

## *Nyctalus plancyi* and *Falsistrellus petersi* (Chiroptera: Vespertilionidae) from northern Luzon, Philippines: ecology, phylogeny, and biogeographic implications

LAWRENCE R. HEANEY<sup>1,5</sup>, DANILO S. BALETE<sup>1</sup>, PHILLIP ALVIOLA<sup>2</sup>, ERIC A. RICKART<sup>3</sup>, and MANUEL RUEDI<sup>4</sup>

<sup>1</sup>Department of Zoology, Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, USA

<sup>2</sup>Museum of Natural History, University of the Philippines at Los Baños, College, Laguna 4031, Philippines

<sup>3</sup>Natural History Museum of Utah, 301 Wakara Way, Salt Lake City, UT 84108, USA

<sup>4</sup>Department of Mammalogy and Ornithology, Natural History Museum of Geneva, Geneva, Switzerland

<sup>5</sup>Corresponding author: E-mail: lheaney@fieldmuseum.org

We report the first records of *Nyctalus plancyi* from the Philippines, on the basis of three specimens taken in high-elevation mossy forest in the Central Cordillera of northern Luzon. We also report three new specimens of *Falsistrellus petersi* in the same areas, previously a poorly known species within the Philippines, and provide the first genetic data on the phylogenetic position of the genus. Analysis of sequence data from the mitochondrial gene cytochrome *b* shows ca. 4% divergence of the Philippine *N. plancyi* from a sample from China. Combined sequence data from cytochrome *b* and the nuclear gene RAG2 confirm that *N. plancyi* is related to *Pipistrellus*. They further show that *F. petersi* is related to *Hypsignathos* and *Vesperugo*, and *Philetor brachypterus* is related to *Tylonycteris*, with all of these taxa being members of the Vespertilionini, not the Pipistrellini. *Nyctalus plancyi* is the first mammal species documented to have colonized the main, oceanic body of the Philippines from the north (i.e., Taiwan or mainland China), rather than from the south (Borneo, Sulawesi, or New Guinea).

*Key words:* colonization, cytochrome *b*, RAG2, mossy forest, oceanic islands, Southeast Asia

### INTRODUCTION

The Philippine bat fauna is one of the most diverse in Asia, with 78 species currently formally recognized (Heaney *et al.*, 2010). However, much uncertainty exists about the number of species actually present, due to evidence that some currently recognized species represent species complexes (e.g., Ingle and Heaney, 1992; Rickart *et al.*, 1999; Helgen *et al.*, 2007; Sedlock *et al.*, 2008, 2011; Sedlock and Weyandt, 2009; Esselstyn *et al.*, 2012), documentation of species not previously known from the Philippines (e.g., Balete *et al.*, 1995; Esselstyn *et al.*, 2004; Heaney *et al.*, 2005; Duya *et al.*, 2007), and the continuing discovery of previously unknown endemic species (Esselstyn, 2007; Esselstyn *et al.*, 2008). Further, many of the recorded species are poorly known, with few specimens and little information on ecology and distribution within the archipelago, and much uncertainty about phylogenetic relationships (Heaney *et al.*, 2010). During the course of recent intensive efforts to document the mammal fauna of Luzon Island, the largest

island in the Philippines at ca. 103,000 km<sup>2</sup> (e.g., Duya *et al.*, 2007, 2011; Balete *et al.*, 2009, 2011; Alviola *et al.*, 2011; Heaney *et al.*, 2011; Rickart *et al.*, 2011a, 2011b; Sedlock *et al.*, 2011), we obtained specimens and data on two species of vespertilionids that allow us to add a new and surprising species record to the island's bat fauna, and to clarify the ecology and phylogenetic position of a poorly known species, as documented below.

### MATERIALS AND METHODS

#### *Field and Museum Methods*

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. Specimens were measured in the field with a ruler graduated in millimeters and with Pesola scales graduated to either 1 g (used for *Nyctalus*) or 0.1 g (used for *Falsistrellus*). 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 ankle to the tip of 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 base of the elbow to the wrist, with both joints folded; and body mass, measured in grams. Specimens were preserved in formalin, and later transferred to 70% ethanol, with the skulls removed and cleaned with dermestid beetles and a weak ammonia solution. Our specimens have been cataloged into the collection of the Field Museum of Natural History (FMNH); half of the specimens will later be deposited in the National Museum of the Philippines, Manila.

For existing fluid-preserved specimens housed in the Field Museum, we took external measurements with a ruler graduated in millimeters. We also examined specimens housed in the American Museum of Natural History (AMNH) and United States National Museum of Natural History (USNM). Images of the skulls were obtained with an AMRAY 1810 scanning electron microscope, using uncoated (untreated) skulls.

### Morphological Methods

Heaney took the following measurements on skulls using digital calipers graduated to 0.01 mm. Condylar-incisive length: from the anteriormost point on the incisors to the posteriormost point on the occipital condyles; zygomatic width: taken across the widest points on the zygomatic arches; interorbital width: least width between the orbits; mastoid width: greatest width across the mastoid region; orbito-temporal length: greatest length from the posterior margin of the orbito-temporal fossa to the posterior opening of the infraorbital canal; canine to M<sup>3</sup>: alveolar length from the anterior margin of the upper canine to the posterior margin of the third (last) upper molar; molariform toothrow length: alveolar length from the anteriormost lateral margin of the second (P<sup>4</sup>) premolar to the posterior margin of M<sup>3</sup>; palatal width: alveolar width taken between M<sup>3</sup>s; and palatal length: from the anterior edge of the palate at the midline (not including a spine if present) to the posterior margin of the palate along the midline (including a spine when present).

### Genetic Methods

Tissue samples associated with voucher specimens were obtained from three *N. plancyi*, three *F. petersi*, two *Philetor brachypterus* and three *Pipistrellus cf. javanicus* from the Philippines (Table 1). To place these specimens into a broader phylogenetic perspective, tissue samples from the following range of other vespertilionid species were also analyzed: *Nyctalus lasiopterus*, *N. leisleri*, *N. noctula*, *Glischropus tylopus*, *Scotomanes ornatus*, *Tylonycteris pachypus* and *Vespertilio murinus*. Together, with 22 other species obtained from GenBank and published elsewhere (Ruedi and Mayer, 2001; Hofer and Van Den Bussche, 2003; Sakai *et al.*, 2003; Stadelmann *et al.*, 2004a, 2004b, 2007; Ibáñez *et al.*, 2006; Cui *et al.*, 2007; Thabrah *et al.*, 2007; Trujillo *et al.*, 2009; Lack *et al.*, 2010), this taxon sampling includes representatives of all subfamilies and major tribes recovered in the molecular survey of the family Vespertilionidae by Van Den Bussche and colleagues (Hofer and Van Den Bussche, 2003; Roehrs *et al.*, 2010, 2011), as detailed in Table 1. *Cistugo seabrae*, a representative of the family Cistugidae and sister to the Vespertilionidae (Lack *et al.*, 2010), was chosen as an outgroup.

DNA was isolated from 20–30 mg tissue samples using a DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany) and eluted in 200 µL TE Buffer (provided elution buffer).

The complete mitochondrial cytochrome *b* gene (*cyt b*) and a portion of the nuclear Recombination Activating Gene 2 (RAG2) were amplified and sequenced in both directions following the protocols detailed in Ruedi *et al.* (2012). PCR products were submitted for sequencing to Macrogen Europe (The Netherlands).

The overlapping sequences of each individual were aligned and assembled to produce sequences of 1,140 bp (*cyt b*) or 755 bp (RAG2), using the software Sequencher version 4.6 (Gene Codes Corp.). This program was also used to ensure that all sequences were coding for amino acids, with no stop codons, and hence were assumed to represent orthologous genes. These new sequences were aligned with 24 *cyt b* and RAG2 sequences obtained from GenBank (Table 1). Sequences shorter than the target length were completed with 'N' to replace missing data. For consistency with other molecular studies in bat systematics (see e.g., Bradley and Baker, 2001; Salgueiro *et al.*, 2007), we measured pairwise sequence divergence with the K2P model of substitution (K2P distance), using the program MEGA version 5 (Tamura *et al.*, 2011).

All phylogenetic analyses were repeated for each data set separately and on the combined *cyt b* + RAG2 matrix. We used Bayesian (BA) inference and neighbor-joining (NJ) methods to reconstruct phylogenetic relationships. For each data set, the appropriate model of nucleotide substitutions was determined with the program MrModeltest version 2.2 (Nylander, 2004). The GTR + G + I model of substitution best described the *cyt b* and combined data sets, while the simpler model SYM+G provided the best fit for the RAG2 data set.

Bayesian posterior probabilities (PP) were calculated from four simultaneous chains run for 10 million generations with trees sampled every 1,000 generations, as implemented in MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001). Stationarity of likelihoods were checked with Tracer version 1.5 (Rambaut and Drummond, 2009) and the initial 10% of sampled trees were discarded as burn-in. NJ analyses and 1000 bootstrap replicates were based on the maximum likelihood distance selected with MrModeltest and performed with MEGA.

## RESULTS

### Ecology and Morphological Assessments

#### *Nyctalus plancyi*

On 24 March 2006, we captured a large vespertilionid 0.1 km S of the south peak of Mt. Data at 2,310 m elevation; on 18 February 2007, we captured two specimens of the same species on Mt. Amuyao at 1,730 m elevation, 0.3 km N of the Barlig Municipal Hall. Both localities are in Mountain Province, within the Central Cordillera of northern Luzon Island (Fig. 1).

The specimen from Mt. Data was captured in one of three 12 m mist nets set for three nights (9 net-nights) along the perimeter of a small, shallow pond surrounded by open vegetable fields, less than 100 m from remnant mossy forest, on the rolling plateau that forms the top of Mt. Data; several buildings and other structures existed within a few hundred meters

TABLE 1. Taxonomic sampling (following Hooper and Van Den Bussche, 2003, and Simmons, 2005), voucher number (for newly sequenced individuals) and geographic origin of the bat species included in the phylogenetic reconstructions. GenBank numbers and corresponding bibliographic references are also listed for each gene. FMNH stands for Field Museum of Natural History, MHNG for Natural History Museum of Geneva and EBD for Estación Biológica de Doñana

Classification	Voucher	Origin	Cyt <i>b</i>	Ref	RAG2	Ref
Family Vespertilionidae						
Subfamily Vespertilioninae						
<i>Perimyotis subflavus</i>		USA	AJ504449	c	GU328103	j
Tribe Nycticeiini						
<i>Eptesicus hottentotus</i>		South Africa	AJ841963	b	EU786886	k
<i>Eptesicus serotinus</i>		Azerbaijan/Europe	EU751000		IEU786909	k
<i>Scotomanes ornatus</i>	MHNG 1926.051	Laos PDR	JX570910	m	JX570927	m
Tribe Pipistrellini						
<i>Pipistrellus kuhlii</i>		Greece/Switzerland	AJ504444	c	DQ120829	h
<i>P. pygmaeus</i>		Greece/Spain	AJ504441	c	GU328107	j
<i>P. cf. javanicus</i>	FMNH 194729	Philippines	JX570908	m	JX570924	m
<i>P. cf. javanicus</i>	FMNH 191321	Philippines	JX570896	m	JX570925	m
<i>P. cf. javanicus</i>	FMNH 167237	Philippines	JX570909	m	JX570926	m
<i>Glischropus tylopus</i>	MHNG 1970.063	Malaysia	JX570898	m	JX570915	m
<i>Nyctalus lasiopterus</i>	EBD C-2306	Spain	JX570900	m	JX570916	m
<i>N. leisleri</i>	MHNG 1956.071	Switzerland	JX570901	m	JX570917	m
<i>N. noctula</i>	MHNG 1807.050	Greece	JX570902	m	JX570918	m
<i>N. plancyi</i>		China	DQ435073	d	—	—
<i>N. plancyi</i>	FMNH 193511	Philippines	JX570903	m	JX570919	m
<i>N. plancyi</i>	FMNH 193512	Philippines	JX570904	m	JX570920	m
<i>N. plancyi</i>	FMNH 188236	Philippines	JX570905	m	JX570921	m
Tribe Scotophilini						
<i>Scotophilus heathi</i>		Vietnam	EU750944	l	GU328112	j
<i>S. kuhlii</i>		Philippines	EU750914	l	GU328113	j
Tribe Vespertilionini						
<i>Falsistrellus petersi</i>	FMNH 188235	Philippines	JX570894	m	JX570912	m
<i>F. petersi</i>	FMNH 188238	Philippines	JX570895	m	JX570914	m
<i>F. petersi</i>	FMNH 193513	Philippines	JX570897	m	JX570913	m
<i>Hypsugo savii</i>		Switzerland	AJ504450	c	DQ120827	h
<i>H. cadornae</i>	MHNG 1926.050	Laos PDR	JX570899	m	DQ120828	h
<i>Philetor brachypterus</i>	FMNH 180236	Philippines	JX570906	m	JX570922	m
<i>P. brachypterus</i>	FMNH 191324	Philippines	JX570907	m	JX570923	m
<i>Tylonycteris pachypus</i>	MHNG 1970.041	China/Malaysia	EF517315	f	JX570928	m
<i>Vespertilio murinus</i>	MHNG 1957.087	Switzerland	JX570911	m	JX570929	m
Subfamily Kerivoulinae						
<i>Kerivoula cf. lenis</i>		Vietnam	AJ841970	b	AY141035	i
Subfamily Murininae						
<i>Harpiocephalus harpia</i>		Laos PDR	AJ841971	b	AM265701	g
Subfamily Myotinae						
<i>Myotis alcaethoe</i>		France	JQ044687	n	JQ044698	n
<i>M. annectans</i>		Laos PDR	AJ841956	b	AM265663	g
<i>M. brandtii</i>		Russia	AM261886	g	AM265647	g
<i>M. cf. browni</i>		Philippines	AF376859	a	AM265648	g
<i>M. formosus</i>		Laos PDR	AJ841950	b	AM265658	g
<i>M. gracilis</i>		Japan	AB106609	e	AM265660	g
<i>M. keaysi</i>		Mexico	AF376852	a	GU328083	j
<i>M. myotis</i>		Spain	AM261883	g	AM265679	g
<i>M. nattereri</i>		Greece	AF376863	a	AM265681	g
<i>M. riparius</i>		Brasil	AF376866	a	AM265687	g
Family Cistugidae						
<i>Cistugo seabrae</i>		South Africa	AJ841962	b	GU328052	j

References: a — Ruedi and Mayer (2001); b — Stadelmann *et al.* (2004b); c — Stadelmann *et al.* (2004a); d — Thabah *et al.* (2007); e — Sakai *et al.* (2003); f — Cui *et al.* (2007); g — Stadelmann *et al.* (2007); h — Ibáñez *et al.* (2006); i — Hooper and Van Den Bussche (2003), j — Lack *et al.* (2010); k — J. Juste, P. Benda, J. R. García-Mudarra, and C. Ibáñez (unpublished data); l — Trujillo *et al.* (2009); m — this paper; n — Ruedi *et al.* (2012)

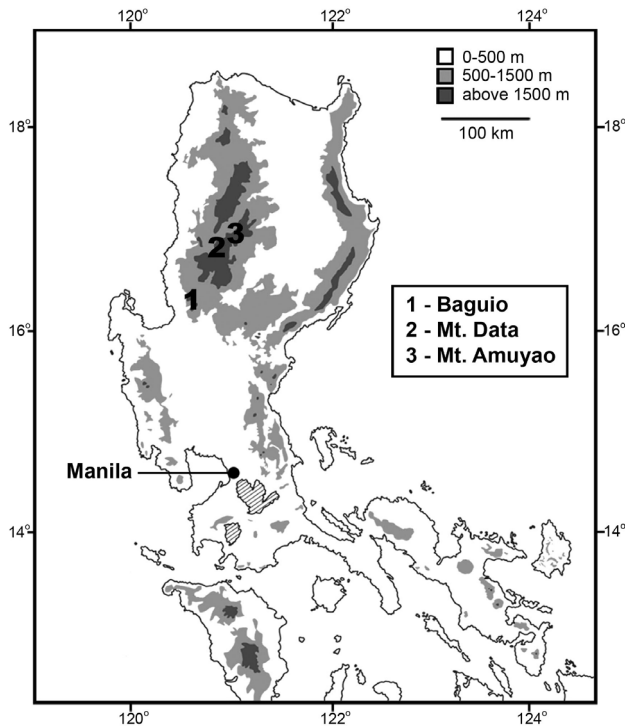


FIG. 1. Map of Luzon Island, Philippines, showing the locations of documented specimens of *F. petersi* (at 1, 2, and 3) and *N. plancyi* (at 2 and 3). See text for details

(Heaney *et al.*, 2006). Other bats captured at the same pond or closer to the nearby remnant forest were *Otopteropus cartilagonodus* ( $n = 4$ ) and *Pipistrellus tenuis* ( $n = 2$ ; specimens in FMNH). Other bats captured nearby were *Cynopterus brachyotis* (1), *Hipposideros diadema* (1), and *Falsistrellus petersi* ( $n = 2$ ; see below).

The second and third specimens, from Mt. Amuyao, were captured in 34 net-nights, in 12 m nets set along the top of a narrow ridge ascending steeply through pine forest with an understory of exotic grasses and small shrubs (especially *Melastoma* spp.); fires sweep over the hillside at least every few years. Lightly disturbed montane forest occurred about 100 m uphill, and many buildings and other structures within 300 m downhill. Other bats captured in the same net-line included *Macroglossus minimus* (one individual), *O. cartilagonodus* (7), and *Ptenochirus jagori* (7).

No known bat from the Philippines matches these specimens, but all of the features of these three specimens are consistent with those of *N. plancyi* from mainland China, northern Vietnam, and Taiwan (Miller, 1907; Bates and Harrison, 1997; Francis, 2008; Wilson, 2008); we follow Simmons (2005) in recognizing *N. plancyi* as distinct from

*N. noctula*. The total, tail, hind foot, ear, and forearm length of the three specimens are similar to those of a series from Szechuan, China (Table 2). The dorsal fur is dark brown, with a deep reddish tint in bright light, and has a glossy sheen; it extends only a short distance onto the patagium. The ventral fur is also brown but paler, sometimes with an orange tint; a fairly dense coat of this fur extends to the elbow both anterior and posterior to the humerus, and a sparse covering of hair extends laterally from the elbow to the proximal base of digits five and four, posterior to the wrist. No fur grows over the humerus or radio-ulna or on the digit bones. A small amount of this ventral fur grows posterior to the basal portion of the femurs, in the vicinity of the anus. The muzzle (Fig. 2A) is darkly pigmented, broad, and nearly naked except for some fine hairs growing on the upper and lower lips. The nostrils are moderately large and project laterally. The ears and tragus are short and broad, and the tragus is sharply curved anteriorly for its upper half. The tip of the tail protrudes a few millimeters beyond the end of the tail membrane, and the calcar is well developed. Adult males have a large, pendulous penis.

The skull (Fig. 3A–F) is relatively short and robust, with broad but slender zygomatic arches and a conspicuous lambdoidal crest. In lateral profile, the rostrum lies on the same plane as the braincase, with virtually no hint of a ‘forehead’ (Fig. 3C). The anterior palatal emargination is large. The dental formula is 2.1.2.3/3.1.2.3 = 34. The lateral upper incisor is slightly smaller in basal cross-section than the medial one (Fig. 3B and 3F). A small upper premolar ( $P^2$ ) lies lingual to the canine, between and in contact with both the canine and a large, molariform premolar ( $P^4$ ); the canine and second premolar ( $P^4$ ) are in contact laterally, and so the first upper premolar ( $P^2$ ) is not visible in the lateral view of the skull. All three upper molars are well developed, with the third molar ( $M^3$ ) about half to two-thirds the size of the second molar ( $M^2$  — Fig. 3F). There are three pairs of tricuspid lower incisors (Fig. 3D and 3E). The anterior lower premolar is about two-thirds the size of the second. Of the three lower molars, the second is the largest (Fig. 3D). The palate is broad, and the posterior margin lies posterior to the edge of the last molar by a distance greater than the width of the last molar (Fig. 3B). The auditory bullae are large, with a well-developed basioccipital pit medial to each bulla, and a smaller and shallower basioccipital pit lies anterior to each (Fig. 3B). Measurements of the crania show only slight differences from a series from Szechuan, China (Table 2).

TABLE 2. External and cranial measurements (in mm, except for body mass in g) of *N. plancyi* and *F. petersi* from Szechuan, China and Luzon, Philippines. See Materials and Methods. Numbers in parentheses indicate sample size when less than shown at top of column

Measurement	<i>N. plancyi</i>				<i>F. petersi</i>	
	Szechuan ( <i>n</i> = 7)		Luzon ( <i>n</i> = 3)		Luzon ( <i>n</i> = 3)	
	$\bar{x} \pm SD$	min-max	$\bar{x} \pm SD$	min-max	$\bar{x} \pm SD$	min-max
Total length	121.8 ± 4.5	117–127	123.3 ± 0.6	123–124	90 (2)	88–92
Tail length	46.2 ± 1.9	44–47	43.0 ± 1.7	42–45	37 (2)	35–39
Hind foot length	11.6 ± 0.5	11–12	12.7 ± 1.2	12–14	9 (2)	9
Ear length	16.6 ± 0.9	16–18	16.7 ± 0.6	16–17	14.3 ± 0.6	14–15
Forearm length	51.8 ± 1.1	50–53	48.7 ± 0.6	48–49	38.7 ± 0.6	38–39
Body mass	–	–	19.7 ± 0.6	19–20	6.3 (2)	6.0–6.6
Condylar-incisive length	17.98 ± 0.47	17.12–18.44	18.21 ± 0.41	17.74–18.49	14.44 ± 0.20	14.24–14.64
Condylar-canine length	17.00 ± 0.41	16.51–17.55	17.31 ± 0.44	16.81–17.62	13.63 ± 0.17	13.48–13.81
Zygomatic width	12.29 ± 0.38	11.82–12.78	12.05 ± 0.59	11.39–12.52	9.15 ± 0.06	9.09–9.21
Interorbital width	5.35 ± 0.06	5.25–5.41	5.00 ± 0.11	4.92–5.13	3.67 ± 0.15	3.52–3.81
Mastoid width	11.21 ± 0.32	10.66–11.74	11.08 ± 0.25	10.92–11.37	7.62 ± 0.09	7.57–7.72
Orbito-temporal length	6.64 ± 0.48	5.62–7.09	7.21 ± 0.14	7.06–7.32	5.47 ± 0.08	5.38–5.52
Canine to M <sup>3</sup>	6.54 ± 0.13	6.41–6.73	6.54 ± 0.23	6.28–6.71	5.40 ± 0.05	5.35–5.42
Molariform length	5.22 ± 0.10	5.09–5.41	5.42 ± 0.07	5.36–5.49	4.27 ± 0.01	4.26–4.28
Palatal width at M <sup>3</sup>	4.48 ± 0.18	4.27–4.78	4.76 ± 0.16	4.58–4.89	3.36 ± 0.04	3.32–3.39
Palatal length	6.60 ± 0.25	6.21–6.97	6.60 ± 0.23	6.34–6.77	5.87 ± 0.14	5.72–6.00

*Falsistrellus petersi*

On 18 and 29 March 2006, we captured two *Falsistrellus petersi* inside a large, old, wooden building located 0.8 km N, 1.5 km E of the south

peak of Mt. Data, at 2,128 m elevation. On 10 March 2007, we captured an additional specimen 0.5 km N, 0.5 km W of the peak of Mt. Amuyao at 2,530 m elevation (Fig. 1). Previous records from the Philippines, which we have re-examined, include one captured at Camp John Hay, Baguio, Benguet Province (ca. 1,250 m elevation; USNM 283870) and one from Panatao, Claver Municipality, Surigao del Norte Province, Mindanao (elevation unknown; AMNH 206748). We re-examined a specimen reported as *F. petersi* by Sedlock *et al.* (2008), and identified it as representing a large member of the *Pipistrellus javanicus* group. *Falsistrellus petersi* is also known from the Crocker Range of Sabah, Borneo; Minahassa, north Sulawesi; and Buru and Ambon islands in the Moluccas. It has been suggested that *F. mordax* (from Java) and *F. affinis* (from Burma, India, Nepal, Sri Lanka, and southwest China) are conspecific (Payne *et al.*, 1985; Francis and Hill, 1986; Corbett and Hill, 1992; Flannery, 1995; Simmons, 2005; Wilson, 2008).

The two specimens captured on Mt. Data were taken by hand inside an old, large, wooden building at 2,128 m in a residential area adjacent to a heavily used road. Scattered pine trees grew nearby among residences, small-scale agricultural plots, and grazing land; remnant mossy forest was ca. 1 km distant. Numerous small bats seen flying in the evenings near the building appeared similar and may have been this species. The third specimen was captured in a mist net set at the top of a steep ridge at 2,530 m elevation on Mt. Amuyao, in an area dominated



FIG. 2. A — *N. plancyi* (FMNH 188236), photographed on 24 March 2006, B — *F. petersi* (FMNH 188238), photographed on 29 March 2006. Both photographs taken on Mt. Data, Mountain Province, Luzon by L. R. Heaney

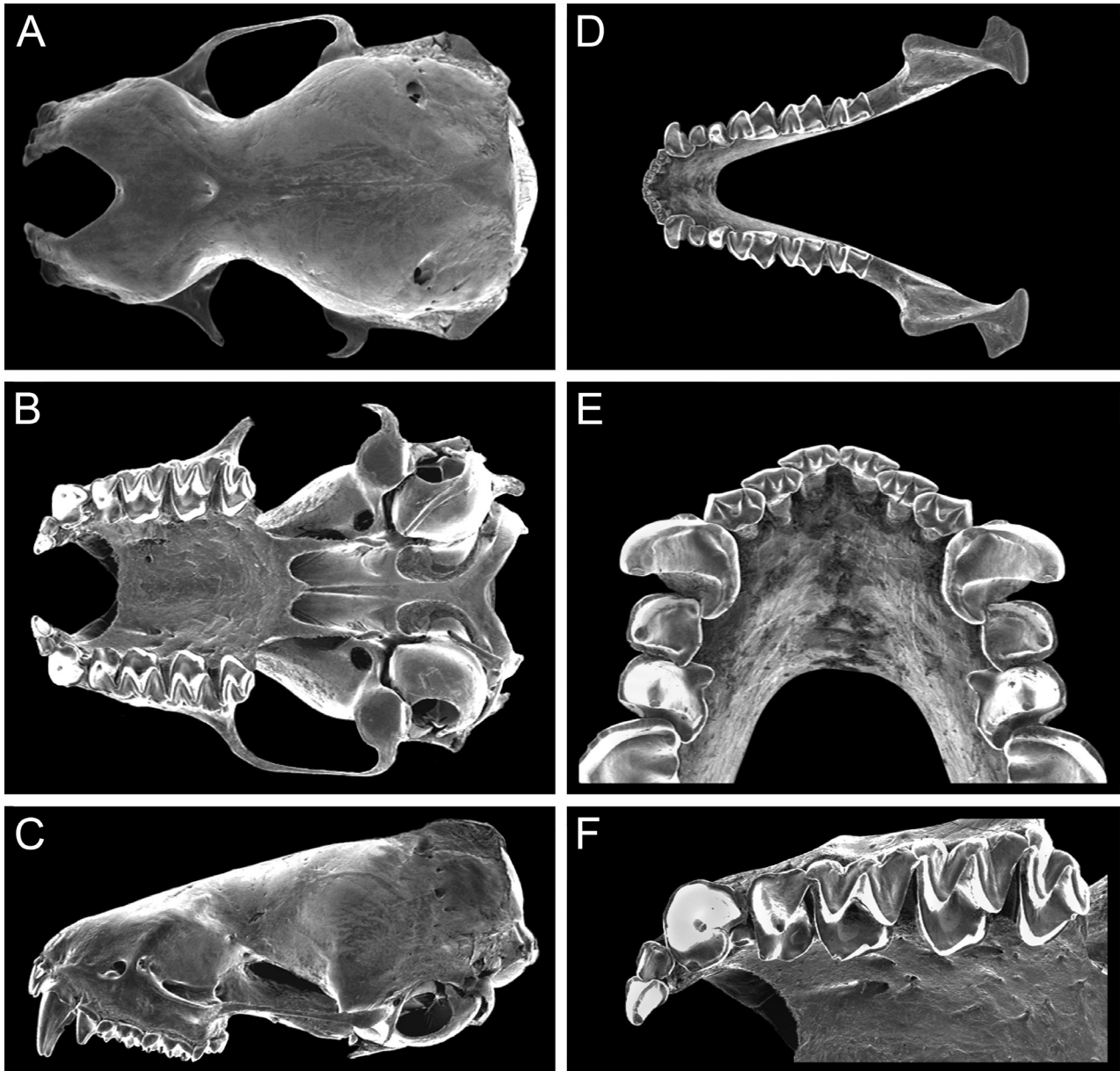


FIG. 3. Scanning electron micrographs of the cranium, dentition, and mandible of *N. plancyi* (FMNH 193511) from Mt. Amuyao, Mountain Province, Luzon

by old-growth mossy forest; the net was set on the ridge where no trees grew, so that the net was above the surrounding vegetation. Scattered pine trees grew nearby along the ridge-top. Other bats captured at this location were *Otopteropus cartilagonodus*, *Rhinolophus* sp. (*R. arcuatus* group), and *Pipistrellus tenuis*. In a small grocery store, made of wood, in the town of Barlig at the base of Mt. Amuyao, ca. 1,500 m elevation, we noted that among the dried luna moths for sale were several bats that appeared to be this species. The owner told us that the bats, like the moths, flew into the store in the evenings and were captured by hand. We saw many

small vespertilionid bats flying over the town in the evenings that may have been this species.

Cranial measurements of our three specimens are consistent with those of specimens in AMNH and USNM (Table 2) and published measurements of *F. petersi* from Borneo and Buru, and *F. affinis* from India (Francis and Hill, 1986). The dorsal fur (Fig. 2B) is soft, dense, and long, somewhat shaggy, and dark brown with pale tips that appear gray or silvery. The ventral pelage is paler with brown tips; the fur extends only a short distance onto the patagium adjacent to the torso. A small amount of pale brown fur extends onto the ventral surface of the femur and

adjacent to the anus. The muzzle is dark brown, and appears narrow and elongated compared to *Pipistrellus javanicus*, with less swelling laterally. The nostrils are slightly elongated. The ears are substantially taller than wide; the tragus is of moderate length and width, and is slightly curved anteriorly. The tip of the tail extends about 1.5 mm beyond the tail membrane. The calcar is well developed, with a slight keel extending medially from the hind foot. Adult males have a long, pendulous penis.

The skull (Fig. 4A–F) is somewhat elongate and narrow, with slender zygomatic arches. The occipital crests are well-developed, and the sagittal and lambdoidal crests are low but present. In lateral view (Fig. 4C), there is a slight inflection from the plane of the rostrum upward to the plane of the braincase, producing a low ‘forehead’. A ridge runs along the superior margin of the orbit from the anterior edge to a supraorbital tubercle. The dental formula is 2.1.2.3/3.1.2.3 = 34. The first upper incisor (Fig. 4F) has prominent anterior and posterior cusps; the second upper incisor has a small postero-lingual cusp, with a basal area similar to that of the first upper incisor. The upper canine is unicuspid and has a prominent lingual cingulum. The first upper premolar (P<sup>2</sup>) has a basal area somewhat smaller than either incisor. In two of three specimens, P<sup>2</sup> is in line laterally with the canine and second premolar (P<sup>4</sup>), and is fully visible in lateral view; in one, it is displaced lingually and invisible in lateral view, and the canine is in full contact with the second upper premolar. The second upper premolar is large, and in contact with the posterior edge of the first premolar (Fig. 4F). The first upper molar is slightly smaller than the second; the third molar is substantially smaller and lacks the hypocone. The palate is noticeably longer than wide, and the tooththrows converge slightly anteriorly. Basioccipital pits are virtually absent.

There are three pairs of lower incisors; all are tricuspidate, with an increase in width posteriorly (Fig. 4C). The lower canine has a small anterior cusp that is in contact with I<sub>3</sub>. The first lower premolar (P<sub>2</sub>) is half to two-thirds the basal area of the canine and the second premolar (P<sub>4</sub>); the canine and second premolar are about equal in height. Of the three lower molars, the first is largest and the third smallest.

#### Genetic Assessments

Seventeen new *cyt b* sequences were obtained and submitted to GenBank (accession numbers JX570894–JX570911 — see Table 1). All three

sequences of *N. plancyi* from the Philippines were identical and differed by 44 point mutations from a sample from China (4% K2P distance). Pairwise comparisons of genetic differentiation with the other *Nyctalus* species were all much higher, ranging from 16.1% (compared to *N. noctula*) to 18.5% (compared with *N. lasiopterus*). For *F. petersi*, two individuals (DSB 3938 and LRH 7476) had identical *cyt b* sequences, while they differed by three point mutations (0.3%) from the third specimen (EAR 6413). These *Falsistrellus* differed at least by 13% from any other vespertilionid analysed here.

Eighteen partial sequences of RAG2 were obtained and deposited in GenBank (accession numbers JX570912–JX570929). Interestingly, the sequence of *T. pachypus* contained two codon insertions (AAG, and CAG, respectively) when aligned with most other vespertilionids. These insertions correspond to a Lysine and a Glutamine residue, respectively, and are located at position 17 and 22 respectively of the amino acid alignment (after residue 84 and 89 in the homologous gene sequence of humans). Likewise, the two sequences of *Philetor* also were longer than in most other bats sequenced due to the same CAG insertion at position 22, but lacked the other inserted codon. A Blast search (as of June 2012) indicates that among the 328 sequences of vespertilionid RAG2 deposited in GenBank, only *T. robustula* also contains the AAG insertion, while the extra CAG codon was found in both *T. robustula* and *Eptesicus dimissus*. These rare codon insertions thus concern only three species that also appear to be closely related in a broader molecular phylogenetic context (Lack *et al.*, 2010), and thus represent singular apomorphic characters that identify this clade.

#### Phylogenetic Reconstructions

As continental *N. plancyi* is represented only by a *cyt b* sequence (Table 1), this reference individual appears only on reconstructions based on that gene, but it is consistently associated with *N. plancyi* from the Philippines (BP/PP 100% in all analyses — Fig. 5). Otherwise, phylogenetic relationships inferred from *cyt b* alone or in combination with RAG2 (Fig. 6) are very similar with no strongly supported node (BP/PP > 80%) conflicting between analyses.

In contrast, analyses of the nuclear data set (RAG2 alone) resulted in much less resolved trees, with rampant low bootstrap or posterior probabilities of nodes (results not shown), but none

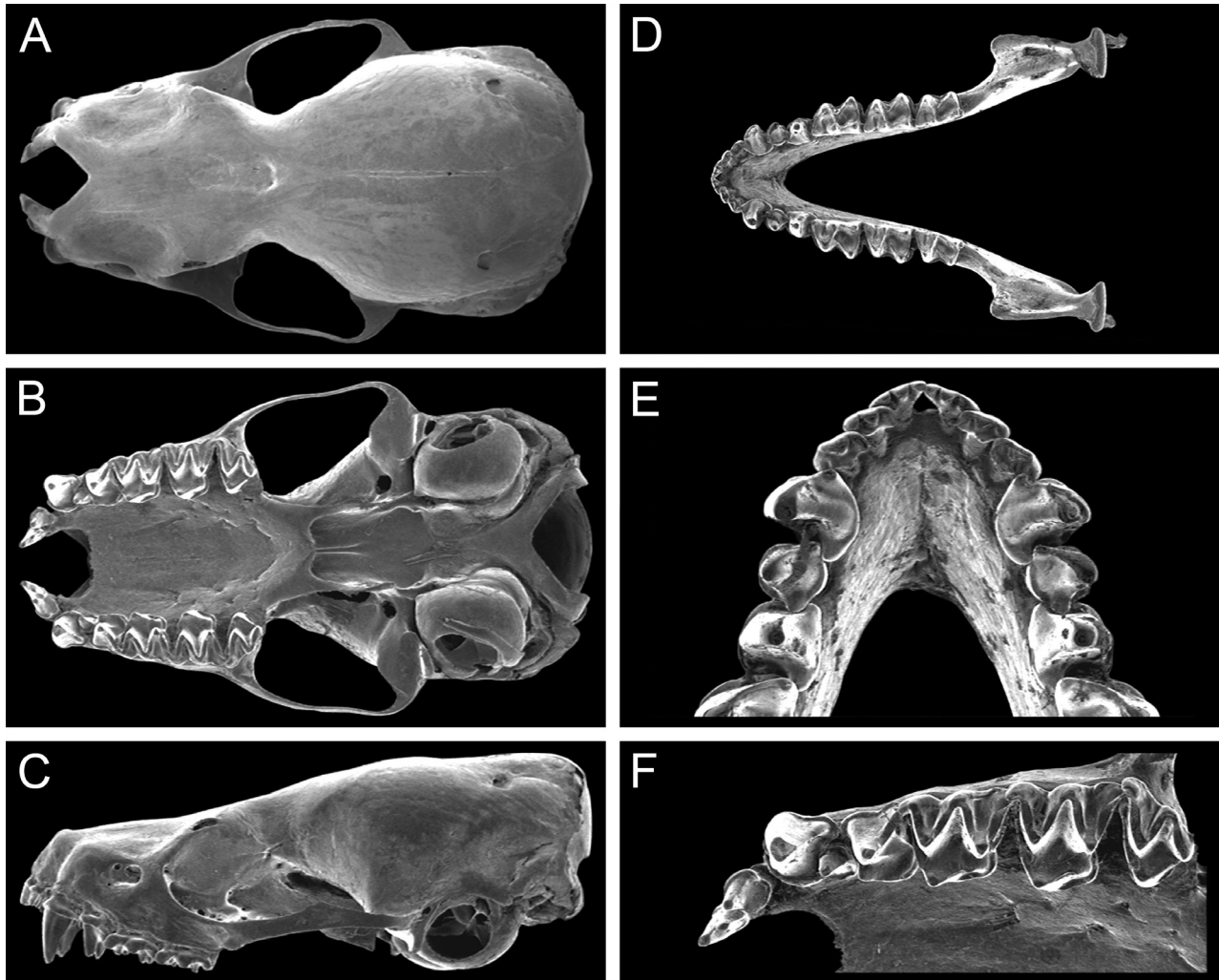


FIG. 4. Scanning electron micrographs of the cranium, dentition, and mandible of *F. petersi* (FMNH 188238 for A, B, C, and F; 188235 for D and E) from Mt. Data, Mountain Province, Luzon

of the supported relationships are in conflict with results from analyses of the other data sets. For instance, this nuclear gene supports strongly (BP/PP > 95%) a Pipistrellini clade comprised of *Glischropus*, *Nyctalus* and *Pipistrellus*, and the sister-group relationship of *Falsistrellus* with *Hypsugo*, and *Philetor* with *Tylonycteris*. These relationships also receive high support in the other reconstructions (Figs. 5 and 6). Other strongly supported relationships include the monophyly of all *Nyctalus* species and the paraphyly of the genus *Pipistrellus*, while the few uncertainties in the molecular analyses include the relative position of *Vespertilio* within the Vespertilionini and of *Perimyotis* and *Scotophilus* within the Vespertilionidae, a situation mirrored by other molecular surveys (e.g., Hofer and Van Den Bussche, 2003; Roehrs *et al.*, 2010, 2011).

## DISCUSSION

### *Molecular Systematics*

Molecular analyses clearly corroborate the morphological evidence that *Nyctalus* specimens from the Philippines are more closely related to the Oriental species *N. plancyi* than to other taxa from the Palearctic region. The reference *cyt b* sequence issued from a Chinese specimen is distinct (4% K2P distance) from those from the Philippines, but still in the upper limits for intra-specific comparisons (Bradley and Baker, 2001; Ruedi and McCracken, 2009). In spite of the large geographic distance and expanses of open water separating these samples, these specimens are likely conspecific. Species from this genus are known to undertake considerable migrations across the European continent



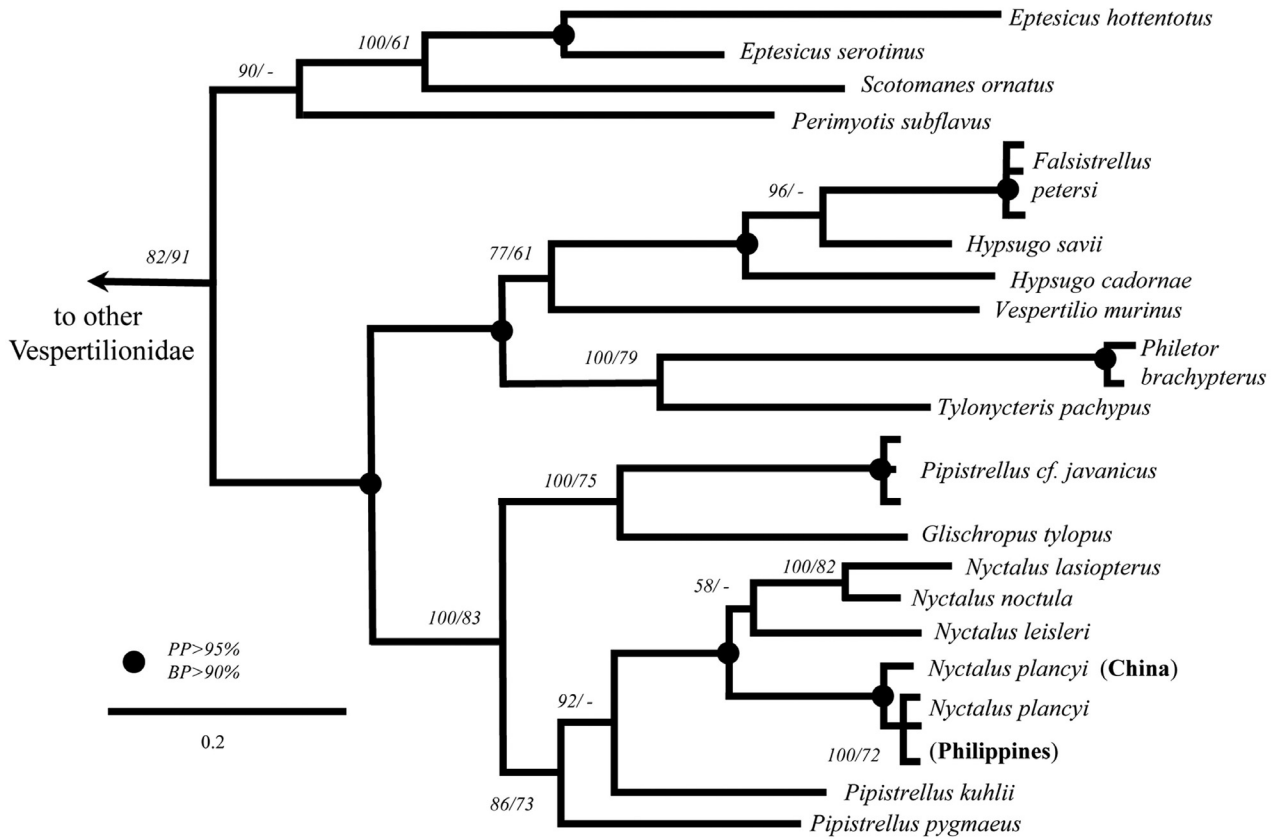


FIG. 5. Part of the Bayesian consensus tree representing the phylogenetic relationships of selected vespertilionid bats based on cytochrome *b* (1140 bp) sequence data. Outgroups and other basal vespertilionids were omitted for simplicity. A solid dot at a node denotes that it is supported by at least 95% posterior probability (PP in BA reconstructions) and 90% bootstrap (BP in NJ reconstructions); other support values are given as percentages (PP listed first and BP second). The scale bar represents 0.2 changes

(Petit and Mayer, 1999, 2000; Hutterer *et al.*, 2005), so have high potential for dispersal, but it is unclear whether they can migrate regularly over large expanses of open sea (Salgueiro *et al.*, 2008). Comparative phylogeographic studies in European *Nyctalus* species (Salgueiro *et al.*, 2007) showed that insular and continental samples of *N. leisleri* differ by less than 3%, while sympatrically-occurring species (*N. leisleri*, *N. noctula*, and *N. lasiopterus*) differ by > 9%.

Phylogenetic analyses suggest that all *Nyctalus* species form a strongly supported clade that is nested within a larger clade containing the paraphyletic genus *Pipistrellus*, and *Glischropus* (Fig. 6). This is in line with recent surveys of molecular relationships within the Vespertilionidae (Hofer and Van Den Bussche, 2003; Francis *et al.*, 2010) and of results suggested by earlier karyological analyses (Volleth and Heller, 1994).

The phylogenetic position of *F. petersi* and *P. brachypterus* based on both mitochondrial and nuclear genes is shown here for the first time (Figs.

5 and 6), and again corroborates the hypothesized position suggested by karyological characters that place these genera in the tribe Vespertilionini (Volleth and Heller, 1994), not in the Pipistrellini. In our sampling, the closest, albeit with high genetic distance (13–16% K2P distance for the *cyt b* gene), taxon to *Falsistrellus* is *Hypsugo*, while *Philetor* is more closely related to the specialized bamboo bats of the genus *Tylonycteris* (Fig. 5). This surprising relationship is further supported by a shared CAG codon insertion in their RAG2 sequence, an insertion also found in the enigmatic species *Eptesicus dimissus* (Lack *et al.*, 2010). These molecular results also support the generic distinction of *Falsistrellus* from *Pipistrellus* suggested by several morphological characters (Kitchener *et al.*, 1986; Hill and Harrison, 1987). The consistently close relationship of *Falsistrellus* with *Hypsugo* in all analyses suggest that the former genus is part of the Hypsugine group recently defined by Roehrs *et al.* (2011), along with other genera of Australian origin (*Chalinolobus* and *Vespadelus*).

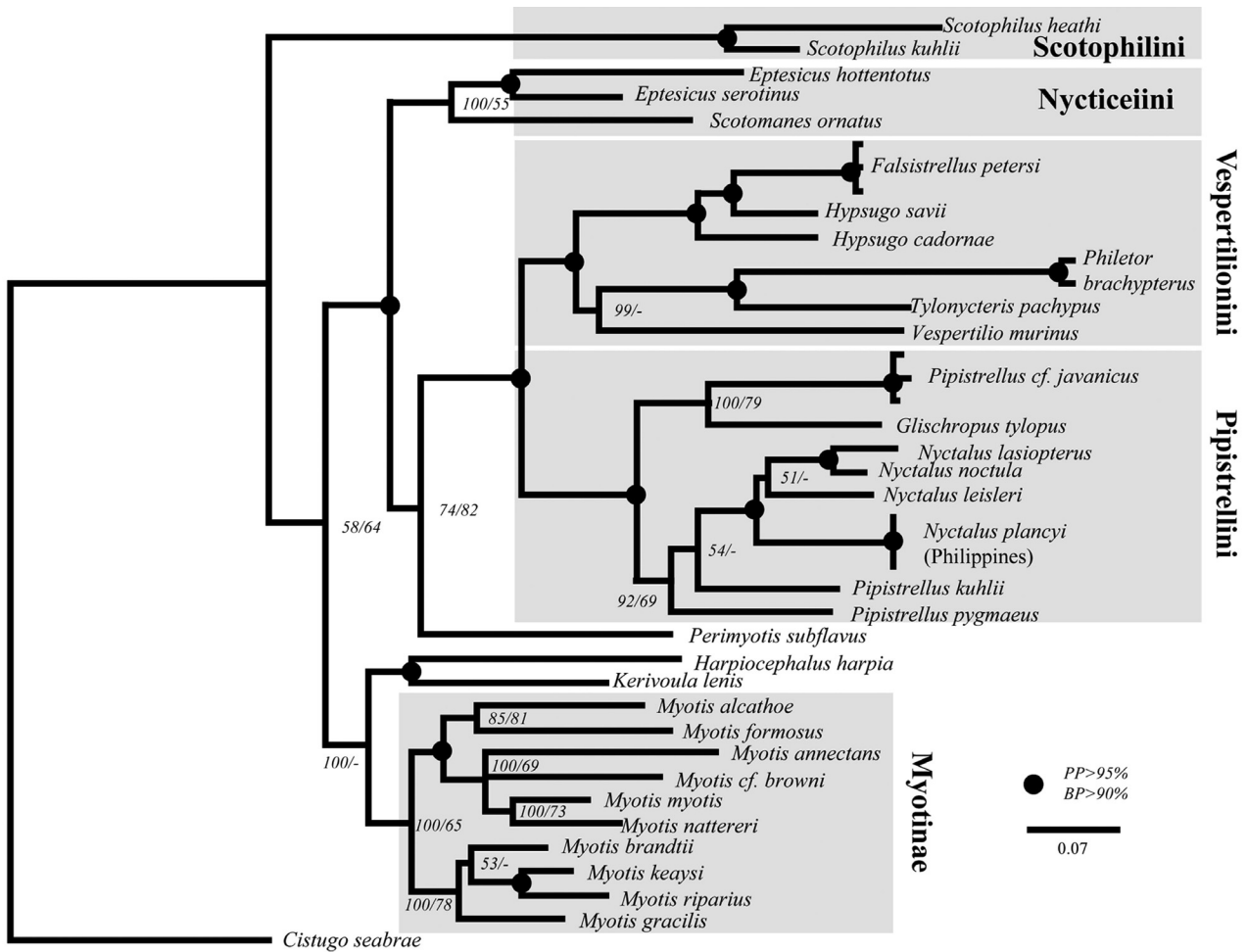


FIG. 6. Bayesian consensus tree representing the phylogenetic relationships of selected vespertilionid bats based on combined cytochrome *b* (1140 bp) and RAG2 (755 bp) sequence data. Clades consistent with the tribal and subfamilial subdivision of the Vespertilionidae (Roehrs *et al.*, 2010) are highlighted in grey. Other conventions are the same as in Fig. 4

### Biogeography

The bats of Luzon Island have been studied for many decades (e.g., Hollister, 1913; Taylor, 1934; Lawrence, 1939; Sanborn, 1952), but most remain poorly known in many respects. Fruit bats are abundant, diverse, and easily captured in mist nets, and most studies have focused on them (e.g., Ingle, 1993, 2003; Roberts, 2006a, 2006b; Sedlock *et al.*, 2008, 2011; Heaney and Roberts, 2009). Insectivorous bats are much less well known, with new records for Luzon taken relatively frequently (e.g., *Coelops hirsutus* and *Kerivoula papillosa* — Duya *et al.*, 2007; *Murina suilla* — Heaney *et al.*, 2010; *Otomops* sp. — Heaney *et al.*, 2005). Further, most studies of bats have been conducted in lowland dipterocarp forest below 800 m, and few records have been available from montane and mossy forest above ca. 800 m, especially for insectivorous bats;

it can be expected that surprising discoveries will be made in such highland areas.

The presence of *N. plancyi* on Luzon represents the first record of a mammal species that occurs both in the main body of the oceanic portions of the Philippines and to the north, on Taiwan and in mainland China. The oceanic Philippines includes most of the islands of the archipelago, which are tectonic/volcanic in origin and have not had dry-land connections to Asia or other land areas (Mitchell *et al.*, 1986; Hall, 1998, 2002), and excludes Palawan and small associated islands, which may have been connected to Borneo during portions of the Pleistocene (Bird *et al.*, 2005; Esselstyn *et al.*, 2010; Piper *et al.*, 2011). It is noteworthy that our records of these bats are from high elevations, ca. 1,700–2,300 m, in cool, moist areas with native vegetation composed of mossy forest, where many plants are most closely related to those of

the temperate zone (e.g., oaks, laurels, myrtles, and gymnosperms — Rickart *et al.*, 2011b). Other species of bats have conspecifics either to the south (Sulawesi), southwest (Borneo and the Sunda Shelf), or over widespread parts of Indo-Australia (Ingle and Heaney, 1992; Heaney and Roberts, 2009; Heaney *et al.*, 2010). Most non-volant mammals on Luzon are members of old endemic clades that probably entered from the Asian mainland ca. 10–15 million years ago; a few probably entered from the south, but did so several million years ago (e.g., Steppan *et al.*, 2003; Jansa *et al.*, 2006; Esselstyn *et al.*, 2009, 2011). The sole exception is one species of shrew (*Crocidura tanakae*) that occurs on Taiwan and nearby mainland China and on several small oceanic islands that lie about mid-way between Taiwan and Luzon (Esselstyn and Oliveros, 2010). The morphological and genetic similarity of the Luzon sample of *N. plancyi* and specimens from mainland China implies that either this species arrived recently on Luzon, or that like its European and some Asian relatives, it is migratory, with individuals moving from Luzon to Taiwan and/or mainland China. Further study is needed to resolve this unique situation among Philippine mammals.

The presence of *F. petersi* at our study areas in the highland Central Cordillera of Luzon is less surprising, given the previous records of the species from Baguio (which is also in the Central Cordillera) and from Mindanao, Borneo, Sulawesi, and the Moluccas (Francis and Hill, 1986), which imply broad distribution over a portion of the Sunda Shelf and Wallacea and, therefore, the ability to cross permanent sea channels. Taken together with the previous record from Baguio, our records imply that this species primarily occurs above 1,500 m, in cool, moist habitats. The specimens from Borneo, like ours, were taken in a house, implying that they may often roost in such places.

These records reinforce the prior perception that the insectivorous bats of the Philippines are still very poorly known, and raise the possibility that highland areas may support additional species that are most closely related to species in temperate continental Asia to the north, rather than on tropical islands to the south. They support the view that some bats (e.g., *Cynopterus brachyotis*, *Macroglossus minimus*, and *Rousettus amplexicaudatus*) have entered the Philippines recently, thus demonstrating their ability to cross permanent salt-water channels, while others that are endemic, and especially those that are members of endemic clades (e.g., *Haplonycteris fischeri* and *Ptenochirus jagori*) have

diversified within the archipelago over a period of millions of years. The dynamics of bat species richness in the Philippines is thus complex, including both shallow- and deep-time events (Heaney and Rickart, 1990; Heaney and Roberts, 2009).

#### ACKNOWLEDGEMENTS

Financial support for this project has been provided by the Barbara Brown and Ellen Thorne Smith Funds of the Field Museum, the Grainger Foundation, and the Negaunee Foundation, for which we are grateful. Permits were provided by the Philippine Department of Environment and Natural Resources (DENR); we especially thank the staff of the Protected Areas and Wildlife Bureau and the DENR Regional Office for the Cordilleran Autonomous Region. Access to specimens at the AMNH and USNM was kindly provided by N. Simmons and R. Voss, and by M. Carleton and R. Thorington Jr., respectively. We thank Andria Niedzielski for her assistance with preparing the figures; Betty Strack for sharing her expertise with the Scanning Electron Microscope; Anna Goldman, John Phelps, and Bill Stanley for their help with preparing the specimens for study; and Janik Pralong for help in the DNA extraction. The manuscript was improved by suggestions from two anonymous reviewers.

#### LITERATURE CITED

- ALVIOLA, P. A., M. R. M. DUYA, M. V. DUYA, L. R. HEANEY, and E. A. RICKART. 2011. Mammalian diversity patterns on Mt. Palali, Caraballo Mountains, Luzon. *Fieldiana Life and Earth Sciences*, 2: 61–74.
- BALETE, D. S., L. R. HEANEY, and R. I. CROMBIE. 1995. First records of *Hipposideros lekaguli* Thonglongya and Hill 1974 from the Philippines. *Asia Life Sciences*, 4: 89–94.
- BALETE, D. S., L. R. HEANEY, M. J. VELUZ, and E. A. RICKART. 2009. Diversity patterns of small mammals in the Zambales Mts., Luzon, Philippines. *Mammalian Biology*, 74: 456–466.
- BALETE, D. S., P. A. ALVIOLA, M. R. M. DUYA, M. V. DUYA, L. R. HEANEY, and E. A. RICKART. 2011. The mammals of the Mingan Mountains, Luzon: evidence for a new center of mammalian endemism. *Fieldiana Life and Earth Sciences*, 2: 75–87.
- BATES, P. J. J., and D. L. HARRISON. 1997. *Bats of the Indian Subcontinent*. Harrison Zoological Museum, Sevenoaks, Kent, 258 pp.
- BIRD, M. I., D. TAYLOR, and C. HUNT. 2005. Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? *Quaternary Science Reviews*, 24: 2228–2242.
- BRADLEY, R. D. and R. J. BAKER. 2001. A test of the genetic species concept: cytochrome *b* sequences and mammals. *Journal of Mammalogy*, 82: 960–973.
- CORBET, G., and J. E. HILL. 1992. *The mammals of the Indo-malayan Region*. Oxford University Press, Oxford, 488 pp.
- CUI, J., N. I. J. HAN, D. STREICKER, G. LI, X. C. TANG, Z. L. SHI, Z. H. HU, G. P. ZHAO, A. FONTANET, Y. GUAN, *et al.* 2007. Evolutionary relationships between bat coronaviruses and their hosts. *Emerging Infectious Diseases*, 13: 1526–1532.
- DUYA, M. R. M., M. V. DUYA, P. A. ALVIOLA, D. S. BALETE, and L. R. HEANEY. 2007. Report on a survey of the mammals of

- the Sierra Madre Range, Luzon Island, Philippines. *Banwa*, 4: 41–68.
- DUYA, M. R. M., M. V. DUYA, P. A. ALVIOLA, D. S. BALETE, and L. R. HEANEY. 2011. Diversity of small mammals in montane and mossy forests on Mount Cetaceo, Cagayan Province, Luzon. *Fieldiana Life and Earth Sciences*, 2: 88–95.
- ESSELESTYN, J. A. 2007. A new species of stripe-faced fruit bat (Chiroptera: Pteropodidae: *Styloctenium*) from the Philippines. *Journal of Mammalogy*, 88: 951–958.
- ESSELESTYN, J. A., and C. H. OLIVEROS. 2010. Colonization of the Philippines from Taiwan: a multi-locus test of the biogeographic and phylogenetic relationships of isolated populations of shrews. *Journal of Biogeography*, 37: 1504–1514.
- ESSELESTYN, J. A., P. WIDMANN, and L. R. HEANEY. 2004. The mammals of Palawan Island, Philippines. *Proceedings of the Biological Society of Washington*, 117: 285–316.
- ESSELESTYN, J. A., H. J. D. GARCIA, M. G. SAULOG, and L. R. HEANEY. 2008. A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. *Journal of Mammalogy*, 89: 815–825.
- ESSELESTYN, J. A., R. M. TIMM, and R. M. BROWN. 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.
- ESSELESTYN, J. A., C. H. OLIVEROS, R. G. MOYLE, A. T. PETERSON, J. A. MCGUIRE, and R. M. BROWN. 2010. Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line. *Journal of Biogeography*, 37: 2054–2066.
- ESSELESTYN, J. A., S. P. MAHER, and R. M. BROWN. 2011. Species interactions during diversification and community assembly in an island radiation of shrews. *PLoS ONE*, 6(7): e21885.
- ESSELESTYN, J. A., J. L. SEDLOCK, F. A. ANWARALI KHAN, B. J. EVANS, and L. R. HEANEY. 2012. Single-locus species delimitation: a test of the mixed Yule-coalescent model, with an empirical application to Philippine round-eared bats. *Proceedings of the Royal Society*, 279B: 3678–3686.
- FLANNERY, T. 1995. *Mammals of the South-West Pacific and Moluccan Islands*. Cornell University Press, Ithaca, 464 pp.
- FRANCIS, C. M. 2008. *A guide to the mammals of Southeast Asia*. Princeton University Press, Princeton, 392 pp.
- FRANCIS, C. M., and J. E. HILL. 1986. A review of the Bornean *Pipistrellus* (Mammalia: Chiroptera). *Mammalia*, 50: 43–55.
- FRANCIS, C. M., A. V. BORISENKO, N. V. IVANOVA, J. L. EGER, B. K. LIM, A. GUILLEN-SERVENT, S. V. KRUSKOP, I. MACKIE, and P. D. N. HEBERT. 2010. The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia. *PLoS ONE*, 5(9): e12575.
- HALL, R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99–131, in *Biogeography and geological evolution of SE Asia* (R. HALL and J. D. HOLLOWAY, eds.). Backhuys Publishers, Leiden, 417 pp.
- HALL, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences*, 20: 353–431.
- HEANEY, L. R., and E. A. RICKART. 1990. Correlations of clades and clines: geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. Pp. 321–332, in *Vertebrates in the tropics* (G. PETERS and R. HUTTERER, eds.). Museum Alexander Koenig, Bonn, 424 pp.
- HEANEY, L. R., and T. E. ROBERTS. 2009. New perspectives on the long-term biogeographic dynamics and conservation of Philippine fruit bats. Pp. 17–58, in *Ecology, evolution, and conservation of island bats* (T. H. FLEMING and P. A. RACEY, eds.). University of Chicago Press, Chicago, 560 pp.
- HEANEY, L. R., D. S. BALETE, G. V. GEE, M. V. LEPITEN-TABAO, E. A. RICKART, and B. R. TABARANZA, JR. 2005. Preliminary report on the mammals of Balbalasang, Kalinga Province, Luzon. *Sylvatrop*, 13 (2003): 51–62.
- HEANEY, L. R., D. S. BALETE, J. SARMIENTO, and P. A. ALVIOLA. 2006. Losing diversity and courting disaster: the mammals of Mt. Data National Park. *Haring Ibon*, 25: 15–23.
- HEANEY, L. R., M. L. DOLAR, D. S. BALETE, J. A. ESSELESTYN, E. A. RICKART, and J. L. SEDLOCK. 2010. Synopsis of Philippine mammals. Available at <http://fieldmuseum.org/explore/synopsis-philippine-mammals>.
- HEANEY, L. R., E. A. RICKART, D. S. BALETE, M. V. DUYA, M. R. M. DUYA, and S. STEPPAN. 2011. Seven new species and a new subgenus of forest mice (Rodentia: Muridae: *Apomys*) from Luzon Island. *Fieldiana Life and Earth Sciences*, 2: 1–60.
- HELGEN, K. M., D. KOCK, R. K. SALVE, C. GOMEZ, N. R. INGLE, and M. H. SINAGA. 2007. Taxonomy and natural history of the Southeast Asian fruit-bat genus *Dyacopterus*. *Journal of Mammalogy*, 88: 302–318.
- HILL, J. E., and D. L. HARRISON. 1987. The baculum in the Vespertilioninae (Chiroptera: Vespertilionidae) with a systematic review, a synopsis of *Pipistrellus* and *Eptesicus* and the description of a new genus and subgenus. *Bulletin of the British Museum (Natural History), Zoology Series*, 52: 225–305.
- HOLLISTER, N. 1913. A review of the Philippine land mammals in the United States National Museum. *Proceedings of the United States National Museum*, 46: 299–341.
- HOOFFER, S. R., and R. A. VAN DEN BUSSCHE. 2003. Molecular phylogenetics of the chiropteran family Vespertilionidae. *Acta Chiropterologica*, 5 (Supplement): 1–63.
- HUELSENBECK, J. P., and F. RONQUIST. 2001. MrBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics Applications Note*, 17: 754–755.
- HUTTERER, R., T. IVANOVA, C. MEYER-CORDS, and L. RODRIGUES. 2005. Bat migrations in Europe. A review of banding data and literature. Federal Agency for Nature Conservation, Bonn, 162 pp.
- IBÁÑEZ, C., J. L. GARCÍA-MUDARRA, M. RUEDI, B. STADELMANN, and J. JUSTE. 2006. The Iberian contribution to cryptic diversity in European bats. *Acta Chiropterologica*, 8: 277–297.
- INGLE, N. R. 1993. Vertical stratification of bats in a Philippine rainforest. *Asia Life Sciences*, 2: 215–222.
- INGLE, N. R. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia*, 134: 251–261.
- INGLE, N. R., and L. R. HEANEY. 1992. A key to the bats of the Philippine Islands. *Fieldiana Zoology (N.S.)*, 69: 1–44.
- JANSA, S. A., F. K. BARKER, and L. R. HEANEY. 2006. The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. *Systematic Biology*, 55: 73–88.
- KITCHENER, D. J., N. CAPUTI, and B. JONES. 1986. Revision of Australo-Papuan *Pipistrellus* and of *Falsistrellus* (Microchiroptera: Vespertilionidae). *Records of the Western Australian Museum*, 12: 435–496.
- LACK, J. B., Z. P. ROEHRS, C. E. STANLEY, M. RUEDI, and R. A. VAN DEN BUSSCHE. 2010. Molecular phylogenetics of

- Myotis* indicate familial-level divergence for the genus *Cistugo* (Chiroptera). *Journal of Mammalogy*, 91: 976–992.
- LAWRENCE, B. L. 1939. Collections from the Philippine islands. *Mammals. Bulletin of the Museum of Comparative Zoology*, 86: 28–73.
- MILLER, G. S. 1907. The families and genera of bats. *United States National Museum Bulletin*, 57: 1–282 + 14 plates.
- MITCHELL, A. H. G., F. HERNANDEZ, and A. P. DELA CRUZ. 1986. Cenozoic evolution of the Philippine Archipelago. *Journal of Southeast Asian Earth Sciences*, 1: 3–22.
- NYLANDER, J. A. A. 2004. MrModeltest v.2. Distributed by the author, Uppsala University, Sweden.
- PAYNE, J., C. M. FRANCIS, and K. PHILLIPPS. 1985. A field guide to the mammals of Borneo. Sabah Society, Kota Kinabalu, 332 pp.
- PETIT, E., and F. MAYER. 1999. Male dispersal in the noctule bat (*Nyctalus noctula*): where are the limits? *Proceedings of the Royal Society of London*, 266B: 1717–1722.
- PETIT, E., and F. MAYER. 2000. A population genetic analysis of migration: the case of the noctule bat (*Nyctalus noctula*). *Molecular Ecology*, 9: 683–690.
- PIPER, P. J., J. OCHOA, E. ROBLES, H. LEWIS, and V. PAZ. 2011. The palaeozoology of Palawan Island, Philippines. *Quaternary International*, 233: 142–158.
- RAMBAUT, A., and A. J. DRUMMOND. 2009. Tracer v1.5. Available from <http://beast.bio.ed.ac.uk/Tracer>.
- RICKART, E. A., J. A. MERCIER, and L. R. HEANEY. 1999. Cyto-geography of Philippine bats. *Proceedings of the Biological Society of Washington*, 112: 453–469.
- RICKART, E. A., D. S. BALETE, R. J. ROWE, and L. R. HEANEY. 2011a. Mammals of the northern Philippines: tolerance for habitat disturbance and resistance to invasive species in an endemic fauna. *Diversity and Distributions*, 17: 530–541.
- RICKART, E. A., L. R. HEANEY, D. S. BALETE, and B. R. TABARANZA, JR. 2011b. Small mammal diversity along an elevational gradient in northern Luzon, Philippines. *Mammalian Biology*, 76: 12–21.
- ROBERTS, T. E. 2006a. History, ocean channels, and distance determine phylogeographic patterns in three widespread Philippine fruit bats (Pteropodidae). *Molecular Ecology*, 15: 2183–2199.
- ROBERTS, T. E. 2006b. Multiple levels of allopatric divergence in the endemic Philippine fruit bat *Haplonycteris fischeri* (Pteropodidae). *Biological Journal of the Linnean Society*, 88: 329–349.
- ROEHRS, Z. P., J. B. LACK, and R. A. VAN DEN BUSSCHE. 2010. Tribal phylogenetic relationships within Vespertilioninae (Chiroptera: Vespertilionidae) based on mitochondrial and nuclear sequence data. *Journal of Mammalogy*, 91: 1073–1092.
- ROEHRS, Z. P., J. B. LACK, and R. A. VAN DEN BUSSCHE. 2011. A molecular phylogenetic reevaluation of the tribe Nycticeiini (Chiroptera: Vespertilionidae). *Acta Chiropterologica*, 13: 17–31.
- RUEDI, M., and F. MAYER. 2001. Molecular systematics of bats of the genus *Myotis* (Vespertilionidae) suggests deterministic ecomorphological convergences. *Molecular Phylogenetics and Evolution*, 21: 436–448.
- RUEDI, M., and G. F. MCCracken. 2009. Genetics and evolution: phylogeographic analysis of bats. Pp. 739–756, in *Ecological and behavioral methods for the study of bats*, 2nd edition (T. H. KUNZ and S. PARSONS, eds.). The Johns Hopkins University Press, Baltimore, 920 pp.
- RUEDI, M., J. BISWAS, and G. CSORBA. 2012. Bats from the wet: two new species of tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. *Revue Suisse de Zoologie*, 119: 111–135.
- SAKAI, T., Y. KIKKAWA, K. TSUCHIYA, M. HARADA, M. KANOE, M. YOSHIYUKI, and H. YONEKAWA. 2003. Molecular phylogeny of Japanese Rhinolophidae based on variations in the complete sequence of the mitochondrial cytochrome *b* gene. *Genes & Genetic Systems*, 78: 179–189.
- SALGUEIRO, P., M. RUEDI, M. M. COELHO, and J. M. PALMEIRIM. 2007. Genetic divergence and phylogeography in the genus *Nyctalus* (Mammalia, Chiroptera): implications for population history of the insular bat *Nyctalus azoreum*. *Genetica*, 130: 169–181.
- SALGUEIRO, P., J. M. PALMEIRIM, M. RUEDI, and M. M. COELHO. 2008. Gene flow and population structure of the endemic Azorean bat (*Nyctalus azoreum*) based on microsatellites: implications for conservation. *Conservation Genetics*, 9: 1163–1171.
- SANBORN, C. C. 1952. Philippine Zoological Expedition 1946–1947. *Mammals. Fieldiana Zoology*, 33: 89–158.
- SEDLACK, J. L., N. R. INGLE, and D. S. BALETE. 2011. Enhanced sampling of bat assemblages: a field test on Mount Banahaw, Luzon. *Fieldiana Life and Earth Sciences*, 2: 96–102.
- SEDLACK, J. L., and S. E. WEYANDT. 2009. Genetic divergence between morphologically and acoustically cryptic bats: novel niche partitioning or recent contact? *Journal of Zoology (London)*, 279: 388–395.
- SEDLACK, J. L., S. E. WEYANDT, L. CORCORAN, M. DAMEROW, S.-H. HWA, and B. PAULI. 2008. Bat diversity in tropical forest and agro-pastoral habitats within a protected area in the Philippines. *Acta Chiropterologica*, 10: 349–358.
- SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529, in *Mammal species of the World* (D. E. WILSON and D. M. REEDER, eds.). The Johns Hopkins University Press, Baltimore, 2142 pp.
- STADELMANN, B., G. HERRERA, J. ARROYO-CABRALES, and M. RUEDI. 2004a. Molecular systematics of the piscivorous bat *Myotis (Pizonyx) vivesi*. *Journal of Mammalogy*, 85: 133–139.
- STADELMANN, B., D. JACOBS, C. SCHOEMAN, and M. RUEDI. 2004b. Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome *b* sequences. *Acta Chiropterologica*, 6: 177–192.
- STADELMANN, B., T. H. KUNZ, L. K. LIN, and M. RUEDI. 2007. Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution*, 43: 32–48.
- STEPHAN, S., C. ZAWADZKI, and L. R. HEANEY. 2003. Molecular phylogeny of the endemic Philippine rodent *Apomys* and the dynamics of diversification in an oceanic archipelago. *Biological Journal of the Linnean Society*, 80: 699–715.
- TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI, and S. KUMAR. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28: 2731–2739.
- TAYLOR, E. H. 1934. Philippine land mammals. *Monographs of the Bureau of Science, Manila*, 30: 1–548 + 25 pls.
- THABAH, A., G. LI, Y. N. WANG, B. LIANG, K. L. HU, S. Y. ZHANG, and G. JONES. 2007. Diet, echolocation calls, and phylogenetic affinities of the great evening bat (*Ia io*;

- Vespertilionidae): another carnivorous bat. *Journal of Mammalogy*, 88: 728–735.
- TRUJILLO, R. G., J. C. PATTON, D. A. SCHLITTER, and J. W. BICKHAM. 2009. Molecular phylogenetics of the bat genus *Scotophilus* (Chiroptera: Vespertilionidae): perspectives from paternally and maternally inherited genomes. *Journal of Mammalogy*, 90: 548–560.
- VOLLETH, M., and K.-G. HELLER. 1994. Phylogenetic relationships of vespertilionid genera (Mammalia: Chiroptera) as revealed by karyological analysis. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 32: 11–34.
- WILSON, D. E. 2008. Chiroptera. Pp. 327–387, in *A guide to the mammals of China* (A. T. SMITH and YAN XIE, eds.). Princeton University Press, Princeton, 544 pp.

*Received 31 August 2012, accepted 03 December 2012*