bartelsi* Jentink, 1910 (Java and Bali), *M. formosus* (Hodgson, 1835) (Afghanistan, India, Nepal, China, Taiwan, and Vietnam), *M. hermani* Thomas, 1923 (Sumatra, Thailand, and Malaysia), *M. rufoniger* (Tomes, 1858) (Korea, Japan, China, Taiwan, Laos, and Vietnam), *M. rufopictus* (Waterhouse, 1845) (Philippines), and *M. weberi* (Jentink, 1890) (Sulawesi).

Key words: identification key, mouse-eared bats, phylogeny, systematics, taxonomy

DOI: 10.1644/13-MAMM-A-200

Chrysopteron Jentink, 1910 is 1 of the 7 subgenera of *Myotis* Kaup, 1829 recognized by Tate (1941; alongside *Selysius* Bonaparte, 1841, *Isotus* Kolenati, 1856, *Paramyotis* Bianchi, 1916, *Myotis*, *Leuconoe* Boie, 1830, and *Rickettia* Bianchi, 1916) and traditionally comprises Asian and African species characterized by conspicuously parti-colored wing membranes. Originally established by Jentink (1910) for *C. bartelsi* from Java, several Asian forms with similar dichromatic wing patterns (*Vespertilio formosa* Hodgson, 1835; *V. rufopictus* Waterhouse, 1845; *V. rufoniger* Tomes, 1858;

Kerivoula pallida Blyth, 1863; *V. auratus* Dobson, 1871; *V. dobsoni* Anderson, 1881; *K. weberi* Jentink, 1890; *V. andersoni* Trouessart, 1897; *M. tsuensis* Kuroda, 1922; *M. hermani* Thomas, 1923; *M. watasei* Kishida, 1924; *M. chofukusei* Mori, 1928; and *M. flavus* Shamel, 1944) were described and subsequently included in major treatments as separate species, subspecies, or synonyms within *Chrysopteron* (Tate 1941; Honacki et al. 1982; Koopman 1989; Corbet and Hill 1992; Simmons 2005). The African species *M. welwitschii* (Gray, 1866) and its synonym *M. venustus* Matschie, 1899 also have been included in the subgenus (Tate 1941; Meester et al. 1986).

Definition of *Myotis* subgenera has long challenged taxonomists, and their compositions have consequently varied from author to author. *Chrysopteron* is no exception. Tate (1941:539) defined *Chrysopteron* as "near *Myotis* [the subgenus], but distinguished by peculiar dichromatic wing-pattern, somewhat like that of *K. picta*, and by the presence of four well-developed lobes on i1 and i2. Braincase rather higher and rostrum lower than in *Myotis*." He admitted, however, that these craniodental characters showed no clear segregation, for example, "in *Chrysopteron* the braincase is slightly fuller and rostrum a little more depressed," and "the 4-cusped condition of i1 and i2 … present also in true *Myotis*" (Tate 1941:541). Tate's (1941) remark that M3 shows reduction in *Myotis*, but not in *Chrysopteron*, also does not appear to be true.

When Findley (1972) included *Chrysopteron* in the subgenus *Myotis* in his phenetic treatment, he found evidence that *M. flavus*, *M. formosus*, *M. hermani*, *M. rufoniger*, *M. rufopictus*, and *M. welwitschii* form a separate clade that he named the *formosus*-group, and linked these species to his newly established *emarginatus*-group (including *M. tricolor*, *M. emarginatus*, and *M. goudoti*). While Findley (1972) also found *M. bocagii* was placed close to *M. goudoti*, he regarded this position as "misplaced" (Findley 1972:38). Although the above Asian taxa were listed as operational taxonomic units and occupied positions similarly separated from each other as from other species in his depictions of phenetic space, all of these taxa were subsumed under the species *M. formosus* within the *formosus*-group without explanation in his classification (Findley 1972:42). This view was followed by Honacki et al. (1982), and subsequently, these sometimes conspicuously different forms were generally regarded as conspecifics. For instance, Corbet and Hill (1992) retained *Chrysopteron* as a valid subgenus (with just 2 species, *M. formosus* and *M. hermani*) and separated it from the subgenus *Myotis* by its wing coloration and differences in the dorsal profiles of the skull. The latter view is, however, hardly justifiable, because all Indomalayan *Chrysopteron* have gradually sloping braincases similar to those of several species assigned by the same authors to the subgenus *Myotis*. Koopman (1994) also adopted Findley's (1972) treatment, including the segregation of 2 externally similar species into 2 different subgenera, namely: *M. scotti* to *Selysius* and *M. bocagii* (regarded by Tate [1941] as belonging to *Selysius*) to the large-footed *Leuconoe*, but in the latter case also remarking, "foot relatively small" (Koopman 1994:106).

In the era of molecular systematics, growing evidence has revealed the paraphyletic nature of *Myotis* subgenera. Characters once thought to be diagnostic are often now regarded as convergent morphological traits related more to modes of food procurement than phylogeny (Stadelmann et al. 2004b). Some analyses also suggest that the biogeographical origins of species are a better predictor of phylogenetic relationships than morphology (Stadelmann et al. 2007). Nonetheless, species once treated as belonging or relating to *Chrysopteron* by Findley (1972) have been shown to have close relationships irrespective of their geographic origin. For instance, Ruedi and Mayer (2001) found *M. welwitschii* (from Uganda and South Africa) and *M. emarginatus* (from Greece) monophyletic in all analyses. In incorporating *M. formosus* from South Korea in their phylogenetic study, Kawai et al. (2003) placed the taxon in a group that included *M. welwitschii*, *M. emarginatus*, and *M. dasycneme*. Although subsequent molecular investigations have not placed *M. dasycneme* among these species (Ruedi et al. 2013), they have proven the validity of grouping *M. formosus* with the other species.

The work of Stadelmann et al. (2004b) was the 1st study of *Myotis* to include all of the traditional subgenera and biogeographic regions. This also included additional African species (*M. bocagii*, *M. tricolor*, *M. goudoti*, and *M. scotti*) in a phylogenetic analysis inferred from cytochrome-*b* (*Cytb*) sequences that found that (together with *M. emarginatus* and *M. formosus*) these form a well-supported lineage, which they named the "Ethiopian clade." Sampling completeness was further improved by the phylogenetic study of Jiang et al. (2010), which included *M. watasei* and *M. flavus* and concluded that the Indomalayan taxa investigated represented more than 1 species, and that these also nested within the "Ethiopian clade" of Stadelmann et al. (2004b, 2007). Unfortunately, however, the nomenclature used by Jiang et al. (2010) seriously misconceived the taxa involved (see details under the headings "*Status of Chrysopteron*" and "*Taxonomic remarks*" of *M. formosus*) and consequently lent further confusion to taxonomic and nomenclatural questions surrounding Asian *Chrysopteron*. Finally, Ruedi et al. (2013), using an even wider sample and a combination of mitochondrial and nuclear sequences, confirmed the monophyly of the "Ethiopian clade" with the additional inclusion of *M. anjouanensis* (from Anjouan, Comoro Islands).

It has long been supposed that the pelage colors of *Chrysopteron* species are species-specific (hence the many species descriptions emphasizing differences between pale yellowish and deep reddish taxa), yet, with the exception of Jiang et al. (2010), systematic and taxonomic studies of Asian *Myotis* that recognize the importance of color differences are thus far confined to Taiwanese field guides (Fang 2007; Cheng et al. 2010) and 1 university thesis (Chou 2004). Major contemporary treatments admit only 2 species (*M. formosus* and *M. hermani*) distinguished by size (Simmons 2005; Francis 2008; Smith and Xie 2008), and critical investigation of these has been hampered by their apparent rarity. As noted by Corbet and Hill (1992:121) "known specimens are quite inadequate for any study of infraspecific variation." In light of this, and following examination of material (including available type specimens) in 21 European, North American, and Asian collections, we discuss the validity of the subgenus *Chrysopteron*, revise the taxonomy of the named Asian forms, and review their distinguishing characters, distributions, and taxonomic histories. A key to the Asian species of *Chrysopteron* also is provided.

MATERIALS AND METHODS

Materials.—All specimens examined are listed under the corresponding taxa in Appendix I. Abbreviations referring to collections include AMNH: American Museum of Natural History, New York, United States; BMNH: The Natural History Museum (formerly British Museum [Natural History]), London, United Kingdom; CPC: Cuc Phuong National Park Reference Collection, Cuc Phuong, Vietnam; DWNP: Department of Wildlife and National Parks, Kuala Lumpur, Malaysia; FMNH: Field Museum of Natural History, Chicago, United States; HNHM: Hungarian Natural History Museum, Budapest, Hungary; IEBR: Institute of Ecology and Biological Resources, Hanoi, Vietnam; MHC: Harada Collection, Osaka City University, Osaka, Japan; MHNG: Muséum d'histoire naturelle de Genève, Geneva, Switzerland; MNHN: Museum national d'histoire naturelle, Paris, France; MZB: Museum Zoologicum Bogoriense, Bogor, Indonesia; NF: Kim Hy Nature Reserve Collection, Hanoi, Vietnam; NSMT: National Museum of Nature and Science (formerly National Science Museum), Tokyo, Japan; NMNS: National Museum of Natural Science, Taichung, Taiwan; PSUZC: Prince of Songkla University Zoological Collection, Hat Yai, Thailand; RMNH: Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands; ROM: Royal Ontario Museum, Toronto, Canada; SMC: Sumiko Matsumura Collection, Yamaguchi, Japan; SMF: Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt a. M., Germany; THU: Tunghai University, Taichung, Taiwan; USNM: National Museum of Natural History (formerly United States National Museum), Washington, D.C, United States; ZMB: Museum für Naturkunde (formerly Zoological Museum), Berlin, Germany.

Measurements.—Forearm length (FA) data were compiled from the literature or measured by the authors from 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. Abbreviations and definitions for craniodental measurements follow Bates and Harrison (1997) and are: GTL—greatest length of skull, from the anterior of the 1st upper incisor to the most posteriorly projecting point of the occipital region; CCL—condylo–canine length, from the exoccipital condyle to the most anterior part of the canine; CCW—greatest width across the upper canines from their buccal borders; M3M3W—greatest width across the crowns of the last upper molars from their buccal borders; IOW—least width of the interorbital constriction; ZYW—greatest width of the skull across the zygomatic arches; MAW—greatest distance across the mastoid region; BCW—greatest width of the braincase; BCH—braincase height, from the basisphenoid at the level of the hamular processes to the most dorsal part of the skull, including the sagittal crest (if present); CM3L—maxillary toothrow length, from the anterior of the upper canine to the posterior of the crown of the 3rd molar; CP4L—distance from the anterior of the upper canine to the posterior of the crown of the last 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 anterior of the lower canine to the posterior of the crown of the 3rd lower molar; and CPH—height of the coronoid process, from its dorsal tip to the apex of the indentation on the ventral surface of the ramus adjacent to the angular process.

All statistical analyses were carried out with R 2.13.2 (R Development Core Team 2012). Measurements were compared using Welch 2-sample *t*-tests. A 1-way analysis of variance (ANOVA) model with Tukey's pairwise tests was used for comparisons of selected external and craniodental measurements. All variables showed normal distributions in quantile-comparison plots and all tests were 2-tailed. To eliminate false discoveries in multiple tests, the adjustment method of Benjamini and Hochberg (1995) was applied.

Phylogenetic reconstruction.—Thirty-six *Cytb* sequences (1,140 base pairs) were downloaded from GenBank to build a phylogenetic tree of available species belonging to *Chrysopteron* and a number of other representative *Myotis* taxa (Table 1). In addition, homologous sequences of 3 outgroup taxa (*Murina cyclotis*, *Mu. pluvialis*, and *Kerivoula papillosa*) were used to root the trees. Sequences were aligned in MEGA5 (Tamura et al. 2011), and the analyses were completed in MrBayes version 3.2.1 (Ronquist and Huelsenbeck 2003) using the Bayesian interference method and in RAxML (Stamatakis 2006) to obtain a maximum-likelihood tree. Reliability of nodes in maximum-likelihood analyses was assessed by 1,000 standard bootstraps with RAxML. All analyses were done using a partitioned scheme where each codon position was allowed to have specific model parameters. The general time reversible model with "gamma" and "invariant sites" was used in each partition, as suggested by the results of jModelTest version2.1.3 (Darriba et al. 2012) applied to the alignment.

To obtain Bayesian interference trees, MrBayes was run for 10×10^6 generations and sampled every 1,000 generations. The first 1×10^6 generations were discarded as burn-in. Posterior probabilities were subsequently computed from the consensus of the remaining sampled trees. Two independent replicate analyses were performed on the same data set, and the results were then combined. Effective sample sizes for the estimated parameters and posterior probability were calculated

TABLE 1.—Origin and GenBank numbers with corresponding references of the 39 cytochrome-*b* sequences from *Myotis* analyzed. Both species of *Murina* and *Kerivoula* were used as outgroups for the phylogenetic reconstructions.

Species	Locality	GenBank name	GenBank no.	Reference
M. albescens	Bolivia		AF376839	Ruedi and Mayer (2001)
M. anjouanensis	Comoros		GU116765	Weyeneth et al. (2011)
M. bechsteinii	Switzerland		AF376843	Ruedi and Mayer (2001)
M. blythii	Kirghizstan		AF376840	Ruedi and Mayer (2001)
M. bocagii bocagii	Ghana		AJ504408	Stadelmann et al. (2004a)
M. b. cupreolus	Tanzania		KF312502	Ruedi et al. (2013)
M. brandtii	Russia		AM261886	Stadelmann et al. (2007)
M. chinensis	China		EF555227	Zhang et al. (2009)
M. chinensis	China		EF555228	Zhang et al. (2009)
M. emarginatus	Greece		AF376849	Ruedi and Mayer (2001)
M. fimbriatus	China		KF312517	Ruedi et al. (2013)
M. formosus sensu stricto	Taiwan	*M.* "*formosus flavus*"	KF312518	Ruedi et al. (2013)
M. formosus sensu stricto	China	*M.* "*flavus*"	EF555233	Jiang et al. (2010)
M. formosus sensu stricto	Taiwan	*M.* "*flavus*"	EU434932	Jiang et al. (2010)
M. rufoniger	Taiwan	*M.* "*watasei*"	EU434933	Jiang et al. (2010)
M. rufoniger	Taiwan	*M.* "cf. *formosus*"	KF312519	Ruedi et al. (2013)
M. rufoniger	China	*M.* "*formosus*"	EF555234	Jiang et al. (2010)
M. rufoniger	China	*M.* "*formosus*"	EF555235	Jiang et al. (2010)
M. rufoniger	South Korea	*M.* "*formosus*"	AB106592	Kawai et al. (2003)
M. rufoniger	Laos	*M.* "*formosus*"	AJ841950	Stadelmann et al. (2004b)
M. rufoniger	Korea	*M.* "*formosus*"	HQ184048	Kim et al. (2011)
M. frater	Japan		AB106593	Kawai et al. (2003)
M. goudoti	Madagascar		AJ504451	Stadelmann et al. (2004a)
M. goudoti	Madagascar		GU116756	Weyeneth et al. (2011)
M. goudoti	Madagascar		GU116761	Weyeneth et al. (2011)
M. goudoti	Madagascar		GU116762	Weyeneth et al. (2011)
M. goudoti	Madagascar		GU116768	Weyeneth et al. (2011)
M. latirostris	Taiwan		AM262330	Stadelmann et al. (2007)
M. pilosus	China		AJ504452	Stadelmann et al. (2004a)
M. ruber	Brazil		AF376867	Ruedi and Mayer (2001)
M. scotti	Ethiopia		AJ841958	Stadelmann et al. (2004b)
M. tricolor	South Africa		AJ841952	Stadelmann et al. (2004b)
M. tricolor	South Africa		AJ841953	Stadelmann et al. (2004b)
M. welwitschii	South Africa		AF376874	Ruedi and Mayer (2001)
M. welwitschii	Guinea		AJ841954	Stadelmann et al. (2004b)
M. welwitschii	Uganda		AF376873	Ruedi and Mayer (2001)
Kerivoula papillosa	Malaysia		EU188782	Anwarali et al. (2010)
Murina cyclotis	Laos		JQ044692	Ruedi et al. (2012)
Murina pluvialis	India		JQ044689	Ruedi et al. (2012)

with Tracer version 1.5 (Rambaut and Drummond 2007) and were all higher than 200.

The genetic distances between and within each species were calculated in MEGA5 (Tamura et al. 2011) using the Kimura 2-parameter model (Kimura 1980).

RESULTS

Status of Chrysopteron.—The monophyletic lineage known as the "Ethiopian clade" within the phylogenetic tree of *Myotis* (Stadelmann et al. 2004b, 2007; Jiang et al. 2010; Ruedi et al. 2013) was recovered in our analyses with high support (> 95% posterior probability and boostrap value) and includes 6 Ethiopian, 1 Palearctic, and 2 Indomalayan species (Fig. 1). The majority of the taxa grouped in this clade had previously been regarded as closely related based on phenetic analyses (Findley 1972). The species referred to as "*M. flavus*" (e.g., Jiang et al. 2010) is identified by us as *M. formosus*, and it does not form a sister group with *M. rufoniger*, the other species of Indomalayan parti-colored bat (variously designated as "*M. watasei*" or "*M. formosus*" by different authors [e.g., Jiang et al. 2010]). Rather, *M. formosus* (as understood here) is associated with the European *M. emarginatus* and the African *M. tricolor* (low nodal support among these 3 species impedes more precise understanding of their phylogenetic relationships), whereas *M. rufoniger* is sister to the African *M. welwitschii* (with high support). The Ethiopian clade is itself part of the Old World species assemblage as detailed in a more comprehensive analysis of the genus (Ruedi et al. 2013).

Although our investigations did not reveal any craniodental characters distinguishing these taxa from all other species of *Myotis*, 1 phenetic character was shared by all of the studied taxa. This is the characteristic reddish or yellowish dorsal fur that strongly differentiates these bats from congeners. An additional feature that may be a synapomorphic character of

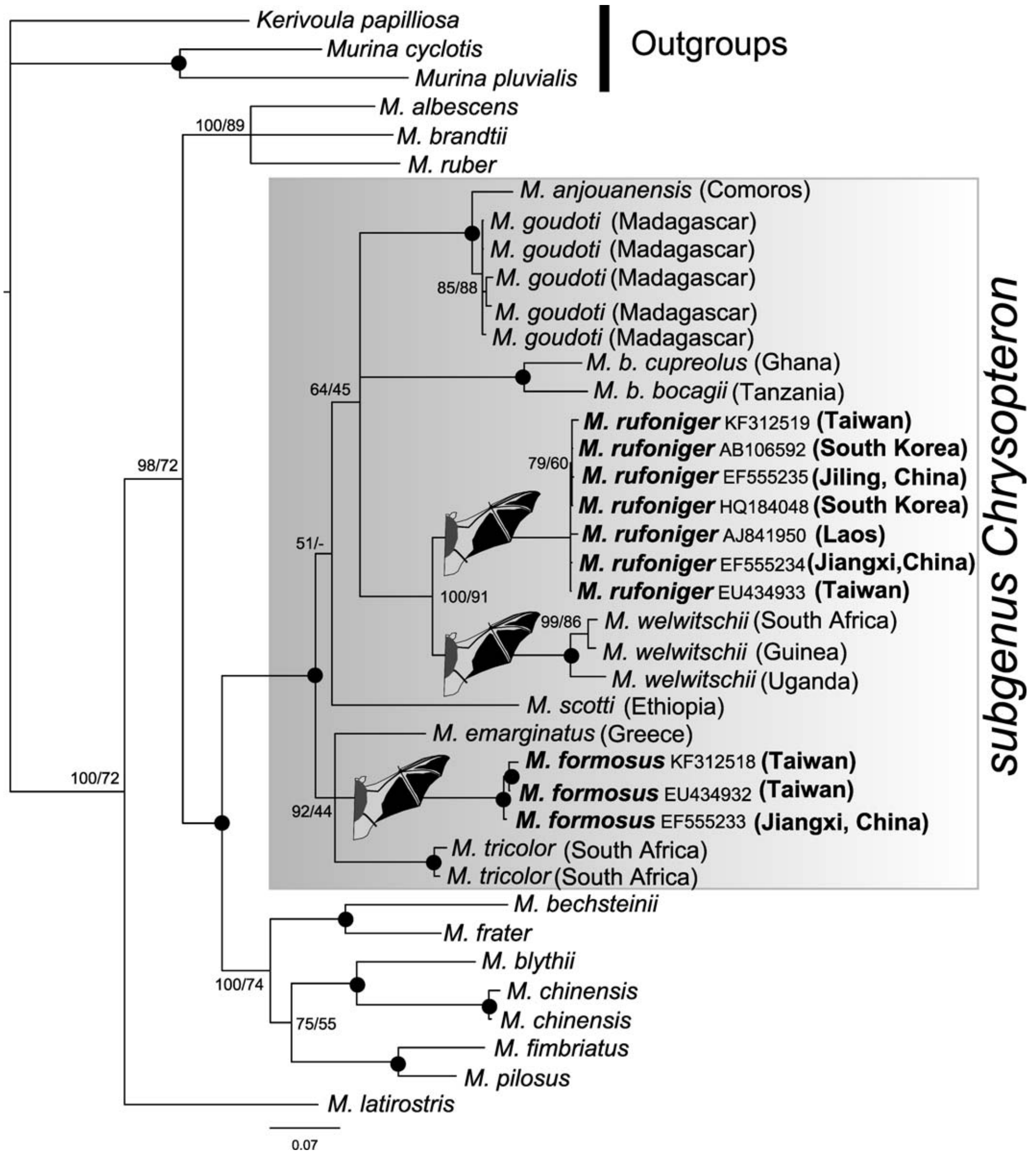

FIG. 1.—Bayesian consensus tree for 19 species of *Myotis* and 3 outgroup species based on an alignment of 1,140 base pairs of the cytochrome-*b* gene. Nodal support is represented as percent posterior probabilities (PP) obtained with MrBayes and standard bootstrap value (BP) obtained with RaxML. Nodes supported by values higher than 95% in both analyses are indicated by a filled circle. Clades showing the typical dichromatic wing pattern are marked with a pictogram. For the GenBank names of the taxa pertaining to the *M. formosus*-complex refer to Table 1.

Chrysopteron is the peculiar texture of the hairs, variously described as "thick and woolly" (Dobson [1871:187] for *V. auratus* and Yoshiyuki [1989:110] for *M. tsuensis*), "cottony" (Tomes [1858:84] for *V. rufoniger*), "woolly" (Blyth [1863:34] for *K. pallida*, Hill and Morris [1971:43] for *M. morrisi*, and Dietz et al. [2009:242] for *M. emarginatus*), "thick, soft and cottony" (Tomes [1858:81] for *V. emarginatus*), or "shaggy" (Rosevear [1965:303] for *M. bocagii*). This feature also is reflected in the vernacular name, "hairy bats," frequently used for Ethiopian species (Taylor 2000), and, with the exception of 2 sister species, *M. goudoti* and *M. anjouanensis* from islands in the Indian Ocean, is typical for all *Chrysopteron* species investigated by us.

Chrysopteron is the earliest available name for the "Ethiopian clade." Its type species, *bartelsi* Jentink, 1910 from Java, is currently considered a subspecies of *M. formosus* (Simmons 2005), which, in turn, is part of the "Ethiopian clade." This renders *Chrysopteron* the only traditional subgenus of *Myotis* currently validated by molecular systematics.

With the separation of *Cistugo* from *Myotis* (Stadelmann et al. [2004b]; subsequently confirmed by Horácek et al. [2006] and Lack et al. [2010]), all sub-Saharan species of *Myotis* were regarded (or anticipated in the case of *M. morrisi*) as part of the "Ethiopian clade" by Stadelmann et al. (2004b). Our morphological examination of the holotype of *M. morrisi* indicated that the species has the fur characters regarded here as diagnostic of *Chrysopteron*, thereby justifying its inclusion in the "Ethiopian clade." The 2 Indian Ocean insular species, *M. goudoti* and *M. anjouanensis*, which are clearly part of the Ethiopian clade in molecular reconstructions (Ruedi et al. 2013; Fig. 1), also have very strong overall reddish to orange dorsal fur. In contrast, the recently recognized species *M. dieteri* Happold, 2005 may be distinct from the "Ethiopian clade." Although *M. dieteri* resembles *M. bocagii* in size, Happold (2005) noted its dorsal fur coloration as dark brown with a pale auburn tip (among other distinguishing characters), instead of reddish brown with a rufous tip, as in *M. bocagii*. Based on this external characteristic *M. dieteri* would be the only sub-Saharan *Myotis* that does not belong to *Chrysopteron*, but molecular data are needed to substantiate this interpretation.

Although Stadelmann et al. (2004b) supposed the dichromatic wing coloration evolved only once within the "Ethiopian clade," the presence of the conspicuous black-and-orange pattern in 2 independent lineages of *Chrysopteron* and in several genetically unsampled species suggests that the developmental pathway may be conserved in many (if not all) species of the subgenus. It is, however, worth noting that within the subgenus this wing coloration is always accompanied by large body size and is observed only in *M. welwitschii*, the largest Ethiopian species (Taylor 2000; Ratcliffe 2002), and much less conspicuously so in some specimens *M. tricolor* from Malawi (M. Happold, pers. comm.) and in similar-sized Asian taxa. Interestingly, the distantly related *K. picta* (Vespertilionidae: Kerivoulinae) also shows the very same dichromatic pattern, suggesting that this peculiar coloration has appeared more than once in the evolution of bats.

Biogeographic inferences based on a likelihood model of ancestral area reconstruction (DEC model—Ree and Smith 2008) and a nearly complete, worldwide taxonomic sampling of *Myotis* species (Ruedi et al. 2013) indicate that species of *Chrysopteron* evolved after an initial range expansion of an Asian ancestor. This widespread ancestor radiated in sub-Saharan Africa to give rise to several taxa. The 2 lineages that led to the current, nonsister species *M. rufoniger* and *M. formosus* apparently resulted from 2 independent recolonizations of the Asian continent by these African forms.

Revision of Asian species of Chrysopteron.—The 1st publication that grouped all of the Asian dichromatic taxa into a single species was that of Findley (1972), who provided limited justification for this action. However, his opinion was adopted by Honacki et al. (1982), Koopman (1989, 1994), and, with the exception of recognizing *M. hermani* as a distinct species, by Corbet and Hill (1992) and Simmons (2005). The presence of more than 1 species within *M. formosus* sensu lato is suggested by more recent publications employing external traits (Cheng et al. 2010), craniodental features (Heaney et al. 1998; Chou 2004), and molecular genetic studies (Jiang et al. 2010; Ruedi et al. 2013).

Our phylogenetic reconstruction (Fig. 1) confirms that specimens formerly included in the *M. formosus* complex are not monophyletic, but form 2 strongly supported, nonsister clades. The nomenclature used in the tree is based on our identification of voucher specimens or is inferred from distributional information and genetic distances.

One of these clades includes all representatives of *M. formosus* (= *M. flavus* sensu Jiang et al. 2010), whereas the remaining sequences, including those representing *M. rufoniger* (= *M. watasei* sensu Jiang et al. 2010), group in a distinct clade. The latter clade is clearly sister to *M. welwitschii* from Africa in all reconstructions (Fig. 1), but the phylogenetic position of the *M. formosus* clade is uncertain within a group that also contains *M. emarginatus* and *M. tricolor* with no bootstrap or posterior probability supporting either sister-group relationship. The mean Kimura 2-parameter genetic distance is about 2 orders of magnitude larger between (18.9%) than within (0.2%) these 2 clades and corresponds well to a pattern of interspecific and intraspecific comparisons, respectively (Bradley and Baker 2001).

Myotis formosus sensu lato, in fact, contains several forms that are morphologically distinct and can be found either in sympatry (e.g., in Taiwan) or in widely separated geographic localities. Having investigated specimens from the entire distribution, we recognize 6 species (*M. bartelsi*, *M. formosus*, *M. hermani*, *M. rufoniger*, *M. rufopictus*, and *M. weberi*), revise their distributions, and summarize their distinguishing characters. In view of the history of taxonomic confusion, a brief review of previous taxonomic opinions also is included.

SYSTEMATIC BIOLOGY

Subgenus *Chrysopteron* Jentink, 1910

Chrysopteron Jentink, 1910:74. Original designation, type species *Chrysopteron bartelsi*.

Dichromyotis Bianchi, 1916:78. Original designation, type species *Myotis formosus*.

Myotis bartelsi Jentink, 1910

Chrysopteron Bartelsii Jentink, 1910:74. Type locality Mt. Pangrango, Java, Indonesia.

Myotis bartelsi: Tate 1941:542. First use of current name combination.

Myotis formosus: Honacki et al. 1982:187 (part). Name combination.

Myotis formosus bartelsi: Koopman 1994:101. Name combination.

Description.—This is a large species of *Chrysopteron* (Table 2). Individual dorsal hairs are black basally, pale yellow distally, then darken to deep red before terminating in a black tip. The general impression of the dorsal fur is thus red tipped with black. Individual ventral hairs possess a black base, followed by either a pale yellow section that progressively darkens distally to deep red, or are otherwise entirely deep red. The ear is conspicuously edged with black and the thumb and underside of hind foot are entirely black. This combination of fur and flesh coloration is henceforth referred to as the

TABLE 2.—Selected external and craniodental measurements (in mm) of Asian *Chrysopteron* (*Myotis*) species. Values are given as mean ± *SD* ($n \geq 5$), minimum–maximum (*n*). Acronyms and definitions for measurements are given in the text.

	M. bartelsi	*M. formosus*	*M. hermani*	*M. rufopictus*	*M. rufoniger*	*M. weberi*
FA	53.4	49.3 ± 2.13	58.7	51.8	49.0 ± 2.46	51.6
		45.5–53.0 (12)	56.1–60.0 (3)	51.0–52.5 (2)	45.0–56.0 (24)	49.7–53.5 (2)
GTL	20.42	18.62 ± 0.46	20.94	18.22	18.16 ± 0.55	19.41
		17.97–19.45 (17)	20.10–21.77 (2)		16.98–19.24 (26)	19.15–19.72 (3)
CCL	18.25	16.61 ± 0.39	19.43	16.1	16.29 ± 0.58	17.17
		15.85–17.30 (18)			15.27–17.71 (28)	16.87–17.59 (3)
CCW	6.04	5.31 ± 0.20	6.2	4.76	4.93 ± 0.21	5.29
		4.98–5.68 (18)	6.00–6.30 (3)	4.75–4.76 (2)	4.37–5.37 (31)	5.10–5.67 (4)
M3M3W	8.63	7.90 ± 0.24	8.9	7.43	7.15 ± 0.24	8
		7.45–8.22 (14)	8.80–9.10 (3)	7.23–7.63 (2)	6.59–7.54 (27)	7.68–8.33 (4)
IOW	4.09	4.48 ± 0.14	4.29	4.19	4.08 ± 0.13	4.37
		4.00–4.66 (19)	4.20–4.36 (3)		3.84–4.44 (31)	3.98–5.24 (4)
ZYW	13.41	12.23 ± 0.32	13.75	11.71	11.30 ± 0.45	12.52
		11.76–12.94 (16)	13.40–14.10 (2)		10.04–12.24 (24)	12.37–12.67 (2)
MAW	10.21	9.33 ± 0.22	11.03	8.73	8.93 ± 0.28	9.59
		8.86–9.73 (17)			8.37–9.34 (26)	9.27–10.05 (3)
BCW	8.8	8.61 ± 0.23	9.22	8.27	8.03 ± 0.21	8.53
		8.13–9.05 (17)			7.61–8.03 (29)	8.12–9.23 (3)
BCH	7.39	6.50 ± 0.24	8.03	6.14	6.33 ± 0.25	6.97
		5.89–6.91 (13)			6.00–7.16 (22)	6.96–6.98 (2)
CM3L	8.44	7.44 ± 0.23	8.7	7.36	7.54 ± 0.29	7.87
		6.92–7.90 (18)	8.60–8.79 (2)	7.22–7.50 (2)	6.88–8.14 (31)	7.57–8.14 (4)
CP4L		3.40 ± 0.18	4.25	3.35	3.81 ± 0.21	3.84
		3.05–3.70 (13)		3.20–3.49 (2)	3.33–4.21 (26)	3.70–3.98 (3)
ML		13.98 ± 0.39	16.45	13.66	13.77 ± 0.55	14.51
		13.18–14.53 (15)		13.35–13.97 (2)	12.69–15.17 (27)	14.33–14.62 (3)
cm3L		7.96 ± 0.24	9.44	7.88	8.00 ± 0.29	8.4
		7.41–8.37 (14)		7.80–7.96 (2)	7.50–8.66 (27)	8.17–8.60 (3)
CPH		4.53 ± 0.22	6.03	4.36	4.12 ± 0.27	4.96
		4.07–4.53 (15)		4.17–4.54 (2)	3.58–4.83 (27)	4.78–5.13 (2)

"*rufoniger*-type," this being the 1st taxon described to have these characters (Figs. 2 and 3a).

The skull has a definite, albeit shallow, rostral depression, and an elongated supraorbital region. The sagittal crest is prominent, and the lambdoid crests are strong. The dentition is robust. The upper canine has a wide base, and attains a height twice that of P4. P3 is fully out of line of the rest of the toothrow, has less than half the basal area of P2, and is not visible in lateral view of the skull. The mandible of the holotype is missing (Fig. 4).

Taxonomic remarks.—In describing *C. bartelsi* (separated from *C. weberi* from Sulawesi based on its larger size and small differences in color patterns), Jentink (1910) differentiated the cranial (flatter head) and dental (smaller middle upper premolar and number of cusps on lower incisors) features of these 2 species from another, unrelated genus containing parti-colored bats, *Kerivoula*, and placed both in his newly established genus *Chrysopteron*. He also noted that the species of *Chrysopteron* "have some characters in common with … *Myotis*" (Jentink 1910:73) and tentatively included *M. formosus* in the new genus.

This taxon is quite similar to *M. hermani* in craniodental traits. Although *M. bartelsi* is smaller in several mensural characters (e.g., FA, M3M3W, IOW, and CM3L; and is therefore tentatively regarded here as a separate species), in other measurements (e.g., GTL, CCW, and ZYW) it falls within the known variation of *M. hermani*. When more specimens and genetic information for both taxa become available, they may prove to be conspecific.

Distribution.—Indonesia (Java and Bali [Fig. 5]). Kitchener and Foley (1985) recorded the species (as *M. formosus*) from Bali.

Myotis formosus (Hodgson, 1835)

Vespertilio formosa Hodgson, 1835:700. Type locality Kathmandu Valley, Nepal.

Kerivoula pallida Blyth, 1863:34. Type locality Chaibassa, Orissa, India.

Vespertilio auratus Dobson, 1871:186. Type locality Darjeeling, West Bengal, India.

Vespertilio dobsoni Anderson, 1881:143. Type locality Purnia, Bihar, India. Not *V. dobsoni* Trouessart, 1878.

Vespertilio Andersoni Trouessart, 1897:129. Replacement name for *Vespertilio dobsoni* Anderson, 1881, preoccupied by *V. dobsoni* Trouessart, 1878.

Myotis formosus: Tate 1941:541. First use of current name combination.

Myotis flavus Shamel, 1944:191 Type locality Yuanli, Miaoli, Taiwan.

Myotis formosus formosus: Koopman 1994:101. Name combination.

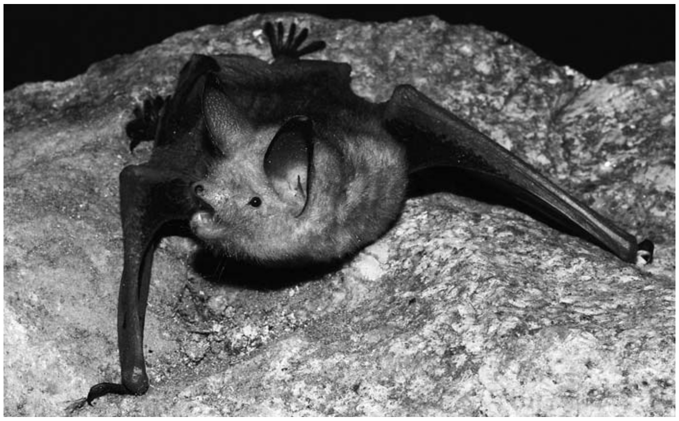

Fig. 2.—Live *Myotis rufoniger* from China, illustrating "*M. rufoniger*-type" pelage (photo: Wen-Hua Yu and Yi Wu).

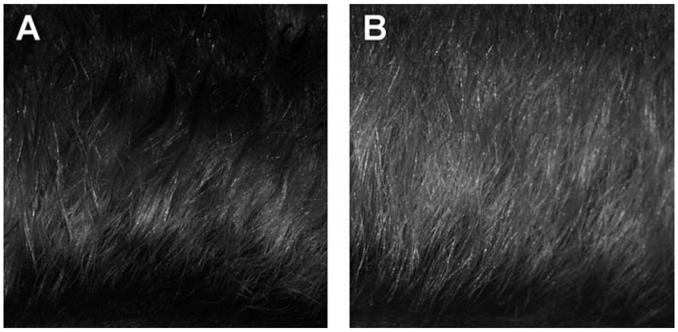

Fig. 3.—Detailed view of dorsal pelage of a) *Myotis rufoniger* from South Korea (HNHM 2003.37.8.) and b) *M. formosus* from Nepal (HNHM 98.8.22.).

Description.—A medium-sized species of *Chrysopteron* (Table 2). Individual dorsal hairs are mid-brown at base (approximately 10% of hair length), pale yellow distally for 80–100% of hair length, or instead terminate in a mid-brown tip slightly darker than the base. Banding is sometimes not evident as the color changes gradually. The general aspect of the dorsal fur is light yellow-brown. Ventral hairs either possess a mid-brown base followed distally by pale yellow, or are entirely light yellow. The darker hair bases are not apparent from a superficial view. The ear is only faintly edged with black, and the thumb and hind foot are brown, not black. This combination of fur and flesh coloration is henceforth referred to as the "*formosus*-type," this being the 1st taxon having these characters to be described (Figs. 3b and 6).

The skull has a distinctly elevated frontal region, with a globose braincase. The sagittal crest is missing or very weak and the lambdoid crests are weakly developed. The upper canine is moderately robust. P3 occupies at most half the basal area of P2, is fully or mostly out of the toothrow (sometimes missing), and is not visible in lateral view of the skull. The lower middle premolar (p3) occupies approximately half the basal area of p2 and is usually situated within the toothrow (Fig. 7).

Taxonomic remarks.—The very vague description of *K. pallida* given by Blyth (1863:34) contains a short comparison with *Kerivoula picta* and is limited to some external measurements.

Dobson's (1871:187) description of *V. auratus* "… hairs tipped with light golden brown; beneath light fawn color" defines it as having the same general color as *M. formosus*, with which he later (together with *K. pallida*) synonymized the taxon (Dobson 1878). Without referring to *M. formosus*, Shamel (1944:191) described *M. flavus* from Taiwan and characterized it as a "pale yellow bat." He pointed out that this taxon is larger than *M. rufoniger* and *M. watasei* and that its P3 is much more reduced. He also described the characteristically differing coloration of *M. watasei* from a Taiwanese specimen (Shamel 1944:192). Lacking exact information on the characters of *M. formosus* sensu stricto, Jiang et al. (2010) mistakenly thought that *M. flavus* and *M. formosus* differ in coloration and craniodental traits (they likely regarded *M. formosus* as the same taxon as *M. rufoniger*). Although they correctly recognized that 2 separate species occur in Taiwan and in mainland Asia, these populations were subsequently associated with the wrong names. As a consequence, they named the larger, yellow species "*flavus*" and the smaller, reddish one "*formosus*," and *M. watasei* was regarded as a junior synonym of *M. formosus*. The specific identity of the

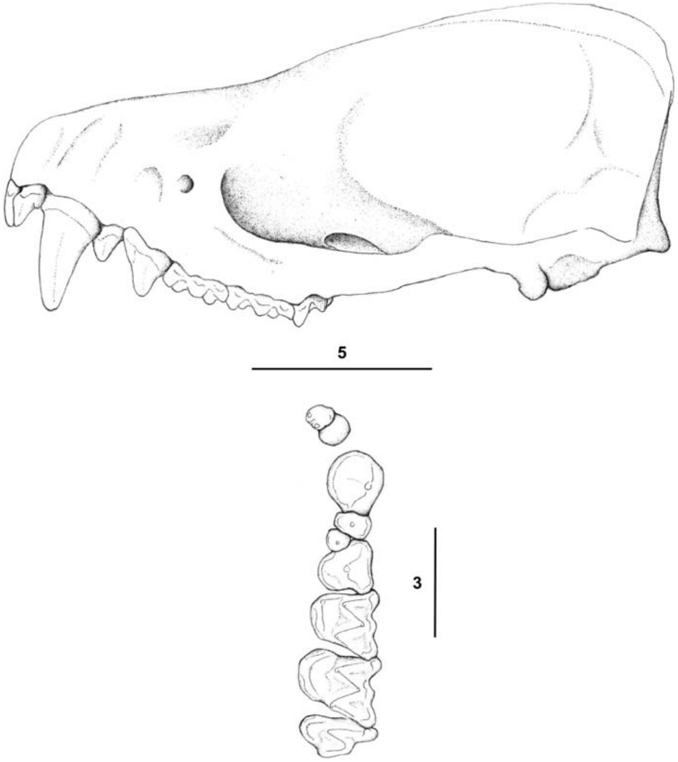

Fig. 4.—Lateral view of skull and occlusal view of left upper dentition of *Myotis bartelsi* (holotype, MZB 10573). Scale bar in millimeters.

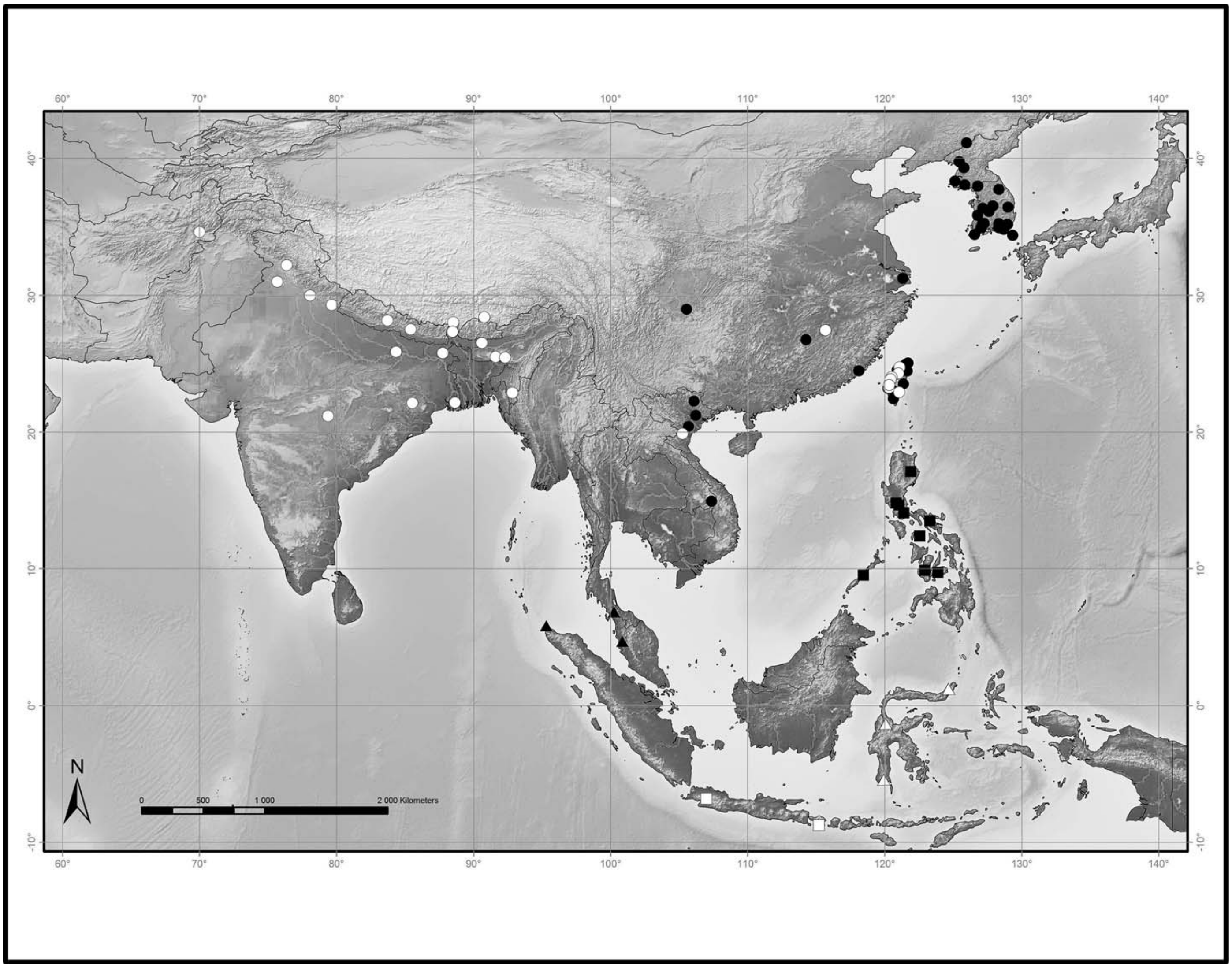

FIG. 5.—Distribution map of Asian *Chrysopteron* species: *Myotis formosus* (empty circles), *M. rufoniger* (full circles), *M. rufopictus* (full squares), *M. hermani* (full triangles), *M. bartelsi* (empty squares), and *M. weberi* (empty triangles).

Jianxi (China) specimen (Jiang et al. 2010) is confirmed by the accompanying photographs (Jiang et al. 2010:46–47) and its *Cytb* sequence (Fig. 1).

Although the limited geographic coverage does not suggest major genetic subdivision within *M. formosus* ($n = 19$), based on Welch 2-sample *t*-tests, the Taiwanese population (*M. flavus*, $n = 12$) is significantly larger than the mainland population in the following measurements: M3M3W ($t_{10.34} = 3.42$, $P = 0.006$), CM3L ($t_{9.26} = 3.89$, $P = 0.003$), CP4L ($t_{10.89} = 3.36$, $P = 0.006$), cm3L ($t_{7.62} = 3.75$, $P = 0.006$), ML ($t_{7.39} = 2.92$, $P = 0.021$) and CCW ($t_{8.54} = 2.41$, $P = 0.041$). After controlling for false discoveries in multiple tests, differences in M3M3W, CM3L, CP4L, and cm3L remain significant ($P = 0.023$ in each case). We regard *M. formosus flavus* herein as a valid subspecies.

Distribution.—Afghanistan, India (Jammu and Kashmir, Himachal Pradesh, Punjab, Maharashtra, Uttar Pradesh, Bihar, West Bengal, Sikkim, Assam, and Meghalaya—for details see Bates and Harrison [1997] and Mandal et al. [2000]), Nepal, China (Tibet and Jianxi), Taiwan, and Vietnam (Fig. 5). The IEBR XL-15B specimen from Thanh Hoa Province, Vietnam (an adult female, collected on 18 April 2012), represents the 1st and only record of *M. formosus* sensu stricto from the country.

Myotis hermani Thomas, 1923

Myotis hermani Thomas, 1923:252. Type locality Sabang Island, Aceh, Sumatra, Indonesia.

Myotis formosus: Findley 1972:42 (part). Name combination.

Myotis formosus hermani: Koopman 1994:101. Name combination.

Description.—The largest species of the subgenus (Table 2). The coloration is of the "*rufoniger*-type" (Figs. 2 and 3a).

Fig. 6.—Live *Myotis formosus* from Taiwan, illustrating "*M. formosus*-type" pelage (photo: Cheng-Han Chou).

The skull is very robust with a shallow but distinct frontal depression, posteriorly elongated supraoccipitale, and exceptionally developed sagittal and lambdoid crests. The basal dimensions of C1 exceed those of P4, whereas P3 is minute, fully displaced lingually, and obscured in lateral view of the skull. The lower middle premolar (p3) is half the size of p2 and partly out of the toothrow (Fig. 8).

Taxonomic remarks.—Thomas (1923) allied *M. hermani* with *M. weberi* and *M. bartelsi* and noted that *M. hermani* is much larger size and has a well-marked sagittal crest. He also briefly discussed the earlier generic placements of *M. weberi* and *M. bartelsi* (in *Kerivoula* and *Chrysopteron*, respectively) and was the first to recognize that all 3 species belong to *Myotis*.

Although larger, *M. hermani* is evidently closely related to, and might be conspecific with *M. bartelsi*, in which case *M. bartelsi* would have priority (see also remarks under that species).

Distribution.—Indonesia (Sumatra), Thailand (Songkhla [in Bumrungsri et al. 2006]), and Malaysia (Perak [in Francis 1995; Fig. 5]).

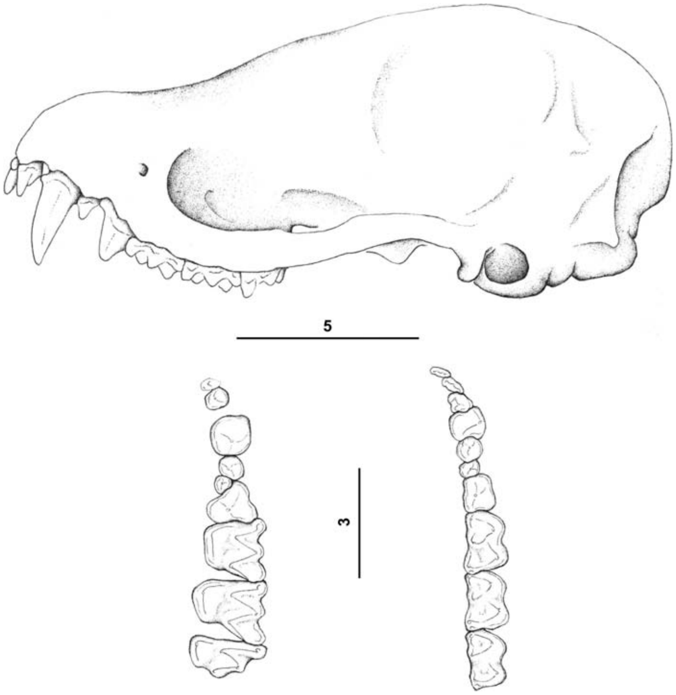

Fig. 7.—Lateral view of skull and occlusal view of left upper and right lower dentition of *Myotis formosus* (Nepal, HNHM 98.8.22.). Scale bar in millimeters.

Myotis rufoniger (Tomes, 1858)

Vespertilio rufo-niger Tomes, 1858:82. Type locality Shanghai, China.

Myotis tsuensis Kuroda, 1922:43. Type locality Tsushima Island, Japan.

Myotis Watasei Kishida, 1924:36. Type locality Manjhou, Pingtung, Taiwan.

Myotis chofukusei Mori, 1928:389. Type locality "Kaishu," Hwanghae-Namdo, North Korea.

Myotis formosus chofukusei: Kuroda 1938:97. Name combination.

Myotis formosus tsuensis: Kuroda 1938:97. Name combination.

Myotis formosus watasei: Kuroda 1938:97. Name combination.

Myotis rufoniger: Tate 1941:541. First use of current name combination.

Myotis sicarius tsuensis?: Tate 1941:548. Name combination.

Myotis formosus: Findley 1972:42 (part). Name combination.

Myotis formosus rufoniger: Koopman 1994:101. Name combination.

Myotis formosus tsuensis: Koopman 1994:101. Name combination.

Myotis formosus watasei: Koopman 1994:101. Name combination.

Description.—On average one of the smallest of *Chrysopteron* species in Asia (Table 2). Coloration is of the "*rufoniger*-type" (Figs. 2 and 3a).

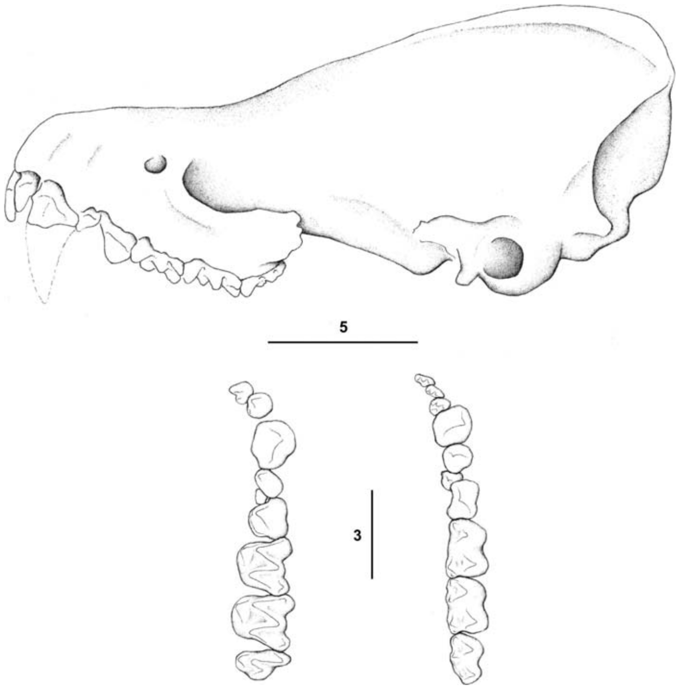

Fig. 8.—Lateral view of skull and occlusal view of left upper and right lower dentition of *Myotis hermani* (holotype, BMNH 23.1.2.13). Scale bar in millimeters.

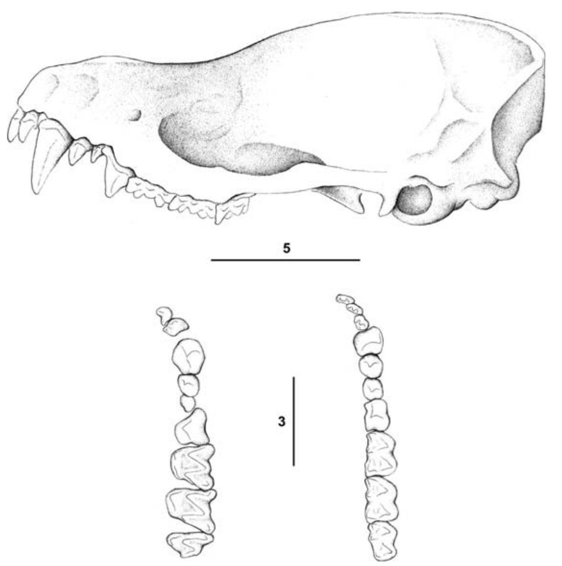

Fig. 9.—Lateral view of skull (Taiwan, MHC 7223) and occlusal view of left upper and right lower dentition (holotype, BMNH 57.4.16.1) of *Myotis rufoniger*. Scale bar in millimeters.

The skull has a slightly, but distinctly, elevated frontal part, and moderately strong sagittal and lambdoid crests. The dentition (including the canines) is moderately robust. The basal area of P3 is approximately two-thirds that of P2, and is usually in line and visible from outside, but rarely displaced inward. The lower middle premolar (p3) is well developed and at least two-thirds of the size of p2 basally, but often closely approaches its basal dimensions (Fig. 9).

Taxonomic remarks.—Tomes (1858) provided a diagnosis for his *V. rufoniger* based on the color differences (ears edged with black, and dorsal and ventral hairs tipped with bright rufous) but hesitated to recognize it as a distinct species or a "variety" of *V. formosus*.

When Kuroda (1922) described *M. tsuensis* as having reddish brown fur dorsally and ventrally and compared it only with *M. macrodactylus* and *M. nattereri bombinus*, he unsurprisingly found it specifically distinct. Details provided by Kishida (1924:40) for *M. watasei* unambiguously define the species from Taiwan as belonging to the "*rufoniger*-type": "ear red brown at base, edged with black ... upper [dorsal] and under [ventral] body fur basal two-thirds brown-yellow, terminal one-third brown ... feet black" (translated from Japanese).

Mori (1928:390) compared *M. chofukusei*, characterized by its "capucine orange" dorsal fur and ears emarginated with dark margins, with *M. bechsteinii*. Under the heading of *formosus*, Howell (1929:15) stated "the mainland bat of this rufous and black type has been described under the name *rufoniger* Tomes, but I believe that the validity of the latter has not been satisfactorily established." The geographical basis of this remark likely stemmed from his erroneous idea that *M. formosus* was described from Formosa (= Taiwan).

Imaizumi (1970:223), however, regarded *M. tsuensis* as "indistinguishable from *M. chofukusei* described from Korea" and gave its range as Tsushima and the Korean Peninsula. Yoshiyuki (1989) and Yoon (2010) also regarded the Korean population as belonging to the subspecies *M. formosus tsuensis*.

Kim et al. (2011) published the complete mitochondrial genome of a specimen of "*M. formosus*" from South Korea (GenBank accession number is HQ184048, not HQ184084 as published in Kim et al. 2011); genetically, this corresponds fully (100% match at *Cytb*, see Fig. 1) to "*M. formosus*" in Kawai et al. (2003) and "*M. watasei*" in Jiang et al. (2010) and thus represents *M. rufoniger*, not *M. formosus* sensu stricto.

Although earlier studies (Imaizumi and Yoshiyuki 1969) found no differences between specimens from Tsushima Island (*M. tsuensis*) and the geographically closer Korean Peninsula (*M. chofukusei*), in 1-way ANOVA models the Tsushima Island population ($n = 4$) proved to be significantly smaller than either *M. chofukusei* ($n = 10$) or the Taiwan population (*M. watasei*, $n = 8$), respectively, in the following measurements GTL ($P = 0.020$ and 0.006, $F = 4.82$), MAW ($P = 0.005$ and 0.010, $F = 5.36$), CM3L ($P = 0.037$ and 0.001, $F = 5.39$), CP4L ($P = 0.005$ and 0.001, $F = 11.11$), and CPH ($P = 0.021$ and 0.001, $F = 9.36$). After controlling for false discoveries in multiple tests, differences between *M. tsuensis* and *M. chofukusei* in MAW and CP4L remained significant ($P = 0.038$ in both cases). For *M. tsuensis* versus *M. watasei*, all of the above differences remained significant ($P = 0.023$, 0.03, 0.005, 0.005, and 0.005, respectively). Abe et al. (2008) asserted that the Tsushima population was vagrant from the

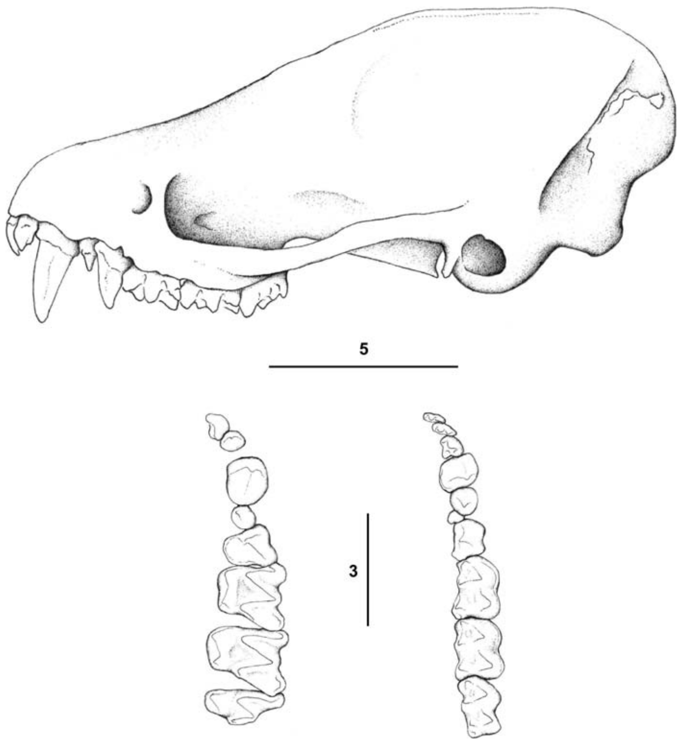

Fig. 10.—Lateral view of skull and occlusal view of left upper and right lower dentition of *Myotis rufopictus* (holotype, BMNH 7.1.1.533). Scale bar in millimeters.

Korean Peninsula and did not breed on the island although a female with young had been reported on Tsushima Island in August by Imaizumi (1970). Recent observations indicate these bats are present year-round on the island (S. Matsumura, pers. comm.). Specimens from Tsushima have not yet been included in phylogenetic analysis, but all other samples studied show almost identical *Cytb* sequences, indicating no major genetic subdivision within the species.

The only known Lao record of *M. rufoniger* is included in several phylogenetic reconstructions (Stadelmann et al. 2004b; Jiang et al. 2010; Ruedi et al. 2013; present paper). Its specific identity is supported by the color plate provided by Francis et al. (1999) and by its genetic data (e.g., approximately 0.8% sequence divergence from South Korean or Taiwanese *M. rufoniger*).

Distribution.—North Korea, South Korea, Japan (Tsushima), China (Fujian, Jiangxi, Jilin, Shanghai, and Sichuan), Taiwan, Laos, and Vietnam (Fig. 5). The Vietnamese specimens from the provinces of Hai Duong, Bac Kan, and Ninh Binh represent the 1st published records of the species from the country.

Myotis rufopictus (Waterhouse, 1845)

Vespertilio rufo-pictus Waterhouse, 1845:8. Type locality Philippines.

Myotis rufopictus: Tate 1941:541. First use of current name combination.

Myotis formosus: Findley 1972:42 (part). Name combination.

Myotis formosus rufopictus: Koopman 1994:101. Name combination.

Description.—A medium-sized species of the Asian members of the subgenus (Table 2). The fur color is the "*formosus*-type" (Figs. 3b and 6).

The skull profile ascends almost evenly with no frontal depression. The sagittal and lambdoid crests are only moderately developed, whereas the skull is globose posteriorly. The canines are moderately strong, and the upper molars are relatively robust with developed talons. The P3s are missing from the holotype. The p3s are very small and intruded lingually half-way out of the line of the toothrow (Fig. 10).

Taxonomic remarks.—Waterhouse (1845) gave a detailed description of the fur of his new species, which was compared by him only with *K. picta* and separated from that species by its much larger size and differently shaped ear.

Tomes (1858) directly compared the type specimens of *M. rufopictus* and *M. formosus* and noted the larger size (despite immaturity) and missing middle premolars of the former.

Large differences in skull measurements within the Philippines (CCL 16.1–17.9, and CM3L 7.1–8.5, $n = 4$) are reported by Ingle and Heaney (1992) and records of a reddish form in the islands (L. Heaney, Field Museum of Natural History, pers. comm., 2013) imply the presence of a 2nd species in addition to *M. rufopictus*.

Distribution.—Philippines (Fig. 5). An overview of the distribution and habitat of the species is given by Ong et al. (2008).

Myotis weberi (Jentink, 1890)

Kerivoula weberi Jentink, 1890:129. Type locality Loka, Bantaeng, Sulawesi, Indonesia.

Myotis weberi: Tate 1941:542. First use of current name combination.

Myotis formosus: Honacki et al. 1982:187 (part). Name combination.

Myotis formosus weberi: Koopman 1994:101. Name combination.

Description.—A relatively large species of the subgenus (Table 2). The fur coloration is the "*rufoniger*-type" (Figs. 2 and 3a).

The skull has a distinct frontal depression, moderately developed sagittal and lambdoid crests, and posteriorly elongated supraoccipital region. The upper canine has a wide base but is not especially high, whereas P2 is much reduced in size, fully or partly displaced lingually, and is accordingly obscured or visible in the lateral view. The p3 occupies half the basal area of p2 at most and is situated within the toothrow (Fig. 11).

Taxonomic remarks.—In placing *M. weberi* in the genus *Kerivoula*, Jentink (1890) was misled by the apparent similarity of their wing patterns, and within that genus he distinguished his new species by its larger size; comparisons were inappropriately confined to *K. picta*.

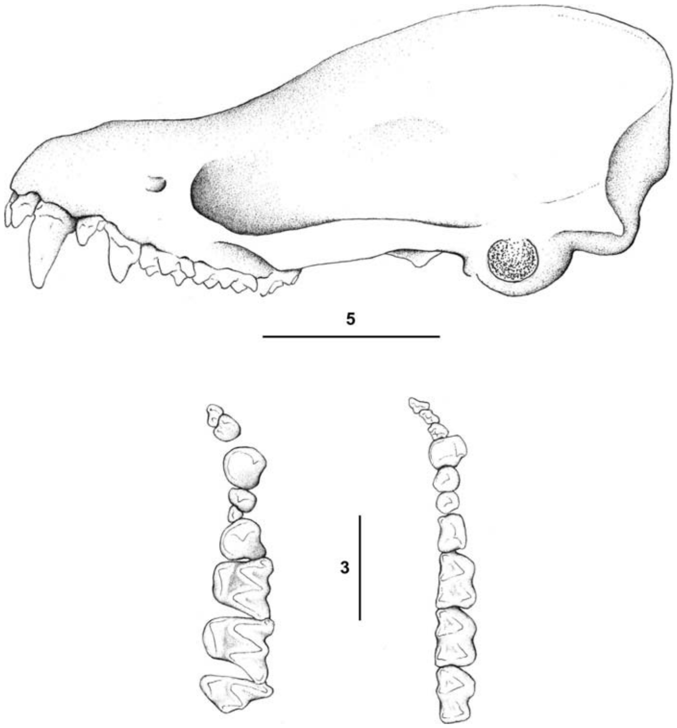

Fig. 11.—Lateral view of skull and occlusal view of left upper and right lower dentition of *Myotis weberi* (holotype, RMNH 35827). Scale bar in millimeters.

Myotis weberi is erroneously given by Yoshiyuki (1989) as the type species of *Chrysopteron*.

Distribution.—Indonesia (Sulawesi [Fig. 5]).

KEY TO THE ASIAN SPECIES OF *CHRYSOPTERON*

1a. Dorsal hairs tipped with black, general impression dark red; supraoccipital region of skull elongated with developed crests ("red" species; Figs. 2, 3a, and 4) 2

1b. Dorsal hairs tipped with light brown, general impression pale yellow; braincase globose, sagittal crest weak or moderately developed ("yellow" species; Figs. 3b, 6, and 7) 5

2a. M3M3W $<$ 7.6 mm; basal area of P3 more than half of P2 ("mainland red" species; Fig. 9)........... *M. rufoniger*

2b. M3M3W $>$ 7.6 mm; basal area of P3 less than half of P2 ("Sunda red" species)............................... 3

3a. Sagittal crest moderately developed; CCL $<$ 18.0 mm; M3M3W $<$ 8.5 mm (Sulawesi; Fig. 11)...... *M. weberi*

3b. Sagittal crest very strong; CCL $>$ 18.0 mm; M3M3W $>$ 8.5 mm... 4

4a. FA $>$ 56 mm; M3M3W $>$ 8.8 mm (Sumatra and Malay Peninsula; Fig. 8)......................... *M. hermani*

4b. FA 53.4 mm; M3M3W 8.63 mm (Java and Bali; Fig. 4) .... *M. bartelsi*

5a. Skull with distinct frontal depression; very weak sagittal crest; CCW near or over 5 mm ("mainland yellow" species; Fig. 7) .... *M. formosus*

5b. Cranial profile straight; moderately developed sagittal crest; CCW 4.75–4.76 mm ("Philippine yellow" species; Fig. 10) .... *M. rufopictus*

ACKNOWLEDGMENTS

We thank N. Simmons and E. Westwig (AMNH); P. Jenkins and R. Portela Miquez (BMNH); Le Trong Dat (CPC); L. Heaney (FMNH); M. Harada (MHC); J. Cuisin and Jean-Marc Pons (MNHN); Shin-Ichiro Kawada and S. Shimoinaba (NSMT); Yen-Jean Chen (NMNS); C. Satasook and P. Soisook (PSUZC); C. Smeenk, S. van der Mije, and W. van Bohemen (RMNH); B. K. Lim and J. L. Eger (ROM); S. Matsumura (SMC); K. Krohmann (SMF); K. Helgen and D. Lunde (USNM); and F. Mayer and N. Lange (ZMB) for kindly providing essential information and access to specimens in their care. We are grateful to P. Racey (University of Exeter) and P. Bates (Harrison Institute) for their longstanding support of bat research in Southeast Asia, to Z. Vas for his help with the statistical comparisons, and to A. Honfi for the final elaboration of drawings. This research received support from the SYNTHESYS Project, which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program, the NHMG, the FMNH, and the Smithsonian Institution. Field studies in Vietnam were funded by the National Foundation for Science and Technology Development of Vietnam (project 106.11–2012.02) and helped by the Directorate and Scientific Council of IEBR, and Le Dinh Thuy.

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Submitted 16 August 2013. Accepted 31 January 2014.

Associate Editor was Neal Woodman.

Appendix I

Specimens examined

Kerivoula sp.—JAVA: RMNH 35401 (registered as *M. formosus*). *Myotis anjouanensis*—COMOROS: MNHN 1886-266, 1886-1265, 1886-1267, 1886-1269, 1886-1536. *M. bartelsi*—JAVA: MZB 10573 (holotype). *M. bocagii*—CAMEROON: BMNH 3.2.4.6, 89.723; DR CONGO: BMNH 59.508, 59.509; GABON: MNHN 1985-1928; KENYA: BMNH 3.3.2.2 (holotype of *M. hildegardeae*); MALAWI: BMNH 87.1080, 87.1081. *M. emarginatus*—HUNGARY: HNHM 71.7.1; PAKISTAN: BMNH 1909.1.4.33 (holotype of *M. desertorum*). *M. formosus*—AFGHANISTAN: SMF 38752; NEPAL: BMNH 43.1.12.141 (holotype), HNHM 98.8.22; NORTH INDIA: BMNH 6.12.24.4, 79.11.21.175, 79.11.21.176, FMNH 85057; TAIWAN: USNM 239908 (holotype of *M. flavus*), BMNH 66.6.17.1, 66.6.17.2, HNHM B000054, MHNG B000065, B000100, NMNS t-4607, t-4614, t-4546, THU B000060, B030004, ZMB 54193; TIBET: BMNH 15.2.21.4; VIETNAM: IEBR XL-15B; UNKNOWN: BMNH 60.5.4.45. *M. goudoti*—MADAGASCAR: BMNH 7.4.1.503 (holotype of *M. madagascariensis*), 87.146, 87.147, 99.9, MNHN 1949-310, 1981-869. *M. hermani*—SUMATRA: BMNH 23.1.2.13 (holotype); THAILAND: PSUZC M05.1. *M. morrisi*—ETHIOPIA: BMNH 70.488 (holotype); NIGERIA: BMNH 84.840. *M. scotti*—ETHIOPIA: BMNH

27.3.4.1–27.3.4.5 (paratypes). *M. rufoniger*—CHINA: BMNH 57.4.16.1 (holotype), 7.1.1.502, 88.1.16.1, AMNH 84843, USNM 241369, ZMB 4139; JAPAN (TSUSHIMA ISLAND): NSMT 11886, 21191, without number; SOUTH KOREA: FMNH 48375, HNHM 2003.37.8–2003.37.10, 2003.37.24, 2003.37.45, MHC 5289, 5296, NSMT 5732, 5888, 11671, 27178; TAIWAN: MHC 7222, 7223, MHNG B030022, B000098, NMNS t-4613, t-4611, THU B000048, B000053, B030063, B030046, USNM 239909, ZMB 88447, 88448; VIETNAM: IEBR T.080511.1, NF 170906.7, CPC DB0295; UNKNOWN: NSMT 34440. *M. rufopictus*—PHILIPPINES: BMNH 7.1.1.533 (holotype), FMNH 1114. *M. tricolor*—KENYA: BMNH 76.29.30, 76.29.31; SOUTH AFRICA: BMNH 1881.17.1. *M. weberi*—SULAWESI: AMNH 224579, RMNH 35827 (holotype), ZMB 5416, 88450.