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Philippine bats of the genus *Kerivoula* (Chiroptera: Vespertilionidae): Overview and assessment of variation in *K. pellucida* and *K. whiteheadi*

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Abstract

Bats of the genus *Kerivoula* (Mammalia, Chiroptera) are widespread in the Philippines with four reported species, but have been poorly known due to a paucity of specimens. We provide the first molecular phylogeny for Philippine *Kerivoula*, which supports the existence of four distinct clades that we treat as species (*K. hardwickii*, *K. papillosa*, *K. pellucida*, and *K. whiteheadi*); these four overlap broadly geographically. Each of these may be recognized on the basis of cytochrome b sequences and external and craniodental morphology. Detailed examination of *K. pellucida* shows little geographic differentiation within the Philippines, but they differ subtly from those on the Sunda Shelf. We consider *K. whiteheadi* to be composed of four recognizable clades, each restricted to a geographic region within the Philippines. We consider *K. bicolor*, from peninsular Thailand, and *K. pusilla*, from Borneo, to be distinct from *K. whiteheadi.* Our data indicate the presence of two species within the Philippines currently lumped as *K. hardwickii*; further study of these is needed. A calibrated phylogeny suggests that *Kerivoula* began arriving in the Philippines about 10 MYA, with each of the four current lineages arriving independently.

Key words: biogeography, cytochrome *b*, echolocation, ecology, morphology, phylogeny, Southeast Asia

Introduction

The Philippine archipelago is composed of about 7,000 islands, ranging in area up to 103,000 km^2 that are largely of oceanic origin; only the Palawan region may have been connected to the Asian mainland by dry-land connection (Piper *et al.* 2011; Hall 2012, 2013; Heaney *et al.* 2016). During Pleistocene periods of low sea level, some oceanic islands formed into several large aggregates, but many islands remained isolated by permanent sea channels (Inger 1954; Heaney 1985; Brown *et al.* 2013; Heaney *et al.* 2016). Thus, the archipelago is an ideal place for studying the relative success of groups of organisms in crossing oceanic channels and the impact of the subsequent isolation on diversification.

With at least 80 species of bats recorded (Heaney *et al.* 2010, 2012), the Philippines has a rich fauna that provides opportunity for such studies. Among Philippine bats, the family Pteropodidae, with 26 species, has been the most extensively studied, including ecology, geographic patterns of genetic variation and gene flow, the relationship of species richness and island area, and the frequency and sources of colonization to the Philippines from other geographic sources (e.g., Heaney 1991; Heideman 1995; Heideman & Utzurrum 2003; Ingle 2003; Sedlock *et al.* 2008, 2011, 2014a; Heaney & Roberts 2009).

In contrast, the insectivorous bats of the Philippines, which currently include about 54 species in seven families, are less thoroughly studied. Identification keys, brief descriptions, and illustrations have been published (Ingle & Heaney 1992; Heaney *et al.* 2016), and habitat selection (e.g., Sedlock *et al.* 2008, 2011, 2014a), foraging behavior, and echolocation (Sedlock 2001; Sedlock *et al.* 2014b) have been investigated for selected species. However, numerous authors have commented on the uncertainty regarding species definitions and distributions and the likelihood that more species are present than are currently recognized (e.g., Ingle & Heaney 1992; Patrick *et al.* 2013; Heaney *et al.* 2016).

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Among these poorly-known insectivorous Philippine bats is the genus *Kerivoula*. Hill (1965) provided a detailed assessment of the species then known, noting that few specimens were available from Asia. For most species, Hill's work remains the basis for current taxonomy of *Kerivoula* in the Philippines, and our assignments of specimens to species are based on the characters he cited, as implemented in Ingle & Heaney (1992) and discussed below. About 24 species are currently recognized from tropical Africa, through South and Southeast Asia, to New Guinea and the Bismarck Archipelago (Bates *et al.* 2004, 2007; Simmons 2005; Francis *et al.* 2007; Kuo *et al.* 2017), but recent studies have pointed to the likely existence of additional, currently unnamed species (e.g., Khan *et al.* 2010; Hasan & Abdullah 2011; Douangboubpha *et al.* 2015). Until recently, based on a small number of specimens, three species had been reported from the Philippines: *K. hardwickii*, *K. pellucida*, and *K. whiteheadi* (Sanborn 1952; Hill 1965; Ingle & Heaney 1992; Heaney *et al.* 1998). However, extensive field research during the last two decades has produced additional specimens from many parts of the archipelago (e.g., Alviola *et al.* 2011; Balete *et al.* 2011, 2013; Esselstyn *et al.* 2004; Sedlock *et al.* 2008, 2011, 2014a; Heaney *et al.* 2016). As a result of those studies, *K. papillosa* has been reported from Luzon (Duya *et al.* 2007) and Bohol (Sedlock *et al.* 2014). Heaney *et al.* (2016) noted additional specimens and their similarity to specimens of *K. papillosa* from Vietnam, but considered the referral to be tentative and in need of further study. Hill (1965) and Heaney *et al.* (2016) also noted geographic variation among specimens referred to *K. whiteheadi* that deserves study.

This paper presents a broad overview of the diversity of *Kerivoula* within the Philippines, based on morphological and genetic studies made possible by recently obtained specimens. In this paper, we define phylogenetic relationships and circumscribe all species groups, note potential species, and discuss the likely biogeographic implications of these data. Finally, we present an assessment of variation within two of the species, *K. pellucida* and *K. whiteheadi*, and summarize our data on their ecology. We plan to present similarly detailed data on the other Philippine species of *Kerivoula* in a subsequent publication.

Material and methods

Taxonomic sampling for morphological analysis

We examined 157 *Kerivoula* specimens (Appendix A). The majority of these are at the Field Museum of Natural History (FMNH) and were collected by our team over the past 20 years, but we also examined specimens from the Museum of Natural History, University of Kansas (KU), the Natural History Museum, London (BMNH), the Philippine National Museum (PNM), and the Harrison Institute, Sevenoaks (HZM; Appendix A). The adults (with skulls in good condition) were used in the morphometric analyses described below (see Appendix A).

Morphological measurements and analyses

Prior to preservation, specimens were measured in the field with a ruler graduated in millimeters and with Pesola scales graduated to 0.1 g. The following measurements were taken: total length, from the tip of the rostrum to the tip of the tail vertebrae; tail length, from the base of the tail at the pelvis to the tip of the tail vertebrae; hind foot length, from the heel to the further point on the longest claw; ear length, from the notch at the base of the external ear (pinna) to the dorsal tip of the pinna; forearm length, from the point of the elbow to the wrist, with both joints folded; and weight. Specimens were preserved in formalin, and later transferred to 70% ethanol. For previously existing fluid-preserved specimens, we took external measurements with a ruler graduated in millimeters. Skulls from fluid-preserved specimens we collected were later removed and cleaned with dermestid beetles and a weak ammonia solution. Images of skulls were obtained with an AMRAY 1810 scanning electron microscope, using uncoated (untreated) skulls. Our specimens are cataloged into the collection of the Field Museum of Natural History (FMNH); half of these will later be deposited in the Philippine National Museum of Natural History, Manila. Field studies were conducted under permits from the Philippine Department of Environment and Natural Resources; all relevant Philippine rules and regulations regarding the capture, handling, and exportation of specimens were followed.

To standardize measurements, JLS took all of the following measurements from adult specimens using digital calipers graduated to 0.01 mm. Two external measurements included forearm length (FA) taken as described above, and tibia length (TIB) taken from the ankle to the knee joint, and 10 cranial and dental measurements: greatest length of skull (GTL), from the alveolus of the first incisor to the most posterior point of the skull; condylo-canine length (CCL), from the alveolus of a canine to the posterior edge of the exoccipital condyles; greatest width of the braincase (GBB), taken at the widest points across the braincase; braincase height (BH), from the highest point of the skull to the basisphenoid; post-orbital constriction (PC), the narrowest width of the skull between the orbits; maxillary toothrow length (C–M^3), from the most anterior point of the canine to the posterior edge of the third molar; molar width (M^2–M^{2ext}), between the buccal edges of the second molars; canine width (C^1–C^1), from the labial edges of the canines; mandibular toothrow length (C–M_3), from the anterior edge of the canine to the posterior edge of the third molar; and mandible length (MDL), from the most anterior part of the mandible not including the incisors to the most posterior part of the condyle.

We assessed multivariate variation in craniodental morphology among taxa using a Principle Components Analysis (PCA) in R (R Development Core Team 2018). We ran the PCA on a correlation matrix of eight log-transformed variables. In order to maximize the number of specimens included in the analysis, we excluded three of the craniodental measurements often missing due to skull damage (GTL, C–$M_{3,}$ MDL). We also plotted condylo-canine length against braincase height, since the PCA indicated that these two measurements reflect much of the variation in Philippine *Kerivoula*, as discussed below.

For morphological comparison, we included representative samples of *Kerivoula* species from outside the Philippines that occur within the Philippines (*K. hardwickii*, *K. pellucida*, *K. papillosa*, *K. whiteheadi*) including specimens from Borneo and mainland Southeast Asia (we use "mainland" to refer to the region encompassing Indochina and Peninsular Malaysia). Additionally, we included several species that occur near the Philippines, including *K. titania, K. intermedia*, and *K. minuta*. We did not include several members of the *K. hardwickii* group, a complex that requires much detailed study (e.g., *K. depressa*, *K. krauensis, K. furva* or *K. kachinensis;* see Bates *et al.* 2007; Francis *et al.* 2007; Khan *et al.* 2010; Douangboubpha *et al*. 2015; Son *et al*., *et al.* 2015; Struebig *et al.* 2016; Kuo *et al.* 2017; Tu *et al.* 2018).

Taxon sampling for genetic analyses

A representative subsample of 33 *Kerivoula* specimens from the Philippines was selected for the genetic analyses, including seven *K. pellucida* from Mindanao and Bohol, 19 *K. whiteheadi* from Bohol, Camiguin Norte, Cebu, Luzon, Mindanao, and Siquijor, five *K. hardwickii* from Bohol and Mindanao, and two *K. papillosa* from Bohol and Luzon. We include specimens of *K. hardwickii*, *K. papillosa*, and *K. pellucida* from outside the Philippines, plus four species some authors have suggested are related to *K. papillosa* (*K. lenis*) and *K. hardwickii* (*K. furva, K. intermedia,* and *K. minuta*), and two outgroup species, *Murina cyclotis* and *Phoniscus jagorii* (see Appendix B for details; we follow Tu *et al.* (2018) for use of *K. furva* for specimens from southern China and Taiwan previously assigned to *K. titania*).

DNA amplification and sequencing

Total genomic DNA was isolated from about 20-40 μg of tissue preserved in ethanol, using the DNeasy Blood & Tissue Kit (Qiagen, Switzerland) and following manufacturer's instructions. The purified DNA was eluted into 200 μl of TE buffer. The complete mitochondrial cytochrome *b* gene (Cyt *b*; 1140 bp) was amplified and sequenced in both directions using the forward primer Molcit-F (Ibáñez *et al.* 2006) and reverse primer CYTB-H (Weyeneth *et al.* 2008). The PCR cocktail for amplifications was achieved in a 25 μl reaction volume, including 2.5 μl 10× Buffer, 1 μM MgCl2, 0.8 mM dNTP, 0.2 μM of each primer, 1 U Taq Qiagen (Qiagen, Switzerland) and 4 μl of extracted DNA. The thermal cycling program started with an initial denaturation at 93°C for 3 min, followed by five touchdown cycles with 45 s denaturation at 93°C, 45 s annealing at a temperature set between 50 and 45°C (with a decreasing pitch of 1°C) and 1 min extension at 72°C, followed by 35 cycles with an annealing temperature set at 45°C and a final extension for 5 min at 72°C. The PCR product was purified using the High Pure PCR Product Purification Kit (Roche, Switzerland). PCR products were sequenced for both strands by a commercial facility (Macrogen Europe, Netherlands). Sequences were visually checked with Sequencher v4.10.1 (Gen Codes, Co) for possible double peaks, stop codons or indels, which would indicate the presence of paralogs. Two identical sequences (GB MG194442) presented such anomalies and were excluded from further analyses. The remaining sequences were assumed to be the functional mitochondrial gene and alignments were straightforward. Fragments shorter than the target length were also completed by Ns to replace missing data.

To extend genetic comparisons to the extensive dataset of DNA sequences publicly available the Barcode of Life Data system version 3.0 (Ratnasingham & Hebert 2007), we also sequenced a subset of the same specimens for the Cytochrome C oxidase subunit I gene (COI; Appendix B). Part of this gene was obtained using the primer pair

UTyr (5'-ACCYCTGTCYTTAGATTTACAGTC-3') and C1L705 (5'-ACTTCDGGGTGNCCRAARAATCA-3') published by Hassanin *et al.* (2012). Except for a slightly distinct cycling program (5 cycles at 60° annealing temperature, followed by 32 cycles at 55°), the same procedure as for the Cyt *b* gene was used to generate a fragment of about 700 bp of the COI.

Phylogenetic analyses

In addition to the sequences of Cyt *b* we generated for this paper, we downloaded from the GenBank and aligned a set of representative *Kerivoula* lineages from Southeast Asia published by Khan *et al.* (2010), 2 sequences (JN112244 and JN112246) assigned to *K. titania* by Wu *et al.* (2012) and subsequently reassigned to *K. furva* by Tu *et al.* (2018), and one unpublished sequence of *K. pellucida* (AB444717; Bastian Jr, S.T., Malcampo, R.A., Yamagata, T. & Namikawa, T.) from the Philippines (Appendix B). We noticed that a series of sequences of *K. intermedia* (EU188789–188791) are wrongly labelled as *K. whiteheadi* in the GenBank, while a series of *K. minuta* (EU188774–188778) are wrongly labelled as *K. intermedia*. As both series are correctly referenced in the Appendix I of Khan *et al.* (2010), we follow this original publication to label representatives of these lineages (see Appendix B).

Methods used to reconstruct phylogenetic trees included the Maximum Likelihood (ML) approach implemented in iQ-Tree (Nguyen *et al.* 2015) and Bayesian inferences (BI) in MrBayes v3.2.0 (Ronquist & Huelsenbeck 2003). All analyses were done on a fully partitioned model, where each codon partition was allowed to have partition-specific model parameters. The most appropriate model of nucleotide substitution for each partition was evaluated using MrModeltest 2.3 (Nylander 2004) and the Akaike Information Criterion (AIC). The General Time Reversible (GTR) model with rate variation among sites (G) represent the best fit model of nucleotide substitution for the first positions, HKY (Hasegawa *et al.* 1985) with a proportion of invariable sites (I) model for the second positions and GTR + G + I model for the third positions. Tree searches were initiated from random trees.

Bayesian analyses were performed with MCMC chains run for 10 million generations, with a sampling every 1000 generations. The chains were checked for convergence and appropriate effective sample size (ESS>200) with TRACER v.1.5 (Rambaut & Drummond 2009). The initial 10% of sampled trees were discarded as burn-in. Posterior probabilities (PP) were subsequently computed from the consensus of the remaining trees. Reliability of nodes in the ML analyses was assessed by 1000 Ultrafast bootstraps (BP) with iQ-TREE (Hoang *et al.* 2018).

Molecular dating analyses

We estimated the mean divergence times between taxa by a relaxed uncorrelated lognormal molecular clock as implemented in BEAST v1.7.4 (Drummond & Rambaut 2007). Similar to the MrBayes analyses, we used the Cyt *b* dataset partitioned into 3 categories with the most appropriate model of nucleotide substitution for each codon partition determined with MrModeltest. Tree searches started from a random tree and assumed a constant lineage birth rate for each branch (Yule tree prior; Drummond *et al.* 2006). All other parameters were kept at default values. Markov Chains Monte Carlo (MCMC) were sampled every 1000 generations over 10 million generations, with a burn-in of 10%. Kerivoulinae-like fossils have been recorded in various parts of the Northern Hemisphere (Horácek 2001; Gunnell *et al.* 2012), but their precise phylogenetic position within the Vespertilionidae radiation is very contentious and cannot serve to calibrate precise nodes in modern phylogenies. Instead, as the Myotinae are closely related to the Kerivoulinae (e.g., Kawai *et al.* 2002; Hoofer & Van den Bussche 2003), we used two fossil-calibrated nodes of the former radiation as a secondary calibration for the *Kerivoula* divergence. For this purpose, we included as additional outgroups in the BEAST analysis sequences of *Myotis daubentonii*, *M. bechsteinii*, and *Submyotodon latirostris* (see Appendix B) and placed the following temporal constraints on two nodes, as minimum and maximum soft bounds (Ruedi *et al.* 2013). The first calibration point was the split of *M. daubentonii* and *M. bechsteinii*, estimated to have diverged between 5 MYA (Topál 1983) and 11.6 MYA. We used an exponential prior distribution (offset 5.0, mean 2.5) to encapsulate this calibration in the 95% CI. The second calibration concerned the most recent common ancestor of Myotinae, which diverged some 20-31 MYA, with an associated lognormal prior distribution to this basal node (offset 20.0, S.D. 1.6).

Genetic distances between lineages were also estimated with the Kimura two parameter model implemented in MEGA (Tamura *et al.* 2013) to assess their distinctness and for comparisons with values given for population- or species-level differentiation in bats (Bradley & Baker 2001; Khan *et al.* 2010). To aid species comparisons based on barcodes, we submitted our COI sequences to the BOLD system to obtain a Barcode Index Number (BIN, Ratnasingham & Hebert 2013).

Echolocation call analysis

We recorded echolocation calls from 21 individuals—5 *K. pellucida* and 16 *K. whiteheadi*—from free-flying bats in either a small tent (1.2 m height, 2 m length, 2 m width), a mobile flight cage (3 x 3 x 2 m), or a small room (approx. 4 x 4 x 2.5 m). Calls were recorded using an Ultrasoundgate 116 (Avisoft Bioacoustics, Inc.) detector with a sampling rate of 500 kHz and stored onto a laptop computer. Sound analysis was conducted in SASLabPro (version 5.2.12, Avisoft Bioacoustics, Inc.). Measurements were taken from a spectrogram generated with a fast Fourier transform (FFT) length of 256 kHz and a Hann window. This resulted in a frequency resolution of 1.9 kHz and a time resolution of 0.02 ms. To improve visualization we used a 96% temporal overlap and enlarged the spectrogram by two. For each individual call, the automatic measurement function was used to measure the duration, start frequency, and terminal frequency at -25 dB from peak amplitude. Peak frequency was measured as the frequency with the highest energy across the entire call. Bandwidth was calculated as the start minus the terminal frequency. All measurements were taken on the first harmonic. We measured up to 10 calls from each individual and calculated the mean peak frequency and duration, the maximum bandwidth and start frequency, and the minimum terminal frequency for each individual. These values were used in subsequent summary statistics by species. We tested for differences between species for each measurement using Welch's t-test in R (R Development Core Team 2018).

Results

Molecular phylogeny

We obtained mitochondrial Cyt *b* sequence data from all four species currently recognized from the Philippines. In this study, we include individuals of *K. pellucida* and *K. whiteheadi* from all localities from which we have specimens, and representatives of other known and suspected Philippine species, plus representatives of four species that occur in countries adjacent to the Philippines. Detailed assessments of specimens and species limits in the *K. hardwickii* and *K. papillosa* groups will be presented in a later publication. The new Cyt *b* sequences generated in this study are deposited in the Genbank (MG194437–MG194468).

All phylogenetic analyses of these data (Fig.1; Appendix B) strongly support the monophyly of *K. pellucida* and *K. whiteheadi*, and further show both as members of a well-supported (BP and PP >0.99), high-level clade within the genus. Hereafter, we refer to both of these lineages as belonging to the *K. pellucida* species group. Our assessment of variation within these two species is given below. A previous study of Malaysian *Kerivoula* found *K. pellucida* to be basal among the 7 species included (*K. whiteheadi* was not represented; Khan *et al.* 2010).

Our analyses identified *K. lenis* and *K. papillosa* as members of a second well-supported (BP 0.94 and PP 1.0), high-level clade, as did Khan *et al.* (2010), who also reported evidence of a third, undescribed species from Sarawak (Malaysia) within this clade; we refer to this clade below as the *K. papillosa* species group. We note that our specimens from the Philippines tentatively referred to *K. papillosa* are members of a clade (**K** in Fig. 1) with the taxon that Khan *et al.* (2010) considered to represent the undescribed species (sequence stored in the GenBank with number GU585651). A specimen from Sarawak, Borneo that Khan *et al.* (2010) considered to represent *K. papillosa* (**L**) is sister to *K. lenis* (**M**).

Finally, there is a third high-level clade that includes *K. intermedia*, *K. minuta*, *K. furva* (see Tu *et al.* 2018), and various individuals considered to represent *K. hardwickii* including five from the Philippines. Hereafter, we refer to this as the *K. hardwickii* species group. In these analyses, there is strong support (BP 94and PP 1.0) for *K. intermedia* (**J** in Fig. 1), from the Malay Peninsula and Borneo, as basal to all other species in the clade. The phylogenetic position of *K. minuta* (**I**), also from the Malay Peninsula, is ambiguous (BP = 0.76). There is strong support (BP 0.91 and PP 1.0) for *K. furva* (**H**) from Taiwan and Hainan (Bates *et al.* 2007; Tu *et al.* 2018) and *K. hardwickii* (**G**), which occurs widely from Myanmar to the Philippines and the Lesser Sunda Islands (Bates & Harrison 1997; Simmons 2005; Tu *et al.* 2018), as sister-taxa. Within the *K. hardwickii* clade (**G**), there are two well-supported groups—one from the Philippines (BP 0.99 and PP 1.0) and the other from Borneo (BP 0.98 and PP 0.9). Finally, there are two distinct lineages of *K. hardwickii* within the Philippines (one from Mindanao and one from Bohol).

Within *K. pellucida*, our specimens from Bohol and Mindanao, which are in the southern Philippines and were part of the Late Pleistocene island of Greater Mindanao (Heaney 1985), are part of a well-supported clade (BP 0.92 and PP 1.0; **A** in Fig. 1) within which branch lengths are short (mean K2P genetic distance 2.3%). Previously published data from *K. pellucida* from the Malay Peninsula and northern Borneo (Khan *et al.* 2010) show them to form a moderately well supported clade (BP 0.92 and PP 0.97, **B**) that differs from the Philippine clade by 5.6%.

TABLE 1. Mean (± standard deviation) and range of cranial-dental measurements of adult *K. whiteheadi* and *K. pellucida*, and comparison groups. Holotypes indicated with an asterisk. n = sample size

Taxon Locality	n	GTL	CCL	GBB	BH	PC	C–M^3	M^2–M^{2ext}	C^1–C^1	C–M$_3$	MDL
K. whiteheadi											
Camiguin Norte		14.61	13.66	7.14	6.09	3.26	5.94	5.11	1.93	6.32	11.24
Luzon											
N. Luzon	4	13.80 ± 0.30	12.11 ± 0.24	7.04 ± 0.17	5.69 ± 0.25	3.12 ± 0.09	5.63 ± 0.07	4.80 ± 0.09	1.74 ± 0.14	5.95 ± 0.15	10.42 ±0.23 (2)
		13.54–14.13	11.88–12.32	6.86–7.26	5.43–5.94	3.03–3.22	5.53–5.68	4.74–4.93	1.60–1.92	5.74–6.10	10.26–10.58
Mt. Irid		13.50	11.80	6.91	5.25	2.96	5.46	4.61	1.67	5.81	
Mt. Makiling	4	13.66 ± 0.24	12.10 ± 0.28	6.84 ± 0.10	5.72 ±0.06	2.97 ± 0.10	5.57 ±0.15	4.73 ± 0.06	1.78 ± 0.13	5.91 ±0.16	10.31 ± 0.39 (3)
		13.35–13.94	11.75–12.36	6.72–6.95	5.64–5.76	2.85–3.10	5.42–5.77	4.65–4.78	1.60–1.88	5.77–6.14	10.04–10.75
Mt. Banahaw	8	13.71 ± 0.13	12.31 ± 0.13	6.80 ± 0.18	5.79 ± 0.12	2.99 ± 0.11	5.58 ± 0.12	4.75 ± 0.15	1.62 ± 0.19	5.96 ± 0.17	10.35 ± 0.13
		13.52–13.93	12.08–12.43	6.52–6.97	5.64–6.04	2.80–3.09	5.42–5.76	4.54–4.99	1.26–1.79	5.70–6.20	10.18–10.51
Mt. Isarog	5	13.47 ± 0.25	12.03 ± 0.16	6.76 ± 0.16	5.59 ± 0.07	3.01 ± 0.07	5.48 ± 0.07	4.66 ± 0.07	1.81 ±0.13	5.83 ± 0.09	10.30 ± 0.15 (4)
		13.20–13.86	11.87–12.24	6.53–6.95	5.49–5.67	2.94–3.10	5.40–5.55	4.57–4.77	1.63–1.93	5.76–5.99	10.15–10.48
Lubang	1	14.00	12.69	7.11	5.93	3.05	5.68	4.76	1.60	5.94	
Mindoro	6	13.82 ± 0.33	12.35 ± 0.24	6.91 ± 0.18	5.94 ± 0.17	2.94 ± 0.05	5.71 ± 0.06	4.70 ± 0.25	1.94 ± 0.08	6.04 ± 0.10	10.39 ± 0.21 (5)
		13.50–14.24	12.05–12.67	6.70–7.19	5.80–6.25	2.87–2.99	5.64–5.78	4.37–4.93	1.81–2.01	5.93–6.19	10.09–10.57
Sicogon- Tumaguin	2	13.33 ± 0.10	11.72 ± 0.06	6.53 ± 0.03	5.44 ± 0.09	3.04 ± 0.12	5.47 ± 0.02	4.76 ± 0.04	1.78 ± 0.09	5.84 ± 0.04	10.4 (1)
		13.23–13.42	11.66–11.78	6.50–6.55	5.35–5.53	2.92–3.16	5.45–5.48	4.72–4.79	1.69–1.86	5.80–5.88	
Bohol	2	13.01 ± 0.33	11.72 ± 0.32	6.79 ±0.13	5.46 ± 0.06	2.96 ± 0.14	5.28 ± 0.01	4.50 ± 0.16	1.77 ± 0.01	5.59 ± 0.14	9.66 ± 0.01
		12.78–13.24	11.49–11.94	6.69–6.88	5.42–5.50	5.27–5.29	5.27–5.29	4.38–4.61	1.76–1.78	5.49–5.69	9.65–9.66
Cebu	6	13.11 ± 0.19	11.67 ± 0.20	6.65 ± 0.09	5.53 ± 0.08	2.93 ± 0.08	5.34 ± 0.17	4.62 ± 0.09	1.84 ± 0.02	5.68 ± 0.07	9.79 ± 0.28
		12.82–13.30	11.31–11.94	6.55–6.83	5.42–5.64	2.77–3.02	5.03–5.61	4.51–4.80	1.80–1.87	5.59–5.80	9.51–10.28
Siquijor	5	13.45 ± 0.32	11.97 ± 0.11	6.70 ± 0.02	5.63 ± 0.19	3.11 ± 0.06	5.54 ± 0.10	4.69 ± 0.05	1.64 ± 0.14	5.92 ± 0.09	9.95 ± 0.04 (4)
		13.13–13.89	11.84–12.13	6.66–6.73	5.40–5.58	3.04–3.18	5.40–5.66	4.60–4.74	1.48–1.81	5.82–6.05	9.91–9.99
Mindanao	6	12.53 ± 0.26	11.24 ± 0.26	6.58 ± 0.12	5.33 ± 0.13	3.05 ± 0.10	5.11 ± 0.17	4.43 ± 0.11	1.61 ± 0.17	5.47 ± 0.15	9.57 ± 0.15 (5)
		12.16–12.93	11.08–11.77	6.42–6.70	5.15–5.56	2.92–3.18	4.89–5.33	4.31–4.53	1.34–1.78	5.23–5.63	9.22–10.04

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TABLE 1. (Continued)

Taxon Locality	n	GTL	CCL	GBB	BH	PC	$C–M^3$	$M^2–M^{2ext}$	$C^1–C^1$	$C–M_3$	MDL
*K. pusilla bicolor**		13.47		5.48	4.74	2.81	5.19	4.4	1.62		8.8
*K. p. pusilla**			11.39	5.86	4.96	2.78	5.01	4.49	1.43	5.27	8.66
*K. whiteheadi**										5.94	9.55
K. pellucida											
Bohol	12	14.40 ± 0.26 14.06–15.00	13.17 ± 0.19 12.75–13.44	7.29 ± 0.11 7.14–7.55	6.01 ± 0.13 5.80–6.23	3.07 ± 0.05 2.98–3.15	5.85 ± 0.12 5.63–6.02	5.02 ± 0.09 4.92–5.19	1.80 ± 0.04 1.71–1.86	6.27 ± 0.13 6.05–6.50	10.57 ± 0.35 10.19–11.12
Cebu	1	14.66	13.39	7.50	5.60	3.08	5.95	5.12	1.95	6.37	10.83
Mindanao	4	14.53 ± 0.51 13.82–15.03	13.11 ± 0.21 12.82–13.27	7.08 ± 0.05 7.04–7.15	5.93 ± 0.28 5.69–6.33	3.10 ± 0.06 3.02–3.15	5.91 ± 0.14 5.73–6.05	5.03 ± 0.12 4.88–5.16	1.72 ± 0.09 1.62–1.82	6.31 ± 0.12 6.13–6.38	10.85 ± 0.32 10.40–11.16
Palawan	2	14.41 ± 0.07 14.36–14.46	13.02 ± 0.23 12.86–13.18	7.19 ± 0.18 7.06–7.31	5.81 ± 0.04 5.78–5.83	3.12 ±0.05 3.08–3.15	5.70 0.01 5.69–5.71	5.04 ± 0.13 4.94–5.13	1.81 ± 0.01 1.80–1.81	6.11 ± 0.00	10.95 ± 0.18 10.82–11.08
Borneo	1	13.78	12.14	7.07	5.74	2.97	5.37	4.59	1.68	5.39	9.51
P. Malaysia	5	14.27 ± 0.24 (4) 14.00–14.58	12.52 ± 0.19 12.23–12.72	7.11 ± 0.17 6.96–7.30	5.74 ± 0.11 5.64–5.90	3.09 ± 0.09 2.94–3.18	5.58 ± 0.06 5.50–5.66	4.94 ± 0.11 4.79–5.07	1.83 ± 0.10 1.73–1.98	5.85 ± 0.13 (4) 5.73–6.03	9.80 ± 0.12 (4) 9.64–9.93
*K. pellucida**			13.31	7.18	5.95	3.11	5.26	4.98	1.75	6.22	10.22

There are no published sequence data from *K. whiteheadi* from Borneo (*K. w. pusilla*) or the Malay Peninsula (*K. w. bicolor*). We have been unable to locate specimens from the Malay Peninsula that have been obtained since the original description of *K. w. bicolor* (Thomas 1904; Corbet & Hill 1992; Francis 2008). Since the description of *K. w. pusilla*, several records have been reported from Sabah and Sarawak (Thomas 1894; Medway 1977; Payne *et al.* 1985; Corbet & Hill 1992), and we examined the holotype, as described below, but no suitable tissues or genetic sequences are available. Within the Philippines, three somewhat distinctive clades are evident. Clade **C** (BP 0.96 and PP 1.0) includes specimens from northern Luzon, Lubang, Mindoro, and Camiguin Norte islands (Figs. 1, 2). Branch lengths within this clade are short (mean K2P 1.6%), but differ considerably from the next clades (> 9.0% K2P). FMNH 206007 was captured in Peñablanca Municipality, Cagayan Province, about 75 km north of the type locality of *K. whiteheadi*, and FMNH 190762 about 115 km southwest of the type locality (M. van Weerd, pers. com); since these localities bracket the type locality, we consider clade **C** to represent the nominate form. Clade **D** includes specimens from central and southern Luzon Island, and clade **E** from Cebu and Siquijor islands in the central Philippines; these clades appear to be sister-taxa (BP 0.68 and PP 1.0) and differ from each other by only 4.6%. Clade **F** (BP 0.96 and PP 1.0) is represented by specimens from Bohol and Mindanao islands, both of which were part of Late Pleistocene Greater Mindanao (Figs. 1, 2), and branch lengths between them are substantial (9.5% K2P).

Craniodental Metric Analysis

Species-level taxonomy of *Kerivoula* has traditionally emphasized pelage characters and qualitative assessment of cranial shape and dental features. We based our initial identifications on these features following Hill (1965), Corbet & Hill (1992), and Ingle & Heaney (1992), and summarize them in the species accounts that follow.

A principal components analysis (PCA) of craniodental measurements of *Kerivoula* found in the Philippines, plus representatives of additional species from Borneo and mainland Southeast Asia (Table 2), showed that 83% of the variation was explained by the first axis, with an eigenvalue of 5.81 (Table 2). All variables loaded at 0.84 or higher, with condylo-canine length (CCL) loading most strongly at 0.97. The second axis showed low loadings for all measurements, with braincase height loaded most heavily at -0.45; but this axis had an eigenvalue of 0.59, which is below the minimum of 1.0 for an axis to be interpretable. These results show that the great majority of the variation in our total sample was associated with a generalized size axis (83%), with the implication that braincase height (BH) and post-orbital constriction (PC) supplied much of the variation that was not correlated with size.

TABLE 2. Results of principle components analysis of craniodental measurements given in Table 1; see methods for measurement descriptions.

Variable	PC1	PC2
CCL	0.970	-0.084
GBB	0.955	0.086
BH	0.845	-0.447
PC	0.849	0.432
$C–M^3$	0.921	-0.272
$M^2–M^{2ext}$	0.960	0.072
$C^1–C^1$	0.869	0.222
Proportion variance	0.83	0.07
Eigen value	5.81	0.53

Although the eigenvalues preclude use of the second axis, and therefore preclude a plot of the scores of individuals on the first vs. the second axis, the results of the PCA indicate that a bivariate plot of condylo-canine length (CCL) vs. braincase height (BH) would represent much of the variation that is present. In a plot of these variables (Fig. 3; Tables 1, 3), specimens referred to as *K. papillosa* from the Philippines, Borneo and Vietnam are the largest, overlap substantially, and are widely separated from all other specimens. Two reference samples of *K. minuta*, one

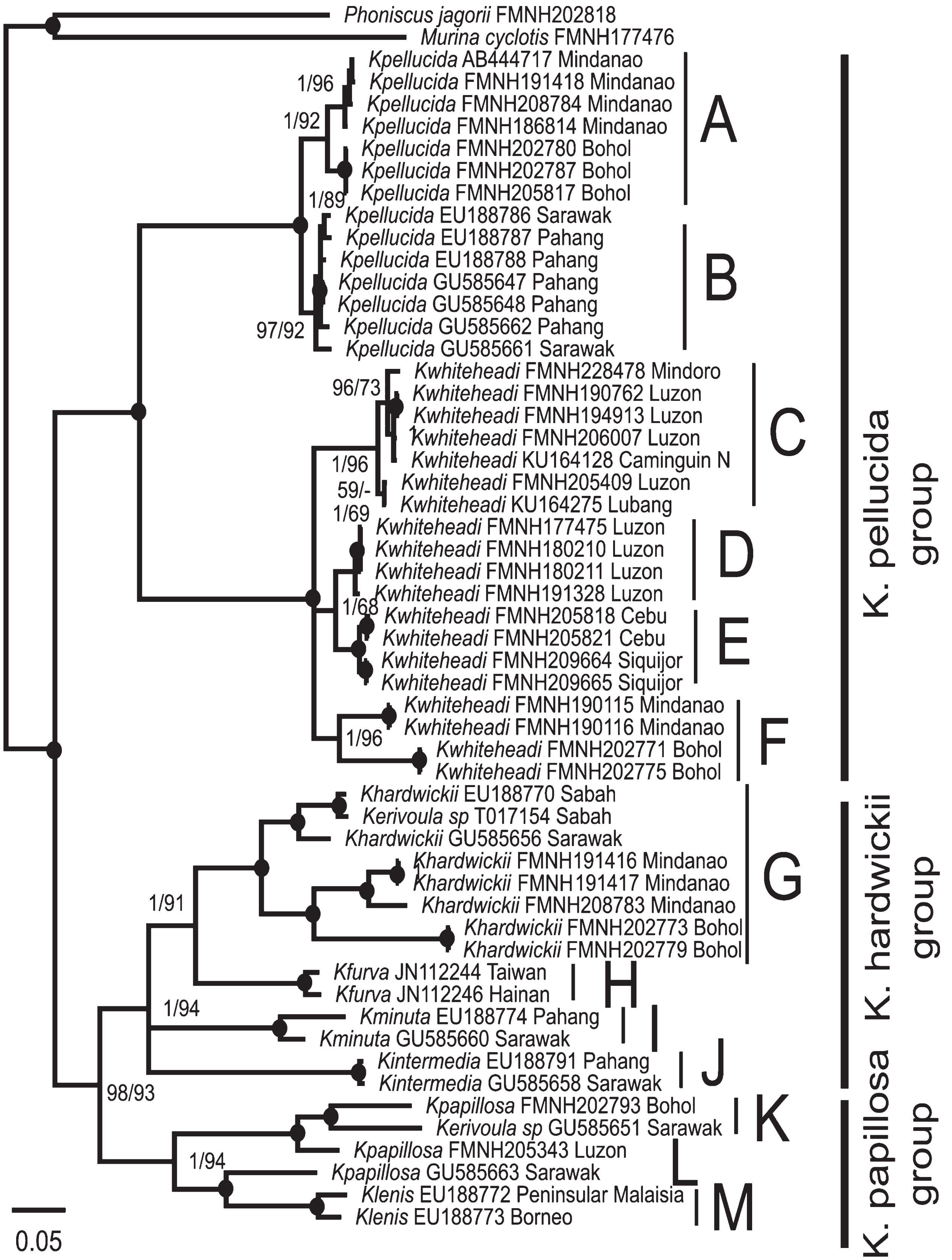

FIGURE 1. Phylogenetic relationships of East Asian *Kerivoula* and two outgroup species based on Cyt *b* haplotypes. This topology results from a Bayesian analysis. Numbers at each node correspond to the Bayesian posterior probabilities (left) and to the proportion of bootstrap support of a maximum likelihood reconstruction (right). If both analyses supported a node by 98% or more support, this node is symbolized with a plain circle. The letters to the right of each clade refer to the groups discussed in the text. The scale bar corresponds to a branch length of 0.05 substitution per site.

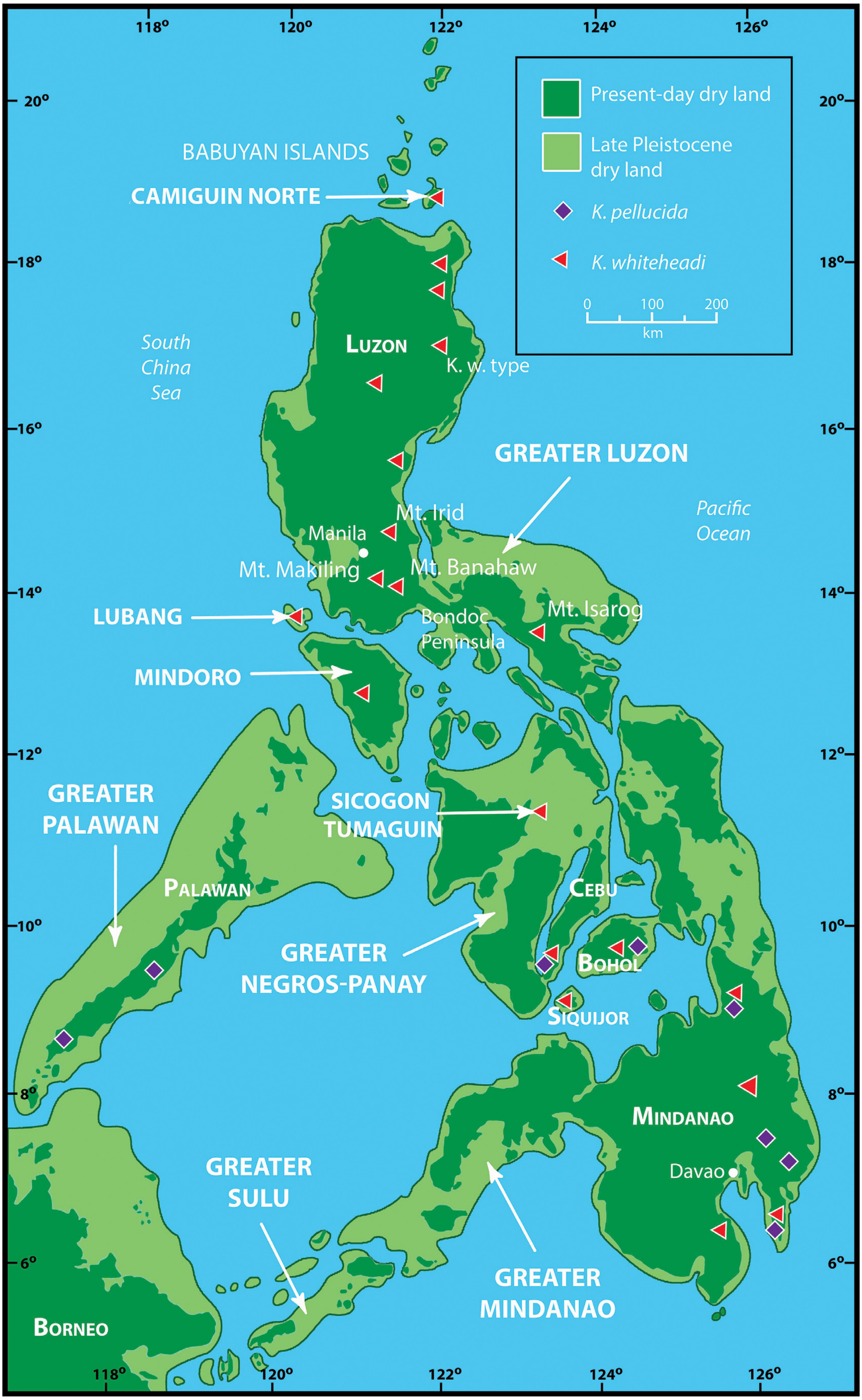

FIGURE 2. Map of the Philippines indicating the collecting localities of *Kerivoula pellucida* and *K. whiteheadi*. The land exposed during the Pleistocene Last Glacial Maximum is shown in light green.

from Sabah (BMNH 84.2042) and one from Peninsular Mayalsia (FMNH 110752), are the smallest animals. The holotypes of *K. intermedia* and *K. pusilla* have similar and slightly greater CCL than *K. minuta*, with the latter two distinguished by *K. pusilla* having a higher braincase. Specimens referred to *K. "hardwickii* A*"* from the Philippines and Sulawesi overlap in condylo-canine length with *K. intermedia* and *K. pusilla*, but have higher braincases. Specimens of *K. hardwickii* from the mainland, including the Malay Peninsula, Cambodia, Myanmar, and Vietnam, (labelled "mainland" in Fig. 3) differ from *K. hardwickii* from Sulawesi and K. "*hardwickii* A" from the Philippines in averaging greater in CCL and lower BH. Specimens of *K. hardwickii* from Borneo fall between specimens from the mainland and the Philippines. Some *K.* "*hardwickii* A" specimens from eastern Mindanao, Philippines overlap on these two dimensions with *K. pellucida* from the Philippines and some *K. hardwickii* from the mainland, but differ from other Philippine *K.* "*hardwickii* A" in having a greater CCL. Specimens we have designated *K.* "*hardwickii* B" from the Philippines overlap in CCL with mainland and Borneo *K. hardwickii*, but have longer CCL than Philippine *K.* "*hardwickii* A". We will deal with Philippine *Kerivoula hardwickii* and *K. papillosa* in a subsequent publication.

In this bivariate comparison, our large sample of *K. whiteheadi* from throughout the Philippines forms a large cloud of points with no immediately apparent geographic structure (Figs. 2, 3). This sample of *K. whiteheadi* from the Philippines overlaps widely on these axes with *K.* "*hardwickii* A" from the Philippines and a single specimen from Sulawesi, and overlap to a limited amount with those from Borneo. However, Philippine *K. whiteheadi* have a consistently shorter CCL than *K.* "*hardwickii* B" from the Philippines. Philippine *K. whiteheadi* specimens do not overlap with *K. hardwickii* from mainland Southeast Asia, mainland differing in having a lower braincase (Fig. 3). Specimens of *K. pellucida* from the mainland overlap with *K. whiteheadi* from the Philippines in braincase height, but *K. pellucida* from the Philippines consistently have greater condylo-canine length than *K. whiteheadi.* Several specimens of *K. titania* have greater condylo-canine length than any of these samples of *Kerivoula*, with the exception of *K. papillosa*. Finally, our sample of Philippine *K. pellucida* specimens have a greater condylo-canine length than mainland specimens and the single specimen from Borneo, but have similar braincase height (Fig. 3; Table 1).

The status of *K. bicolor* and *K. pusilla*

Two taxa originally named as distinct species, *K. bicolor* Thomas 1904 and *K. pusilla* Thomas 1894, were considered by Hill (1965) to represent subspecies of *K. whiteheadi*, and have been provisionally dealt with in that fashion subsequently (e.g., Corbet & Hill 1992; Francis 2008). At the time, Hill (1965) had only the holotype of *K. whiteheadi* from Luzon, a badly damaged specimen, for comparison with *K. bicolor*, also represented only by the holotype, and with *K. pusilla*, represented by two specimens. He also noted two specimens referred to as *K. pusilla* by Sanborn (1952), which he did not examine. We know of no specimens of *K. bicolor* collected since the holotype, and only a few *K. pusilla* have been reported from Borneo (Phillipps & Phillipps 2016), but we have obtained large numbers of *K. whiteheadi* from the Philippines that allow some morphological assessment of the distinctiveness of these three taxa.

As shown in Figure 3, a plot of condylo-canine length vs. braincase height of specimens of *K. whiteheadi* from the Philippines form a cloud of points that represents the range of variation in the nominate form. The two specimens referred to *K. pusilla* by Sanborn (FMNH 56687 and 61077) have the shortest condylo-canine length of our Philippine sample, but they fall within the range of other specimens from Mindanao and within the cloud of Philippines points overall. Our measurements of the holotype of *K. pusilla* from Borneo show it to be similar in condylo-canine length, but with a notably lower braincase height, well below that of any Philippine specimen (Fig. 3; Tables 1, 3). Additionally, our examination of the cranium of the holotype showed it to have unusually large cochlea, as described by Thomas (1894) and confirmed by Hill (1965). While the cochlea of *K whiteheadi* is large (Fig. 6), the *K. pusilla* holotype's cochlea (from a photograph we took) is proportionately substantially larger. Given the difference in braincase height and cochlea size in comparison to our large sample, we recommend that *K. pusilla* not be treated as a subspecies of *K. whiteheadi*.

We also examined the holotype (and only known specimen) of *K. bicolor*. The cranium is badly damaged, and we were unable to measure the condylo-canine length. Further, the cochlea were not present for comparison. However, the braincase height (4.74 mm) is well below the range shown by *K. whiteheadi* (Fig. 3; Table 1). Given the comment by Hill (1965:531) that "both [*K. bicolor* and *K. pusilla*] have greatly expanded cochlea", and that *K. w. bicolor* "closely resembles *K. w. pusilla*, differing … only in its white-tipped wings, white and not grayish underparts, slightly narrower rostrum and slightly less pronounced rostral sulcus … [which] seem only of subspecific importance", we provisionally conclude that these should not be considered conspecific with *K. whiteheadi*, and can be treated as subspecies of a single species, *K. p. pusilla* and *K. p. bicolor*, until further specimens are available for more detailed study.

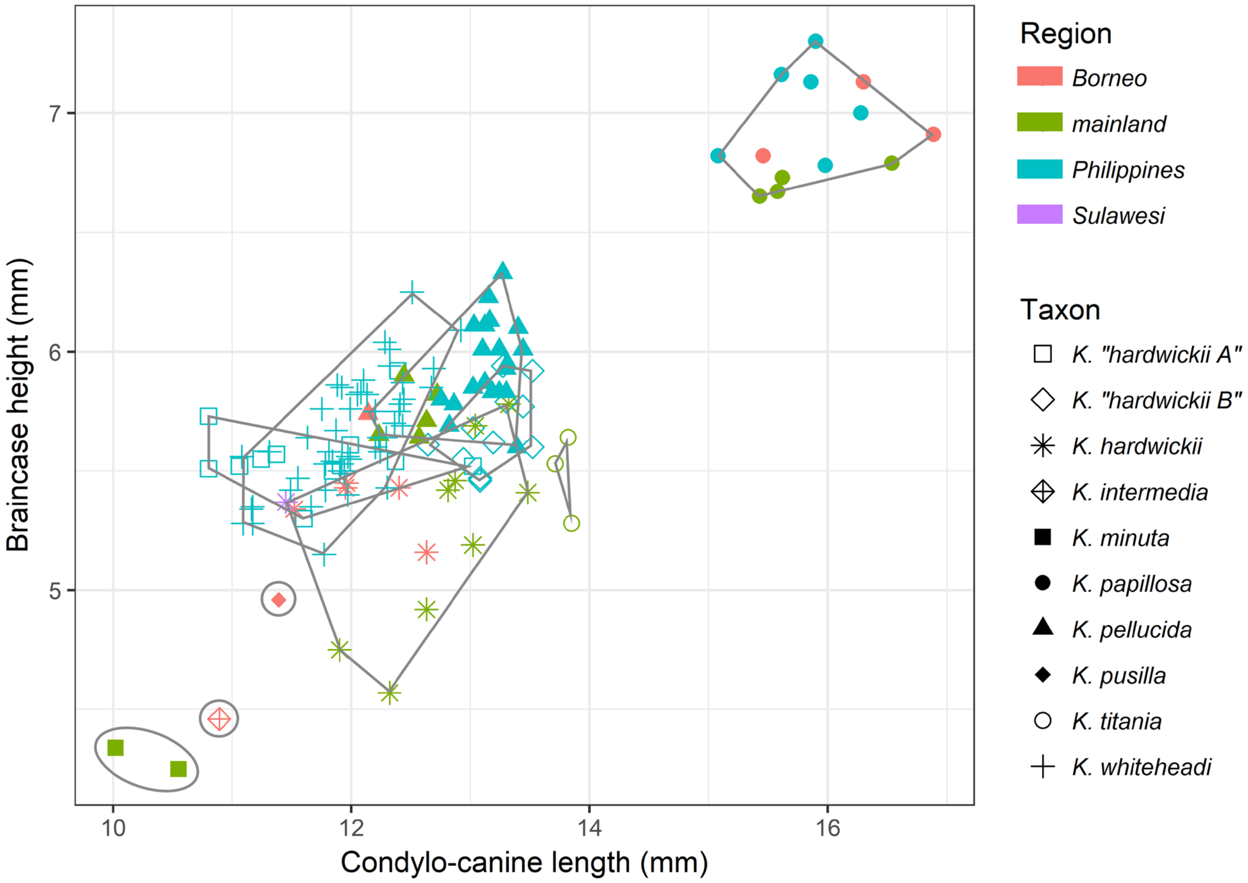

FIGURE 3. Bivariate plot of condylo-canine length vs. height of braincase for specimens of *Kerivoula* summarized in Tables 1 and 3. Color indicates geographic region and symbol indicates taxon. Philippine specimens of each taxon are enclosed within polygons.

Biogeography and diversification

Our time-calibrated phylogenetic tree of Cyt *b* sequences obtained with BEAST has implications for the timing and geography of diversification of *Kerivoula* in the Philippines and adjacent areas (Fig. 4). As noted above, support for many nodes is strong, but confidence limits (i.e. 95% HPD intervals) on the timing of most nodes are broad, so that caution is warranted. All mention of dates that follow are given as the average; these should be viewed as rough estimates, plus or minus about 30%, with the confidence limits shown in Fig. 4.

The genus *Kerivoula* is here estimated to have diverged from *Phoniscus*, its sister-genus, about 27 million years ago (MYA; Fig. 4). The initial split between the *K. pellucida* species group (A–F) and all other species took place about 25 MYA, and the split between the *K. papillosa* species group (K–M) and the *K. hardwickii* species group (G–J) about 21 MYA. Thus, initial diversity within *Kerivoula* in Southeast Asia appears to have been well established by more than about 20 MYA.

Diversification within the species groups has been more recent. *K. pellucida* (**A**–**B**) and *K. whiteheadi* (**C**–**F**) last shared a common ancestor about 18 MYA, but diversification within these species (as currently defined) began about 3.7 MYA and 7.1 MYA, respectively. Members of the *K. papillosa* group (**K**–**M**) last shared a common ancestor about 15.3 MYA, but most species have diverged within the last 10 MYA (Fig. 4). Members of the *K. hardwickii* species group (**G**–**J**) last shared a common ancestor about 17.2 MYA, with subsequent diversification.

We note that most diversification within the Philippines is relatively recent. *Kerivoula pellucida* in the Philippines diverged from their Sunda Shelf conspecifics about 3.7 MYA, but divergence within the Philippines (clade **A**) appears to have begun only about 2.0 MYA. Populations referred to *K. whiteheadi* last shared a common ancestor about 7.1 MYA, and have formed geographically cohesive clades (**C**, **D**, **E**, and **F**) subsequently, with specimens from northern Luzon, Camiguin Norte, Lubang, and Mindoro (**C**) sharing a common ancestor about 1.4 MYA. The oldest clade that includes *K. papillosa* in the Philippines diverged about 7.0 MYA, but this includes a specimen from Sarawak, which makes the interpretation of diversification within the Philippines ambiguous. Finally, Philippine populations of *K. hardwickii* (G') diverged from their Sunda Shelf relatives (G") by about 9.6 MYA, the oldest of the implied colonizations of the Philippines by *Kerivoula*.

These data imply that *Kerivoula* arrived in the Philippines by about 10 MYA. *Kerivoula whiteheadi* occurs throughout the entire Philippines (Esselstyn *et al.* 2004; Heaney *et al.* 2010; Fig 2). However, *K. pellucida* occurs only on Greater Mindanao, Greater Negros-Panay, and Greater Palawan; *K. hardwickii* only occurs in Greater Mindanao and Greater Palawan; *K. papillosa* only occurs in Greater Luzon and Greater Mindanao (Fig. 2). Thus, only one of the four species is widespread within the Philippine archipelago, and it (*K. whiteheadi*) exhibits only a moderate level of incipient speciation that began about 7 MYA.

However, our genetic data (Figs. 1, 4) indicate the presence of two distinct clades within the Philippine *K. hardwickii* lineage that are morphologically distinct, and our morphological data (Fig. 3; Table 3) show that both occur on Mindanao (Appendix A). We take this as tentative evidence of speciation in *Kerivoula* within the archipelago that has progressed to the point of secondary sympatry. This requires further study, but suggests that although in places where more than one species of *Kerivoula* is present, each is usually the product of a separate colonization from other regions in Southeast Asia. Where divergence dates among sympatric taxa are deeper, in the case of the *K. hardwickii* group, some full diversification within the archipelago may have taken place, in this oldest of the Philippine lineages.

TABLE 3. Mean (± standard deviation) and range of condylo-canine length (CCL) and braincase height (BH) for those specimens not included in Table 1. n = sample size.

Taxon Locality	n	CCL	BH
K. hardwickii			
Borneo	5	12.09 ± 0.43 11.52–12.63	5.36 ± 0.12 5.16–5.45
mainland	15	12.60 ± 0.47 11.90–13.48	5.11 ± 0.36 4.57–5.78
Sulawesi	1	11.45	5.37
K. "*hardwickii* A"			
Philippines	9	11.45 ± 0.54 10.80–12.37	5.54 ± 0.10 5.34–5.54
K. "hardwickii B"			
Philippines	12	13.17 ± 0.26 12.64–13.52	5.66 ± 0.16 5.46–5.94
K intermedia			
Borneo	1	10.89	4.46
K. minuta			
Borneo	1	10.02	4.34
mainland	1	10.55	4.25
K. papillosa			
Borneo	1	16.89	6.91
mainland	6	15.82 ± 0.47 15.43–16.54	6.79 ±0.17 6.65–7.13
Philippines	6	15.79 ± 0.41 15.08–16.28	7.03 ± 0.20 6.78–7.30
K. titania			
mainland	3	13.79 ± 0.07 13.71–13.85	5.48 ± 0.18 5.28–5.64

Finally, we note that *K. whiteheadi* from southern Luzon (clade **D**) are more closely related to specimens from the central Philippines (clade **E**) than they are to those from central and northern Luzon and adjacent islands (clade **C**; Fig. 4). Although it is initially surprising that all populations from Luzon are not monophyletic, the geological history of the Philippines is consistent with this. The estimated divergence date of 5.8 MYA for clades **D** and **E** from clade **C** reflects the fact that southern Luzon (the area represented by clade **D**) was a distinct island that first arose about 6.6 MYA. However, this island did not become connected to central and northern Luzon until roughly 0.5 MYA when the Bondoc Peninsula and adjacent areas were uplifted (Aurelio *et al.* 1991; Heaney *et al.* 2016:49-50; Fig. 2). Thus, the sister-group relationship of clades **D** and **E** appears to reflect the prior history of southern Luzon and Greater Negros-Panay (including Cebu) as two separate but nearby islands at the time of this phylogenetic split, 5.8 MYA.

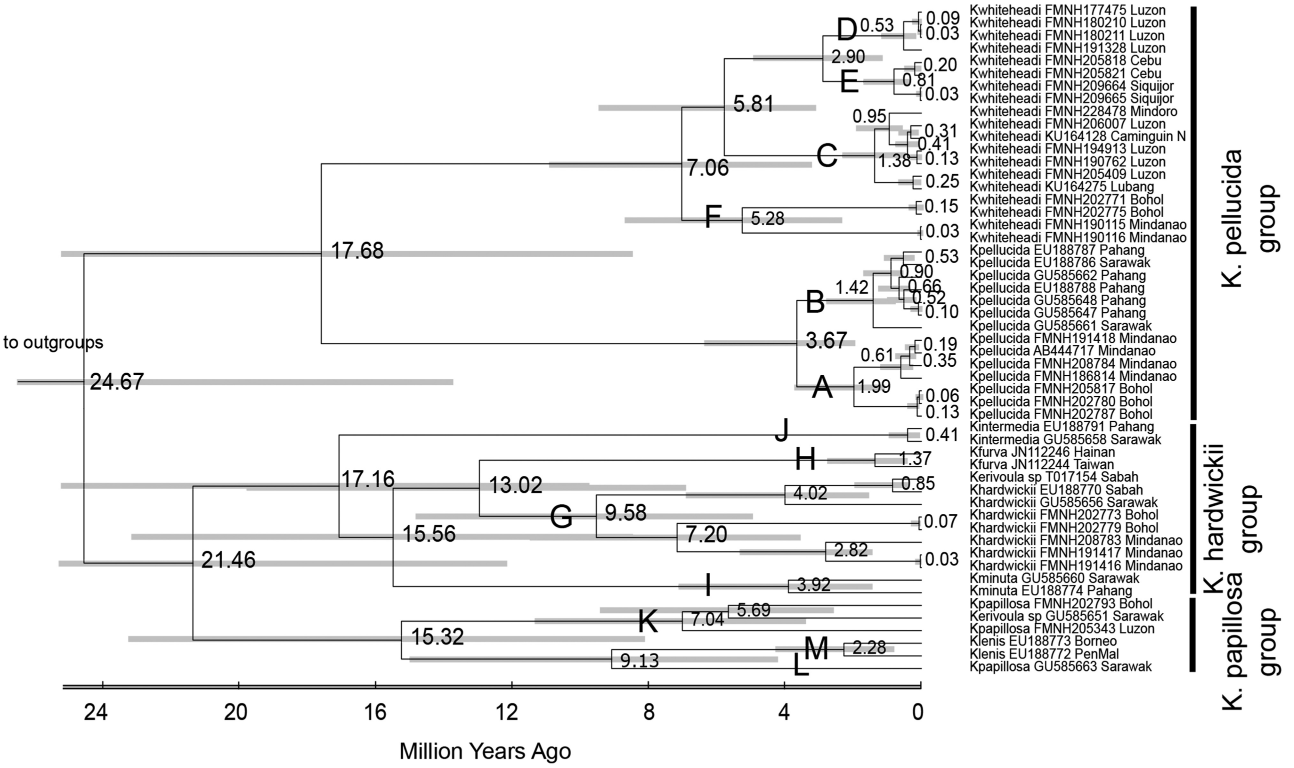

FIGURE 4. Time-calibrated phylogeny of *Kerivoula* species based on Cyt *b* haplotypes. Outgroups were omitted for ease of readability. The greyed boxes represent 95% highest posterior density (HPD) intervals of node ages derived from a BEAST analysis. Time is expressed in million years.

Species Accounts

In this section, we provide detailed assessments of the geographic variation and species limits in Philippine *K. pellucida* and *K. whiteheadi*, along with ecological information on these poorly-known species. Equivalent information on other Philippine *Kerivoula* will be published subsequently.

Kerivoula pellucida Waterhouse 1854

Type locality: Philippines.

Specimens examined. Given in Appendix A.

Distribution. Borneo, Java, the Malay Peninsula, the Philippines (Cebu, Jolo, Mindanao, Mindoro, and Palawan), and Siberut (Fig. 2; see also Corbet & Hill 1992: 154).

Description. Total length 83–97 mm, tail 43–50 mm, ear 16–18.5 mm, forearm 31.1–35.2 mm, tibia 16.6–19.4, mass 4.0–5.7 mm (Table 4). Dorsal pelage is long and soft with a slightly woolly appearance, and pale reddish-brown buff; hairs slightly paler at base than at tips, lacking distinct color bands; ventral pelage paler (Fig. 5D, E). The ears are pale brown, and unusually large (Fig. 5A, B). A thin scattering of inconspicuous hairs is present over the dorsal surface of the interfemoral membrane, some of which project over its posterior edge (Fig. 5A). The wing and tail membranes are very pale brown, nearly translucent (Fig. 5A, C). Tragus long and slender (Fig. 5B). Skin is nearly transparent giving the face, wing- and leg bones a reddish-pink hue in live animals. The wing membrane inserts onto the side of the outer toe well above the base, not at its base (Fig. 5C). There do not appear to be striking regional differences within the Philippines in appearance; however, specimens from Bohol are slightly darker brown than those from Mindanao and Cebu; those from Palawan are palest. Palawan specimens have more reddish-brown tips on the dorsum than those from Bohol and Cebu.

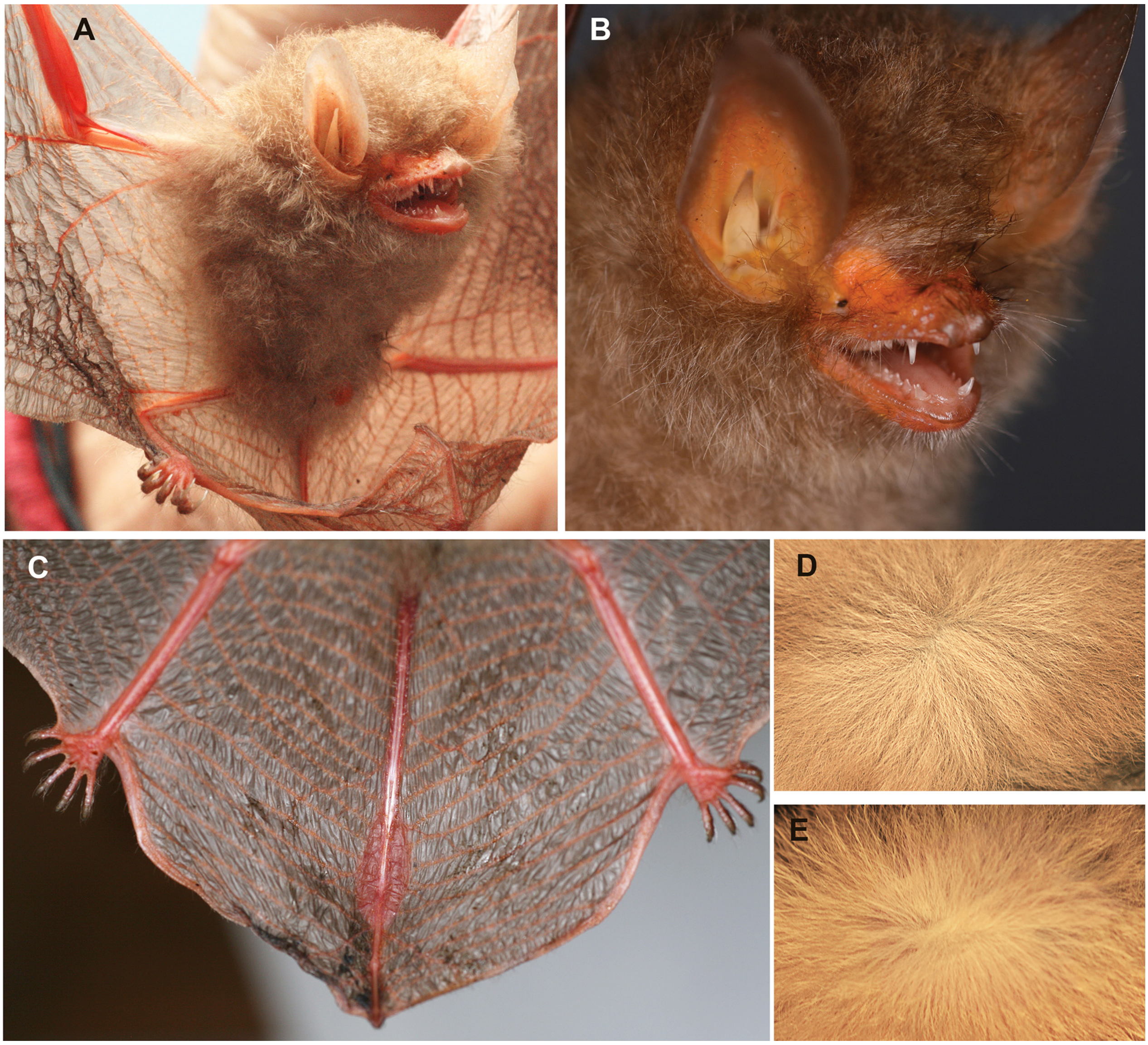

FIGURE 5. Photograph composite of *K. pellucida* showing the nearly translucent wing membranes (A), pelage color, and ears with tapered tragus (B), membrane attachment on foot and membrane with male gland (C), dorsal (D) and ventral (E) pelage lacking distinct color bands. A: Bohol I. (no voucher); B–C: FMNH 205817, Cebu I.; D–E: FMNH 202785, Bohol I.

Skull as shown in Figure 6. GTL14.06–15.03, CCL 12.75–13.44 mm, GBB 7.04–7.55 mm, BH 5.69–6.33 mm, PC 2.98–3.15, C–M^3 5.63–6.05 mm, M^2–M^{2ext} 4.88–5.16 mm, C^1–C^1 1.62–1.86 mm, C–M_3 6.05–6.50 mm, MDL 10.19–11.16 mm (Table 1). The skull is narrow with a highly inflated braincase that forms a steep forehead. The post-palatal region extends far posterior to the molar tooth row, and the bullar cochleae are moderately large. The upper tooth rows are slightly convergent anteriorly. Infraorbital canal is short, above P^3 to middle of M^1. The upper incisors are conical; the first upper incisor is more than twice the height of the second upper incisor, which is often separated from the canine by a narrow space. The first lower incisor (Fig. 7B) usually has four cusps (occasionally three), the second has three cusps, and the third has two prominent cusps and usually a third (at the posterior edge). The upper and lower canines are high and conical with a cingulum that extends from the anterior edge lingually to the posterior margin, about twice the height of the first premolars. The first upper premolar is nearly circular in outline, and the second is slightly compressed laterally (Fig. 7A). The third upper premolar is partially molariform, with a broad lingual shelf. The first lower premolar is roughly circular in outline only slightly compressed laterally; the second and third are more compressed laterally, but not strongly so. The upper and lower molars are typical for the genus (Hill 1965). Philippine specimens are slightly larger than a small series from Malaysia (Fig. 3; Tables 1, 4).

Comparisons. *Kerivoula pellucida* differs from *K. whiteheadi* in having dorsal and ventral pelage that is paler at the base than at the tips (Fig. 5D, E) (rather than dark at the base), reddish-brown at the tips, and slightly paler at mid-shaft, giving a tri-banded appearance. The wing and interfemoral membranes of *K. pellucida* are pale and nearly transparent, rather than moderately dark brown as those of *K. whiteheadi*. The tail membrane of *K. pellucida* has shorter, less conspicuous hairs (though still few and scattered) than that of *K. whiteheadi*. The wing membrane inserts up onto the side of the toe (Fig. 5C), rather than at the base of the outer toe. Most individuals of *K. pellucida* have greater total length than in *K. whiteheadi*, but much of this is due to having a longer tail (at least 43 mm, rather than 41 mm or less). The forearm is typically longer (usually 32 or more, rather than 31 mm or less), and the ear averages longer, though there is overlap (Table 4). The rostrum, palate, and braincase of *K. pellucida* are proportionately broader than those of *K. whiteheadi* (Fig. 6), the upper and lower premolars are less laterally compressed, there is more space between the molars lingually in *K. pellucida*, and the toothrows are typically longer (Fig. 7). The posterior palatal extension in *K. pellucida* is longer and narrower.

Kerivoula pellucida differs from the Philippine *K. hardwickii* (i.e., *K.* "*hardwickii* A" and *K.* "*hardwickii* B") in having larger and more pointed ears (rather than smaller and rounded; Heaney *et al.* 2010, 2016). The pelage of *K. pellucida* is paler at the base of each hair (Fig. 5D, E), rather than much darker at the base. Wing membranes of *K. pellucida* are pale and nearly transparent (Fig. 5A), rather than moderately dark brown and not transparent. Skin over the wing bones on individuals in the *K. hardwickii* group are darkly pigmented, not nearly transparent giving the bones the appearance of white stripes in preserved specimens and a pinkish hue in live animals, as in *K. pellucida*. Hairs on the tail membrane of Philippine *K. hardwickii* are very sparse and short, but a fringe of short hairs is often visible along the posterior edge. The wing membranes attach at the base of the outer toe, not part way up as in *K. pellucida* (Fig. 5C). The average total length of *K. pellucida* (91.4 mm) is longer than *K. "hardwickii* A" (82.8 mm) and *K.* "*hardwickii* B" (85.0 mm); but the average forearm length of *K. pellucida* (32.9 mm) is similar to *K.* "*hardwickii* A" (33.0 mm) and smaller than *K.* "*hardwickii* B" (35.0 mm) (Table 4; Heaney *et al.* 2010; unpublished data). The skull in *K. pellucida* is generally proportionately longer and narrower than Philippine *K. hardwickii* (Fig. 8). The post-palatal extension of Philippine *K. hardwickii* is broader and shorter than that of *K. pellucida*. Finally, the palate is proportionately narrower in *K. pellucida* than in Philippine *K. hardwickii*.

Kerivoula pellucida differs from Philippine *K. papillosa* in being much smaller in all respects (Fig. 3; Heaney *et al.* 2010, 2016); the average forearm length of *K. pellucida* is 32.9 mm compared to 42.6 mm in *K. papillosa* (Heaney *et al.* 2010; unpublished data). The pelage of *K. pellucida* is much paler overall than *K. papillosa*, which is a dark brown. The skull is smaller and more delicate, with conspicuously narrower rostrum, palate, and braincase (Figs. 6, 9). The second upper incisor reaches only one-third toward the tip of the first incisor, rather than more than halfway (Figs. 7A, B, 10A, B). All of the premolars and molars are proportionately more massive.

Echolocation. Philippine *K. pellucida* (4 individuals from Bohol, 1 from Cebu) have extremely broadband (132 kHz), short duration (2 ms), high frequency (peak = 138 kHz) calls similar to those recorded in Peninsular Malaysia (Fig. 11; Table 5; Kingston *et al.* 1999, Schmieder *et al.* 2010). They are also similar to those of Philippine *K. whiteheadi* with respect to peak frequency, although *K. pellucida* calls had a broader bandwidth (Table 5). Both species' calls start at a similarly high frequency (194 kHz), but *K. pellucida* calls terminate at a lower frequency.

Ecology. In the Philippines, *K. pellucida* occupies a broad range of elevations (sea level to about 1200 m), though most records are from below 700 m. They also occupy a wide range of habitats; examples include an isolated patch of second growth forest surrounded by vegetable farms on Cebu Island, disturbed second growth forest on limestone on Bohol Island, and pristine montane forest on Mindanao Island. Its roosting habits are poorly known in the Philippines, but one adult female with a suckling young was captured by hand from dried banana leaves on Palawan Island (J. Esselstyn, pers. com.). Payne *et al.* (1985) also reported it roosting in dried banana leaves, and Kingston (2006) reported a group roosting in a clutter of dead understory leaves. In Peninsular Malaysia, they roost in small groups of up to 15 individuals and appear to have small home ranges, evidenced by short recapture

TABLE 4. Mean (± standard deviation) and range of external body measurements (in mm) of *K. whiteheadi* and *K. pellucida*. n = sample size

Taxon Locality	n	Total	Tail	Hind foot	Ear	Forearm	Tibia	Mass (g)
K. whiteheadi								
Camiguin Norte		82	42	8	17	34.84	16.33	5.7
Luzon								
N. Luzon	4	76.2 ± 3.3	39.0 ± 2.16	6.5 ± 1.0	14.2 ± 1.26	31.29 ± 1.02	15.56 ± 0.26	3.87 ± 0.55
		74.0–81.0	36.0–41.0	5.0–7.0	13.0–16.0	30.10–32.46	15.32–15.92	3.50–4.50
Mt. Irid		78.0	42.0	8.0	14.0	31.70	15.63	3.50
Mt. Makiling	4	79.0 ± 3.46	36.0 ± 2.83	7.0 ± 0.0	14.0 ± 0.0	30.23 ± 0.77	15.42 ± 0.63	3.73 ± 0.21
		76.0–82.0	34.0–40.0			29.39–31.21	14.68–16.19	3.50–4.00
Mt. Banahaw	9	83.22 ± 2.86	34.7 ± 2.1	8.0 ± 0.35	14.9 ± 0.7	31.13 ± 1.27	15.75 ± 0.43	4.18 ±0.32
		80.0–89.0	31.0–39.0	7.5–8.5	14.0–16.0	29.11–33.04	15.14–16.30	3.70–4.50
Mt. Isarog	7	82.9 ± 2.8	35.4 ± 1.5	8.3 ± 0.5	15.0 ± 1.79	31.75 ±0.87	15.87 ± 0.41	4.53 ± 0.55
		78.0–86.0	34.0–38.0	8.0–9.4	13.0– 18.0	30.35–32.66	15.32–16.49	3.90–5.48
Lubang		84.0	43.0	7.0	14.0	32.97	16.15	4.5
Mindoro	8	79.4 ± 1.92	38.7 ± 3.77	6.7 ± 0.71	14.0 ±0.76	31.64 ± 0.76	15.94 ± 0.41 (5)	4.11 ± 0.47
		77.0–82.0	30.0–41.0	6.0–8.0	13.0–15.0	30.71–32.97	15.41–16.53	3.36–4.80
Sicogon-Tumaguin	2					30.76 ± 0.18	15.30 ± 0.39	
						30.52–30.88	14.91–15.69	
Bohol	2	85.0 ± 0	36.0 ± 1.4	8 ± 0	13.5 ± 0.7	31.10 ± 0.16	15.53 ± 0.30	3.73 ± 0.18
			35.0–37.0		13.0–14.0	30.98–31.21	15.31–15.74	3.60–3.85
Cebu	6	79.5 ± 1.3	32.7 ± 1.9	8.7 ± 1.0	15.5 ± 0.6	30.76 ± 1.24	15.19 ± 0.48	3.35 ± 0.18
		77.0–81.0	29.0–34.0	7.0–10.0	15.0–16.5	28.04–32.47	14.67–16.06	3.10–3.60
Siquijor	6	81.7 ± 1.37	33.1 ± 1.8	8.0 ± 1.10	13.9 ± 0.66	31.40 ± 0.51	15.37 ± 0.45	3.60 ± 0.09
		80.0–84.0	31.0–35.0	6.0–9.0	13.0–15.0	30.66–32.01	14.98–16.10	3.50–3.70
Mindanao	6	71.5 ± 3.27	35.3 ± 2.94	7.8 ±0.4	13.8 ± 1.4	29.61 ± 1.17	14.21 ± 0.68	3.00 ± 0.45
		67.0–76.0	32.0–39.0	7.0–8.0	12.0–16.0	28.09–31.41	13.35–15.16	2.50–3.50

......*continued on the next page*

TABLE 4. (Continued)

Taxon Locality	n	Total	Tail	Hind foot	Ear	Forearm	Tibia	Mass (g)
*K. pusilla**								
Borneo						27.77	13.10	
*K. whiteheadi**								
Luzon						31.28	15.61	
K. pellucida								
Bohol	12	92.1 ± 2.6	44.4 ± 4.8	8.1 ± 0.6	16.7 ± 0.8	32.94 ± 0.80	18.49 ± 0.47	4.60 ± 0.16
		87.0–96.0	35.0–50.0	6.6–9.0	16.0–18.5	31.70–34.14	17.81–19.47	4.30–4.90
Cebu	1	97.0	49.0	8.5	19.0	33.35	18.65	5.10
Mindanao	3	87.7 ± 3.51	45.7 ± 3.0	7.5 ± 0.5	16.7 ± 0.6	33.04 ± 1.69 (4)	18.31 ± 1.18 (4)	4.67 ± 0.58
		83.0–90.0	43.0–49.0	7.0–8.0	16.0–17.0	31.12–35.24	16.68–19.22	4.00–5.00
Palawan	2	91.0 ±8.49	49.0 ± 4.24	7.5 ± 0.71	17.5 ± 0.71	32.34 ± 1.61	17.26 ± 0.66	5.70
		85.0–97.0	46.0–52.0	7.0–8.0	17.0–18.0	31.20–33.48	16.79–17.73	
Malaysia	2	86.5 ± 3.54	46.5 ± 3.54		15.5 ± 0.7	31.40 ± 1.02 (8)	17.07 ± 0.94 (6)	4.5 ± 0.7
		84.0–89.0	44.0–49.0		15.0–16.0	29.76–32.47	15.80–18.46	4.0–5.0
*K. pellucida**						32.78	19.69	

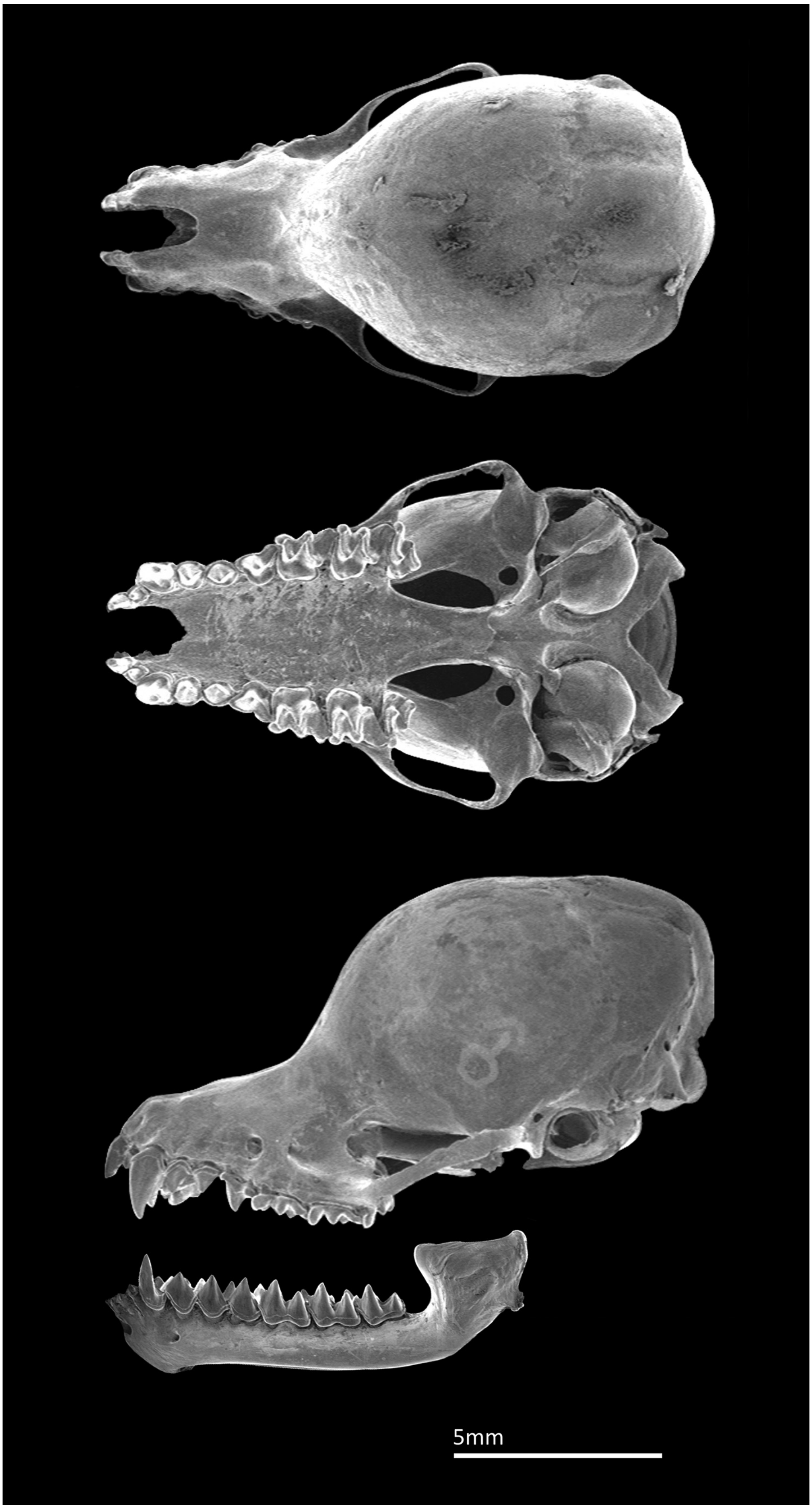

FIGURE 6. Scanning electron microscope images of *K. pellucida* cranium and mandible, FMNH 202782 from Bohol Island, Philippines.

distances (< 100 m) and distinct "hot spots" of high genetic autocorrelation among individuals (Rossiter *et al.* 2012). On Bohol Island, on three occasions, multiple individuals were captured either in the same or adjacent harp traps simultaneously, usually a male and a female (Sedlock *et al.* 2014). In Peninsular Malaysia, *K. pellucida* exhibits asynchronous reproduction giving birth throughout the year, although the highest proportion of pregnant individuals was captured during the rainy season when insect abundance was highest (Nurul-Ain *et al.* 2017). In the Philippines, five lactating females were captured in July, during the rainy season (Sedlock *et al.* 2014), and one female was captured with a suckling young in late March (J. Esselstyn, pers. com.). Its echolocation behavior is highly adapted for distinguishing prey from background clutter at close range allowing it to forage within the forest understory (Schmieder *et al.* 2012).

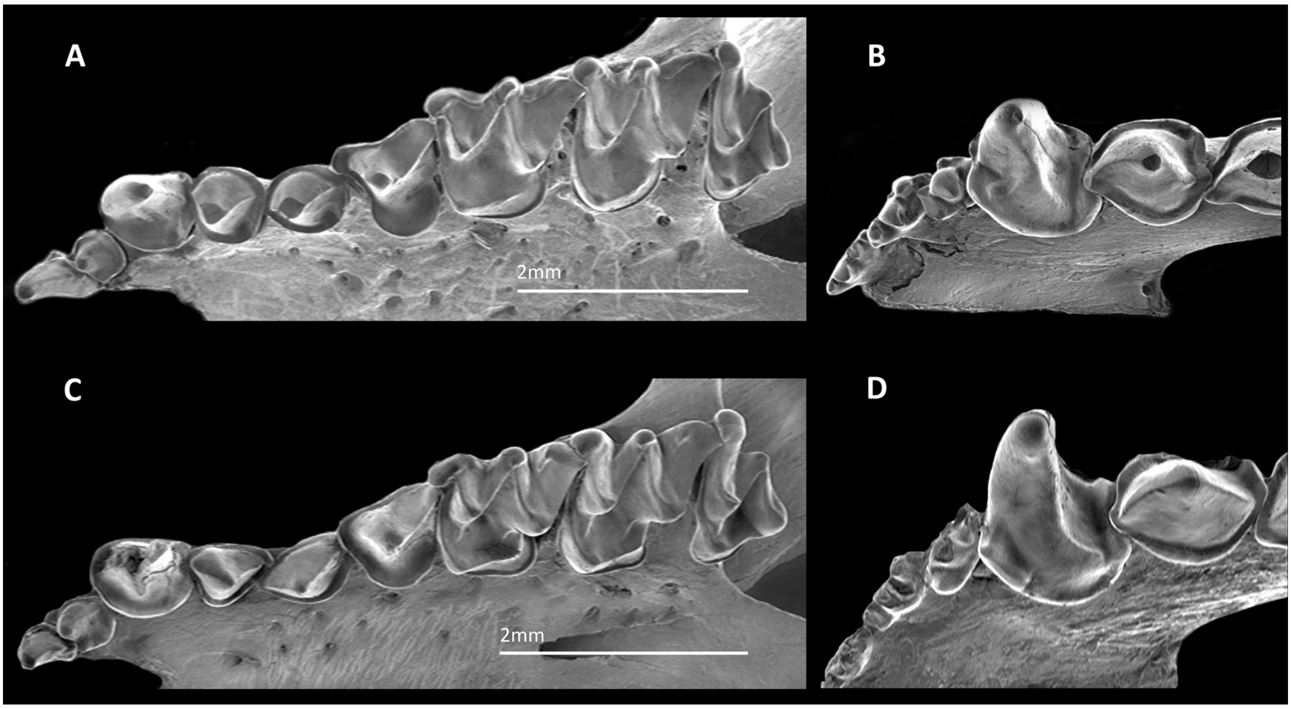

FIGURE 7. Scanning electron microscope images of upper toothrow and lower incisors of *K. pellucida* (FMNH 202782, A and B) and *K. whiteheadi* (FMNH 214092, C and D).

Kerivoula whiteheadi Thomas, 1894

Type locality: Molino, Isabela Province, Luzon.

Specimens examined. Philippine specimens examined are listed in Appendix A.

Distribution. Endemic to the Philippines (Bohol, Camguin Norte, Cebu, Lubang, Luzon, Mindanao, Mindoro, Palawan, Sicogon, Siquijor and Tumaguin; Fig. 2). The type locality "Molino" probably refers to a currently non-existent village on the east bank of the Ilagan River downstream from the city of San Mariano (M. van Weerd, pers. com., 6 May 2019).

Description. Total length 67–86 mm, tail 29–41mm, ear 12–18 mm, forearm 29–33 mm, mass 2.5–5.5 g (Table 1). A clear north-south gradient in size exists from Camiguin Norte Island (north of Luzon, largest) to southern Mindanao (smallest; Tables 1 and 4). A small, delicate bat (Fig. 12A) with funnel-shaped ears, a long, slender tragus, and simple nostrils (Fig. 12C). The dorsal fur varies from dark brown (on Luzon) to reddish brown (on Mindanao), with the ventral fur somewhat paler (Fig. 12A, B). Each hair in the dorsal pelage has three bands (dark gray-brown base, light buff mid-band, and rufus-brown to bright rufus tips (Fig. 12D). The ventral hairs are also banded with a dark gray-brown base and light brown tips (Fig. 12E). The wing and tail membranes are dark. A scattering of a few short hairs is present along the posterior margin of the interfemoral membrane, but there is no definite fringe. Thick hair is present along the dorsal tail membrane, along the legs and on the feet (Fig. 12B).

Skull as shown in Figure 13. GTL12.16–14.60, CCL 11.08–13.66 mm, GBB 6.42–7.14 mm, BH 5.15–6.09 mm, PC 2.92–3.26, C–M^3 4.89–5.94 mm, M^2–M^{2ext} 4.31–5.11 mm, C^1–C^1 1.36–1.93 mm, C–M_3 5.23–6.32 mm, MDL 9.22–11.24 mm (Table 1). The skull of *K. whiteheadi* (Fig. 13) is small and the braincase is highly inflated, producing a pronounced forehead. The rostrum narrows anteriorly, and the upper toothrows converge moderately. The center of the dorsal surface of the rostrum often has a ventral depression along the midline, above the level of the molars. The cochlea are large, and the basioccipital region is narrow. The height of the second upper incisor is half or slightly more than half of the first incisor. The first and second upper premolars, and all three lower premolars, are of nearly equal crown area, and are strongly laterally compressed (Fig. 7C). The lingual shelves of M^1 and M^2 are relatively small, leaving a broad embrasure at their posterior margins. The first lower incisor usually has three cusps, the second has three cusps, and the third usually has three cusps but occasionally two; they overlap substantially (Fig. 7D).

Comparisons. *Kerivoula whiteheadi* differs from *K. pellucida* as noted above. *Kerivoula whiteheadi* and *K. "hardwickii* A" are similar in size (average forearm length 31.1 and 33.0 mm, CCL 11.9 and 11.6 mm, respectively), but where they overlap geographically, *K. hardwickii* are slightly larger. *K. whiteheadi* is smaller overall than *K.* "*hardwickii* B" (forearm length 35.0 mm, CCL 13.2 mm). The dorsal pelage of *K. whiteheadi* has a reddish tone (Fig. 12B, D), rather than medium or dark brown in the Philippine *K. hardwickii*. Both species have hairs that are dark at the base on the dorsum and venter with color bands—three dorsally and two ventrally (Fig. 12D, E). *K. whiteheadi* overall appears more bicolored than Philippine *K. hardwickii* with a rufus-brown dorsum and grayish-brown venter, whereas Philippine *K. hardwickii* appears brown overall (although there is some variation). A fringe of short, inconspicuous hairs along the posterior edge of the interfemoral membrane is present on Philippine *K. hardwickii*, but absent on *K. whiteheadi* (Fig. 12A). The wing attaches at a similar point below the outside toe of both species (Fig. 12A). The penis of male *K. whiteheadi* does not widen distally and lacks a characteristic nub that is present on the penis of males in Philippine *K. hardwickii* (J. Sedlock, pers. obs.). The skulls of *K. whiteheadi* usually have a more abrupt forehead than Philippine *K. hardwickii*. The latter often has a slight sagittal crest posterior to the interorbital region, a structure that is absent in *K. whiteheadi* (Figs. 8, 13). The depression along the midline of the rostrum in *K. whiteheadi* is absent in Philippine *K. hardwickii*. The teeth of Philippine *K. hardwickii* are proportionately substantially larger and more robust than those of *K. whiteheadi* (Fig. 10A, B). In Philippine *K. hardwickii*, the second upper incisor is about one-third the height of the second incisor; in *K. whiteheadi*, the second incisor is half or more the height of the first incisor (Figs. 7C, D, 10A, B). Finally, Philippine *K. hardwickii* lack the conspicuous lateral compression of the premolars present in *K. whiteheadi*.

Kerivoula whiteheadi differs from *K. papillosa* in being much smaller overall in size (mean total length 79.9 mm and forearm length 31.1 mm, rather than 101.6 mm and 42.5 mm, respectively, mean CCL 11.99 mm rather than 15.78 mm; Table 1, 3; Heaney *et al.* 2010; unpublished data). The dorsal pelage of *K. whiteheadi* has a reddish tone with a distinct banding patterns on hairs (Fig. 12), rather than medium or dark brown with no clear banding pattern (but darker at base). *K. whiteheadi*'s skull is small and delicate lacking a sagittal crest (Fig. 13), rather than larger and more robust with a sagittal crest (Fig. 9). Premolars are elongate (Fig. 7C, D), rather than round (Fig. 10C, D).

Echolocation. The echolocation calls of *K. whiteheadi* in the Philippines are similar to those of *K. pellucida* in that they are broadband, high frequency, and short duration (Fig. 11; Table 5). Peak frequency of *K. whiteheadi* calls is 138 kHz. However, as stated above, *K. whiteheadi* calls are significantly shorter in duration and have a narrower bandwidth than those of *K. pellucida* (Table 5). There were no significant differences in call attributes among populations from Bohol, Cebu and Siquijor islands; however, we had sufficient recordings from only those three central Philippine islands and not from Luzon and Mindanao, which represent the largest and smallest individuals within the species, respectively.

TABLE 5. Mean ± standard deviation and range of five call parameter measurements of Philippine *Kerivoula pellucida* and *K. whiteheadi*. Descriptions of measurements given in methods. *p*-values represent results of Welch's t-test comparing species.

Species	n	Duration (ms)	Start frequency (kHz)	Terminal frequency (kHz)	Bandwidth (kHz)	Peak frequency (kHz)
K. pellucida	5	2.17 ± 1.12	194.19 ± 20.14	55.53 ± 17.28	132.39 ± 4.90	138.92 ± 11.92
		4.17-1.47	221.08-169.5	80.49-33.92	139.14-126.65	147.43-118.14
K. whiteheadi	16	1.77 ± 0.56	194.38 ± 18.75	75.77 ± 15.55	112.19 ± 25.85	138.09 ± 5.69
		2.73-0.84	223.06-160.4	107.51-48.24	152.02-66.03	144.74-125.06
p-value		$p = 0.028$	n.s.	$p = 0.000$	$p = 0.000$	n.s.

FIGURE 8. Photographs of *K. hardwickii* cranium and mandible, FMNH 202779 from Bohol Island, Philippines.

FIGURE 9. Photographs of *K. papillosa* cranium and mandible, FMNH 205342 from Luzon Island, Philippines.

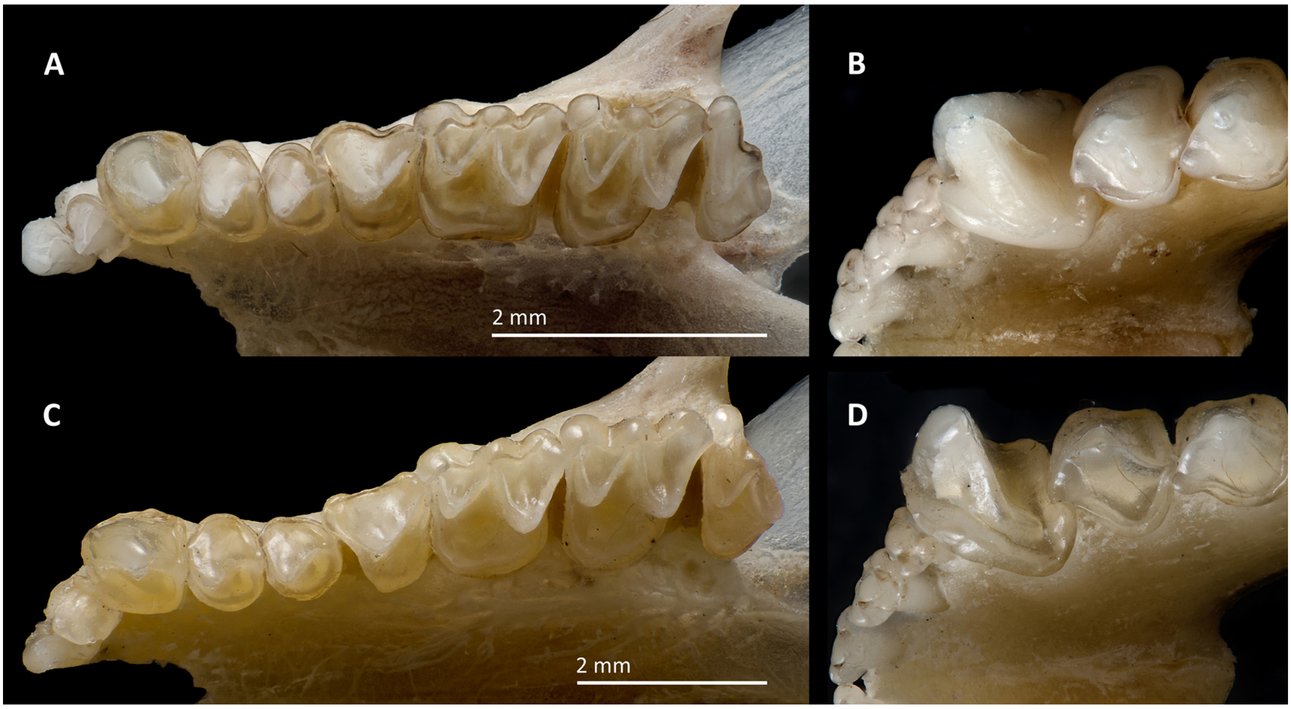

FIGURE 10. Photographs of upper toothrow and lower incisors of *K. hardwickii* (FMNH 202779, A and B) and *K. papillosa* (FMNH 205342, C and D).

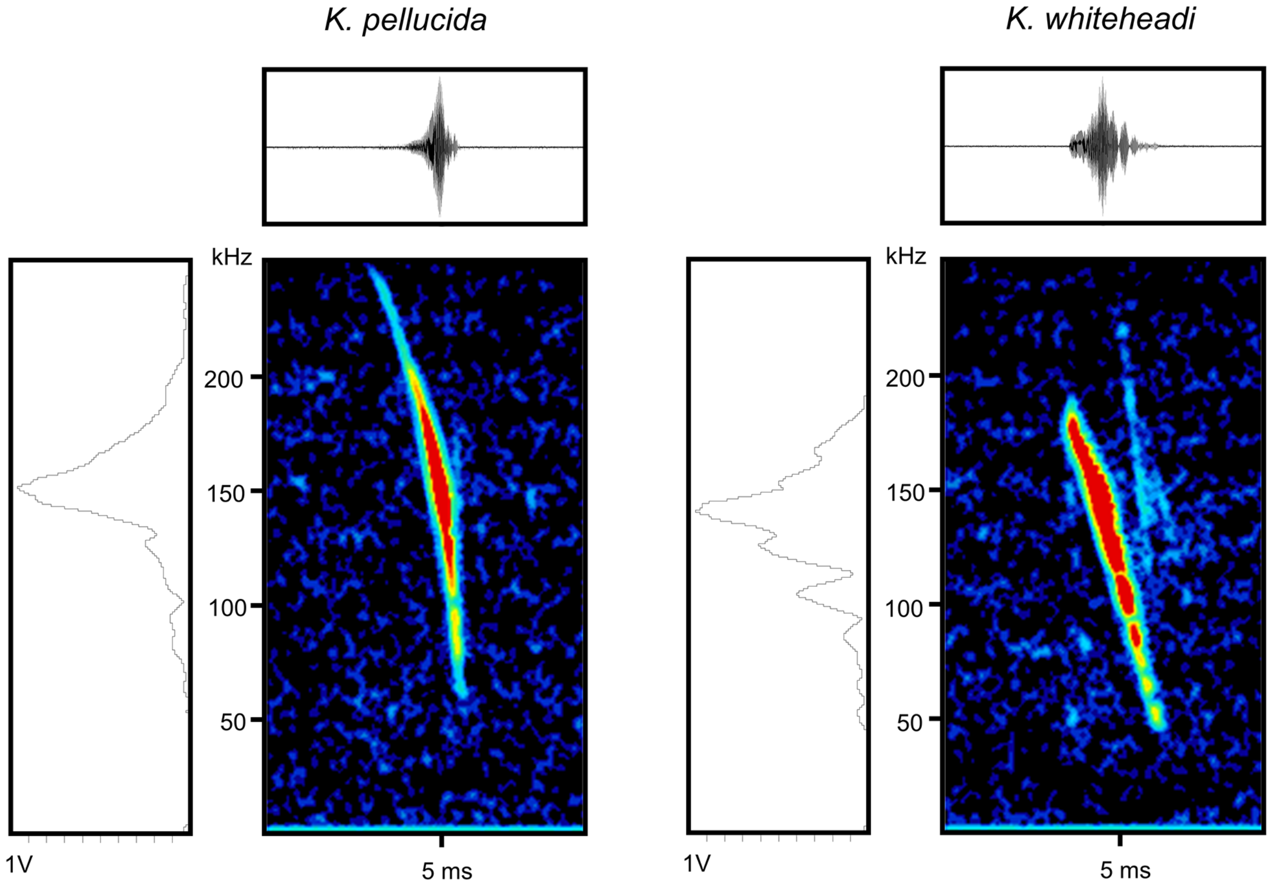

FIGURE 11. Power spectra, waveform and spectrograms of representative *K. pellucida* and *K. whiteheadi* calls (frequency in kilohertz on y-axis, time in milliseconds on x-axis; FFT 512).

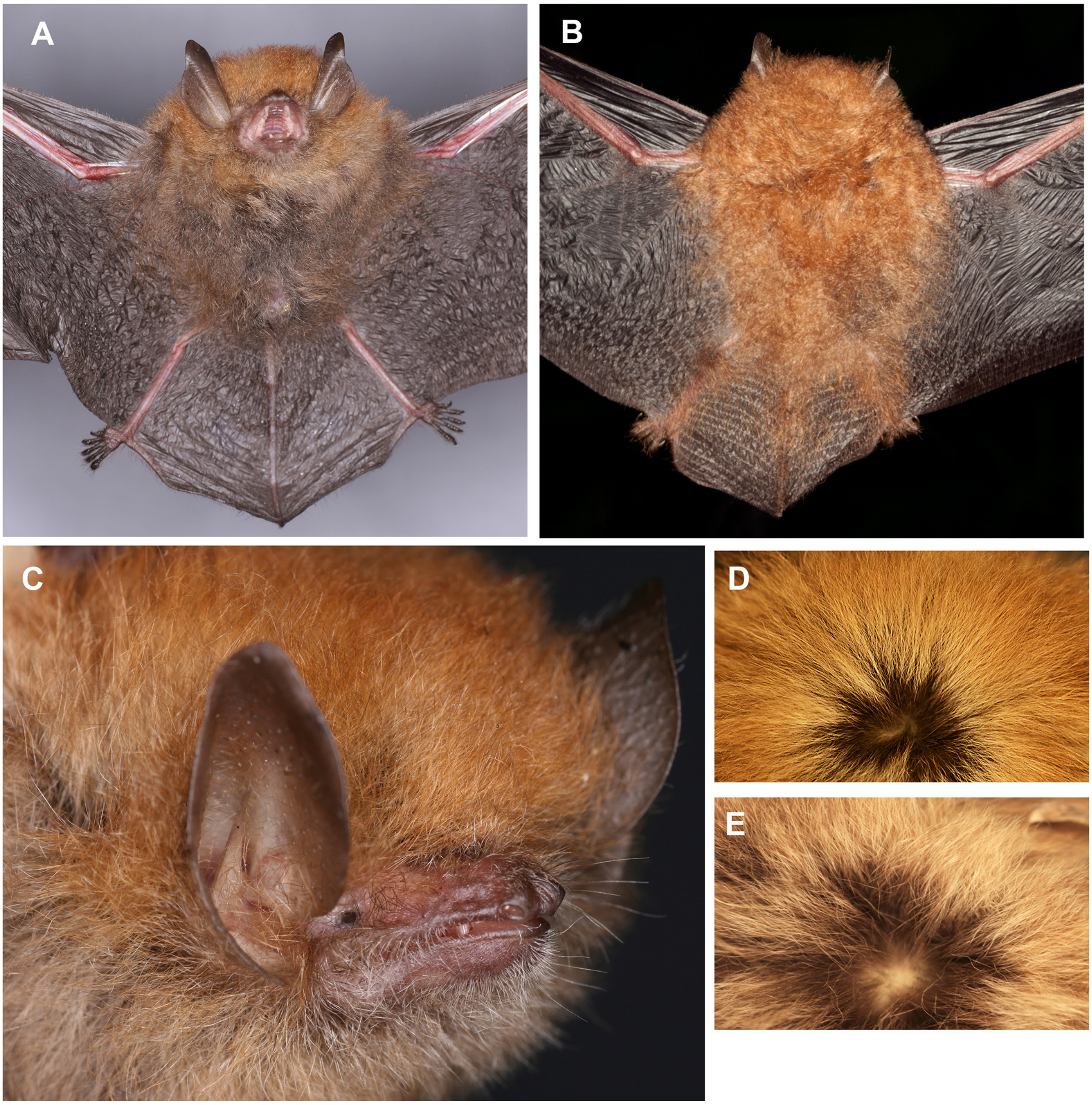

FIGURE 12. Photo composite of *K. whiteheadi* venter with membrane attachment to foot and bicolor pelage (A), dorsum with fur-lined legs and feet (B), head with pointed tragus and high forehead (C), dorsal (D) and ventral (E) pelage with three distinct color bands. A and C: FMNH 205818, Cebu I.; B: FMNH 191330, Luzon I.; D–E: FMNH 205819, Cebu I.

Ecology. *Kerivoula whiteheadi* exhibits a broad tolerance of vegetation types and elevations in the Philippines, from highly disturbed and fragmented lowland forest near sea level, to pristine montane forest at 1465 m above sea level (Sedlock 2002; Sedlock *et al*. 2008, 2011, 2014; Heaney *et al*. 2016). It has also been reported in karst areas within disturbed forest on limestone in the central Philippines and on Palawan Island (Esselstyn *et al*. 2004; Sedlock *et al*. 2014). Pregnant females have been captured in April, June and August, suggesting an asynchronous reproductive period as in *Kerivoula* species in Peninsular Malaysia (Nurul-Ain *et al.* 2017). No reports of roosting behavior exist from the Philippines. The authors have observed its slow and maneuverable flight, and its keen ability to quickly find and retreat into hollows or holes when released within a flight tent or room. For example, one individual flew up the leg of a pair of pants hanging over a line within minutes of release. When perching on the net wall of the flight tent, *K. whiteheadi* curls up with its head upright rather than hanging down (Sedlock 2002).

FIGURE 13. SEM images of *K. whiteheadi* cranium (FMNH 214092) from Luzon Island, Philippines.

Discussion

Our results support the prior recognition of four lineages of *Kerivoula* in the Philippines, including *K. pellucida*, *K. whiteheadi, K. papillosa*, and *K. hardwickii*, that we provisionally treat as species, each of which is distinguishable on genetic, external and craniodental features. *K. hardwickii* appears to comprise at least two more recently diverged lineages that require further study. Each of the four main lineages appears to have arrived in the Philippines independently from roughly 10 MY to about 2 MYA. This was a period during which the Philippine islands grew in size and proximity to one another, from their smaller size and greater isolation—a process that began with the emergence of the first islands some 35 MYA (Hall 2012, 2013). Thus, our data suggest that the first *Kerivoula* lineage to arrive in the Philippines did so at about the same time as the seemingly less vagile cloud rats (Phloeomyini) and earthworm mice (Chrotomyini) that are thought to have arrived about 12 and 8 MYA, respectively (Rowsey *et al.* 2019), but that at least one (*K. pellucida*) is likely to have arrived much more recently.

Within the Philippines, *K. whiteheadi* is widespread and shows evidence of some incipient speciation, as shown by the presence of four genetically identifiable, geographically allopatric clades and some geographic variation in body and cranium size. Our review of the few available specimens of *K. bicolor* and *K. pusilla*, which have in recent decades been treated as subspecies of *K. whiteheadi*, leads us to accept the original conclusion by Thomas (1894, 1904) that they are morphologically distinct from *K. whiteheadi*. Therefore, we recommend that they not be regarded as conspecific with *K. whiteheadi*; rather, *K. pusilla* should provisionally be treated as a distinct species. Moreover, given only subtle differences that have been noted between *K. pusilla* and *K. bicolor*, we suggest *K. bicolor* be assigned as a subspecies of *K. pusilla* until further comparative material is available. *K. whiteheadi* thus is defined here as being entirely endemic within the Philippines.

We provisionally treat *K. pellucida* as occurring in the Philippines, as well as on the Sunda Shelf. However, we note that bats from these two regions form reciprocally monophyletic units (**A** and **B** in Fig. 1 and 4), and our limited samples from Bohol and Mindanao are also genetically distinct. Further studies may support recognizing additional distinct species. Because of the current uncertainty about phylogeny, taxonomy, and distributions in *K. papillosa* and its close relatives (Khan *et al.* 2010; Figs. 1, 4), we continue the conservative treatment of Philippine populations as part of a single species, *K. papillosa*, but recognize the need for further study of them as well.

Although *K. whiteheadi* is widespread in the Philippines, the other three species occupy only parts of the archipelago, suggesting that they may have limited dispersal ability; further detailed study of genetic variation within *K. hardwickii* and *K. papillosa*, which are not documented in detail here, may provide important insights. Our preliminary analysis of *K. hardwickii* suggests that diversification may have taken place within the Philippine archipelago, specifically within Greater Mindanao. Therefore, with the possible exception of the *K. hardwickii* group, we conclude that the current diversity of *Kerivoula* in the Philippines has developed by direct colonization from external regions, with little of the speciation within the archipelago that is so prominent among non-flying small mammals (e.g., Jansa *et al.* 2006; Esselstyn *et al.* 2009; Justiniano *et al.* 2015 & Heaney *et al.* 2018).

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References

Alviola, P.A., Duya, M.R.M., Duya, M.V., Heaney, L.R. & Rickart, E.A. (2011) Mammalian diversity patterns on Mt. Palali, Caraballo Mountains, Luzon. *Fieldiana Life and Earth Sciences*, 2011 (2), 61–74. https://doi.org/10.3158/2158-5520-2.1.61

Aurelio, M.A., Barrier, E., Rangin, C. & Müller, C. (1991) The Philippine fault in the Late Cenozoic tectonic evolution of the Bondoc-Masbate-N. Leyte area, Central Philippines. *Journal of Southeast Asian Earth Sciences*, 6 (3–4), 221–238. https://doi.org/10.1016/0743-9547(91)90069-A

Balete, D.S., Alviola, P.A., Duya, M.R.M., Duya, M.V., Heaney, L.R. & Rickart, E.A. (2011) The mammals of the Mingan Mountains, Luzon: evidence for a new center of mammalian endemism. *Fieldiana Life and Earth Sciences*, 2011 (2), 75–87. https://doi.org/10.3158/2158-5520-2.1.75

Balete, D.S., Heaney, L.R. & Rickart, E.A. (2013) The mammals of Mt. Irid, Southern Sierra Madre, Luzon Island, Philippines. *National Museum of the Philippines Journal of Natural History*, 1, 15–29.

Bates, P.J. & Harrison, D.L. (1997) *Bats of the Indian Subcontinent*. Harrison Zoological Museum, Sevenoaks, Kent, 258 pp.

Bates, P.J.J., Struebig, M.J., Rossiter, S. J., Kingston, T., Oo, S.S.L. & Mya, K.M. (2004) A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from Myanmar (Burma). *Acta Chiropterologica*, 6 (2), 219–226. https://doi.org/10.3161/001.006.0203

Bates, P.J., Struebig, M.J., Hayes, B.D., Furey, N.M., Mya, K.M., Thong, V.D., Tien, P.D., Son, N.T., Harrison, D.L., Francis, C.M. & Csorba, G. (2007) A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from Southeast Asia. *Acta Chiropterologica*, 9 (2), 323–337. https://doi.org/10.3161/1733-5329(2007)9[323:ANSOKC]2.0.CO;2

Bradley, R. & Baker, R. (2001) A test of the genetic species concept: cytochrome b sequences and mammals. *Journal of Mammalogy*, 82 (4), 960 – 973. https://doi.org/10.1644/1545-1542(2001)082<0960:ATOTGS>2.0.CO;2

Brown, R.M., Siler, C.D., Oliveros, C.H., Esselstyn, J.A., Diesmos, A.C., Hosner, P.A., Linkem, C.W., Barley, A.J., Oaks, J.R., Sangulia, M.B., Welton, L.J., Blackburn, D.C. Moyle, R.G., Pterson, A.T. & Alcala, A.C. (2013) Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution, and Systematics*, 44, 411–435. https://doi.org/10.1146/annurev-ecolsys-110411-160323

Corbet, G.B. & Hill, J.E. (1992) *The Mammals of the Indomalayan Region: A systematic Review*. Oxford University Press, Oxford, 488 pp.

Douangboubpha, B., Bumrungsri, S., Satasook, C., Wanna, W., Soisook, P. & Bates, P.J.J. (2015) Morphology, genetics and echolocation calls of the genus *Kerivoula* (Chiroptera: Vespertilionidae: Kerivoulinae) in Thailand. *Mammalia,* 80, 1–27. https://doi.org/10.1515/mammalia-2014-0004

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214. https://doi.org/10.1186/1471-2148-7-214

Drummond, A.J., S.Y.W., Ho, Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *Plos Biology*, 4, 699–710. https://doi.org/10.1371/journal.pbio.0040088

Duya, M.R.M., Alviola, P.A., Duya, M.V., Balete, D.S. & Heaney, L.R. (2007) Report on a survey of mammals of the Sierra Madre Range, Luzon Island, Philippines. *Banwa*, 4 (1), 41–68.

Esselstyn, J.A., Timm, R.M. & Brown, R.M. (2009) Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. *Evolution*, 63, 2595–2610. https://doi.org/10.1111/j.1558-5646.2009.00743.x

Esselstyn, J.A., Widmann, P. & Heaney, L.R. (2004) The mammals of Palawan Island, Philippines. *Proceedings of the Biological Society of Washington*, 117, 271–302.

Francis, C.M., Kingston, T. & Zubaid, A. (2007) A new species of *Kerivoula* (Chiroptera: Vespertilionidae) from peninsular Malaysia. *Acta Chiropterologica*, 9, 1–12. https://doi.org/10.3161/1733-5329(2007)9[1:ANSOKC]2.0.CO;2

Francis, C.M. (2008) *A Guide to the Mammals of Southeast Asia*. Princeton University Press, Princeton, New Jersey, 392 pp.

Gunnell, G.F., Eiting, T.P. & Simons, E.L. (2012) African Vespertilionoidea (Chiroptera) and the antiquity of Myotinae. *In*: Gunnell, G.F. & Simmons, N.B. (Eds.), *Evolutionary history of bats. Fossils, molecules and morphology*. Cambridge Uni-

versity Press, New York, pp. 252–266.
https://doi.org/10.1017/CBO9781139045599.008

Hall, R. (2012) Late Jurassic-Cenozoic reconstructions of the Indonesian region and the Indian Ocean. *Tectonophysics*, 570–571, 1–41.
https://doi.org/10.1016/j.tecto.2012.04.021

Hall, R. (2013) The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology*, 72 (2), 1–17.
https://doi.org/10.4081/jlimnol.2013.s2.e1

Hasegawa, M., Kishino, H. & Yano, T. (1985) Dating the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, 21, 160–174.
https://doi.org/10.1007/BF02101694

Hasan, N.H. & Abdullah, M.J. (2011) A morphological analysis of Malaysian *Kerivoula* (Chiroptera, Vespertilionidae). *Mammal Study*, 36 (2), 87–97.
https://doi.org/10.3106/041.036.0207

Hassanin, A., Delsuc, F., Ropiquet, A., Hammer, C., Van Vuuren, B.J., Matthee, C., Ruiz–Garcia, M., Catzeflis, F., Areskoug, V., Nguyen, T.T. & Couloux, A. (2012) Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies*, 335, 32–50.
https://doi.org/10.1016/j.crvi.2011.11.002

Heaney, L.R. (1985) Zoogeographic evidence for Middle and Late Pleistocene land bridges to the Philippine Islands. *Modern Quaternary Research in Southeast Asia*, 9, 127–144.

Heaney, L.R. (1991) An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). *Bulletin of the American Museum of Natural History*, 206, 145–167.

Heaney, L.R., Balete, D.S., Dolar, M.L., Alcala, A.C., Dans, A.T.L., Gonzales, P.C., Ingle, N.R., Lepiten, M.V., Oliver, W.L.R., Ong, P.S., Rickart, E.A., Tabaranza Jr., B.R. & Utzurrum, R.C.B. (1998) A synopsis of the mammalian fauna of the Philippine Islands. *Fieldiana Zoology*, New Series, 88, 1–61.
https://doi.org/10.5962/bhl.title.3419

Heaney, L.R., Dolar, M.L., Balete, D.S., Esselstyn, J.A., Rickart, E.A. & Sedlock, J.L. (2010) *Synopsis of Philippine Mammals*. Available from: http://www.fieldmuseum.org/philippine_mammals/ (accessed 8 May 2019)

Heaney, L.R., Balete, D.S., Alviola, P.A., Rickart, E.A. & Ruedi, M. (2012) *Nyctalus plancyi* and *Falsistrellus petersi* (Chiroptera: Vespertillionidae) from northern Luzon, Philippines: ecology, phylogeny, and biogeographic implications. *Acta Chiropterologica*, 14, 265–278.
https://doi.org/10.3161/150811012x661602

Heaney, L.R., Balete, D.S. & Rickart, E.A. (2016) *The Mammals of Luzon Island: Biogeography and Natural History of a Philippine Fauna*. Johns Hopkins University Press, Baltimore. xi + 287 pp.

Heaney, L.R., Kyriazis, C.C., Balete, D.S., Steppan, S.J. & Rickart, E.A. (2018) How small an island? Speciation by endemic mammals (*Apomys*, Muridae) on an oceanic Philippine island. *Journal of Biogeography*, 45, 1675–1687.
https://doi.org/10.1111/jbi.13352

Heaney, L.R. & Roberts T.E. (2009) New perspectives on the long–term biogeographic dynamics and conservation of Philippine fruit bats. *In*: Fleming, T.H. & Racey, P. (Eds.), *Ecology, Evolution, and Conservation of Island Bats*. University of Chicago Press, Chicago, pp. 17–58.

Heideman, P.D. (1995) Synchrony and seasonality of reproduction in tropical bats. *Symposia of the Zoological Society of London*, 67, 141–165.

Heideman, P.D. and Utzurrum, R.C.B. (2003) Seasonality and synchrony of reproduction in three species of nectarivorous Philippines bats. *BMC Ecology*, 3, 11.
https://doi.org/10.1186/1472-6785-3-11

Hill, J.E. (1965) Asiatic bats of the genera *Kerivoula* and *Phoniscus* (Vespertilionidae), with a note on *Kerivoula aerosa* Tomes. *Mammalia*, 29, 524–556.
https://doi.org/10.1515/mamm.1965.29.4.524

Hoofer, S.R. & Van den Bussche, R.A. (2003) Molecular phylogenetics of the chiropteran family Vespertilionidae. *Acta Chiropterologica*, 5 (Supplement), 1–63.
https://doi.org/10.3161/001.005.s101

Horácek, I. (2001) On the early history of vespertilionid bats in Europe: the Lower Miocene record from the Bohemian Massif. *Lynx*, 32, 123–154.

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35, 518-522.
https://doi.org/10.1093/molbev/msx281

Ibáñez, C., García-Mudarra, J.L., Ruedi, M., Stadelmann, B. & Juste, J. (2006) The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterologica*, 8, 277–297.
https://doi.org/10.3161/1733-5329(2006)8[277:TICTCD]2.0.CO;2

Inger, R.F. (1954) Philippine Zoological Expedition 1946–1947. Systematics and zoogeography of the Philippine Amphibia. *Fieldiana: Zoology*, 33, 181–531.
https://doi.org/10.5962/bhl.title.5571

Ingle, N.R. (2003) Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation.

Oecologia, 134, 251–261.
https://doi.org/10.1007/s00442-002-1081-7

Ingle, N.R. & Heaney, L.R. (1992) A key to the bats of the Philippine Islands. *Fieldiana: Zoology*, New Series, 69, 1–44.
https://doi.org/10.5962/bhl.title.3504

Jansa, S., Barker, K. & Heaney, L.R. (2006) The pattern and timing of diversification of Philippine endemic rodents: Evidence from mitochondrial and nuclear gene sequences. *Systematic Biology*, 55, 73–88.
https://doi.org/10.1080/10635150500431254

Justiniano, R., Schenk, J. J., Balete, D.S., Rickart, E.A., Esselstyn, J.A., Heaney, L.R. & Steppan, S.J. (2015) Testing diversification models of endemic Philippine forest mice (*Apomys*) with nuclear phylogenies across elevational gradients reveal repeated colonization of isolated mountain ranges. *Journal of Biogeography*, 42, 51–64.
https://doi.org/10.1111/jbi.12401

Kawai, K., Nikaido, M., Harada, M., Matsumura, S., Lin, L.K., Wu, Y., Hasegawa, M. & Okada, N. (2002) Intra- and interfamily relationships of Vespertilionidae inferred by various molecular markers including SINE insertion data. *Journal of Molecular Evolution*, 55, 284–301.
https://doi.org/10.1007/s00239-002-2326-0

Kingston, T., Jones, G., Akbar, Z. & Kunz, T.H. (1999) Echolocation signal design in Kerivoulinae and Murininae (Chiroptera: Vespertilionidae) from Malaysia. Journal of Zoology, 249, 359–374.
https://doi.org/10.1017/S0952836999009917

Kingston, T., Boo Liat, L. & Akbar, Z. (2006) *Bats of Krau Wildlife Reserve*. Penerbit Universiti Kebangsaan Malaysia, Bangi, 141 pp.

Khan, F.A.A., Solari, S., Swier, V.J., Larsen, P.A., Abdullah, M.T. & Baker, R.J. (2010) Systematics of Malaysian woolly bats (Vespertilionidae: *Kerivoula*) inferred from mitochondrial, nuclear, karyotypic, and morphological data. *Journal of Mammalogy*, 91, 1058–1072.
https://doi.org/10.1644/09-MAMM-A-361.1

Kuo, H.-C., Soisook, P., Ho, Y.-Y., Csorba, G., Wang, C.-N. & Rossiter, S.J. (2017) A Taxonomic Revision of the *Kerivoula hardwickii* Complex (Chiroptera: Vespertilionidae) with the Description of a New Species. *Acta Chiropterologica*, 19, 19–39.
https://doi.org/10.3161/15081109ACC2017.19.1.002

Medway, L. (1977) *Mammals of Borneo*. *Monographs of the Malaysian Branch of the Royal Asiatic Society No. 7*. Printed for MBRAS by Mas, Kuala Lumpur, xii + 172 pp.

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.
https://doi.org/10.1093/molbev/msu300

Nurul-Ain, E., Rosli, H. & Kingston, T. (2017) Resource availability and roosting ecology shape reproductive phenology of rain forest insectivorous bats. *Biotropica*, 49, 382–394.
https://doi.org/10.1111/btp.12430

Nylander, J.A.A. (2004) *MrModeltest. Version 2.3*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala. [program]

Patrick, L.E., McCulloch, E.S. & Ruedas, L.A. (2013) Systematics and biogeography of the arcuate horseshoe bat species complex (Chiroptera, Rhinolophidae). *Zoologica Scripta*, 42, 1–38.
https://doi.org/10.1111/zsc.12026

Payne, J., Francis C.M. & Phillipps, K. 1985. *A field guide to the mammals of Borneo*. Sabah Society, Kota Kinabalu, 332 pp.

Phillipps, Q. & Phillipps, K. (2016) *Mammals of Borneo and their ecology*. John Beaufoy Publishing Ltd, Oxford, 400 pp.

Piper, P.J., Ochoa, J., Robles, E., Lewis, H. & Paz, V. (2011) The palaeozoology of Palawan Island, Philippines. *Quaternary International*, 233, 142–158.
https://doi.org/10.1016/j.quaint.2010.07.009

R Developer Core Team (2018) R: A language and environment for statistal computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org (accessed 19 February 2020)

Rambaut, A. & Drummond, A.J. (2009) Tracer. Version 1.5. Available from: http://beast.bio.ed.ac.uk/Tracer (accessed 8 July 2017)

Ratnasingham, S. & Hebert, P.D.N. (2007) The Barcode of Life Data System (http://www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364.
https://doi.org/10.1111/j.1471-8286.2007.01678.x

Ratnasingham, S. & Hebert, P.D.N. (2013) A DNA-based registry for all animal species: the Barcode Index Number (BIN) system. *Plos One* 8, 8 (7), e66213.
https://doi.org/10.1371/journal.pone.0066213

Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180

Rossiter, S.J., Zubaid, A., Mohd-Adnan, A., Struebig, M.J., Kunz, T.H., Gopal, S., Petit, E.J. & Kingston, T. (2012) Social organization and genetic structure: Insights from codistributed bat populations. *Molecular Ecology*, 21, 647–661.
https://doi.org/10.1111/j.1365-294X.2011.05391.x

Rowsey, D.M., Heaney, L.R. & Jansa, S.A. (2019) Tempo and mode of mandibular shape and size evolution reveal contrasting support for incumbency effects in two clades of island-endemic rodents (Muridae: Murinae). *Evolution*, 73 (7), 1411–1427.
https://doi.org/10.1111/evo.13737

Ruedi, M., Stadelmann, B., Gager, Y., Douzery, E.J.P., Francis, C.M., Lin, L.-K., Guillén-Servent, A. & Cibois, A. (2013) Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus *Myotis* (Mammalia, Chiroptera). *Molecular Phylogenetics and Evolution*, 69, 437–449.
https://doi.org/10.1016/j.ympev.2013.08.011

Sanborn, C.C. (1952) Philippine Zoological Expedition 1946–1947: Mammals. *Fieldiana: Zoology*, 33, 89–158.

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. (2010) Breaking the trade-off: rainforest bats maximize bandwidth and repetition rate of echolocation calls as they approach prey. *Biology Letters*, 6, 604–609.
https://doi.org/10.1098/rsbl.2010.0114

Schmieder, D.A., Kingston, T., Hashim, R. & Siemers, B.M. (2012) Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. Sensory constraints on prey detection performance in an ensemble of vespertilionid understorey rain forest bats. *Functional Ecology*, 26, 1043–1053.
https://doi.org/10.1111/j.1365-2435.2012.02024.x

Sedlock, J.L. (2002) Autecology and the conservation of insectivorous bats on Mt. Makiling, Philippines. *Silliman Journal*, 42 (1), 163–201.

Sedlock, J.L., Ingle, N.R. & Balete, D.S. (2011) Enhanced sampling of bat assemblages: a field test on Mount Banahaw, Luzon. *Fieldiana: Life and Earth Sciences*, 2, 96–102.
https://doi.org/10.3158/2158-5520-2.1.96

Sedlock, J.L., Jose, R.P., Vogt, J. M., Paguntalan, L.M.J. & Carino, A.B. (2014) A survey of bats in a karst landscape in the central Philippines. *Acta Chiropterologica*,16, 197–211.
https://doi.org/10.3161/150811014X683390

Sedlock, J.L., Krüger, F. & Clare, E.L. (2014) Island bat diets: Does it matter more who you are or where you live? *Molecular Ecology*, 23 (15), 3684–3694.
https://doi.org/10.1111/mec.12732

Sedlock, J.L., Weyandt, S.E., Cororan, L., Damerow, M., Hwa, S. & Pauli, B. (2008) Bat diversity in tropical forest and agro-pastoral habitats within a protected area in the Philippines. *Acta Chiropterologica*, 10 (2), 349–358.
https://doi.org/10.3161/150811008X414926

Simmons, N. (2005) Order Chiroptera. *In*: Wilson, D. & Reeder, D.M. (Eds.), *Mammal Species of the World, A Taxonomic and Geographic Reference*. The Johns Hopkins University Press, Baltimore, Maryland, pp. 312–525.

Son, N.T., Motokawa, M., Oshida, T. & Endo, H. (2015) A morphological analysis of the skull size and shape of Kerivoulinae (Chiroptera: Vespertilionidae) from Vietnam. *Journal of Veterinary Medical Science*, 78, 187–198.
https://doi.org/10.1292/jvms.15-0270

Stuebig, M.J., Huang, J.C., Mohamed, N.Z., Noerfahmy, S., Schoner, C.R, Schoner, M.G. & Francis, C.M. (2016) Forest surveys extend the range of the Krau woolly bat (*Kerivoula krauensis*) in the Malay-Thai Peninsula, Borneo, and Sumatra. *Mammalia*, 81 (2), 1–5.
https://doi.org/10.1515/mammalia-2015-0114

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
https://doi.org/10.1093/molbev/mst197

Thomas, O. (1894) Descriptions of two new bats of the genus *Kerivoula*. *Annals and Magazine of Natural History*, 14, 460–462.
https://doi.org/10.1080/00222939408677834

Thomas, O. (1904) Three new bats, African and Asiatic. *Annals and Magazine of Natural History*, 13, 384–388.
https://doi.org/10.1080/00222930408562462

Topál, G. (1983) New and rare fossil mouse–eared bats from the Middle Pliocene of Hungary (Mammalia, Chiroptera). *Fragmenta Mineralogica et Palaeontologica*, 11, 43–54.

Tu, V.T., Hassanin, A., Furey, N.M., Son, N.T. & Csorba, G. (2018) Four species in one: multigene analyses reveal phylogenetic patterns within Hardwicke's woolly bat, *Kerivoula hardwickii*-complex (Chiroptera, Vespertilionidae) in Asia. *Hystrix–Italian Journal of Mammalogy*, 29 (1), 111–121
https://doi.org/10.4404/hystrix-00017-2017

Waterhouse, G.R. (1845) Descriptions of species of bats collected in the Philippines Islands. *Proceedings of the Zoological Society of London*, 13, 3–10.

Weyeneth, N., Goodman, S.M., Stanley, W.T. & Ruedi, M. (2008) The biogeography of *Miniopterus* bats (Chiroptera: Miniopteridae) from the Comoro Archipelago inferred from mitochondrial DNA. *Molecular Ecology*, 17, 5205–5219.
https://doi.org/10.1111/j.1365-294X.2008.03994.x

Wu, Y., Li, Y., Lin, L.-K., Harada, M., Chen, Z. & Motokawa, M. (2012) New Records of *Kerivoula titania* (Chiroptera: Vespertilionidae) from Hainan Island and Taiwan. *Mammal Study*, 37, 69–72.
https://doi.org/10.3106/041.037.0109

APPENDIX A. List of all *Kerivoula* specimens examined. Specimens included in morphological analysis and comparisons are in bold. § Holotypes * Paratype.

Species	sex	Country	Island	Province/State	Catalog number
Kerivoula "hardwickii A"	m	Philippines	Bohol	Bohol	**FMNH 202773**
Kerivoula "hardwickii A"	m	Philippines	Bohol	Bohol	**FMNH 202774**
Kerivoula "hardwickii A"	f	Philippines	Bohol	Bohol	**FMNH 202777**
Kerivoula "hardwickii A"	f	Philippines	Bohol	Bohol	**FMNH 202779**
Kerivoula "hardwickii A"	m	Philippines	Mindanao	Bukidnon	**FMNH 147081**
Kerivoula "hardwickii A"	m	Philippines	Mindanao	Bukidnon	**FMNH 166467**
Kerivoula "hardwickii A"	m	Philippines	Mindanao	Davao Oriental	**FMNH 186809**
Kerivoula "hardwickii A"	f	Philippines	Mindanao	Davao Oriental	**FMNH 186810**
Kerivoula "hardwickii A"	m	Philippines	Mindanao	Davao Oriental	**FMNH 208783**
Kerivoula "hardwickii A"	m	Philippines	Mindanao		**BMNH 87.10.31.1**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Agusan del Norte	**FMNH 191414**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Agusan del Norte	**FMNH 191415**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Agusan del Norte	**FMNH 191416**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Agusan del Norte	**FMNH 191417**
Kerivoula "hardwickii B"	f	Philippines	Palawan	Palawan	**FMNH 168948**
Kerivoula "hardwickii B"	m	Philippines	Palawan	Palawan	**FMNH 168953**
Kerivoula "hardwickii B"	m	Philippines	Palawan	Palawan	**FMNH 195213**
Kerivoula "hardwickii B"	f	Philippines	Mindanao	Surigao del Sur	**FMNH 190110**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Surigao del Sur	**FMNH 190111**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Surigao del Sur	**FMNH 190112**
Kerivoula "hardwickii B"	m	Philippines	Mindanao	Surigao del Sur	**FMNH 190113**
Kerivoula hardwickii	f	Cambodia		Preah Vihear	**HZM 11.3379**
Kerivoula hardwickii	m	Indonesia	Borneo	Central Kalimantan	**HZM 11.3654**
Kerivoula hardwickii	m	Indonesia	Sulawesi	South Sulawesi	**BMNH 97.1.3.21**
Kerivoula hardwickii	f	Malaysia	Balambangan	Sabah	**FMNH 141414**
Kerivoula hardwickii	f	Malaysia	Balambangan	Sabah	**FMNH 141415**
Kerivoula hardwickii	f	Malaysia	Balambangan	Sabah	**FMNH 141416**
Kerivoula hardwickii	m	Malaysia	Banggi	Sabah	**FMNH 141334**
Kerivoula hardwickii	m	Malaysia	Borneo	Sarawak	**BMNH 64.43**
Kerivoula hardwickii	f	Malaysia		Selangor	**FMNH 110229**
Kerivoula hardwickii	f	Malaysia		Selangor	**FMNH 110751**
Kerivoula hardwickii	f	Malaysia		Selangor	**FMNH 110756**
Kerivoula hardwickii	f	Malaysia		Selangor	**FMNH 110757**
Kerivoula hardwickii	f	Malaysia		Selangor	**FMNH 110765**
Kerivoula hardwickii	f	Myanmar		Kachin	**HZM 10.35963**
Kerivoula hardwickii	f	Vietnam		Nghệ An	**HZM 4.31763**
Kerivoula hardwickii	f	Vietnam		Nghệ An	**HZM 6.31778**
Kerivoula intermedia§	m	Malaysia	Borneo	Sabah	**BMNH 86.356**
Kerivoula minuta	m	Malaysia	Borneo		**BMNH 84.2042**
Kerivoula minuta	m	Malaysia		Selangor	**FMNH 110752**
Kerivoula pusilla§	f	Malaysia	Borneo	Sarawak	**BMNH 94.9.29.17**
Kerivoula p. bicolor§	f	Malaysia		Biserak, Jalor	BMNH 3.2.6.91
Kerivoula papillosa	m	Indonesia	Borneo	Central Kalimantan	**HZM 1.36538**

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APPENDIX A . (Continued)

Species	sex	Country	Island	Province/State	Catalog number
Kerivoula papillosa	f	Malaysia		Selangor	**FMNH 110761**
Kerivoula papillosa	f	Malaysia		Selangor	**FMNH 67812**
Kerivoula papillosa	m	Malaysia		Selangor	**FMNH 67813**
Kerivoula papillosa	f	Malaysia			**BMNH 47.1438**
Kerivoula papillosa	f	Philippines	Bohol	Bohol	**FMNH 202793**
Kerivoula papillosa	f	Philippines	Bohol	Bohol	**FMNH 202794**
Kerivoula papillosa	f	Philippines	Luzon	Cavite	**FMNH 205342**
Kerivoula papillosa	m	Philippines	Luzon	Cavite	**FMNH 205343**
Kerivoula papillosa	m	Philippines	Luzon	Cavite	**FMNH 205344**
Kerivoula papillosa	m	Philippines	Luzon	Quirino	**FMNH 180286**
Kerivoula papillosa	m	Vietnam		Darlac	**FMNH 46564**
Kerivoula papillosa	f	Vietnam		Darlac	**FMNH 46623**
Kerivoula pellucida	f	Malaysia	Borneo	Sabah	**BMNH 84.2058**
Kerivoula pellucida	f	Malaysia		Selangor	**FMNH 109035**
Kerivoula pellucida	f	Malaysia		Selangor	**FMNH 110749**
Kerivoula pellucida	f	Malaysia		Selangor	FMNH 110750
Kerivoula pellucida	f	Malaysia		Selangor	FMNH 110759
Kerivoula pellucida	f	Malaysia		Selangor	FMNH 110760
Kerivoula pellucida	f	Malaysia		Selangor	**FMNH 110856**
Kerivoula pellucida	f	Malaysia		Selangor	FMNH 67816
Kerivoula pellucida	m	Malaysia		Selangor	**FMNH 67817**
Kerivoula pellucida	f	Malaysia		Selangor	**HZM 1.352**
Kerivoula pellucida§	m	Philippines			**BMNH 55.12.26.264**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202780**
Kerivoula pellucida	f	Philippines	Bohol	Bohol	**FMNH 202781**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202782**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202783**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202784**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202785**
Kerivoula pellucida	f	Philippines	Bohol	Bohol	FMNH 202786
Kerivoula pellucida	f	Philippines	Bohol	Bohol	**FMNH 202787**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202788**
Kerivoula pellucida	f	Philippines	Bohol	Bohol	**FMNH 202789**
Kerivoula pellucida	f	Philippines	Bohol	Bohol	**FMNH 202790**
Kerivoula pellucida	f	Philippines	Bohol	Bohol	**FMNH 202791**
Kerivoula pellucida	m	Philippines	Bohol	Bohol	**FMNH 202792**
Kerivoula pellucida	m	Philippines	Cebu	Cebu	**FMNH 205817**
Kerivoula pellucida	m	Philippines	Mindanao	Agusan del Norte	FMNH 191418
Kerivoula pellucida	f	Philippines	Mindanao	Davao del Norte	**FMNH 61078**
Kerivoula pellucida	m	Philippines	Mindanao	Davao Oriental	**FMNH 186814**
Kerivoula pellucida	m	Philippines	Mindanao	Davao Oriental	**FMNH 186815**
Kerivoula pellucida	m	Philippines	Mindanao	Davao Oriental	**FMNH 208784**
Kerivoula pellucida	f	Philippines	Palawan	Palawan	**FMNH 168949**

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APPENDIX A . (Continued)

Species	sex	Country	Island	Province/State	Catalog number
Kerivoula pellucida	f	Philippines	Palawan	Palawan	**KU 165441**
*Kerivoula titania**	f	Cambodia		Mondul Kiri	**HZM 3.38179**
Kerivoula titania	f	Myanmar		Kachin	**HZM 2.35962**
Kerivoula titania	f	Vietnam		Gia Lai	**HZM 5.31779**
Kerivoula whiteheadi	m	Philippines	Bohol	Bohol	**FMNH 202771**
Kerivoula whiteheadi	m	Philippines	Bohol	Bohol	FMNH 202772
Kerivoula whiteheadi	m	Philippines	Bohol	Bohol	**FMNH 202775**
Kerivoula whiteheadi	f	Philippines	Camiguin Norte	Cagayan	**KU 164128**
Kerivoula whiteheadi	m	Philippines	Cebu	Cebu	**FMNH 205818**
Kerivoula whiteheadi	m	Philippines	Cebu	Cebu	FMNH 205819
Kerivoula whiteheadi	f	Philippines	Cebu	Cebu	**FMNH 205820**
Kerivoula whiteheadi	f	Philippines	Cebu	Cebu	**FMNH 205821**
Kerivoula whiteheadi	m	Philippines	Cebu	Cebu	**FMNH 205822**
Kerivoula whiteheadi	m	Philippines	Cebu	Cebu	FMNH 205823
Kerivoula whiteheadi	m	Philippines	Cebu	Cebu	**FMNH 205824**
Kerivoula whiteheadi	m	Philippines	Cebu	Cebu	**FMNH 205825**
Kerivoula whiteheadi	m	Philippines	Lubang	Lubang	**KU 164275**
Kerivoula whiteheadi	m	Philippines	Luzon	Aurora	**FMNH 190762**
Kerivoula whiteheadi	m	Philippines	Luzon	Cagayan	**FMNH 206007**
Kerivoula whiteheadi	m	Philippines	Luzon	Cagayan	**FMNH 214092**
Kerivoula whiteheadi	m	Philippines	Luzon	Camarines Sur	**FMNH 186084**
Kerivoula whiteheadi	m	Philippines	Luzon	Camarines Sur	**FMNH 186085**
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	FMNH 186086
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	**FMNH 186087**
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	FMNH 186088
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	**FMNH 186089**
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	**FMNH 191328**
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	**FMNH 191329**
Kerivoula whiteheadi	f	Philippines	Luzon	Camarines Sur	FMNH 191330
Kerivoula whiteheadi	m	Philippines	Luzon	Laguna	FMNH 166421
Kerivoula whiteheadi	m	Philippines	Luzon	Laguna	**FMNH 177473**
Kerivoula whiteheadi	m	Philippines	Luzon	Laguna	**FMNH 177474**
Kerivoula whiteheadi	m	Philippines	Luzon	Laguna	**FMNH 177475**
Kerivoula whiteheadi	m	Philippines	Luzon	Laguna	**FMNH 177476**
Kerivoula whiteheadi	m	Philippines	Luzon	Nueva Viscaya	**FMNH 194913**
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	**FMNH 180204**
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	FMNH 180205
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	**FMNH 180206**
Kerivoula whiteheadi	f	Philippines	Luzon	Quezon	**FMNH 180207**
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	**FMNH 180208**
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	**FMNH 180209**
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	**FMNH 180210**
Kerivoula whiteheadi	f	Philippines	Luzon	Quezon	**FMNH 180211**

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APPENDIX A . (Continued)

Species	sex	Country	Island	Province/State	Catalog number
Kerivoula whiteheadi	f	Philippines	Luzon	Quezon	FMNH 180212
Kerivoula whiteheadi	m	Philippines	Luzon	Quezon	**FMNH 180213**
Kerivoula whiteheadi	m	Philippines	Luzon	Rizal	FMNH 205409
Kerivoula whiteheadi	f	Philippines	Mindanao	Davao del Norte	**FMNH 61077**
Kerivoula whiteheadi	m	Philippines	Mindanao	Davao del Sur	**FMNH 56687**
Kerivoula whiteheadi	m	Philippines	Mindanao	Davao Oriental	**FMNH 186811**
Kerivoula whiteheadi	f	Philippines	Mindanao	Davao Oriental	**FMNH 186812**
Kerivoula whiteheadi	f	Philippines	Mindanao	Davao Oriental	FMNH 186813
Kerivoula whiteheadi	f	Philippines	Mindanao	Surigao del Sur	FMNH 190114
Kerivoula whiteheadi	m	Philippines	Mindanao	Surigao del Sur	**FMNH 190115**
Kerivoula whiteheadi	f	Philippines	Mindanao	Surigao del Sur	**FMNH 190116**
Kerivoula whiteheadi	m	Philippines	Mindoro	Occidental Mindoro	**FMNH 228477**
Kerivoula whiteheadi	f	Philippines	Mindoro	Occidental Mindoro	**FMNH 228478**
Kerivoula whiteheadi	m	Philippines	Mindoro	Occidental Mindoro	FMNH 228479
Kerivoula whiteheadi	m	Philippines	Mindoro	Occidental Mindoro	FMNH 228480
Kerivoula whiteheadi	m	Philippines	Mindoro	Occidental Mindoro	**FMNH 228481**
Kerivoula whiteheadi	m	Philippines	Mindoro	Occidental Mindoro	**FMNH 228785**
Kerivoula whiteheadi	f	Philippines	Mindoro	Occidental Mindoro	**FMNH 228786**
Kerivoula whiteheadi	m	Philippines	Mindoro	Occidental Mindoro	**FMNH 228787**
Kerivoula whiteheadi	m	Philippines	Sicogon	Iloilo	**PNM 5212**
Kerivoula whiteheadi	m	Philippines	Siquijor	Siquijor	**FMNH 209661**
Kerivoula whiteheadi	m	Philippines	Siquijor	Siquijor	**FMNH 209662**
Kerivoula whiteheadi	m	Philippines	Siquijor	Siquijor	**FMNH 209663**
Kerivoula whiteheadi	m	Philippines	Siquijor	Siquijor	**FMNH 209664**
Kerivoula whiteheadi	f	Philippines	Siquijor	Siquijor	**FMNH 209665**
Kerivoula whiteheadi	m	Philippines	Siquijor	Siquijor	FMNH 209666
Kerivoula whiteheadi	m	Philippines	Tumaguin	Iloilo	**PNM 5213**
Kerivoula whiteheadi§	m	Philippines	Luzon	Isabella	**BMNH 94.10.9.2**

APPENDIX B. Tissue samples included and GenBank numbers for Cyt *b* and CO1 sequences.

Species	Country	Region	Catalog number	Cyt *b*	COI	Citation
Kerivoula furva (*titania* in GB)	China	Hainan		JN112246		Wu *et al*. 2012
Kerivoula furva (*titania* in GB)	Taiwan	Kaohsiung		JN112244		Wu *et al*. 2012
Kerivoula hardwickii	Philippines	Bohol	FMNH202773	MN367904		present paper
Kerivoula hardwickii	Philippines	Bohol	FMNH202779	MN367904	MN367905	present paper
Kerivoula hardwickii	Philippines	Mindanao	FMNH191416	MN367903		present paper
Kerivoula hardwickii	Philippines	Mindanao	FMNH191417	MN367903	MN36791	present paper
Kerivoula hardwickii	Philippines	Mindanao	FMNH208783	MG194460	MN367906	present paper
Kerivoula hardwickii	Malaysia	Sabah, Borneo		EU188770		Anwarali *et al*. 2010
Kerivoula hardwickii	Malaysia	Sarawak, Borneo		GU585656		Anwarali *et al*. 2010
Kerivoula intermedia (*whiteheadi* in GB)	Malaysia	Pahang		EU188791		Anwarali *et al*. 2010
Kerivoula intermedia	Malaysia	Sarawak, Borneo		GU585658		Anwarali *et al*. 2010
Kerivoula lenis	Malaysia	Pahang		EU188772		Anwarali *et al*. 2010
Kerivoula lenis	Malaysia	Sarawak, Borneo		EU188773		Anwarali *et al*. 2010
Kerivoula minuta (*intermedia* in GB)	Malaysia	Pahang		EU188774		Anwarali *et al*. 2010
Kerivoula minuta	Malaysia	Sarawak, Borneo		GU585660		Anwarali *et al*. 2010
Kerivoula papillosa	Malaysia	Sarawak, Borneo		GU585663		Anwarali *et al*. 2010
Kerivoula papillosa	Philippines	Bohol	FMNH202793	MG194453	MN367907	present paper
Kerivoula papillosa	Philippines	Luzon	FMNH205343	MG194454		present paper
Kerivoula pellucida	Malaysia	Sarawak, Borneo		EU188786		Anwarali *et al*. 2010
Kerivoula pellucida	Malaysia	Sarawak, Borneo		GU585661		Anwarali *et al*. 2010
Kerivoula pellucida	Malaysia	Pahang		EU188787		Anwarali *et al*. 2010
Kerivoula pellucida	Malaysia	Pahang		EU188788		Anwarali *et al*. 2010
Kerivoula pellucida	Malaysia	Pahang		GU585648		Anwarali *et al*. 2010
Kerivoula pellucida	Malaysia	Pahang		GU585662		Anwarali *et al*. 2010
Kerivoula pellucida	Philippines	Bohol	FMNH202780	MG194451		present paper
Kerivoula pellucida	Philippines	Bohol	FMNH202787	MG194452	MN367908	present paper
Kerivoula pellucida	Philippines	Bohol	FMNH205817	MG194456		present paper
Kerivoula pellucida	Philippines	Mindanao		AB444717		Bastian *et al*. unpl 2008
Kerivoula pellucida	Philippines	Mindanao	FMNH186814	MG194441		present paper
Kerivoula pellucida	Philippines	Mindanao	FMNH191418	MG194447		present paper
Kerivoula pellucida	Philippines	Mindanao	FMNH208784	MG194461	MN367909	present paper

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APPENDIX B. (Continued)

Species	Country	Region	Catalog number	Cyt *b*	COI	Citation
Kerivoula sp.	Malaysia	Sarawak, Borneo		GU585651		Anwarali *et al*. 2010
Kerivoula sp.	Malaysia	Sabah, Borneo	T017154	MG194468		present paper
Kerivoula whiteheadi	Philippines	Bohol	FMNH202771	MG194449		present paper
Kerivoula whiteheadi	Philippines	Bohol	FMNH202775	MG194450	MN367913	present paper
Kerivoula whiteheadi	Philippines	Cebu	FMNH205818	MG194457	MN367914	present paper
Kerivoula whiteheadi	Philippines	Cebu	FMNH205821	MG194458		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH177475	MG194438		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH180210	MG194439		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH180211	MG194439		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH190762	MG194445		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH191328	MG194446		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH194913	MG194448		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH205409	MG194455		present paper
Kerivoula whiteheadi	Philippines	Luzon	FMNH206007	MG194459		present paper
Kerivoula whiteheadi	Philippines	Mindanao	FMNH190115	MG194443	MN367912	present paper
Kerivoula whiteheadi	Philippines	Mindanao	FMNH190116	MG194443		present paper
Kerivoula whiteheadi	Philippines	Siquijor	FMNH209664	MG194462		present paper
Kerivoula whiteheadi	Philippines	Siquijor	FMNH209665	MG194463		present paper
Kerivoula whiteheadi	Philippines	Mindoro	FMNH 228478	MG194437	MN367911	present paper
Kerivoula whiteheadi	Philippines	Camiguin Norte	KU164128	MG194464		present paper
Kerivoula whiteheadi	Philippines	Lubang	KU164275	MG194465	MN367915	present paper
Murina cyclotis	Philippines	Luzon	FMNH177471	MG194466		present paper
Phoniscus jagorii	Philippines	Bohol	FMNH202818	MG194467	MN367916	present paper
Myotis daubentonii	Germany			AF376847		Ruedi & Mayer 2001
Myotis bechsteinii	Switzerland			AF376843		Ruedi & Mayer 2001
Submyotodon latirostris	Taiwan			AM262330		Stadelmann *et al*. 2007