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A new small montane species of *Philautus* (Amphibia: Anura: Rhacophoridae) from Gunung Kinabalu, Sabah, Malaysia (Borneo)

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Abstract. Three populations of small montane bush frogs previously assigned to *Philautus mjobergi* were compared using morphological, bioacoustic, and genetic (mitochondrial 16S rRNA sequence) data. The comparison revealed that the population from Gunung Kinabalu in Sabah, Malaysia, represents a distinct species that is described herein. Although the new species differs from *P. mjobergi* in few morphological characters, most notably the acuminate snout, it is distinguished from this species and all other Bornean congeners by a unique advertisement call and large genetic differences. The population from Gunung Mulu assigned to *P. mjobergi* differs from the topotypic population from Gunung Murud in its advertisement call and 16S rRNA sequence and probably represents another, undescribed species.

Key words. DNA barcoding, advertisement call, *Philautus mjobergi*, Gunung Mulu, Sarawak, frog.

Introduction

Bush frogs of the genus *Philautus* are represented by 19 species in Borneo (Dehling & Dehling 2013), all of which except *P. petersi* (Boulenger, 1900) are endemic. Dring (1987) revised the Bornean species and arranged them in four groups, the most speciose being the *P. aurifasciatus* (Schlegel, 1837) group that currently comprises nine Bornean species (Malkmus & Riede 1996, Inger & Stuebing 1996, Matsui 2009, Dehling 2010, Dehling & Dehling 2013). Species of the *P. aurifasciatus* group share a similar habitus and are therefore difficult to distinguish morphologically. However, they differ in characteristics of their advertisement calls, which can therefore be used for species differentiation (Dring 1987, Malkmus & Riede 1996, Matsui 2009, Dehling 2010, Dehling & Dehling 2013). The use of molecular techniques such as DNA barcoding has furthered the work on the taxonomy of this group of frogs (Dehling & Dehling 2013).

Philautus mjobergi Smith, 1925 was one of the first *Philautus* species that were described from Borneo. The type specimens were collected at higher altitudes of Gunung Murud in eastern Sarawak (Smith 1925a), and the species has subsequently been reported from several montane sites in Borneo, including Gunung Kinabalu in Sabah (e.g., Smith 1931, Inger 1966 [as *P. aurifasciatus*], Dring 1987, Malkmus 1989, Inger & Stuebing 1992, Malkmus 1994, Malkmus & Riede 1996, Inger et al. 1996, 2000, Malkmus et al. 2002) and Gunung Mulu in Sarawak (e.g., Dring 1987, Dehling 2008, 2010, Haas et al. 2012, Hertwig et al. 2012). Herein, we report on the results of a comparison of voucher specimens of the population from Gunung Kinabalu, which had been assigned to *P. mjobergi*, with the type specimens of the species and recently collected specimens from near the type locality and specimens collected at Gunung Mulu in Sarawak. We applied an integrative approach that combined morphological examination of the voucher specimens with analyses of advertisement calls and molecular genetics. Our comparison revealed that the population from Gunung Kinabalu is not conspecific with *P. mjobergi* but represents an undescribed species, which we name herein.

Materials and methods

Fieldwork was carried out at Mount Kinabalu from July through August 2005 and from December 2014 through January 2015. Fieldwork at Gunung Murud and its surroundings was conducted in January 1991, August 2009,

and August 2010; fieldwork at Camp 3 on Gunung Mulu in January 2008. Specimens were collected at night and photographed in situ prior to collection. They were euthanised by submersion in chlorobuthanol solution, fixed and initially stored in 10% buffered formalin and transferred to 70% ethanol about two weeks after collection. Liver or muscle tissue samples were taken from several specimens prior to fixation and stored separately in 98% ethanol. Voucher specimens are stored in the collections of the Institute for Tropical Biology and Conservation, University Malaysia Sabah (BORNEENSIS); the Graduate School of Human and Environmental Studies, Kyoto University, Japan (KUHE); and the Sabah Parks Zoological Museum, Kinabalu Park Headquarters, Ranau District, Sabah, Malaysia (SP).

We took the following measurements (abbreviations in parentheses, listed alphabetically) to the nearest 0.1 mm, using digital callipers: Horizontal eye diameter (ED); inter-eye distance (EE, distance between anterior margins of eyes); eye to nostril distance (EN, distance between anterior margin of eye and centre of nostril); upper eyelid width (EW); foot length (FOT, from proximal end of inner metatarsal tubercle to tip of fourth toe); head length (HL, distance from rear end of jaw to tip of snout); hand length (HND, distance from proximal end of palmar tubercle to tip of third finger); head width (HW, measured at the level of the jaw joint); interorbital distance (IO, shortest distance between upper eyelids); total hind limb length (LEG, from vent to tip of fourth toe with leg fully extended and being held perpendicularly to median body plane); internarial distance (NN, distance between centres of nostrils); nostril to snout distance (NS, distance between centre of nostril and tip of snout); snout length (SL, distance between anterior margin of eye to tip of snout); snout–vent length (SVL); horizontal tympanum diameter (TD); tibiofibula length (TFL, measured with both knee and tibiotarsal articulation flexed). The webbing formulae are given as proposed by Myers & Duellman (1982). Notes on colour in life are based on digital photographs taken in situ on the day following the collection.

For morphological comparisons, we examined voucher specimens assigned to *Philautus mjobergi* and of several species of *Philautus* including their types (see Appendix) from the collections of The Natural History Museum, London, United Kingdom (BMNH); The Field Museum, Chicago, Illinois, USA (FMNH); Naturhistorisches Museum der Burgergemeinde Bern, Switzerland (NMBE); Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS); and Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Germany (ZMB). The sexes of voucher specimens were identified by examination of external secondary characters, including nuptial pads and vocal sacs, or the gonads by means of dissection. Information on morphological characters and the distribution of other species of *Philautus* was taken from Dring (1987), Brown & Alacala (1994), Malkmus & Riede (1996), Malkmus et al. (2002), and Matsui (2009).

Advertisement calls of the population from Gunung Kinabalu were recorded in the habitat in the headquarters area of the Kinabalu National Park, Sabah, as uncompressed wav-files at 96 kHz/24 bit, using a Sony J PCM–D50 Linear PCM Recorder with stereo microphones. Stereo recordings were converted to mono at a sampling rate of 44.1 kHz and resolution of 16 bits. Advertisement calls of *Philautus mjobergi* were recorded at Pa Ramapuh, near Bario, Sarawak, on 25 January 1991 using a stereo cassette recorder (Sony TC-D5M) with a microphone (Sony ECM-23F), and on 19 August 2009 using a digital recorder (Olympus LS-11) at 44.1 kHz/16 bits, and at Camp 3 on Gunung Mulu, Sarawak, in January 2008 using a Sony WM-D6C stereo cassette recorder and a Sony ECM-S959C microphone. We also re-analysed a call recording of *P. mjobergi* from Gunung Mulu made in 1978 by Julian Dring (Dring 1987). All tape recordings were digitised at 44.1 kHz with 16 bit resolution. We generated waveforms and sound spectrograms of call recordings using Adobe Audition 1.5 software. Sound spectrograms were obtained applying a Blackman-Harris Fast Fourier transformation with a FFT size of 512 Hz. Definitions of acoustic parameters follow Duellman (1970) and Matsui (1997). Values are given as ranges (mean±SD).

DNA sequence data were obtained from tissue samples using the same methods for DNA extraction, amplification, and sequencing of the mtDNA fragments as those reported by Matsui et al. (2011) and Shimada et al. (2011). The resultant sequences of the mitochondrial 16S rRNA gene were deposited in GenBank (Table 1). We aligned the newly obtained sequences with those of several Bornean and Philippine species of *Philautus* as well as some species of *Rhacophorus*, *Polypedates*, and *Buergeria* from GenBank (Table 1). For phylogenetic analyses, we used PAUP* 4.0b10 (Swofford 2002) to conduct a Maximum Likelihood (ML) analysis, based on the substitution model and phylogenetic parameters derived from a hierarchical likelihood ratio test (hLRT) in Modeltest 3.06 (Posada & Crandall 1998). The confidence values of the consensus tree were tested with bootstrap (BS) analyses (Felsenstein 1985) with 500 replicates (Hedges 1992). We also used MrBayes 3.1.1 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) to conduct a Bayesian Inference analysis with the model derived from an hLRT in MrModeltest (Nylander 2002). Two independent Metropolis-coupled Monte Carlo Markov Chain (Larget & Simon 1999) analyses were run for 10 million generations, each with one hot and three cold chains and the temperature set at 0.2. Trees were sampled every 100 generations. The first 10,000 samples of each run were discarded as burn-ins, and the remaining trees from both runs were used to calculate a consensus tree and Bayesian posterior probabilities (BPP). Pairwise comparisons of corrected sequence divergences (Kimura's two-parameter [K2p] distances [Kimura 1980]) were calculated in PAUP*.

Table 1. Samples of species used for molecular genetic analyses, their geographic origins, voucher specimens, GenBank accession numbers, and original sources.

Species	Origin	Voucher	GenBank #	Source
Buergeria buergeri	Ota River, Hiroshima, Japan	IABHU 41011	AB127977	Sano et al. 2004
Philautus acutirostris	Philippines	RMB 613	AF458137	Wilkinson et al. 2002
Philautus aurifasciatus	Java, Indonesia	MZB 1639	KJ802924	Nguyen et al. 2014
Philautus acutus	Gunung Mulu, Sarawak, Malaysia	NMBE 1056431	JN705366	Hertwig et al. 2011
Philautus aurantium	Crocker Range, Sabah, Malaysia	UNIMAS 8666	JN705367	Hertwig et al. 2011
Philautus bunitus	Kinabalu, Sabah, Malaysia	UNIMAS 9045	JN705368	Hertwig et al. 2011
Philautus davidlabangi	Batang Ai, Sarawak, Malaysia	NMBE 1056444	JN705386	Hertwig et al. 2011
Philautus disgregus	Lahad Datu, Sabah, Malaysia	FMNH231141	GQ204704	Meegaskumbura et al. 2015
Philautus everetti	Palawan, Philippines	KU 309610	JN705377	Hertwig et al. 2011
Philautus hosii	Usun Apau, Sarawak, Malaysia	NMBE 1057287	JN705384	Hertwig et al. 2011
Philautus ingeri	Gunung Mulu, Sarawak, Malaysia	NMBE 1056435	JN705385	Hertwig et al. 2011
Philautus juliandringi	Gunung Api, Sarawak, Malaysia	NMBE 1056439	JN705378	Hertwig et al. 2011
Philautus kakipanjang	Gunung Serapi, Sarawak, Malaysia	NMBE 1060433	KF240718	Dehling & Dehling 2013
Philautus macroscelis	Gunung Mulu, Sarawak, Malaysia	NMBE 1056486	JN705375	Hertwig et al. 2011
Philautus mjobergi	Bario, Sarawak, Malaysia	KUHE 53096	KT445972	this study
Philautus mjobergi	Gunung Mulu, Sarawak, Malaysia	NMBE 1056434	JN705380	Hertwig et al. 2011
Philautus nephophilus	Kinabalu, Sabah, Malaysia	BORN 22665	KT445970	this study
Philautus nephophilus	Kinabalu, Sabah, Malaysia	BORN 22666	KT445971	this study
Philautus petersi	Gunung Mulu, Sarawak, Malaysia	NMBE 1056443	JN705381	Hertwig et al. 2011
Philautus refugii	Gunung Penrissen, Sarawak, Malaysia	NMBE 1057544	JN705382	Hertwig et al. 2011
Philautus surdus	Mt Maquiling, Luzon, Philippines	CAS 219932	AF458138	Wilkinson et al. 2002
Philautus tectus	Gunung Mulu, Sarawak, Malaysia	NMBE 1056451	JN705370	Hertwig et al. 2011
Philautus umbra	Gunung Api, Sarawak, Malaysia	NMBE 1056454	JN705379	Hertwig et al. 2011
Polypedates leucomystax	Kota Kinabalu, Sabah, Malaysia	BORN12420	AB728138	Kuraishi et al. 2012
Rhacophorus borneensis	Maliau Basin, Sabah, Malaysia	BORN 22410	AB781693	Matsui et al. 2013

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new name contained herein is available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:1FFA8A5B-7D69-4BB4-920E-B0D1D130B38F. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: www.salamandra-journal.com.

Taxonomy and systematics

Philautus nephophilus sp. n.

ZooBank LSID: urn:lsid:zoobank.org:act:091637D9-BB17-49DF-942B-57C5B2961092.

Philautus aurifasciatus (nec *Hyla aurifasciatus* Schlegel, 1837): Inger 1966: 341–344 (partim).

Philautus mjobergi (nec *Philautus mjöbergi* Smith, 1925): Smith 1931: 21 (partim); Dring 1987: 38–41 (partim); Malkmus 1989: 193; Inger & Stuebing 1992: 46; Malkmus 1994: 230; Inger et al. 2000: 17; Malkmus et al. 2002: 187–188.

Philautus mjöbergi (nec *Philautus mjöbergi* Smith, 1925): Inger et al. 1996: 360, 363 (partim); Inger & Stuebing 1997: 170.

Philautus mjoebergi (nec *Philautus mjöbergi* Smith, 1925): Malkmus & Riede 1996: 29, 31.

Holotype: SP 27443, adult male, from the Silau-Silau Trail (6°00'23.2" N, 116°32'44.7" E; 1,525 m a.s.l.), Kinabalu National Park, Sabah, Malaysia, collected by P. Yambun Imbun and J. M. Dehling, 30 December 2014.

Paratypes: BORNEENSIS 22665, 22667, 22694, three adult males, Headquarters, Kinabalu National Park, Sabah, Malaysia, collected by M. Matsui, K. Nishikawa, and T. Shimada, 30 July 2005; SP 27440–42, three adult males, same collection details as holotype; SP 27444, adult female, 27445–46, two adult males, from the Liwagu Trail (6°00'39.5" N, 116°32'47.1" E; 1,475 m a.s.l.), Kinabalu National Park, collected by P. Yambun Imbun and J. M. Dehling, 30 December 2014.

Referred material: BORNEENSIS 22751, 22779, two adult males, 22666, 22695–96, 22750, 22752, 22964, 23018, sev-

en adult females, Headquarters, Kinabalu National Park, Sabah, Malaysia, collected by M. Matsui, K. Nishikawa, and T. Shimada, in July and August 2005.

Diagnosis**:** Currently, there are no synapomorphic morphological characters considered diagnostic for the genus *Philautus*. We therefore assign the new species to this genus based on its close morphological and bioacoustic resemblance and genetic similarity to several of the Bornean species assigned to the genus. The new species differs from its congeners by the combination of the following characters: size small (SVL of adult males 16.4–18.6 mm, females 20.3–23.1 mm); hind limbs long, tibiotarsal joint reaching beyond tip of snout when legs are stretched forward and adpressed to body, TFL/SVL 0.57–0.63; snout acuminate in dorsal view, shorter than eye diameter; heel with small conical tubercle; nuptial pads small, prominent; toes moderately webbed, formula **I**2–2.5**II**1.75–3**III**2–3.25**IV**3.25–2**V**; iris reddish in life, lightened to bright yellow on the dorsal rim, darkened to greyish brown on the ventral rim; advertisement call consisting of a series of pulsed notes, followed by one or two additional single notes after a distinct interval; furthermore, the new species differs from its congeners by substantial genetic differentiation.

Description of holotype: Measurements are provided in Table 2. Body moderately sturdy, widest across temporal region, tapering to groin (Fig. 1); head large (HL/SVL 0.39, HW/SVL 0.42), slightly wider than long (HW/HL 1.09); snout long (SL/HL 0.45), acuminate in both dorsal view and lateral profile, slightly projecting beyond lower jaw, wider than long (SL/EE 0.76); canthus rostralis distinct, straight-lined in profile, moderately concave in dorsal view; loreal region oblique, concave; nostrils rounded, directed laterally; situated closer to tip of snout than to eye (EN/NS 1.11), separated from each other by a distance larger than that between eye and nostril (NN/EN 1.31); eyes directed anterolaterally, protruding, moderately large (ED/HL 0.40); pupil horizontal; eye diameter shorter than snout length (ED/SL 0.88); interorbital distance wider than upper eyelid (IO/EW 1.14) and greater than internarial distance (IO/NN 1.11); tympanum distinctly visible, its posterodorsal edge concealed by supratympanic fold, separated from eye by about half its diameter; tympanum moderately large (TD/ED 0.47); upper jaw with dentition; choanae small, oval, located far anterolaterally at margins of roof of the mouth, partly concealed by maxillary fringe in ventral view; vomerine processes and teeth absent; tongue long and broad, bilobed for one-fifth of its length, free distally for three-fourths of its length; median lingual process absent; vocal sac single, median, subgular; vocal sac apertures on each side of the mouth, slit-like, long, directed longitudinally, situated close to corner of mouth.

Dorsal faces, especially those of head and upper eyelids covered with large, subconical tubercles; supratympanic fold thick and conspicuous, straight-lined, extending from posterior corner of eye to level of insertion of forelimb; another, slightly less prominent dermal fold extending posteromedially from posterior edge of eye to scapular region where the folds of both sides meet; ventral sides of trunk and limbs shagreened; row of large tubercles along ventral edge of lower jaw; very small tubercle present at tibiotarsal joint; vent without dermal appendages.

Forelimbs slender; hand moderately large (HND/SVL 0.28); tips of fingers enlarged into broad oval disks, those of Fingers I and II slightly wider than those of Fingers III and IV and about twice as wide as the respective penultimate phalanges; each disc with circummarginal groove; relative lengths of fingers: I < II < IV < III; subarticular tubercles rounded, well developed, numbering one on Fingers I and II, two on Fingers III and IV, with proximal tubercles on Fingers III and IV being much smaller than distal ones; rudimentary webbing between fingers, formula being **I**2.5–2.75**II**2.5–3.75**III**3–2.5**IV**; thenar tubercle distinct, about one-fourth the size of base of Finger I; palmar tubercles not discernible; nuptial pads on dorsal face of Fingers I and II, most conspicuously developed as prominent, large (about twice the size of disc of Finger I), smooth pad on dorsal face of metacarpus of Finger I, otherwise as callous tissue

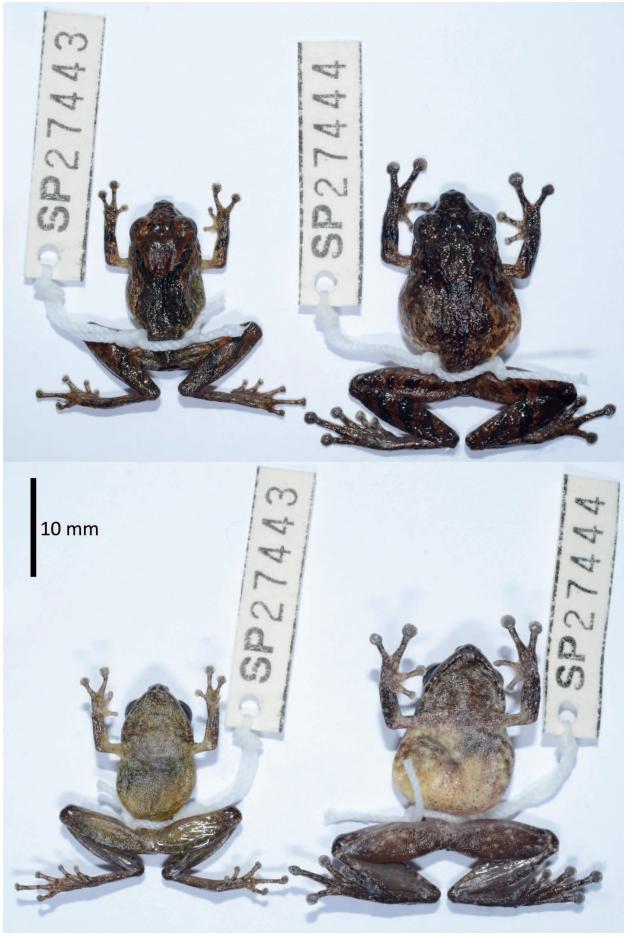

Figure 1. Dorsal (top) and ventral views (bottom) of the preserved adult male holotype (SP 27443; left) and the preserved adult female paratype (SP 27444; right) of *Philautus nephophilus*.

Table 2. Measurements of the holotype and paratypes of *Philautus nephophilus*. For abbreviations see Materials and methods.

SP	27443	27440	27441	27442	27445	27446	27444
status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
origin	Silau-Silau	Silau-Silau	Silau-Silau	Silau-Silau	Liwagu	Liwagu	Liwagu
sex	male	male	male	male	male	male	female
SVL	17.5	18.1	17.0	17.8	17.7	18.6	21.6
TFL	10.3	11.4	10.7	10.7	10.6	10.7	12.4
Fot	8.0	8.8	7.7	8.1	8.0	7.7	9.7
Hnd	4.9	5.4	5.0	4.9	5.3	5.4	6.8
HW	7.4	7.3	7.4	7.7	7.2	7.1	8.7
HL	6.8	7.2	7.0	7.2	7.1	6.9	8.4
IO	2.4	2.2	2.3	2.4	2.3	2.4	2.7
EW	2.1	1.7	1.8	1.9	2.0	1.7	2.0
ED	2.7	2.6	2.4	2.8	3.1	2.7	3.1
TD	1.3	1.2	1.5	1.4	1.5	1.5	2.0
EN	1.7	1.8	1.8	2.0	1.9	1.8	2.1
EE	4.1	4.1	4.0	4.4	4.1	4.0	4.5
NS	1.5	1.6	1.7	1.5	1.6	1.5	1.8
SL	3.1	3.1	3.2	3.2	3.3	3.5	4.0
NN	2.2	2.1	2.2	2.1	2.4	2.2	2.7

on proximal phalanx of Finger I and metacarpus and proximal phalanx of Finger II.

Hind limbs slender, long; tibiotarsal articulation reaching by about one SL beyond tip of snout when legs are adpressed forwardly to body; tibiofibula very long (TFL/SUL 0.63), longer than thigh; heels overlapping each other slightly when knees are flexed and thighs held perpendicularly to median plane; foot much shorter than tibiofibula (FOT/TFL 0.78); tips of toes expanded into broad oval disks, each with circummarginal groove; discs of toes smaller than those of fingers; relative lengths of toes: I < II < III < V < IV; subarticular tubercles numbering one on Toes I and II, two on Toes III and V, and three on Toe IV; pedal webbing formula **I**2–2.5**II**1.75–3**III**2–3.25**IV**3.25–2**V**; inner metatarsal tubercle relatively large (length 0.8 mm), about one-third of length of Toe I (2.3 mm), elongated, prominent; outer metatarsal tubercle low, indistinct.

Dorsal coloration in life varied strikingly between night- and daytime. During the night, dorsal sides of head and shoulder region more strongly pigmented than rest of body, light brown with dark olive brown spots; dark olive brown band along lateral edge of posteromedial fold, fading into light olive brown on dorsal side of trunk; lateral faces of trunk and dorsal faces of limbs light brown to cream-coloured; limbs with light grey crossbars; groin, lateral sides of thigh and venter bright yellow; lateral side of head light grey with cream-coloured spots and stripes; tympanic region yellowish; iris reddish, lightened to bright yellow on the dorsal edge, darkened to greyish brown on the ventral edge. During the day, the colour pattern was similar to that at night, but areas that were lightly pigmented at night were darker during the day; ventral side yellowish, heavily speckled with dark olive brown. In preservative, pattern and coloration similar to daytime coloration, iris colour faded to greyish blue.

Variation**:** The male paratypes are very similar to the holotype in measurements and proportions (Table 2). The female paratype is significantly larger than the males, but does not differ in body proportions or snout shape (Fig. 1, Table 2).

Bioacoustic differentiation: 55 advertisement calls from six male type specimens, including the holotype, and from seven non-collected individuals were recorded in the field. We consider the recorded call to represent the advertisement call of the species because it was the vocalisation most often emitted. Ambient air temperature varied between 16.5 and 17.5°C. Recordings were made at a distance of about 50–200 cm from the calling individuals. For the call description, we calculated means and SD for the parameters from the respective means of all analysed individual males (n = 13).

The advertisement call consisted of an initial series of 4–12 (9.1 ± 1.8) notes (Fig. 2A, Table 3) that were repeated at a rate of 6.2–6.6 (6.5 ± 0.2) per second. Individual notes consisted of 10–13 (12 ± 0.3) pulses and lasted for 61–80 (74 ± 2.5) ms. Pulse repetition rate at the beginning of the note (120–166; 133 ± 7 per second) was lower than in the middle and at the end of the note (200–260; 235 ± 15 per second). Pulse amplitude increased from the beginning of the note, reached its maximum at about three-fourth of the note length, and slightly decreased towards the end (Fig. 2A). Dominant frequency was at 2,750–3,500 Hz and reached the energy maximum at 3,100–3,250 (3,203 ± 53) Hz. Prominent harmonics were discernible at 6,000–6,300, 9,600–9,900, 12,800–12,900, and 16,000–16,300 Hz

Table 3. Major characteristics of the advertisement call of the Bornean species of the *P. aurifasciatus* group *sensu* Dring (1987). Sources: (1) Malkmus & Riede 1996, (2) Malkmus et al. 2002, (3) Matsui 2009, (4) Dehling 2010, (5) Dehling & Dehling 2013, (6) this study, (7) Dring 1987, (8) unpubl. data of JMD.

Species	Number of notes	Note length [ms]	Number of pulses	Dominant frequency [Hz]	Source
P. amoenus	2–3	110	3–4	1800	1, 2, 8
P. davidlabangi	1	50–80	13–18	2875–3300	3, 4
P. juliandringi	2–9	40–52	7–9	2550–3520	4, 8
P. kakipanjang	1	342–478	9–12	2000–2700	5
P. mjobergi	2	20	3–4	2500–3770	6
P. nephophilus	4–12	61–80	10–13	2750–3500	6
P. petersi	1	1180–1300	51–56	1600–2200	7, 8
P. refugii	1–3	10–20	2–5	3500–4000	4
P. saueri	2–4 [5]	30–40	7–8	1900–2600	1, 2
P. umbra	1	120–587	2–11	1400–2100	4

(Fig. 2A) in recordings made from close up (less than 100 cm). The note series was typically followed by a single additional note after an interval of 754–1032 (852 ± 61) ms. In 12 calls (of three individuals), the additional note was not emitted. In five calls (of three individuals), a second additional note was emitted after another interval of 830–843 (838 ± 4) ms. In three calls (of two individuals), not one but two notes were added after the first interval (at the same repetition rate as in the main note), followed by a single note after a second interval. Two individuals, which initiated calling in a chorus after a longer period of silence, emitted only single notes or short series of only two notes (Fig. 2B), which in one case was followed by a single note after an interval of 1,660 ms. On this occasion, a second call type was also recorded (Fig. 2B). The three recorded calls of this type, emitted by two males, consisted of three notes that were repeated at a higher rate of 15/s. Notes lasted 29–32 (30 ± 1) ms and consisted of 7–8 (7.3) pulses, repeated at a rate of 200–270 (250 ± 36) per second. Their dominant frequency did not differ from that of the advertisement call. The function of this second call type is unclear. It could be an initial call, emitted when the individual restarts calling after a pause, or it could be an aggressive call directed at other males in the surroundings.

We also analysed recordings of the advertisement call of *Philautus mjobergi* recorded at Bario, near the type locality of the species (Fig. 2D, Table 3). The call group includes one to three calls, with a duration of 6.77 s in three successive calls. A call consists of two pulsed notes and lasts for 0.08–0.09 seconds. A note includes 3–4 pulses and lasts for 0.02 seconds. The interval between each two notes is 0.04–0.05 seconds. The pulse repetition rate ranges at 167–235 pulses per second. The dominant frequency is spread over 2,500–3,770 Hz with the maximum energy ranging from 3,030–3,100 Hz. Harmonic frequencies are not clear, but intensity modulation is present.

The advertisement call of the population from Gunung Mulu assigned to *Philautus mjobergi* is somewhat similar to the call of *Philautus nephophilus*. 23 calls of seven individuals were analysed. Ambient temperature during recording in January 2008 was 16.2°C, the recording by Julian Dring was made at "an estimated temperature of 15°C" (Dring 1987). The call typically consisted of an initial long series of notes (Fig. 2C) which was followed by 0–3 (1 ± 0.2) additional shorter series of 1–6 notes, emitted after an interval of 958–1,810 (1,210 ± 320) ms. The number of notes in additional series usually consistently decreased, but in one call, the number of notes in the second series (6) was higher than in the first series (4). The initial note series of an advertisement call lasted for 34–1,121 (745 ± 354) ms and consisted of 1–11 (8 ± 2.5) notes (Fig. 2C). The repetition rate of the notes decreased from the beginning of the series (9.2–12.1; 11.4 ± 0.6 per second) to the end (5.3–8.3; 6.5 ± 1.2 per second). Individual notes lasted for 19–60 (49 ± 28) ms and consisted of 2–7 pulses, with the number of pulses per note increasing from the beginning (2–4 pulses) to the end (6–7 pulses) of the note series (Fig. 2C). Pulses were repeated at a rate of 90–125 (115 ± 19) per second. Energy maximum was at 2,150–2,400 (2,250 ± 120) Hz with little frequency modulation between the notes of a series. Because the recordings were made from a distance of more than 2 m from the calling individuals, no harmonics were discernible.

The advertisement call of *Philautus nephophilus* differs strikingly from the call of *Philautus mjobergi* from Bario in several characteristics, including number of notes (4–12 vs. 2), note repetition rate (6.2–6.6/s vs. 15.2–23.8/s), and the number of pulses per note (10–13 vs. 3–4). It also differs in several characteristics from the call of the population from Mulu assigned to *P. mjobergi*, including number of pulses per note (10–13 throughout the series vs. rising from 2–4 at the beginning of a series to 6–7 towards the end of the series), pulse repetition rate (120–166/s at the beginning to 200–260/s at the end of the note vs. 90–125/s throughout the note), energy maximum (3,100–3,250 vs. 2,150–2,400 Hz), number of additional note series (0–2 vs. 0–3), and the number of notes in second and third note series (1–2 vs. 1–6 notes).

The advertisement call of *Philautus nephophilus* is similar to those of the other Bornean species of the *P. aurifasciatus* group sensu Dring (1987) in their calls being pulsed and only slightly frequency-modulated (see also Dehling 2010, Dehling & Dehling 2013). The calls of all other species of this group differ in main characteristics (Table 3) and can therefore be used to distinguish these species from *P. nephophilus*.

Molecular differentiation and phylogenetic relationships: The consensus trees obtained from ML and BI analyses showed almost identical topologies. The BI tree with support values from both analyses is shown in Figure 3. *Philautus nephophilus* formed a well-supported clade with *P. mjobergi*, *P. juliandringi* Dehling, 2010, and *P. umbra* Dring, 1987. Relationships within this clade were not resolved. The two available sequences of *P. nephophilus* were identical to each other and differed from all other analysed sequences by a minimum of 6.9% (Table 4). The lowest values were shared with *P. umbra* (6.9%) and *P. juliandringi* (8.2%). The sequences of the two populations of *P. mjobergi* from Bario and Mulu differed from each other by 4.8% and from *P. nephophilus* by 9.0 and 8.8 %, respectively. The Bornean and Philippine species of the *P. aurifasciatus* group sensu Dring (1987) formed a well-supported clade (Fig. 3) whereas the name-giving *P. aurifasciatus* from Java, although not strongly supported, was not part of that clade.

Morphological comparison: Bornean species of the *P. aurifasciatus* group sensu Dring (1987; see also Matsui 2009, Dehling 2010, Dehling & Dehling 2013) share certain morphological characters, including a small SVL, presence of the musculus cutaneus pectoris and small, smooth nuptial pads (in males), and lack of vomerine teeth. All other *Philautus* species of the Sunda region lack this character combination and are therefore distinct from this group. The species of the *P. aurifasciatus* group exhibit a high level of intraspecific variability regarding coloration and colour pattern and to some extent skin texture, and at the same time, many species are very similar to each other morphologically, rendering species of this group notoriously difficult to distinguish. *Philautus nephophilus* superficially resembles *P. mjobergi* (Figs 4 and 5) in having long hind limbs, a relatively broad head, half-webbed toes, and a moderately tubercular dorsal side. The two species most notably differ in the shape of the snout, which is acuminate in *P. nephophilus* and broadly rounded in *P. mjobergi* (Fig. 5), in both males and females. There is an overlap in the range of the SVL but *Philautus mjobergi* (17.2–24.1 mm in adult males, 24.0–31.4 mm in adult females) appears

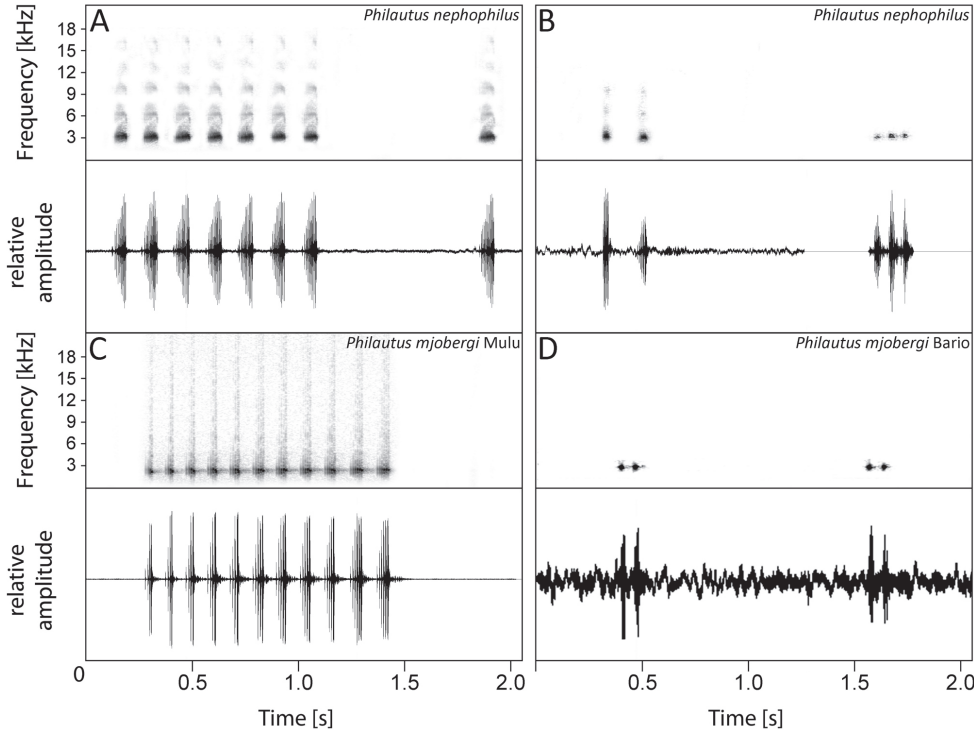

Figure 2. Audiospectrograms (top) and corresponding waveforms (bottom) of A) advertisement call of the holotype of *Philautus nephophilus* (SP 27443), recorded at 17.5°C air temperature at the Silau-Silau Trail, Kinabalu National Park, Sabah; B) two-note call (left) and second call type (right) of a paratype of *Philautus nephophilus* (SP 27445), recorded at 16.8°C at the Liwagu Trail, Kinabalu National Park, Sabah; C) initial note series of an advertisement call of *Philautus mjobergi*, recorded at Camp 3, Gunung Mulu, Sarawak, air temperature about 15°C (see text); D) two-note advertisement call of *Philautus mjobergi* from New Dam, near Bario, Sarawak, air temperature 20.8°C.

to reach larger maximal sizes than *Philautus nephophilus* (SVL of adult males 16.4–18.6 mm, and adult females 20.3–23.1 mm).

Morphological differentiation between species of the *P. aurifasciatus* group is difficult, but the other species of this group can be distinguished from *P. nephophilus* (characters in parentheses) by the following characteristics: *Philautus amoenus* Smith, 1931 is larger with the SVL of adult males being 18.1–24.2 mm (16.4–18.6 mm), has shorter legs with a TFL/SVL of 0.47–0.54 in males (0.58–0.63), and the tibiotarsal articulation reaches to tip of snout or slightly beyond (reaching considerably beyond tip of snout). *Philautus davidlabangi* Matsui, 2009 is larger with the SVL of adult males being 19.9–20.6 mm (16.4–18.6 mm), has shorter legs with a TFL/SVL of 0.52–0.56 (0.58–0.63), and the tibiotarsal articulation reaches between nostril and snout tip (reaching considerably beyond tip of snout), lacks nuptial pads, and has a rounded snout (acuminate). *Philautus juliandringi* has a relatively shorter head with a HL/SVL of 0.31–0.35 (0.37–0.41), a narrower snout with a NN/EN of 0.83–1.00 (1.09–1.30), a relatively larger eye diameter with an ED/HL of 0.46–0.52 (0.35–0.44), and the snout is rounded in dorsal view and obtuse in profile (acuminate). *Philautus kakipanjang* Dehling &

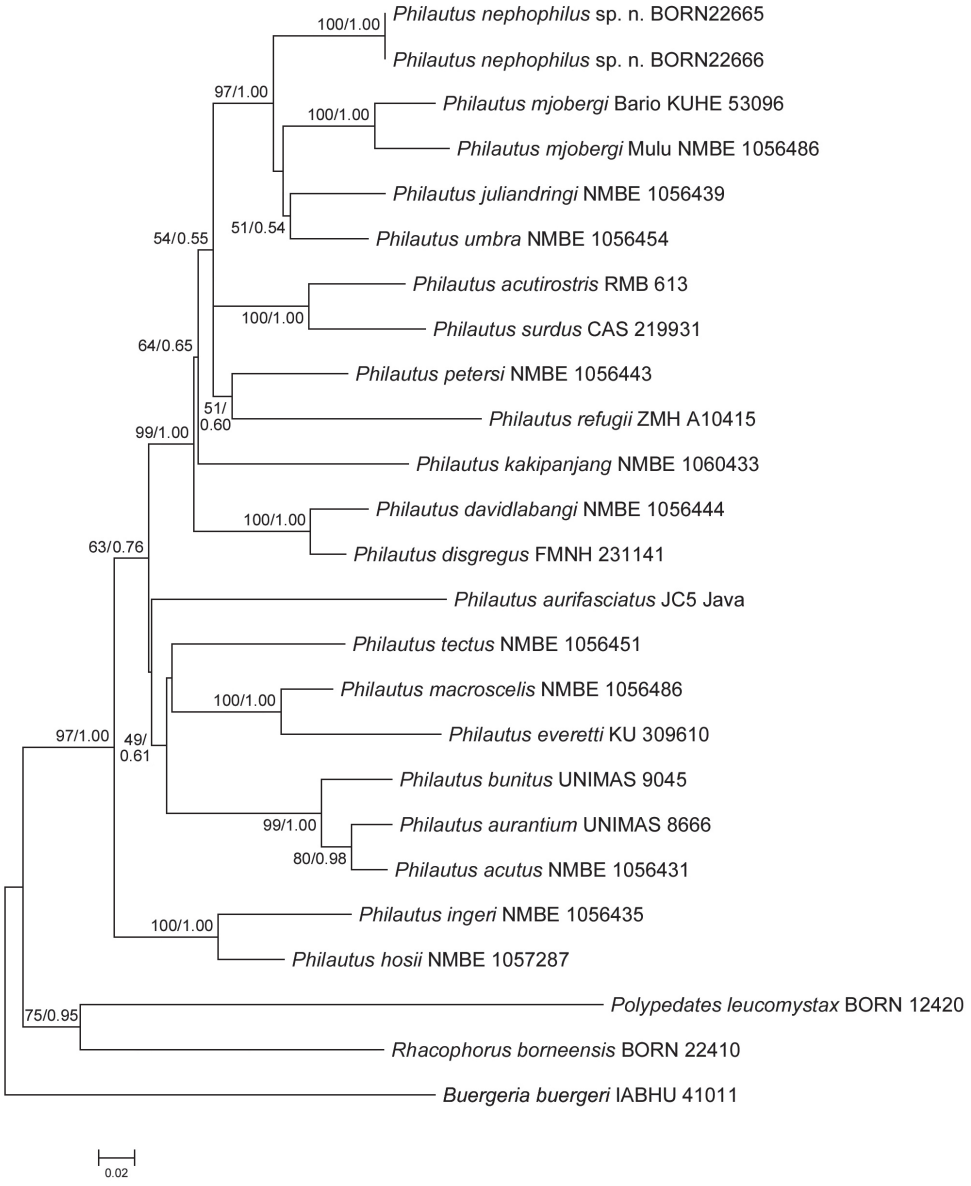

Figure 3. Bayesian phylogram inferred from mitochondrial nucleotide sequence data of 16S rRNA of species of *Philautus* from Borneo as well as some Philippine and Javan species of *Philautus*, and *Buergeria buergeri*, *Polypedates leucomystax*, and *Rhacophorus borneensis* as outgroups. Numbers above branches are non-parametric bootstrap support values from ML, followed by Bayesian posterior probabilities from BI.

Table 4. K2p-distances between *Philautus nephophilus* and other species of *Philautus*, based on comparison of 400 base pairs of mitochondrial 16S ribosomal RNA.

	Species GenBank Accession #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	***Philautus nephophilus*** KT445970																		
2	*Philautus acutirostris* F458137	10.9																	
3	*Philautus acutus* JN705366	12.2	12.2																
4	*Philautus aurantium* JN705367	12.5	12.2	3.5															
5	*Philautus bunitus* JN705368	12.2	10.9	6.1	5.9														
6	*Philautus davidlabangi* JN705386	12.8	12.7	12.2	11.7	12.2													
7	*Philautus disgregus* GQ204704	11.4	12.0	11.4	11.4	11.4	4.0												
8	*Philautus everetti* JN705376	11.2	12.2	10.1	10.9	8.8	12.2	11.4											
9	*Philautus hosii* JN705384	12.5	14.1	11.4	11.4	10.4	14.4	12.5	10.9										
10	*Philautus ingeri* JN705385	12.5	13.6	12.2	12.2	10.9	13.8	12.2	13.3	6.9									
11	*Philautus juliandringi* JN705378	8.2	10.6	14.1	13.3	13.3	13.0	13.0	13.8	14.9	13.6								
12	*Philautus kakipanjang* F240718	11.4	13.0	14.1	14.1	12.8	12.5	12.2	12.8	13.3	14.9	12.0							
13	*Philautus macroscelis* JN705372	12.0	12.7	9.8	9.8	9.3	12.0	11.7	4.5	11.7	12.7	13.0	13.0						
14	*Philautus mjobergi* Bario XXXXXXX	9.0	12.8	14.1	14.1	13.0	13.0	12.8	12.5	14.6	13.8	8.8	13.6	12.8					
15	*Philautus mjobergi* Mulu JN705380	8.8	12.5	14.1	14.6	13.0	12.8	12.0	13.0	14.4	13.3	8.8	14.1	12.8	4.8				
16	*Philautus petersi* JN705381	10.1	9.4	10.9	10.6	10.1	10.4	10.1	8.8	11.4	13.0	11.1	12.0	10.6	11.2	10.6			
17	*Philautus refugii* JN705382	13.6	11.4	13.3	12.8	12.2	13.3	12.5	13.8	14.1	15.4	13.6	13.6	13.3	13.0	13.6	10.1		
18	*Philautus tectus* JN705370	13.8	12.8	10.3	11.2	10.4	14.1	12.5	11.2	11.4	12.2	14.6	14.6	11.4	14.1	16.2	12.0	16.2	
19	*Philautus umbra* JN705379	6.9	10.4	13.6	13.3	13.0	12.8	11.2	12.0	12.5	12.8	7.5	12.0	12.0	7.7	6.7	9.6	13.0	12.8

Dehling, 2013 is larger with the SVL of adult males being 21.2–23.7 mm (16.4–18.6 mm), has a rounded snout in profile (acuminate), has the nostril closer to the tip of snout with an EN/NS of 1.45–1.61 (1.06–1.27), and more extensive toe webbing of **I**2^{-}–2.25**II**1.5–2.75**III**1.75–3**IV**2.75–1.5**V** (**I**2–2.5**II**1.75–3**III**2–3.25**IV**3.25–2**V**). *Philautus petersi* is much larger with the SVL of adult males being 20.4–26.8 mm (16.4–18.6 mm), has a median lingual process (absent); and has shorter legs with the tibiotarsal articulation reaching to tip of snout (reaching considerably beyond tip of snout); females have a distinct tubercle on the snout tip (absent). In *Philautus refugii* Inger & Stuebing, 1996, the interorbital distance is as wide as the upper eyelid (wider than upper eyelid), the snout is rounded in dorsal view (acuminate), the anterior face of the thigh has a barred black and white pattern (lateral sides of thigh bright yellow), and females have a conical rostral tubercle (absent). *Philautus saueri* Malkmus & Riede, 1996 is larger with the SVL of the male holotype being 21.4 mm (16.4–18.6 mm), has shorter legs with a TFL/SVL of 0.54 (0.58–0.63), a rounded snout in both dorsal view and lateral profile (acuminate), and a wider interorbital space with an IO/EW of 1.90 (1.14–1.43). *Philautus umbra* is larger with the SVL of males reaching up to 35.1 mm (16.4–18.6 mm), has a median lingual process (absent), less developed toe webbing, the finger and toe tips are at least twice as wide as the penultimate phalanges (less than twice as wide), its dorsal faces are light grey with darker markings during the night and almost uniformly black during the day (light brown with dark olive brown markings during the night and similar to that during the day, but lightly pigmented areas darker), and the nuptial pads are reduced to pale glandular patches (nuptial pads small, prominent, rounded). *Philautus acutirostris* (Peters, 1867; including its synonyms *P. basilanensis* Tay-

lor, 1922, and *P. woodi* Stejneger, 1905) from the Philippines is larger with an SVL of adult males of 20.8–22.4 mm (16.4–18.6 mm), has a sharply pointed snout (acuminate), frequently with a pale-coloured projection at its tip (absent), less extensive toe webbing with Toe IV being webbed only to the proximal subarticular tubercle (webbed almost to middle tubercle), a median lingual process (absent), and can have vomerine teeth (absent). *Philautus aurifasciatus* from Java is larger with the SVL of males being 18.9–20.6 mm (16.4–18.6 mm), has shorter legs with a TFL/SVL of 0.49–0.58 (0.58–0.63), and the tibiotarsal articulation reaching to nostril or the tip of snout (reaching considerably beyond tip of snout). *Philautus leitensis* (Boulenger, 1897) from the Philippines is larger with the SVL being 19.2–21.9 mm (16.4–18.6 mm) in males and 22.6–26.4 mm (20.3–23.1) in females, and has a rounded snout (acuminate). *Philautus longicrus* (Boulenger, 1894) from the Philippines is larger with the SVL of adult males being 18.0–21.9 mm (16.4–18.6 mm), has a smaller tympanum with a TD/ED of 0.28–0.35 (0.47–0.62); and snout protruding in lateral profile (not protruding). *Philautus schmackeri* (Boettger, 1892) (including *P. mindorensis* [Boulenger, 1897]) from the Philippines is larger with the SVL of adult males being 19.0–21.5 mm (16.4–18.6), has a smaller tympanum with a TD/ED of 0.20–0.35 (0.47–0.62), and more extensive toe webbing of **I**1.5–2**II**1.5–2.75**III**1.75–3**IV**3–2**V**

Figure 4. A) Holotype (SP 27443; adult male) and B) adult male paratype (SP 27442) of *Philautus nephophilus* from Silau-Silau trail, Kinabalu National Park, Sabah, in situ prior to collection; C) *Philautus mjobergi*, adult male from Gunung Mulu (KUHE 54500) in life; D) *Philautus mjobergi*, paratype, adult male from Gunung Murud (BMNH 1925.9.1.2–6); E) *Philautus mjobergi*, adult male from near Bario (KUHE 53518) in life.

(**I**2–2.5**II**1.75–3**III**2–3.25**IV**3.25–2**V**). *Philautus parvulus* (Boulenger, 1893) from Myanmar, Thailand, Cambodia, Vietnam, and Peninsular Malaysia has shorter legs with a TFL/SVL of 0.44–0.51 (0.58–0.63), and the tibiotarsal articulation reaching only to the posterior margin of the eye (beyond tip of snout); the heels barely touch when legs are folded at right angles to the body (overlapping considerably).

Distribution, habitat, and natural history: *Philautus nephophilus* is currently known with certainty only from the headquarters region of the Kinabalu National Park in Sabah where it is found at altitudes between 1,400 and 1,800 m. It probably also occurs at similar altitudes in the neighbouring Crocker Range. Around the headquarters of the Kinabalu NP, it is abundant and one of the most frequently encountered frog species. Calling males form aggregations in lower vegetation and are found on leaves or twigs at heights between 0.3 to 3 m above the ground. Individual males can be spaced from each other by distances of less than one to several meters. Males start calling at dusk and continue until dawn. Calling activity appears to increase after rain and during light rain showers. Calling groups are not found in the immediate vicinity of open water bodies, and the species is presumed to have a direct development without a free-swimming tadpole stage, as is observed in other species of the genus (Malkmus & Dehling 2008, Hertwig et al. 2012).

Etymology: The species epithet is composed of the Ancient Greek words νέφος [néphos], meaning cloud, and φιλεῖν [phileīn], meaning to love; in allusion to the habitat of the new species in montane forest at Gunung Kinabalu that is often covered in clouds. The species is most active during or shortly after rain.

Discussion

Species of the *Philautus aurifasciatus* group sensu Dring (1987) are notoriously difficult to distinguish morphologically and have been confused with each other or considered conspecific in the past. In view of this, most of the earlier original species descriptions or records state none or only few diagnostic characters (Boulenger 1900, Smith 1925a, 1925b, 1931). The first species of the group described from Borneo was *P. petersi*. In its original description, Boulenger (1900) compared it with *P. aurifasciatus* from Java, to which the first specimens collected in Borneo had been referred by Peters (1872). The second description of a species of that group from Borneo was that of *P. mjobergi* from Gunung Murud by Smith (1925a) who, however, compared his new species with *P. vermiculatus* (Boulenger, 1900) from the Malay Peninsula but neither with *P. petersi* nor with *P. longicrus*, for which at the same time he published the first Bornean record (Smith 1925b). This record was based on specimens from Gunung Pueh, which he assigned to *P. longicrus*, a spe-

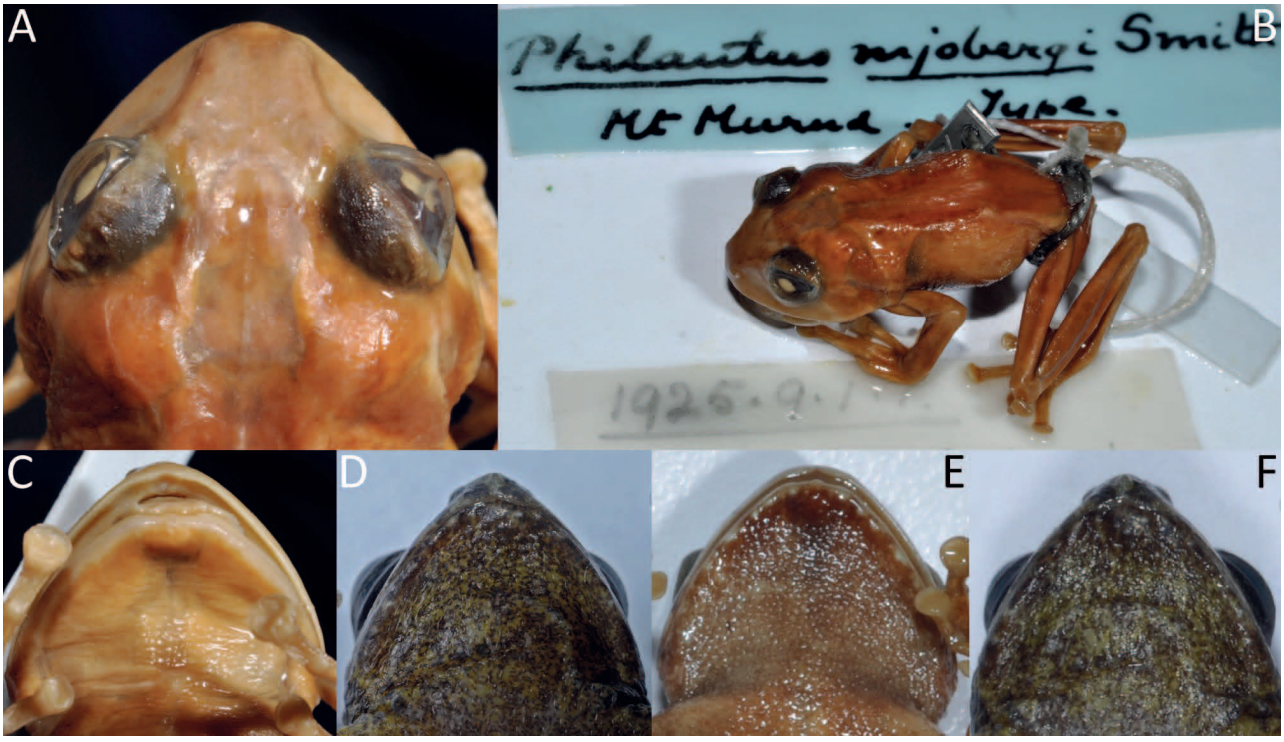

Figure 5. Top row: A) dorsal view of the head; B) dorsolateral view of the holotype of *Philautus mjobergi* (BMNH 1925.9.1.1 = 1947.2.27.13, adult female). Bottom row: Ventral views of the heads of C) female holotype of *Philautus mjobergi*; D) female paratype of *Philautus nephophilus* (SP 27444); E) male paratype of *Philautus mjobergi* (BMNH 1925.9.1.2–6); and F) male holotype of *Philautus nephophilus* (SP 27443), showing the differences in snout shape. Not to scale.

cies that was originally described from Palawan, Philippines, without having examined the type specimens (Smith 1925b, Dehling 2010). A few years later, he assigned eight specimens from Gunung Kinabalu to *P. mjobergi* because they "agreed well with the Mt. Murud specimens". In the same paper, Smith (1931) described another species of the *P. aurifasciatus* group from Gunung Kinabalu, *P. amoenus*, which he only compared with *P. mjobergi*. In his monograph on the amphibians of Borneo, Inger (1966) synonymised the Bornean (and some of the Philippine) species of the group with *P. aurifasciatus*, considering it one highly variable and widespread species, and doubtfully regarded only *P. amoenus* as a distinct species. All these species were later resurrected in the revision by Dring (1987) who for the first time took bioacoustic differences into account. Based on differences in advertisement call and morphology, several more species of the group have since been described from Borneo (Dring 1987, Inger 1989, Malkmus & Riede 1996, Inger & Stuebing 1996, Matsui 2009, Dehling 2010, Dehling & Dehling 2013). The distinct status of the species was further corroborated by comparisons of molecular genetic data (Hertwig et al. 2011, Hertwig et al. 2013, Dehling & Dehling 2013).

Several authors followed Smith's (1931) assignment and reported *P. mjobergi* from Gunung Kinabalu (e.g., Inger 1966 [as *P. aurifasciatus*], Dring 1987, Malkmus 1989, Inger & Stuebing 1992, Malkmus 1994, Malkmus & Riede 1996, Inger et al. 1996, 2000, Malkmus et al. 2002). We have herein demonstrated that the species from Kinabalu is not identical with *P. mjobergi* from Mt. Murud and describe it as a distinct species, *P. nephophilus*. The question arises whether all records from Kinabalu assigned to *P. mjobergi* in fact refer to *P. nephophilus*. Unfortunately, most of the accounts on the species from the headquarters area do not contain detailed morphological descriptions or photographs of the specimens. However, Malkmus & Riede (1996) compared the advertisement call of *P. saueri* to that of "*P. mjoebergi*" from the headquarters at Kinabalu. The latter is unambiguously assignable to *P. nephophilus*. The photos in Inger et al. (1996) and Malkmus et al. (2002), labelled "*P. mjöbergi*" and "*Philautus mjobergi*", respectively, show in fact specimens of *P. nephophilus*. During fieldwork in the headquarters area (1,300–1,900 m a.s.l.), the only species of the *P. aurifasciatus* group we encountered were *P. amoenus*, *P. nephophilus*, and *P. petersi*. We never recorded or heard an advertisement call that could be assigned to *P. mjobergi* either. Although we have not examined all the respective voucher specimens (of which the whereabouts are not always clear), we assume that the records of *P. mjobergi* from the headquarters at Gunung Kinabalu at altitudes between 1,400 and 1,800 m in fact refer to *P. nephophilus*, whereas the record from Pakka Cave at more than 3,000 m (Smith 1931) probably refers to *P. saueri* (Malkmus & Riede 1996).

Philautus nephophilus differs significantly from *P. mjobergi* in its morphological characters, advertisement call, and mitochondrial 16S rRNA gene sequence, and therefore it is justified to regard it as a distinct species. Although the populations of *P. mjobergi* from Gunung Murud and Gunung Mulu were fully supported as sister groups in our phylogeny, comparison revealed a relatively large genetic distance between the two (4.8%). This value is greater than that of species pairs that are otherwise morphologically and/or bioacoustically well distinguished (Table 4), i.e., *P. acutus* / *P. aurantium* (3.5%), *P. davidlabangi* / *P. disgregus* (4.0%), and *P. macroscelis* / *P. everetti* (4.5%). The advertisement calls of the two populations of *P. mjobergi* also appear to differ markedly. Although they are very similar in morphology, Dring (1987) noted subtle differences between the two populations in characters such as the relative position of the nostril, which he stated could be due to the poor state of the preserved material he examined, SVL, and the presence of the lingual papilla. The population on Gunung Mulu therefore probably represents another undescribed species. To address the status of this population, more data on the variation in the advertisement call of the Murud population is needed and larger series of voucher specimens from both populations need to be examined.

The discovery of another new frog species from Gunung Kinabalu once more underlines the potential for unrevealed herpetofaunal diversity in the montane forests of northern and western Sabah (Das 2006, Matsui 2006), which has been demonstrated by recent species descriptions from this area (Matsui et al. 2014, Dehling 2015).

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Appendix

Comparative material examined: *Philautus acutus*: RGS camp 3, Gunung Mulu, 4th Division, Sarawak (BMNH 1978.1765, holotype; 1978.276–279, paratypes; 1978.1766–1770, paratypes); Camp 3 (N 04° 02.284', E 114° 53.285'), Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056429–433). *Philautus amoenus*: "Kina Balu, Borneo, 7000 ft." (BMNH 1929.12.22.25 = 1947.2.6.6–7, holotype); Gunung Kinabalu, Sabah, Malaysia (ZMB 53652–653, 53695, 49019). *Philautus davidlabangi*: Batang Ai Hilton Resort (N 01°09.477', E 111°55.467'), Batang Ai National Park, Sarawak, Malaysia (NMBE 1056444). *Philautus hosii*: Camp 5, Gunung Mulu National Park, Sarawak, Malaysia (SMNS 13628, 13529). *Philautus ingeri*: Camp 3, Gunung Mulu, Sarawak (BMNH 1978.1821–1824, paratypes); Camp 3 (N 04° 02.284', E 114° 53.285'), Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056435–436). *Philautus juliandringi*: Pinnacles Trail (04°07' N, 114°53' E), northern slope of Gunung Api, approx. 1100 m above sea level, Gunung Mulu National Park, Miri Division, Sarawak, Malaysia (NMBE 1056438, holotype; NMBE 1056439, paratype; SMNS 13625–13627, paratypes); 1200 m, Pinnacles camp, G. Api, Gunung Mulu N. P., Sarawak (BMNH 1978.1779–1782), 900 m camp, G. Api, Gunung Mulu N. P., Sarawak (BMNH 1978.1776–1778). *Philautus kakipanjang*: Gunung Serapi (01°35.261' N, 110°11.578' E; 779 m a.s.l.), Matang Range, western Sarawak, Malaysia (NMBE 1060433, holotype; NMBE 1060432, paratype); Gunung Gading, western Sarawak, Malaysia (NMBE 1060427–1060431, paratypes). *Philautus kerangae*: Mentawai Ranger Station, Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056437). *Philautus longicrus*: Brooke's Point, S slope Mt. Balabag, 2800 ft., Palawan, Philippines (FMNH 51339–340), Brooke's Point, S slope Mt. Balabag, 5100 ft., Palawan, Philippines (FMNH 51342, –345, –347, –350, –352, –355, –358), Brooke's Point, S slope Mt. Balabag, 4000 ft., Palawan, Philippines (FMNH 51357). *Philautus mjobergi*: Mt. Murud, 7000–7200 ft., S. Sarawak, N. Borneo (BMNH 1925.9.1.1 = 1947.2.27.13, holotype; 1925.9.1.2–6, paratypes; 1924.5.23.1 = 1947.2.27.11–12, paratypes); Pa Ramapuh, (03°44'N, 115°28'E, ca. 1000 m a.s.l.), Bario, Sarawak, Malaysia (KUHE 12219, 12348, 12390, 12425–29); New Dam (03°45'N, 115°26'E, 1150 m a.s.l.), Bario, Sarawak, Malaysia (KUHE 53067–70, 53096, 53518–19, 53564); Camp 3 (N 04° 02.284', E 114° 53.285'), Gunung Mulu National Park, Sarawak, Malaysia (BMNH 1978.257, 1978.1783; NMBE 1056434); Camp 4, Gunung Mulu National Park, Sarawak, Malaysia (BMNH 1978.258–273, 1978.274–275, 1978.283, 1978.1784–1801). *Philautus petersi*: Mt. Dulit, Borneo (BMNH 92.6.3.16 = 1947.2.27.16, syntype); Camp 3 (N 04° 02.284', E 114° 53.285'), Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056440, 1056441, 1056442, 1056443), Sarawak (ZMB 7145). *Philautus refugii*: Western Sarawak, Malaysia (JMD field numbers 459, 460, 464, 465, 468, 473, 476, 482, 487, 489). *Philautus saueri*: East of Pakka Cave (3050 m), SW-slope of Mount Kinabalu, Sabah, Malaysia (ZMB 53626; holotype). *Philautus tectus*: Base Camp, Gunung Mulu N. P., Sarawak (BMNH 1978.109–111, 1978.1829, paratypes); Camp one, 150 m, Gunung Mulu N. P., Sarawak (BMNH 1978.1830, paratype); Camp two, Gunung Mulu N. P., Sarawak (BMNH 1978.1831, paratype); Camp 5, Gunung Mulu N. P., Sarawak (BMNH 1978.1826–1828, paratypes); Dear cave trail, near Sungai Melinau Paku, Headquarters, Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056450–451); Camp 5, base of Gunung Api, Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056452), Bako National Park, Sarawak, Malaysia (NMBE 1056558). *Philautus umbra*: 900 m camp, Gunung Api, Gunung Mulu N. P., Sarawak (BMNH 1978.1812–1816, paratypes); Pinnacles trail, Gunung Api, Gunung Mulu National Park, Sarawak, Malaysia (NMBE 1056453–456).