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ORIGINAL ARTICLE

Out of the trap: A new phytothelm-breeding species of *Philautus* and an updated phylogeny of Bornean bush frogs (Anura: Rhacophoridae)

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Abstract

Bush frogs of the genus *Philautus* are a species-rich group of the Asian tree frogs Rhacophoridae, which are known for their diverse reproductive biology. Within *Philautus*, reproduction has been described via endotrophic tadpoles and by direct terrestrial development. Here, we provide results of phylogenetic analyses based on the most comprehensive sampling of Bornean *Philautus* to date. As a result of an integrative taxonomic study using mitochondrial and nuclear markers, along with morphological and bioacoustic data, we describe a spectacular new species of this genus from the island of Borneo. The ecology of the new species of *Philautus* is closely associated with the carnivorous pitcher plant, *Nepenthes mollis*. The unusually large eggs are laid in the fluid of the pitcher and the endotrophic tadpoles, characterized by reduced mouthparts, small oral orifice and large intestinal yolk mass, complete their development in this environment. Molecular data and synapomorphic larval characters support the sister group relationship of the new species to *P. macroscelis*: both belong to the early diverged lineages in the *Philautus* tree, whose phylogenetic relationships could not be fully resolved. The new record of endotrophic tadpoles challenges again the hypothesis that terrestrial direct development is the plesiomorphic mode in this genus. Further, we discuss the nature of the frog-plant interaction that could represent a new case of mutualism. The frog provides the plant with a source of nitrogen by depositing yolk-rich eggs in the liquid of the pitcher. The plant, on the other hand, offers an exclusively protected space for the development of tadpoles in a habitat that otherwise has few permanent bodies of water and many competing frog species.

KEYWORDS
direct development, endotrophy, evolution, mutualism, *Nepenthes*

Abstrakt

Die artenreiche Gattung *Philautus* gehört zu den Ruderfröschen (Rhacophoridae), die für ihre vielfältige Fortpflanzungsbiologie bekannt sind. Innerhalb von *Philautus* wurde bisher die Fortpflanzung mit endotrophen Kaulquappen und durch Direktentwicklung

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an Landnachgewiesen. In der vorliegenden Arbeit stellen wir die Ergebnisse phylogenetischer Analysen vor, die auf dem bisher umfangreichsten Sample von *Philautus* von der Insel Borneo basieren. Als Ergebnis dieser integrativen taxonomischen Studie unter Verwendung mitochondrialer und nukleärer Marker, in Kombination mit morphologischen und bioakustischen Daten, beschreiben wir eine spektakuläre neue Art dieser Gattung. Die Ökologie dieser Art ist eng mit der fleischfressenden Kannenpflanze *Nepenthes mollis* verbunden. Die ungewöhnlich großen Eier werden in der Flüssigkeit der Kannenpflanze abgelegt. Die endotrophen Kaulquappen, die durch ein reduziertesMundfeld, eine kleine Mundöffnung und eine große Dottermasse im Darm gekennzeichnet sind, vollenden ihre Entwicklung in den Kannen. Molekulare Daten und synapomorphe larvale Merkmale unterstützen die Schwestergruppenbeziehung der neuen Art zu *P. macroscelis:* beide gehören zu den basalen Linien in der Gattung *Philautus*, deren phylogenetische Beziehungen allerdings nicht vollständig aufgelöst werden konnten. Der neue Nachweis von endotrophen Kaulquappen bei *Philautus* stellt erneut die Hypothese in Frage, dass Direktentwicklung der plesiomorphe Fortpflanzungsmodus in dieser Gattung ist. Weiterhin diskutieren wir die Art der Frosch-Pflanze-Interaktion, die einen neuen Fall von Mutualismus darstellen könnte. Der Frosch bietet der Pflanze eine Stickstoffquelle, indem er dotterreiche Eier in der Flüssigkeit der Kanne ablegt. Die Pflanze wiederum liefert einen exklusiven, geschützten Raum für die Entwicklung der Kaulquappen in einem Habitat, das ansonsten wenige permanente Gewässer und viele konkurrierende Froscharten aufweist.

1 | INTRODUCTION

The inventory of global amphibian diversity remains incomplete although 8,227 species are known to date (Frost, 2020). This can be illustrated by the fact that over the last 16 years, an average of 155 new species descriptions has been published annually (AmphibiaWeb, 2020). This increase is due in large part to the intensified research in the world's biodiversity hotspots, such as Sundaland (Stuart et al., 2008; Myers et al., 2000). The island of Borneo is part of this biogeographical region, which also includes the Malay Peninsula, Sumatra, Java, Bali, and smaller associated islands, together comprising the exposed landmasses of the Sunda shelf. Its high species richness makes Borneo one of the global hotspots for amphibian diversity (de Bruyn et al., 2014). In particular, unraveling the complexes of so-called "cryptic" species accounts for a major part of the new species descriptions in recent years from Sundaland (e.g., Arifin et al., 2018; Dehling et al., 2016; Hamidy & Matsui, 2014; Hamidy et al., 2012; Matsui et al., 2010, 2016; McLeod, 2010; McLeod et al., 2012; Munir et al., 2018; Shimada et al., 2011; Waser et al., 2017). Alongside this hidden sphere of amphibian diversity, unexpected discoveries of completely new frog species (with obviously distinct morphology and life history) were also reported in Borneo during the last decade (e.g., *Ansonia vidua*, Hertwig et al., 2014; *Chiromantis inexpectatus*, Matsui et al., 2014; *Glyphoglossus capsus*, Das et al., 2014).

The frogs of the family Rhacophoridae are known for their high morphological and reproductive diversity (Delorme et al., 2005; Frost et al., 2006; Grismer et al., 2007; Li et al., 2008, 2009; Liem, 1970; Nguyen et al., 2008; Yu et al., 2008, 2009, 2010). The 431 currently known species are distributed with a few representatives in Sub-saharan Africa, while the vast majority of species occur in southern to eastern Asia, namely, from Sri Lanka, Nepal, and India to Japan, the Philippines, Borneo, and Sulawesi (Frost, 2020). Within the rhacophorids, the bush frogs of the genus *Philautus* Gistel, 1848 are closely related to *Gracixalus* Delorme et al., 2005 and *Kurixalus* Ye et al., 1999 (Chan et al., 2018; Feng et al., 2017; Pyron & Wiens, 2011; Wostl et al., 2017). Several phylogenetic studies showed that the genus *Philautus sensu lato*, originally defined by the suggested mode of reproduction (direct development), was not in fact monophyletic (Grosjean et al., 2008; Li et al., 2008; Meegaskumbura et al., 2002; Yu et al., 2008). As a result, most species from India and Sri Lanka were transferred to *Pseudophilautus* (Laurent, 1943) and *Raorchestes* (Biju et al., 2010) (Li et al., 2009). Subsequently, *Philautus everetti* (Boulenger, 1894) and *P. macroscelis* (Boulenger, 1896)—formerly considered members of *Rhacophorus*—were included into *Philautus* (Hertwig et al., 2011). In its current composition, *Philautus* is regarded a natural group of 53 species, that are mainly distributed in Sundaland and the Philippines, only 13 occur on the Asian mainland from Malaysia to India (Frost, 2020; Hertwig et al., 2011; Li et al., 2013; Wostl et al., 2017). It is in the primary and secondary forests of Borneo that one encounters the highest

diversity of bush frogs, with 22 identified species (AmphibiaWeb, 2020), 19 of which are endemic to the island (Frost, 2020; Inger et al., 2017).

Although the mode of reproduction was formerly used as a diagnostic character for the genus before molecular analyses became generally available, it was confirmed unequivocally only in a few species—either by direct observation or genetic matching of the semaphoronts. Apart from those confirmed cases, the mode of reproduction in the vast majority of *Philautus* species remains unknown. Anecdotal reports suggest that some species of *Philautus* lay their eggs on the forest floor in moss (*P. mjobergi* Smith, 1925; Dring, 1987) and underneath dead leaves (*P. tectus* Dring, 1987; Dring, 1987), in leaf axils (*P. bunitus* Inger et al., 1995; Inger et al., 2017) or inside pitcher plants (*P. kerangae* Dring, 1987; Dring, 1987, *P. saueri* Malkmus & Riede, 1996a; Malkmus et al., 2002). Hertwig et al. (2012) genetically matched a clutch of eggs with advanced froglets found underneath leaf litter on the forest floor to *P. acutus* and hence provided a record for direct development in this species. Tadpoles without beaks, oral suckers, external gills, and operculum were reported for *P. hosii* (Boulenger, 1895) (Inger, 1966) and *P. kerangae* Dring, 1987 (Dring, 1987). Similar endotrophic tadpoles were described for *P. macroscelis* (Boulenger, 1896) based on genetically identified material, however, the actual microhabitat of these larvae remains unclear (Hertwig et al., 2011). The proof of tadpoles, however, suggests that at least two reproductive modes exist in *Philautus* and that direct aerial development is not necessarily the plesiomorphic state within the genus (Hertwig et al., 2011).

In 2009, we discovered a single male of an unknown frog of the genus *Philautus* in the Pulong Tau National Park, Sarawak, Malaysia, in north-western Borneo. A second male was collected in 2013. In 2016, we collected a series of adults, eggs, tadpoles, and bioacoustic data of this unknown species. It was found exclusively in close association with the carnivorous Velvet Pitcher-Plant (*Nepenthes mollis* Danser, 1928), a rare endemic of higher elevations in the interior of Borneo. In this study, we present a comprehensive phylogenetic analysis of *Philautus* with a focus on Bornean species. We also demonstrate the status of the new taxon as a valid species distinct from known congeners and provide a formal description using morphological, bioacoustic, and genetic data. The results make a significant contribution to our existing knowledge regarding the amphibian diversity of Borneo and in particular of reproductive strategies in the genus *Philautus* that range from endotrophic tadpoles to direct development. Finally, we discuss possible implications for the ecological interactions between frogs and pitcher plants.

2 | MATERIAL AND METHODS

A total of 134 individuals were included in the phylogenetic analyses (41 obtained from Genbank, 95 sequenced in this study (Appendix 1)). Eight adult specimens and nine tadpoles of the type series were used for morphometrical comparisons. Bioacoustic analysis is based on multiple calls from a single individual.

2.1 | Taxon sampling

Adult specimens and tissue samples used in this study (Appendix 1) were collected by hand between the years 2009 and 2018 in Sabah and Sarawak, Malaysia. Altogether, eight adult specimens (two females and six males) of the unknown species and their tissue samples were collected in 2013 and 2016 (Appendix 1), respectively, at 2,115 m a. s. l. in the Pulong Tau National Park, Sarawak, Malaysia, at the edge of Church Camp, a site comprising wooden houses and a church transiently used by the local people from nearby villages at lower elevations in the Kelabit Highlands of northern Sarawak. Adult specimens were photographed in life with a Canon EOS 5D Mark IV (Canon 100 mm macro lens, various flashes) and euthanized in a ca. 1% aqueous chlorobutanol solution (1,1,1-trichloro-2-methyl-2-propanol). Tissue samples of adult specimens were taken from liver tissue and femoral muscle tissue and stored in RNALater™ Stabilization Solution. Specimens were preserved in 4% neutrally buffered formalin, rinsed in tap water, and transferred to ethanol solution by stepwise increasing the ethanol concentration from 30% to 50% to 75% to minimize shrinkage before long-term storage in 75% ethanol. Specimens comprising the type series are deposited in the collection of the Naturhistorisches Museum Bern (NMBE) (Appendix 1).

Two groups comprising five and six tadpoles were collected from two pitchers of *Nepenthes mollis* in 2016. The two samples were pooled. Two specimens were photographed in life (field number 647P) with a Fuji X-T1 camera, Sigma 105 mm macro lens, and two synchronized flashes (Nikon SB-900, Nissin i40). Afterward, all tadpoles were euthanized by adding a few drops of clove oil to the container (Guenette et al., 2007). Subsequently, nine tadpoles were fixed and stored in 4% neutrally buffered formalin (Histofix®, Roth) and two specimens were transferred to RNALater™ Stabilization Solution for DNA analysis. Tadpoles and adults from the same site were later matched positively by DNA barcoding using a 873 bp fragment of the *16S rRNA* gene. The tadpole specimens are deposited in the collection of the Centrum für Naturkunde (CeNak), University of Hamburg Collection Number ZHM A12303 (Appendix 1).

We included all known Bornean *Philautus* in our phylogenetic analyses (Appendix 1), except for *P. erythrophthalmus* (Stuebing & Wong, 2000), *P. gunungensis* (Malkmus & Riede, 1996b), and *P. saueri* (Malkmus & Riede, 1996a) for which no sequence data are available. For *P. disgregus* (Inger, 1989), reference sequences were available but no tissue samples. *Rhacophorus reinwardtii* (Schlegel, 1840), *Kurixalus chaseni* (Smith, 1924), and *Polypedates leucomystax* (Gravenhorst, 1829) were used as outgroup following recently published phylogenetic hypotheses (Chan et al., 2018).

2.2 | Morphology

The adult voucher specimens were photographed after fixation to acquire 15 morphological measurements (Table 1). The measurements were selected based on two studies (Watters et al., 2016; Wostl et al., 2017). Full-body photographs for the larger

TABLE 1 Body measurements with abbreviations and description of measured distance

Abbr.	Trait	Description
ED	Eye diameter	Largest distance between bony edges of orbit
EN	Eye-nostril distance	Anterior tip of bony orbit to anterior end of nostril
FAL	Forearm length	Greatest distance from proximal end of palmar tubercle to tip of flexed elbow
FOT	Foot length	Distance from proximal end of inner metatarsal tubercle to tip of 4th toe
HL	Head length	Distance from posterior end of jaw bone to tip of snout
HND	Hand length	Distance from proximal end of palmar tubercle to tip of 3rd finger
HW	Head width	Distance between the two angles of the jaw
IN	Internarial distance	Distance between inner edges of nostrils
IO	Interorbital distance	Shortest distance between bony orbits
SL	Snout length	Distance from anterior corner of orbit to tip of snout
SVL	Snout-vent length	Distance from tip of snout to posterior end of vent
TAL	Tarsus length	Distance from tibiotarsal articulation to proximal end of inner metatarsal tubercle
TBL	Tibia length	Distance from distal point of flexed knee to tibiotarsal articulation
THL	Thigh length	Distance from vent to distal point of flexed knee
TYD	Tympanum diameter	Largest distance between bony edges of tympanum

measurements (HW, SVL, TAL, TBL, and THL) were taken with a Canon EOS 700D. Detailed photographs of foot, hand, and head were taken with a calibrated Leica DFC420 camera on a Leica MZ16 Stereomicroscope with motor focus. Measurements were taken from the digital photographs with the software Imagic IMS (Image Bildverarbeitung AG, Glattbrugg, Switzerland). The webbing formula follows Myers and Duellman (1982). Snout shape terms were taken from Savage (2002). Description of the color is based on digital photographs, which were taken *in situ* the day after capture. Sexes were determined by visual inspection of the internal mouth and throat region to check for vocal sac openings and by screening the ventral abdomen and the inguinal region for eggs. The morphological comparison to other species of *Philautus* is based on descriptive data from the literature.

Nine tadpole specimens (all except the ones reserved for DNA work) were subject to digital measurements. Dorsal, ventral, and lateral shots were made using a Keyence VHX 5000 digital microscope equipped with a VHZ20 lens (20–200× zoom). Measurements were taken from digital photographs either with the integrated measuring software of the VHX 5000 or ImageJ software (Schneider et al., 2012).

2.3 | Laboratory protocol

DNA was extracted from adult tissue samples with the DNeasy Blood & Tissue Kit (Qiagen N.V., Hilden, Germany). A total of 14 primer combinations for four mitochondrial loci (*12S-Val-16S*: partial *12S rRNA* gene, intervening *tRNA-Val* gene, partial *16S rRNA* gene: 12Sm + 16Sa, 12L1 + 16Sh, 16SC + 16SD; *CytB*, partial Cytochrome B gene: CB-J-10933 + CytbAR-H) and three partial sequences of nuclear genes (*POMC*, *Proopiomelanocortin-A*: POMC DRV F1 + POMC DRV R1; *BDNF*, *brain-derived neurotrophic factor*: BDNF F1 + BDNF R1; *NTF3*, *Neurotrophin 3*: NTF3 F3 + NTF3 R3) were used for DNA amplification (Table 2). The PCR solution consisted of the following: 6.5 µl nuclease-free water (ddH_2O), 2 µl forward primer (10 µM), 2 µl reverse primer (10 µM), 2 µl sample DNA, 12.5 µl GoTaq® Hot Start Green Master Mix (Promega, Madiso, U.S.). The annealing temperature was set at 94°C for 2 min (3 min for *NTF3*) followed by 35 (40 for *NTF3*) cycles. All three cycle steps were adjusted to primer-specific settings (Table 2). Final extension was performed at 72°C for 5 min (7 min for *NTF3*). PCR Products of the *16S rRNA* gene were cleaned with the Wizard® SV Gel and PCR Clean-up System (Promega, Madiso, U.S.) and sequenced by LGC (LGC Limited, Teddington, UK). All other PCR products were cleaned and subsequently sequenced by LGC (LGC Limited, Teddington, UK). Sequences were managed and checked for ambiguities using Geneious Pro 9.1.8 (Biomatters Ltd., Kearse et al., 2012). The sequences of this study are deposited in GenBank (Appendix 1).

2.4 | Phylogenetic analyses

The sequences were aligned with the MAFFT algorithm plugin in Geneious Pro (Katoh et al., 2002; Katoh & Standley, 2013) and refined with the MUSCLE algorithm plugin in Geneious Pro (Edgar, 2004) with eight iterations. The alignments of each PCR primer combination were checked separately and compared for laboratory or frameshift errors, stop codons and contamination based on preliminary trees obtained with the RAxML–plugin, implemented in Geneious Pro using the GTR GAMMA I nucleotide model, the rapid

TABLE 2 Targeted gene and amplicon length in bold, primer name and primer sequence with corresponding PCR cycle and reference for the used markers. Primer name: F, Forward Primer; R, Reverse Primer. Reference: PHC, Pauly et al. (2004); GDA, Goebel et al. (1999); G, Goebel et al. (1999); P, Pauly et al. (2004); MM, Meegaskumbura and Manamendra-Arachchi (2005); Ve, Vences et al. (2003, 2005); VMW, Vieites et al. (2007); Vi, Vieites et al. (2007); SC, Santos and Cannatella (2010)

		PCR cycles			
Gene and primer name	Primer Sequence (5′-3′)	1st	2nd	3rd	References
***12S-Val-16S*: 12Sm/16Sa: 890-932 bp; 12L1/16Sh: 730-759 bp; 16SC/16SD: 839-885 bp**					
12Sm (F)	GGCAAGTCGTAACATGGTAAG	94°C, 30s	48.2°C, 30s	72°C, 1 min	PHC
16Sa (R)	ATGTTTTTGGTAAACAGGCG	94°C, 30s	48.2°C, 30s	72°C, 1 min	GDA
12L1 (F)	AAAAAGCTTCAAACTGGGATTAGTACCCCACT	94°C, 30s	48.2°C, 30s	72°C, 1 min	G
16Sh (R)	GCTAGACCATKATGCAAAAGGTA	94°C, 30s	48.2°C, 30s	72°C, 1 min	G
16SC (F)	TCAAHTAAGGCACAGCTTA	94°C, 30s	48.2°C, 30s	72°C, 1 min	P
16SD (R)	CTCCGGTCTGAACTCAGATCACGTAG	94°C, 30s	48.2°C, 30s	72°C, 1 min	P
***CytB* : 603 bp**					
CB-J-10933 (F)	TATGTTCTACCATGAGGACAAATATC	95°C, 40s	45°C, 40s	72°C, 40s	MM
CytbAR-H (R)	TAWARGGRTCYTCKACTGGTTG	95°C, 40s	45°C, 40s	72°C, 40s	Ve
BDNF: 645-699 bp					
BDNF F1 (F)	ACCATCCTTTTCCTKACTATGG	94°C, 30s	51.5°C, 30s	72°C, 1 min	VMW
BDNF R1 (R)	CTATCTTCCCCTTTTAATGGTC	94°C, 30s	51.5°C, 30s	72°C, 1 min	Vi
***POMC* : 457-471 bp**					
POMC DRV F1 (F)	ATATGTCATGASCCAYTTYCGCT-GGAA	94°C, 30s	56°C, 30s	72°C, 1 min	Vi
POMC DRV R1 (R)	GGCRTTYTTGAAWAGAGTCATTAGWGG	94°C, 30s	56°C, 30s	72°C, 1 min	Vi
***NTF3* : 556-597 bp**					
NTF 3NTF3 F3 (F)	TCTTCCTTATCTTTGTTGGCATCCACGCTA	95°C, 30s	52.4°C, 30s	72°C, 1 min	SC
NTF3 R3 (R)	ACATTGRGAATTCCAGTGTTTGTCGTCA	95°C, 30s	52.4°C, 30s	72°C, 1 min	SC

bootstrapping and search for best-scoring Maximum Likelihood (ML) tree algorithm and 100 bootstrap replicates.

In a first step, we used an alignment of the 873 bp amplicon of the *16S rRNA* gene obtained with the primer combination 16SC + 16SD to infer a reference tree for genetic barcoding (Figure S1), for comparison with reference sequences obtained from GenBank and to calculate uncorrected pairwise distances (Appendix 1). GenBank sequences of *P. acutirostris*, *P. acutus*, *P. amoenus*, *P. aurantium*, *P. bunitus*, *P. davidlabanig*, *P. disgregus*, *P. everetti*, *P. hosii*, *P. ingeri*, *P. juliandringi*, *P. kakipanjang*, *P. kerangae*, *P. larutensis*, *P. macroscelis*, *P. mjobergi*, *P. nephophilus*, *P. refugii*, *P. surdus*, *P. tectus*, and *P. umbra* were used to confirm the species identification of our samples. The reference tree was estimated with a Maximum Likelihood analysis using RAxML-NG (Kozlov et al., 2019) with 100 bootstrap replicates and the GTR nucleotide model. To reduce the amount of missing data in our final data set, specimens were excluded from final analyses when only data for the *16S rRNA* gene was available. Uncorrected pairwise distances were calculated in MEGA v5.2.2 (Tamura et al., 2011) with transitions and transversions included, without any variance estimation, gaps, and missing data excluded by complete deletion.

For the phylogenetic analyses, the sequences of the *12S rRNA*, *tRNA-Val*, and *16S rRNA* genes were first concatenated and then aligned (2,006 bp, *12S-Val-16S*). The alignments of the different genetic markers were then concatenated into three data partitions: nuclear data partition (nuDNA: *POMC*, *BDNF*, *NTF3*; 90 sequences), mitochondrial data partition (mtDNA: *CytB*, *12S-Val-16S*; 93 sequences), and combined data partition (combDNA: *POMC*, *BDNF*, *NTF3*, *CytB*, *12S-Val-16S*; 93 sequences). The search for the best-fitting partitioning schemes was conducted with PartitionFinder 2 (Lanfear et al., 2016) using the "greedy" algorithm (Lanfear et al., 2012) and PhyML (Guindon et al., 2010) (Table S1). ML analysis was performed with RAxML using 2,000 bootstrap replicates, the GTR Gamma nucleotide model with invariant sites (GTR Gamma + I) and rapid bootstrapping followed by a careful search for the best-fitting ML tree. Bayesian Inference (BI) was conducted using MrBayes 3.2 (Ronquist et al., 2012), the partitioning schemes selected by PartitionFinder 2 (Table S1), and sampling over 10 million generations (20 million for the combined dataset) with a sampling frequency of 1,000 generations. Four independent Markov-Chain Monte Carlo (MCMC) runs were performed with four chains each (one cold and three heated chains), a temperature of 0.2 and a burn-in of 10%. The four independent runs were combined with the "sumt" function. The independent runs were visually inspected in Tracer v1.7.1 (Rambaut et al., 2018) to see whether the trees had reached convergence. The analysis was rejected when the effective sample size (ESS) did not reach 200. Bootstrap values above 70% in ML (Hillis & Bull, 1993) and posterior probability values above 0.95 in BI (Huelsenbeck & Ronquist, 2001) were considered as robust support for the corresponding clade. The resulting trees were visualized in FigTree V 1.4.3

(Rambaut, 2016) and annotated and colored in Inkscape v.0.92.4 (Inkscape Project, 2020). The alignments are available online in the Alignments S1-S8.

2.5 | Bioacoustics

The call of the holotype was recorded on March 9, 2016 at Church Camp, Pulong Tau National Park, Sarawak, Malaysia using an Olympus Linear PCM Recorder LS-10. The recording level was adjusted manually in the field by balancing the signal peaks at 0dB. The advertisement call was analyzed using Raven Pro 1.4 (Bioacoustics Research Program 2014). The call parameters dominant frequency, number of notes per call, note and pulse repetition rates, duration of call, note, pulse, and of intervals were measured in the oscillogram following the step-by-step procedure of Köhler et al. (2017). To eliminate background noise from the sonogram, values below 0.1db were clipped. A note-centered approach was used, defining the parameters as follows: a call is a series of notes, separated by a long silent interval from other calls. Call duration is measured from the beginning of the first note of a call to the end of the last note of the same call. The silent interval is measured from the end of the last note of the call to the beginning of the first note of the consecutive call. Call repetition rate is the number of calls emitted per minute. A note is a series of pulses, separated from the next note by an internote interval. The internote interval is shorter than the silent interval and is measured from the end of the last pulse of one note to the beginning of the first pulse of the consecutive note. Note duration is measured from the beginning of the first pulse to the end of the last pulse of the same note. Note repetition rate is the number of notes emitted per second. A pulse is a single peak of sound energy, not divisible into subunits. Pulses are separated from each other by strong amplitude modulations. Pulse repetition rate is the number of pulses emitted per second. Dominant frequency is the frequency containing the highest sound energy (Köhler et al., 2017). The call recording is available online in the Data S1 of this document.

3 | RESULTS

3.1 | Phylogeny

The nuclear data partition comprised 1,770 bp (nuDNA: *POMC*, *BDNF*, *NTF3*) of 90 individuals. The mitochondrial data partition comprised 2,609 bp (mtDNA: *CytB*, *12S-Val-16S*) of 93 individuals. The combined data set consisted of 4,379 bp (combDNA: *POMC*, *BDNF*, *NTF3*, *CytB*, *12S-Val-16S*) of 93 individuals. The best-fitting partitioning scheme was a gamma-shaped rate variation with a proportion of invariable sites (GTR + I + I) for first and second codon positions of the protein-coding genes and *12S-Val-16S*, and the gamma model for the third codon position (Table S1). In BI analyses, this output of PartionFinder was applied, while the model GTR + G + I was used in ML analyses using RaxML.

The genus *Philautus* is robustly supported as a monophyletic group in all analyses (Figure 1, Figures S2-S5). The new species from Church Camp represents a distinct evolutionary lineage in all analyses and is congruently confirmed as sister group of *P. macroscelis* (Figure 1, Figures S2-S5). Intraspecific pairwise distances, including four adult and five tadpole samples of the new species, are 0–0.25% (NMBE 1065920, NMBE 1073711, NMBE 1073601, NMBE 1073602, lot ZMH A123049) based on 819 bp sequences of the *12S-Val-16S* alignment. The interspecific pairwise distances in comparison with the remaining species of *Philautus* range from 6.81 to 13.76% (Table 3, based on 819 bp including four adult specimens of the new species (NMBE 1065920, NMBE 1073711, NMBE 1073601, NMBE 1073602)).

The phylogenetic relationships of *P. tectus* and as a consequence also the early splitting events within *Philautus* including the relationships (*P. hosii* + *P. ingeri*) and (*P.* sp. + *P. macroscelis*) are not congruently and robustly resolved (BI < 0.9, ML < 70%, Figure 1, Figures S2-S5). The resolution and branching patterns of combDNA and mtDNA trees are congruent but differ in comparison with the nuDNA results (Figure 1, Figures S2-S5). The monophyletic group comprising the remaining *Philautus* species and the clades ((*P. bunitus* + *P. kerangae*) + (*P. acutus* + *P. aurantium*)) and ((*P. amoenus* + *P. nephophilus*) + (*P. umbra* + *P. juliandringi* + *P. mjobergi*)) are robustly and congruently supported in all analyses. The phylogenetic relationships within the subclade (*P. umbra* + *P. juliandringi* + *P. mjobergi*) and of *P. davidlabangi*, *P. kakipanjang*, *P. larutensis*, *P. refugii* and (*P. umbra* + *P. juliandringi* + *P. mjobergi*) remain unresolved, because they received at most moderate support values or differ between the trees obtained using the separate data partitions (Figure 1, Figures S2-S5). The affected nodes of the species with ambiguous relationships received at most moderate support values in all analyses.

3.2 | Bioacoustics

The advertisement call series consists of five calls with each call consisting of three evenly spread notes. The notes are pulsed with visible amplitude modulations. The first note consists of 1–2 low-frequency pulses, two high pulses which are not always completely distinguishable and 1–2 fading, low and rather long pulses. The second note consists of 5–7 pulses with increasing amplitude, the last two being of higher frequency than the two last pulses in the first note. These are followed by 1–3 fading pulses of low frequency. The third and last note consists of six pulses of increasing amplitude, with the highest pulse being of higher frequency than the highest pulse in the second note. The last note ends with 1–2 fading pulses. The call is not continuous, that is, the intercall interval is visible. Average note duration: 36.33 ms, average internote interval: 62.1 ms, average call duration: 164.4 ms, average note repetition rate: 0.064 notes/s, average number of pulses per note: six, average

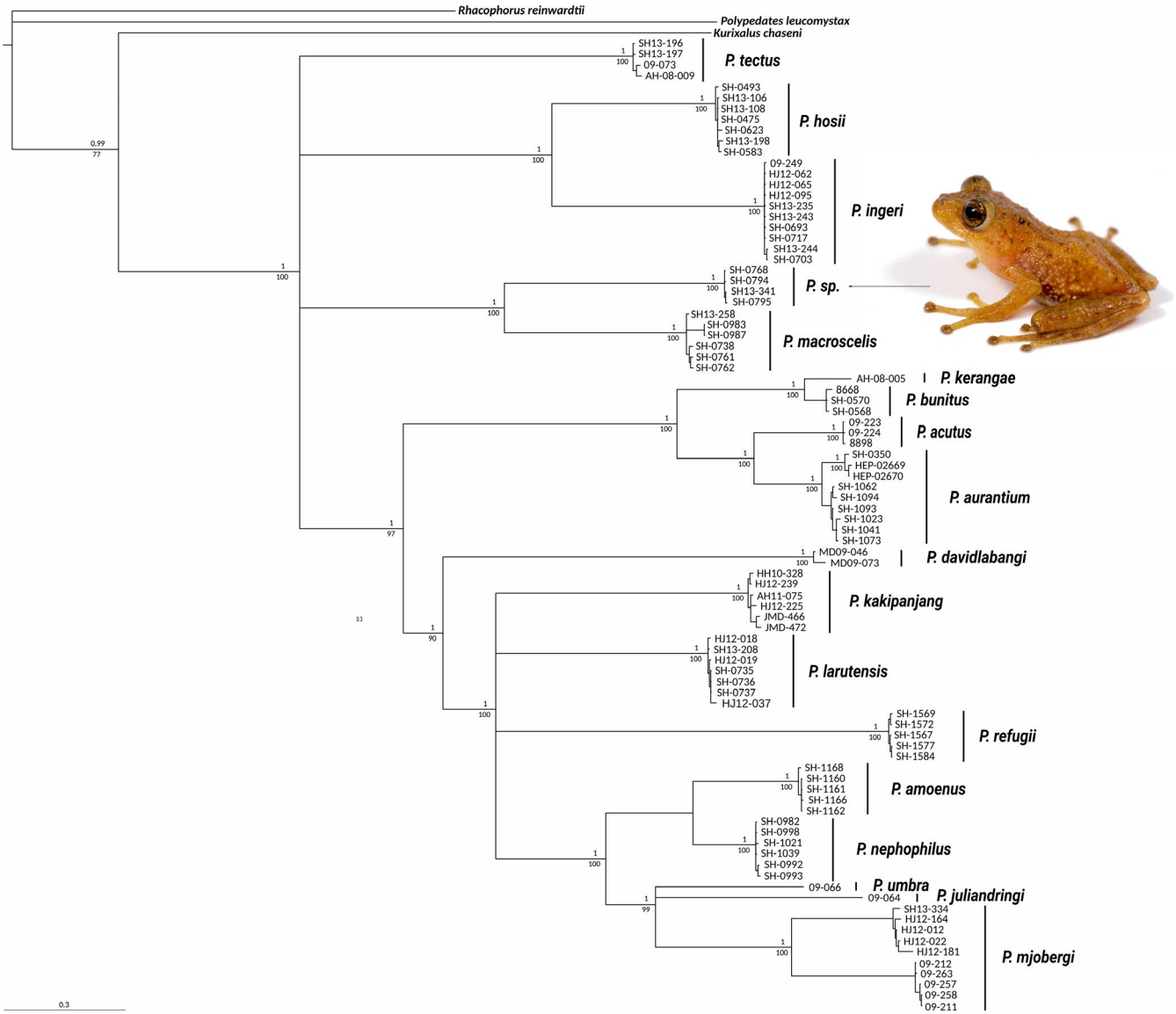

FIGURE 1 Total evidence tree based on the combined nuclear (*POMC*, *BDNF*, and *NTF3*) and mitochondrial DNA (*CytB*, *12S-Val-16S*) data partitions (4379 bp, combDNA). Only congruently and robustly supported nodes are shown (BI > 0.9 and ML > 70%). BI above, ML below branches. See Alignments S1-S8 for the results of the separate analyses of the mitochondrial and nuclear data partitions

note interval: 5.101 s, and average dominant frequency: 2.8125 kHz (Figure 2). The call of the new species differs from the published calls of Bornean *Philautus* species in varying combinations of the following analytical parameters: number of notes, duration of call, duration of notes, and dominant frequency (for details see below section Comparison).

3.3 | Species description

We formally describe the material from Church Camp, the Pulong Tau National Park, Sarawak, Malaysia, as *Philautus nepenthophilus* sp. nov. based on phylogenetic analyses using mitochondrial and nuclear markers (Figure 1, Figures S2-S5), genetic divergence in *16S rRNA* gene (Table 3), and a unique combination of morphological characters of the adults including color pattern, skin structure, head shape; and of the larval stages including shape of snout, structure of the oral disk, presence of a posteroventral skin flap; as well as on bioacoustic evidence. *Philautus macroscelis* is the sister species of *P. nepenthophilus*, but can be clearly distinguished by skin structure, color pattern, and snout shape. For details, see the following sections diagnosis, description, comparisons, and larval description. The new species is registered in Zoobank with the number 4C1B7C00-D110-4EFE-9E50-EBD07003F54A.

3.3.1 | Holotype

NMBE 1073711 (Figures 3a, b, 4a, b, 5a, b), an adult male collected at Church Camp, (N 3°55.603200, E 115°30.867600, 2,115m a.s.l.) Pulong Tau National Park, Sarawak, Malaysia on 9 March 2016 by Flury J., Haas A., Hertwig S. T., Pui Y. M., Reichen N.

TABLE 3 Range of uncorrected pairwise distances (%) inferred with complete deletion, based on 819 bp sequences of the *16S rRNA* gene alignment of all adult *Philautus* species included in the analyses. *P. juliandringi*, *P. kerangae*, and *P. umbra* are represented by only one sequence each. Min. and max. pairwise distance was identical where no range is given. The large pairwise distance of *P. mjobergi* can be explained by the pooling of sequences from two populations

Philautus	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)
acutus (1)																		
aurantium (2)	2.72–3.28	0.00–0.63																
bunitus (3)	4.88–5.00	4.44–4.79	0.00–0.10															
kerangae (4)	5.59	4.91–5.03	2.47–2.58	0														
macroscelis (5)	11.16–11.45	11.05–11.48	10.91–11.32	11.21–11.50	0.00–0.63													
nepenthophilus (6)	12.63–12.77	11.94–12.22	12.19–12.46	13.53–13.67	6.82–7.43	0.00–0.25												
tectus (7)	10.93	11.08–11.35	11.06–11.19	11.49	9.81–10.09	10.81–10.94	0											
amoenus (8)	12.55	11.69–11.95	12.67–12.81	13.11	10.58–10.87	11.31–11.48	11.47	0										
nephophilus (9)	12.54	11.54–11.94	11.86–11.99	12.96	11.13–11.42	11.51–11.65	11.36	3.15	0									
juliandringi (10)	12.89	12.01–12.29	12.23–12.37	12.00	10.87–11.15	12.45–12.59	11.47	7.28	7.30	0								
umbra (11)	12.29	11.82–12.10	11.51–11.64	11.63	10.75–11.15	11.71–11.85	10.76	6.19	5.96	6.04	0							
mjobergi (12)	13.50–13.80	13.01–14.00	13.00–13.43	13.18–13.47	11.75–13.43	13.78–15.83	12.91–13.72	8.88–9.16	8.93–9.21	8.53–8.75	7.04–7.92	0.00–5.90						
kakipanjang (13)	11.59–12.05	11.38–12.26	10.93–11.51	11.33–11.79	9.73–10.58	11.94–12.49	11.11–11.69	9.21–9.60	8.95–9.21	9.09–9.90	9.20–9.60	10.83–11.63	0.10–0.74					
larutensis (14)	10.91–11.04	10.71–11.12	10.62–10.89	11.30–11.44	9.32–10.09	9.95–10.22	10.37–10.50	8.53–8.65	8.54–8.67	8.42–8.55	8.40–8.53	10.00–10.77	7.78–8.17	0.00–0.10				
davidlabangi (15)	11.57–11.70	10.71–11.38	10.96–11.22	11.79–11.93	11.09–11.77	13.16–13.72	10.89–11.03	10.92–11.32	11.08–11.47	10.40–10.79	10.27–10.39	11.11–12.69	9.44–10.25	8.94–9.45	0.00–0.32			
refugii (16)	13.46	12.58–12.86	13.58–13.71	13.19	12.68–12.98	14.56–14.71	14.03	13.57	12.61	12.13	11.05	13.50–13.80	10.97–11.26	10.23–10.37	11.70–11.82	0		
hosii (17)	11.50–11.65	11.78–12.22	11.47–11.89	11.89–12.19	10.96–11.40	12.16–12.46	10.22–10.37	12.48–12.64	12.96–13.12	11.61–11.90	11.98–12.27	13.61–14.37	11.86–12.76	11.22–11.51	11.90–12.20	14.49–14.80	0.00–0.21	
ingeri (18)	13.83	13.51–13.94	12.79–12.92	13.08	12.64–12.95	12.41–12.55	11.66	13.40	12.83	13.29	12.40	14.58–15.05	11.97–12.38	12.79–12.93	12.58–12.72	14.56	7.27–7.40	0

Shaded in grey are the values for the new species.

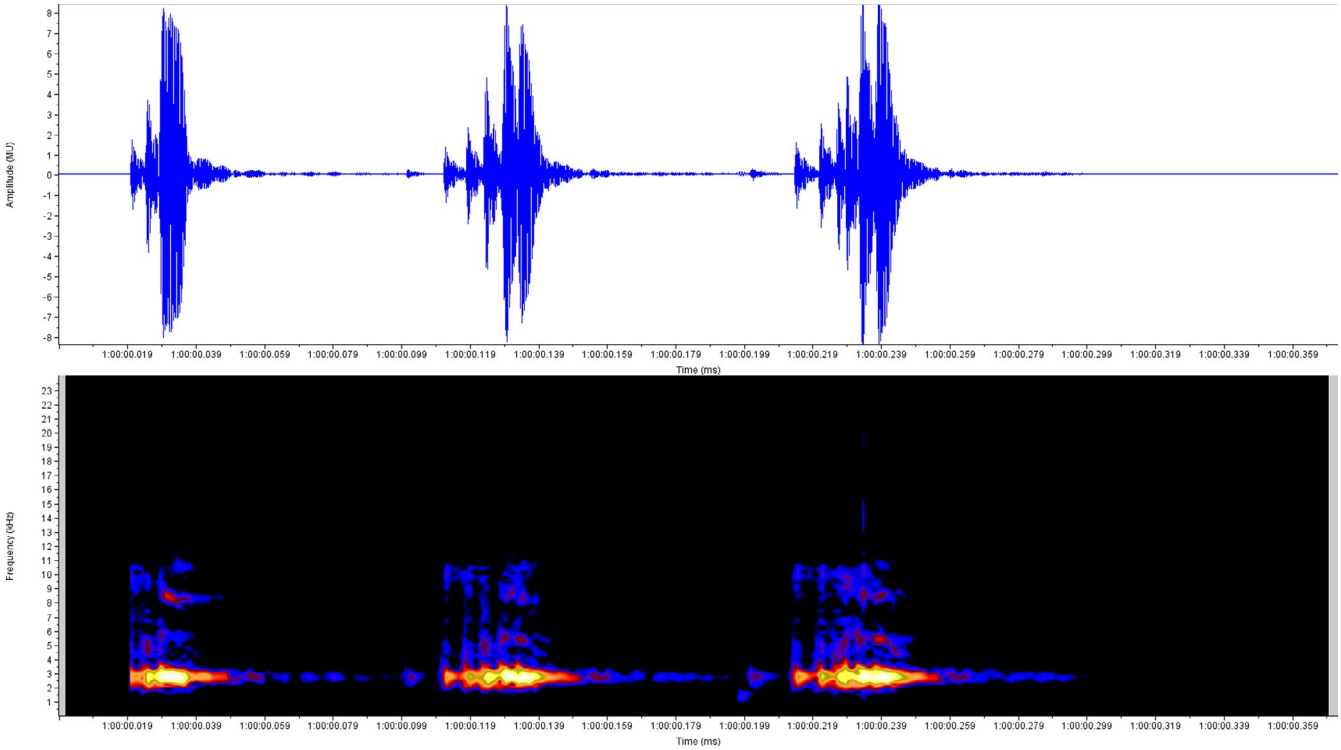

FIGURE 2 Sonogram of one call with three notes of *Philautus nepenthophilus*

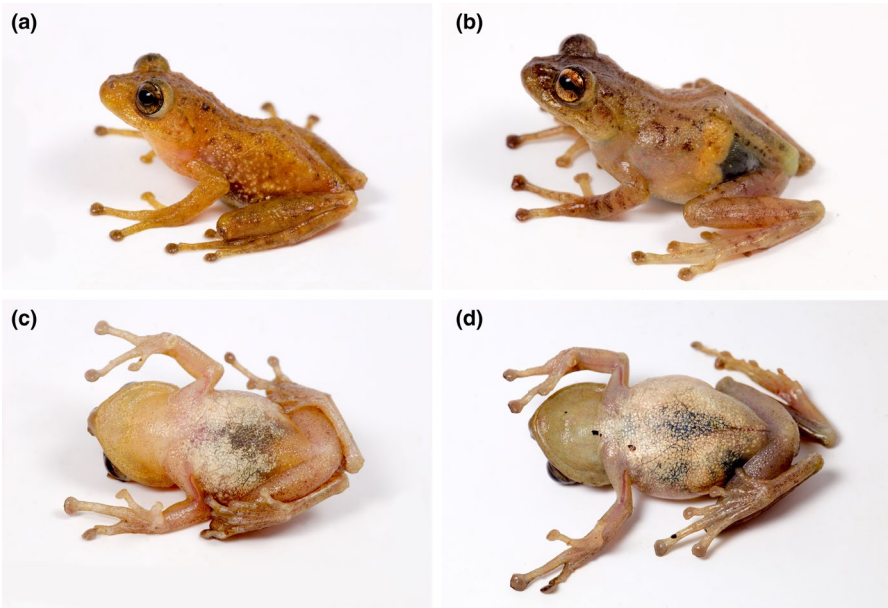

FIGURE 3 Specimens of *Philautus nepenthophilus* photographed alive on the day after capture (a) Male holotype NMBE 1073711 in dorsolateral view (b) Female paratype NMBE 1073601 in dorsolateral view (c) Holotype NMBE 1073711 in ventral view (d) Female paratype NMBE 1073601 in ventral view

3.3.2 | Paratypes

The paratype series consists of seven adults (two females and five males) and five tadpoles (lot ZMH A123049). NMBE 1065920, an adult male collected at the type locality on March 11, 2013 by Hertwig S. T., Pui Y. M., Keilholz T., Einecke T. NMBE 1073601, an adult female, NMBE 1073602 and NMBE 1073580 (Figure 9a), two adult males collected at the type locality on March 9, 2016 by Flury

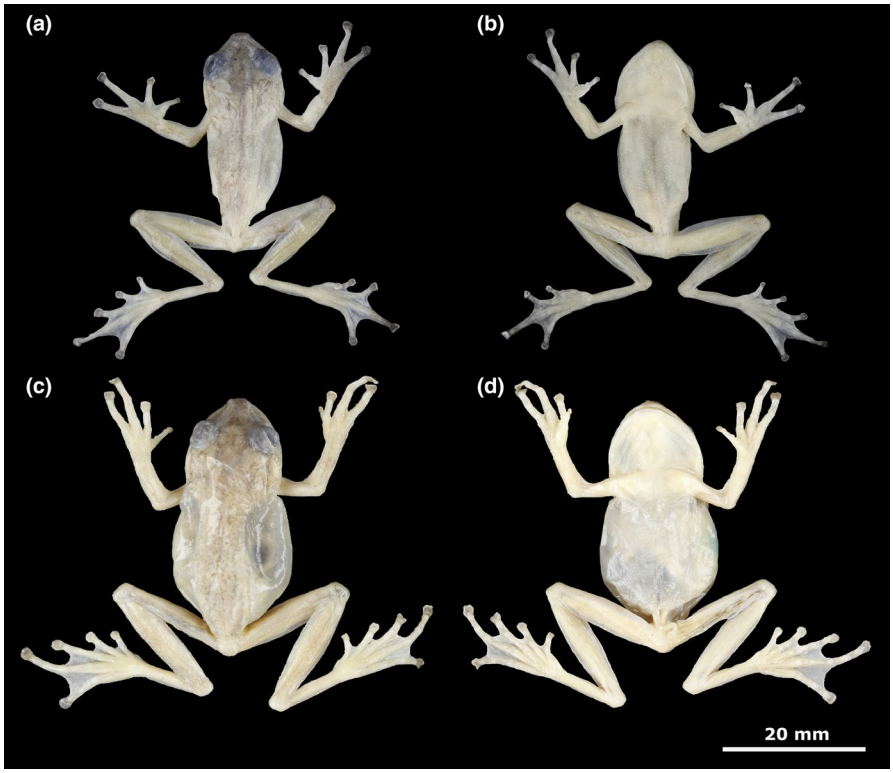

FIGURE 4 (a) Dorsal view and (b) Ventral view of holotype NMBE 1073711 of *Philautus nepenthophilus* (c) Dorsal view and (d) Ventral view of female paratype NMBE 1073577 in preserved condition

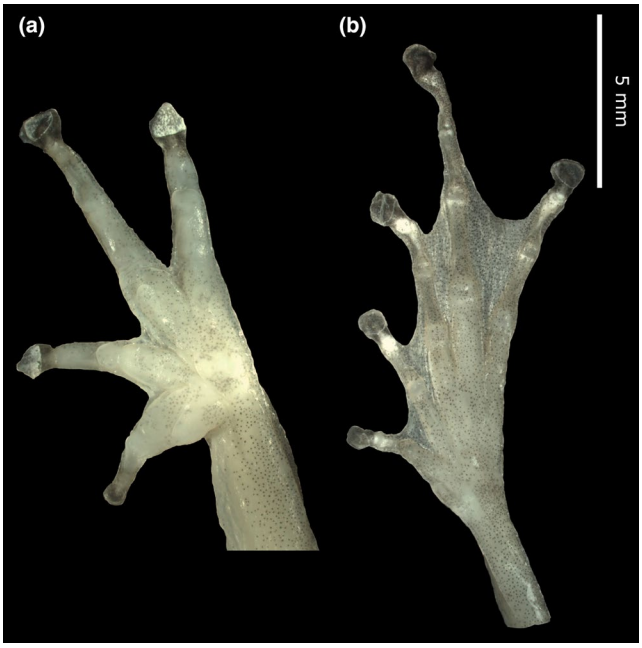

FIGURE 5 (a) Ventral view of left hand and (b) Ventral view of left foot of holotype NMBE 1073711 of *Philautus nepenthophilus* in preserved condition

J., Haas A., Hertwig S. T., Pui Y. M., Reichen N. NMBE 1073577, an adult female (Figure 4c, d), NMBE 1073588, NMBE 1073580 and NMBE 1073591, two adult males and the tadpoles lot ZMH A123049 collected at the type locality on March 12, 2016 by Flury J., Haas A., Hertwig S. T., Pui Y. M., and Reichen N.

3.3.3 | Diagnosis

Philautus nepenthophilus is assigned to the genus *Philautus* based on a robustly supported phylogenetic hypothesis (Figure 1). Morphological synapomorphies of this genus are currently not known after several revisions using molecular data (Hertwig et al., 2013; Li et al. 2008, 2009; Wostl et al., 2017; Yu et al. 2008, 2009). Species are currently assigned to *Philautus* on the basis of morphological similarity to already-described species or of molecular evidence (Dehling & Dehling, 2013; Dehling et al. 2016; Wostl et al., 2017). Diagnostic characters of the adults of the new species in comparison with congeners are as follows: (1) uniform yellow to greenish coloration of head, dorsum, and flanks without a distinct color pattern (Figure 3a, b); (2) low intraspecific variation in color pattern; (3) smooth skin with minuscule keratinous tubercles loosely scattered on eye lids, interorbital region and (in some specimens) snout (Figure S6), enlarged tubercles or projections absent (Figure 4); (4) truncate, rounded, short snout (SL/HL 0.35–0.44) (Figure 6); (5) sexual dimorphism in head shape absent; (6) tympanum moderately large (TYD/ED 0.42–0.52); (7) medium body size (SVL male: 28.67–32.34 mm, female: 35.22–37.24 mm); (8) advertisement call is short, fast and rattling, the three notes with 6–7 pulses each, average note duration is 36.33 ms and the dominant frequency is at 2.8125 kHz (Figure 2); (9)

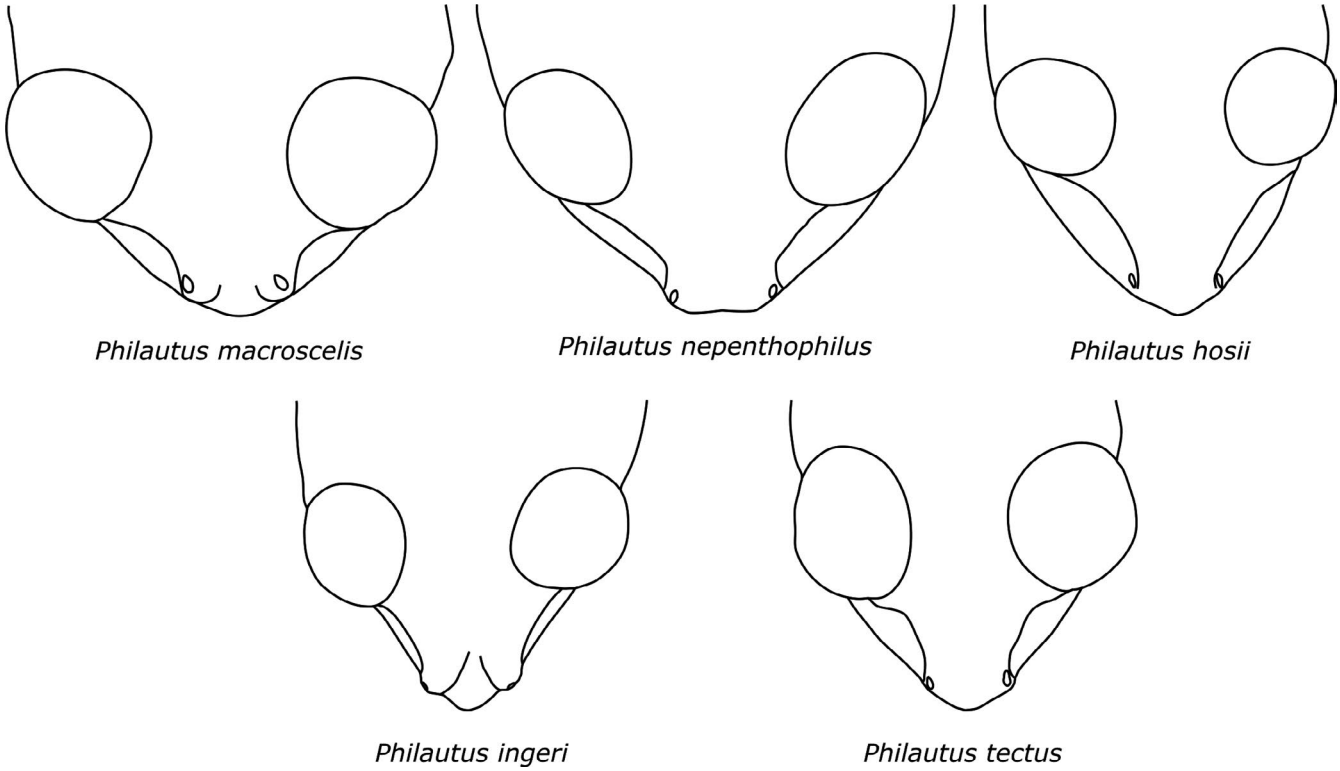

FIGURE 6 Snout shapes of *Philautus* species most closely related to *Philautus nepenthophilus*. Drawings are not to scale to better facilitate shape comparison

presumably endotrophic tadpoles with very short snout, small ventral oral orifice, two pairs of lateral oral papillae, anterolateral nares, unique posteroventral skin flap present (Figure 7c-g); (10) coloration of the tadpoles without iridophores (Figure 7c-g).

3.3.4 | Description of Holotype

Medium-sized body (Figure 4a, b), SVL 30.45 mm (Table 4); head moderately large, rounded, slightly longer than wide (HW/HL 0.95), head width slightly over one-third of snout-vent length (HW/SVL 0.36), head length two-fifths of SVL (HL/SVL 0.38); snout in dorsal view truncate, slightly mucronate, two-fifths of head length (SL/HL 0.37), in profile truncate (vertical) and not clearly pointed, not projecting beyond lower jaw, same length as diameter of eye (SL/ED 0.99); nostrils oval, slightly raised with flap of skin, internarial distance is smaller than eye-nostril distance (EN/IN 1.39); canthus rostralis short but distinct, rounded, in dorsal view slightly curved (Figure 6); interorbital distance is double the size of eye diameter (IO/ED 2.02); lores weekly concave; tympanum weakly distinct, diameter large, two-fifths of eye diameter (TYD/ED 0.42); supratympanic ridge distinct, not curved or angled; eye rather small (ED/HL 0.37) with a horizontal pupil; vomerine teeth absent; tongue triangular with two elongated lobes at posterior end, lingual papilla absent; vocal sac opening slit-like; forelimbs slender, hands large (HND/FAL 1.39), one-third of SVL (HND/SVL 0.32), fingers long and slender, relative lengths: I < II < IV < III, disks rounded, webbing absent, subarticular tubercles weakly distinct, metacarpal tubercles absent, no distinct tubercles on forearm, nuptial pads absent (Figure 5a); Hind limbs long and slender, much longer than SVL ((THL + TBL + TAL + FOT)/SVL 1.73), tibia long (TBL/SVL 0.52), longer than foot (FOT/TBL 0.86) and slightly longer than thigh (TBL/THL 1.13); toe disks rounded, disk of 4th and 5th toe triangular to oval, relative lengths: I < II < III < V < IV, toe webbing moderately developed, generally 2/3. Webbing formula: I1.75–2II1.5–2.75III1.25–3IV2.5–1.5V (Figure 5b); tubercles weakly distinct, outer metatarsal tubercle absent, inner metatarsal tubercle small, oval, subarticular tubercle feebly distinct, rounded, no distinct tubercles on tarsus or heel; skin on dorsum smooth, finely granulated, minuscule whitish transparent tubercles scattered on head, snout, and eyelids with keratinous pointed tips, only visible under high magnification (Figure S6); ventral side of abdomen granular (Figure 3c and 4b).

Color in life—Base color is ocher, with small light brown spots scattered lightly over the entire body (Figure 3a, b). The spots on the dorsum are slightly larger than on the abdomen and are distributed more unevenly. The venter has an areolate white pattern. The flanks bear white spots. The hind limbs are brown, showing a darker tone than the forelimbs. A dark brown band runs along the supratympanic ridge. The throat is smooth without a conspicuous color pattern. The tips of fingers and toes are dark brown, showing the same color as the marks on the dorsum. The toe webbing is of a translucent white color. The eyelids are colored in dark ocher with a green tint and small light brown spots. The iris is black and orange marbled with some gold. The tympanum is indistinctly lighter colored with fewer pale brown spots than on the dorsum.

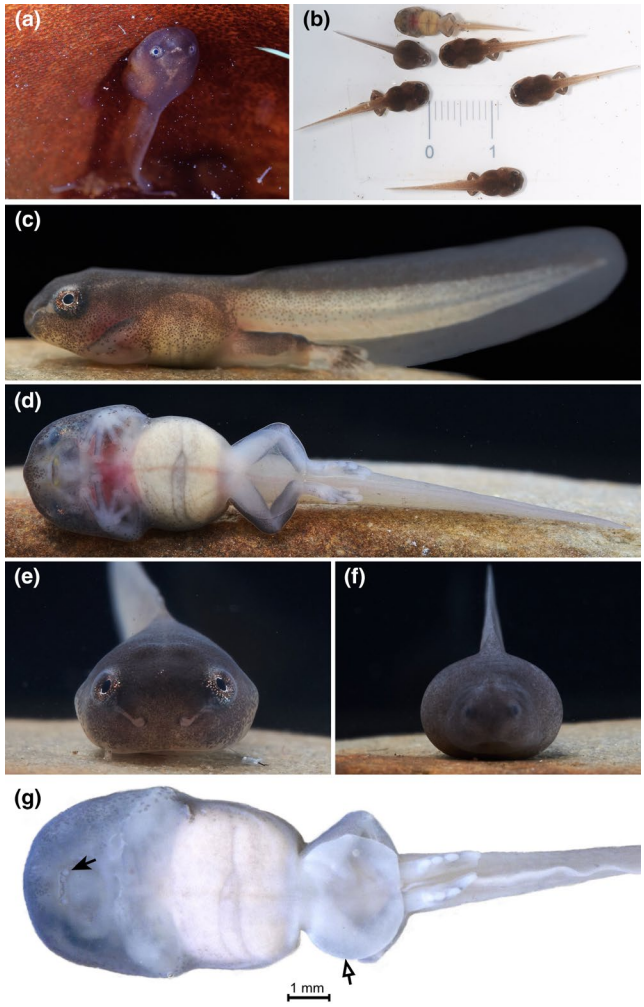

FIGURE 7 Tadpoles of *P. nepenthophilus* photographs not to scale (lot ZMH A12304). (a) Tadpole clinging to the pitcher wall. (b) Group of six tadpoles collected from one pitcher. Note the two different size classes, one specimen being far behind the others in development. Scale 1 cm. (c) Lateral view of specimen 647P–1, showing the short snout and blunt tail tip. (d) Ventral view of the same specimen as in c. The yolk mass in the gut is clearly visible. The circular depression at the gular region and the posteroventral skin flap are difficult to see due to the transparency of the skin. (e) Frontal view of the same specimen as in c, note the far anterior nares, the orbitonasal streak, and the somewhat forward orientation of the eyes. (f) Specimen 647P–2 in frontal view. Note the small head and incompletely developed eyes in this tadpole that was assigned to Stage 27 according to hind limb development. (g) Specimen 647F–1 in ventral view. Lateral oral papilla and posteroventral skin flap indicated by filled and open arrows, respectively

Color in preservation—The color changed to pale brown and sandy white, with darker areas on the dorsum and lighter areas on flanks and abdomen. The areolate white pattern is visible. The tips of toes and fingers are darker brown, like forehead and snout. The dark pattern on dorsum and the brown canthal band are barely visible. The eyelids have a dark gray color (Figure 4a).

TABLE 4 Measurements of all adult *Philautus nepenthophilus* specimens used in this study. Abbreviations and descriptions can be found in Table 1. All measurements in mm. TTTF, THL + TBL+TAL + FOT

NMBE-No.	Sex	EN	ED	TYD	SL	HL	IO	HND	FAL	IN	HW	SVL	THL	TBL	TAL	FOT	TTTF
Holotype																	
1073711	M	2.62	4.27	1.81	4.24	11.55	3.65	9.73	6.98	1.88	10.94	30.45	14.18	15.97	8.86	13.77	52.78
Paratypes																	
1065920	M	2.37	3.87	2.03	3.94	11.24	3.82	10.35	5.58	1.6	10.82	30.45	13.57	14.76	8.2	13.64	50.17
1073577	F	2.87	5.12	2.46	4.88	12.37	4.85	12.19	8.8	2.48	13.16	35.22	17.03	19.26	10.79	17.06	64.14
1073580	M	2.56	4.76	2.38	4.69	10.56	4.01	10.78	7.7	2.33	11.74	32.34	15.09	16.05	9.09	15.49	55.72
1073588	M	2.73	4.31	2.13	4.49	10.64	3.8	10.95	6.56	1.74	10.97	29.91	14.72	15.92	8.12	13.24	52
1073591	M	2.34	4.41	2.03	4.63	11.08	3.36	10.3	6.47	2.39	11.55	31.01	14.79	15.41	8.68	13.66	52.54
1073601	F	2.95	5	2.19	5.11	13.07	4.22	11.9	8.1	2.11	13.9	37.24	16.31	17.97	8.41	17.2	59.89
1073602	M	1.98	4.14	1.84	3.76	10.53	3.19	10.18	6.72	2.25	10.38	28.67	14.54	14.65	8.27	13.69	51.15

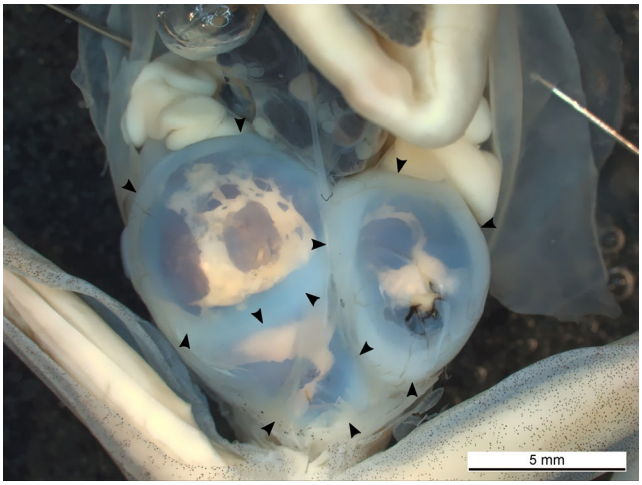

FIGURE 8 Situs of the female paratype NMBE 1073601 of *Philautus nepenthophilus* in preserved condition with three large eggs in the ovaries indicated with arrows

3.3.5 | Variation

The shape of the snout varies slightly in the type series. In the specimens NMBE 1073711, NMBE 1073577, NMBE 1073602, NMBE 1073588, and NMBE 1065920, the nostrils form the anterior-most point (truncate snout), in NMBE 1073580, NMBE 1073591, and NMBE 1073601 it is the small, barely visible snout tip (mucronate snout). The nostrils are of a round, oval, or drop-like shape. The canthus rostralis as well as the tympanum are weakly distinct in NMBE 1073588 and NMBE 1073591. The tips of the digits vary in shape between round and triangular with rounded corners. The length of the 3rd toe is smaller (NMBE 1073711, NMBE 1073588, NMBE 1073601) or equal (NMBE 1065920, NMBE 1073577, NMBE 1073602, NMBE 1073580, and NMBE 1073591) to the length of the 5th toe. The extent of webbing between the toes differs slightly. The variation is included in brackets in the following webbing formula: I(1.75–2.25)–(2–2.5)II(1.25–1.5)–(2–3)III(1–1.75)–(2.75–3)IV(2.5–3.25)–(1.25–2)V. The supratympanic ridge is curved to the arm insertion in NMBE 1065920, NMBE 1073711, NMBE 1073602, NMBE 1073588, NMBE 1073591, NMBE 1073601 and forms a straight line in NMBE 1073577, NMBE 1073580. For variation in measurements, see Table 4.

The female paratype NMBE 1073601 carries three large eggs (diameter: 7.5 mm, 7.7 mm, and 5.4 mm; Figure 8), with visible blood vessels, an indication of fertilized eggs. Additionally, a number of smaller eggs of varying size were found. This suggests that the female produces over a single clutch per year (personal observation by P. H. dos Santos Dias).

Skin—The skin is relatively smooth. The tubercles on the dorsum vary from being rather pronounced to barely distinct. The outer metatarsal tubercle is oval, round, hardly distinct, or completely absent. One specimen (NMBE 1073588) has metacarpal tubercles, one of the females (NMBE 1073601) has a large reniform metatarsal tubercle and a weakly distinct thenar tubercle. On the head, the extent of the keratinous tubercles varies greatly, from loosely scattered in the interorbital region to fully covering interorbital region, head, eyelids, and snout.

Color—The base color varies from pale brown over ocher to a citreous greenish-yellow color. The brown spots scattered on the head and dorsum show high contrast in some specimens and are nearly absent in others. In one individual (NMBE 1073602), these spots form a "W"-shape on interorbital region. In some individuals, the spots on the hind limbs form indistinctive bands. Other individuals do not show any stripes on the hind limbs. The brown band over the supratympanic ridge is not conspicuous in all specimens, but in some it is distinct. The color of the iris is marbled with black. It ranges from amber to dark orange with a green tint.

Sexual dimorphism—The two females are larger (SVL males: 28.67–32.34 mm, SVL females: 35.22–37.24 mm; Figure 4c, d) and do not possess an oval vocal sac opening. The proportion of head width to head length varies more strongly in males than in females (HW/HL males: 0.95–1.11, females: 1.06). The same applies for IN/EN ratio (males: 0.64–1.11, females: 0.72–0.86), IO/ED ratio (males: 1.66–2.02, females: 1.93–1.97), and IO/IN ratio (males: 1.41–2.39, females: 1.96–2.00). Conversely, the FOT/TAL ratio is more variable in females than in males (males: 1.55–1.70, females: 1.58–2.05).

3.4 | Comparisons

Philautus nepenthophilus (values and character states in bold) can be distinguished from other species of *Philautus* from Borneo and from *P. everetti* from Palawan by a unique combination of morphological characters, morphometric measurements (SVL in mean for males and females, respectively), and bioacoustic traits:

Philautus acutus Dring, 1987 (type locality: Camp Three 1,300 m, Gunung Mulu, Fourth Division, Sarawak, Malaysia) is of smaller size (SVL males: 23.4–27.1 mm, female: undescribed vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**), has a red iris and a generally darker skin color. The canthus rostralis is curved in a wider angle than in *P. nepenthophilus*. The call consists of more notes (8–9, named "pulses" by Dring, 1987 vs. **3**) of longer duration (100 ms vs. **36.33 ms**) and of higher dominant frequency (2.6–3.6 kHz vs. **2.8 kHz**) (Dring, 1987).

Philautus amoenus Smith, 1931 (type locality: Kamborangah, 2,1950 m., Mt. Kinabalu, Sabah, Malaysia) is smaller (SVL males: 18.1–24.2 mm, females: 28.3–34.7 vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**), has a smaller tympanum (25 to 30% of eye diameter, smaller than outer finger disks vs. **TYD/ED 0.42–0.52**) and a banded pattern on the lips. The skin has more tubercles, of which some form a clearly defined line from the posterior end of the eye to the dorsum and a cluster on the metatarsals. The call of *P. amoenus* differs in note duration (110 ms vs. **36.33 ms**) and internote interval (150 ms vs. **62.1 ms**) and has a much lower frequency (1.8 kHz vs. **2.8 kHz**) (Inger, 1966; Malkmus et al., 2002; Malkmus & Riede, 1996a; Smith, 1931).

Philautus aurantium Inger, 1989 (type locality: Mendolong, Sipitang District, Sabah, Malaysia) is smaller (SVL males: 23.8–27.7 mm, females: 25.6–26.2 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and shows bright orange marks in the inner and outer articulation of the thighs (vs. **absent**). The tympanum is obscured (vs. **visibly lighter colored**). The frequency of the *P. aurantium* call is similar to *P. nepenthophilus* (2.9 kHz vs. **2.8 kHz**) but consists of many more notes (14–30 vs. **3**) with a longer duration (120–160 ms vs. **36.33 ms**) (Inger, 1989; Malkmus et al., 2002).

Philautus bunitus Inger et al., 1995 (type locality: Mt. Lumaku, 1,350 m, Sipitang District, Sabah, Malaysia) differs in size (SVL males: 34.7–40.8 mm, females: 43.5–46.3 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and in the presence of vomerine teeth (vs. **absence**). The green and black color pattern on the dorsum is markedly different from the yellow color in the new species. The webbing is of yellow color (vs. **white**). *Philautus bunitus* calls at a lower frequency (1.8 kHz vs. **2.8 kHz**) and calls consist of more notes (15–25 vs. **3**) (Inger et al., 1995; Malkmus et al., 2002).

Philautus davidlabangi Matsui, 2009 (type locality: Gunung Serapi (01° 36′ N, 110° 11′E, 330 m), Matang Range, in the suburbs of Kuching, Sarawak, Malaysia) has a subequal body size (SVL males: 19.9–20.6 mm, females: undescribed vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and tympanum diameter (1.3 mm vs. **TYD 1.8–2.5 mm**), and the nostrils are situated in closer proximity to the eye (EN 1.8 mm vs. **2.0–3.0 mm**). The canthus rostralis is curved in a sharp angle in dorsal view (vs. **rounded**). Tubercles form a curved row from the posterior end of the eye to the sacrum (vs. **absent**) and a conspicuous "X"-shaped mark is visible on the dorsum (vs. **absent**). The general color tone is darker than in *P. nepenthophilus*. The call consists of only one single note and is emitted over a longer period of time (note duration 50-60 ms vs. **36.33 ms**) (Matsui, 2009).

Philautus disgregus Inger, 1989 (type locality: Danum Valley Field Centre, Lahad Datu District, Sabah, Malaysia) is much smaller (SVL males: 21.3–23.0 mm, females: 24.4–24.8 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**), has distinct conical tubercles on the upper eye lids (vs. **absent**) and a black and white color pattern below the eye (vs. **plain yellow**) (Inger, 1989).

Philautus erythrophthalmus Stuebing & Wong, 2000 (type locality: Mt. Muruk Mio (4° 22.715′ N, 115° 50.125′ E), Sipitang District, Sabah, Malaysia) is smaller (SVL males: undescribed, female: 26.2 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and possesses a distinctly red iris (vs. **orange marbled**) and bright yellow/golden colored groin (vs. **pale brown**). The tips of fingers and toes are pinkish (vs. **brown**). The tympanum is smaller (30% of eye diameter vs. **TYD/ED 0.42–0.52**) and barely visible. Lingual papillae are present (vs. **absent**), and the supratympanic ridge is indistinct (vs. **highlighted by a distinct brown marking**) (Stuebing & Wong, 2000).

Philautus everetti Boulenger, 1894 (type locality: Palawan, Philippines) is slightly larger (SVL males: 29.6-35.2 mm, females: 41.4-44.3 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and differs in the presence of vomerine teeth (vs. **absent**) and conical tubercles below the anus, along the forearm and on the heels (vs. **absent**). P. everetti also possesses a flap of skin along the outer edge of the forearms and hindlimbs (vs. **absent**). The tympanum is smaller (40% of eye diameter vs. **TYD/ED 0.42–0.52**), the base color is of a pale beige (vs. **greenish-yellow**), the iris is of a pale golden color (vs. **orange marbled**), the skin is finely granulated (vs. **smooth**), and the snout is rounded (vs. **truncate**). (Boulenger, 1894; Inger, 1954b).

Like *Philautus aurantium*, *P. gunungensis* Malkmus & Riede, 1996b (type locality: Mixed fagaceae forest above Silau stream (1,450 m) on the southern slope of Mt. Kinabalu, Sabah, Malaysia) has bright yellow colored thighs (vs. **pale brown**). It is smaller than *P. nepenthophilus* (SVL males: 22.1–25.3 mm, females: undescribed vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and has a much steeper snout slope in profile than *P. nepenthophilus* and palmar, thenar and subarticular tubercles are more distinct. The call of *P. gunungensis* consists of a greater number of pulses (14–30 vs. **6**) and is continuously emitted (vs. **not continuous**) (Malkmus & Riede, 1996b).

Philautus hosii Boulenger, 1895 (type locality: Patah River, northern Sarawak, Malaysia) is considerably larger (SVL males: 40.8–49.1 mm, females: 61.3–62.0 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and has two series of vomerine teeth (vs. **absent**). The iris is bright green (vs. **orange marbled**). The hind limbs show dark crossbars and the sides, as well as the axils, have brown spots. There is a faint X-shaped mark on the dorsum (vs. **absent**) (Boulenger, 1895; Inger, 1966; Wolf, 1936). The snout is longer (Figure 6).

Philautus ingeri Dring, 1987 (type locality: Camp three, 1,300 m, Gunung Mulu, Fourth Division, Sarawak, Malaysia) differs strongly in iris coloration, which is split in an upper pale gray part and a lower, dark brown part (vs. **no split**). The pattern of the eye continues to the tip of the snout. The snout is sharply pointed (vs. **truncate**) and longer (Figure 6). The heels bear spiny tubercles (vs. **absent**) (Dring, 1987).

Philautus juliandringi Dehling, 2010 (type locality: The Pinnacles Trail (04°07′ N, 114°53′ E), northern slope of Gunung Api, approx. 1,100 m, Gunung Mulu N. P., Miri Division, Sarawak, Malaysia) is distinguishable by its small size (SVL males: 14.8–19.2 mm, females: 20.6–24.4 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and the presence of nuptial pads (vs. **absence**). The advertisement call consists of only one note per call (vs. **3**). The dominant frequency is higher (3.2 kHz vs. **2.8 kHz**) (Dehling, 2010; Dring, 1987).

The size of *Philautus kakipanjang* Dehling & Dehling, 2013 (type locality: From below the summit of Gunung Serapi (01°35.261' N, 110°11.578' E; 780 m), Kubah N. P., Sarawak, Malaysia) is smaller (SVL males: 21.2–23.7 mm, females: undescribed vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**). The presence of small but prominent nuptial pads (vs. **absent**), the thick and long supratympanic ridge (vs. **shorter in *P. nepenthophilus***) and the concealed tympanum (vs. **visibly lighter colored**) represent further differences. The call consists of only one note (vs. **3**) and has a slightly lower dominant frequency (2–2.7 kHz vs. **2.8 kHz**) (Dehling & Dehling, 2013).

Philautus kerangae Dring, 1987 (type locality: Kerangas camp 200 m, Gunung Mulu N. P., Fourth Division, Sarawak, Malaysia) differs in the presence of vomerine teeth and tubercles on the heel (vs. **both absent**). There is a conspicuous color pattern with large brown markings on the light green dorsum and the upper side of

the limbs. Likewise, the venter shows blotches of brown on the white, pale blue base color (vs. **aerolate white pattern**). *Philautus kerangae* calls in a lower frequency (1.6–3.0 kHz, most strongly at 2.2–2.5 kHz vs. **2.8 kHz**) and emits more notes per call (8–9 vs. **3**). The call was described with the call-centered approach and thus notes were defined as pulses (Dring, 1987). According to the sonogram in the publication, these pulses equal the definition of notes in our study.

Distinctive features of *Philautus larutensis* Boulenger, 1900 (type locality: Larut Hills at 1,220–1,370 m, Perak, Malaysia) are the well-developed nuptial pads in males (vs. **absent**) and the fleshy tubercle on the rostrum of the females, making the snout acutely pointed (vs. **truncate**). The mandible bears a row of tubercles (vs. **absent**) (Wostl et al., 2017).

Philautus macroscelis Boulenger, 1896 (type locality: Mt. Kinabalu, Sabah) has two groups of vomerine teeth (vs. **absent**). There are conical tubercles on the upper eyelids and a row of small tubercles along the outer edge of the forearms and hind limbs (vs. **both absent**). The forearms and hind limbs bear dark crossbars on the dorsal side (Boulenger, 1896; Inger, 1966; Smith, 1931). The snout is feebly more pointed in dorsal view than that of *P. nepenthophilus* (Figure 6). The tadpole of *P. macroscelis* differs from larvae of *P. nepenthophilus* in coloration (conspicuous scattered white-bluish iridophores vs. **absent**), the position of the nares (ventral vs. **anterolateral**), the relative size of the eyes (larger), relative body width (less broad), and absence of a posteroventral skin flap (vs. **present**) (Hertwig et al., 2011).

Philautus mjobergi Smith, 1925 (type locality: Mt. Murud, 2,134 m, Fourth Division, Sarawak, Malaysia) has a relatively wider head ("much broader than long" Smith, 1925 vs. **HW/HL 0.95–1.11**) and a smaller body size (SVL males: 18.7–24.1 mm, females: 22.7–32.2 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**). Nuptial pads are present and there is a tubercle on the heel (vs. **both absent**). The structure of the call is similar to *P. nepenthophilus* with 4–8 notes (vs. **3**) but has a slightly higher dominant frequency (2.7–3.5 kHz vs. **2.8 kHz**) (Dring, 1987; Malkmus et al., 2002; Smith, 1925).

Philautus nephophilus Dehling, Matsui, & Yambun, 2016 (type locality: Silau Silau Trail, 6°00′23.2″ N, 116°32′44.7″ E; 1,525 m, Kinabalu N. P., Sabah, Malaysia) can be distinguished from the new species by the smaller body size (SVL males: 16.4–18.6 mm, females: 20.3–23.1 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) along with the presence of nuptial pads and a tubercle on the heel (vs. **absence**). The supratympanic fold is strongly pronounced with a pale orange stripe along the fold (vs. **brown stripe**) and the iris is red in color (vs. **orange marbled**). The call consists of a greater number of notes (4–12 vs. **3**) with a longer duration (61–80 ms vs. **36.33 ms**) (Dehling et al., 2016).

Philautus refugii Inger & Stuebing, 1996 (type locality: Bukit Lanjak, 840 m, Lubok Antu District, Sarawak, Malaysia) is of considerably smaller size (SVL males: 16.5–16.8 mm, females: 18.2–20.5 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**). The females bear a tubercle on the rostrum and the males feature nuptial pads (vs. **both absent**). The dorsal color pattern resembles an inverted "V"-shape to some extent and the anterior thighs bear conspicuous brown bars (vs. **absent**) (Inger & Stuebing, 1996; Wostl et al., 2017).

Philautus saueri Malkmus & Riede, 1996a (type locality: *Leptospernum-Dacrydium* forest east of Paka-Cave, 3,050 m, on southwestern slope of Mt. Kinabalu, Sabah, Malaysia) is smaller (SVL male holotype 21.4 mm, females: undescribed vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and bears a light interorbital stripe which is rich in contrast to the dark brown base color (vs. **absent**). The limbs and sides of the dorsum show a distinct reticulate dark gray pattern on the pale whitish gray base color. The supratympanic fold is steeply curved toward the arm insertion (vs. **not curved**) and the snout is protruding (vs. **not protruding**). The call is similar to the call of *P. nepenthophilus* in note duration (30–40 ms vs. **36.33 ms**) but has marginally longer internote intervals (70–100 ms vs. **62.1 ms**) and a subequal frequency (1.9–2.6 kHz vs. **2.8 kHz**) (Malkmus et al., 2002; Malkmus & Riede, 1996a).

Philautus tectus Dring, 1987 (type locality: Camp five, 150 m, Gunung Mulu N. P., Fourth Division, Sarawak, Malaysia) is different from the new species in body size (SVL males: 20.8–23.4 mm, female: 27.3 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) and in having large nuptial pads (vs. **absent**). The canthus rostralis is curved in a larger angle in dorsal view (Figure 6) and bears a small dorsal tubercle in close proximity to the proximal end of the eye (vs. **absent**). The iris is dark brown (vs. **orange marbled**) (Dring, 1987).

Philautus umbra Dring, 1987 (type locality: Pinnacles Camp, 1,200 m, Gunung Api, Gunung Mulu N. P., Fourth Division, Sarawak, Malaysia) has a distinct, sharply angled canthus rostralis (vs. **not curved**). Specimens of *P. umbra* possess lingual papilla and rudiments of a nuptial pad (vs. **both absent**). The uniformly dark brown to dark gray night coloration and the black iris with scattered gray spots are further diagnostic traits that distinguish it from *P. nepenthophilus*. The SVL is similar to the new species (male 24.7–35.1 mm, female 33.3 mm vs. **males: 28.7–32.3 mm, females: 35.2–37.2 mm**) but the smaller EN/IN ratio distinguishes *P. umbra* from the new species (EN/IN 1.06 vs. **1.22**) (Dring, 1987).

3.5 | Larval description

In all larval stages collected, a large mass of yellowish substance was evident through the abdominal body wall. We measured nine formalin-preserved specimens (Table 5). The development of larval features was, however, immature in four early-stage tadpoles, so that we derive the following details on larval morphology from the individuals of advanced stages (Stages 35–38), followed by some comments on the earlier stages (26–27). Color information was obtained from digital color photographs (Figure 7).

Body and tail shape—Maximum total length: 21.55 mm (Stage 38). In dorsal view, the body (here: head and trunk) of the advanced stages is broadly pear-shaped, head slightly narrower than trunk. A soft constriction of the body contour marks the head-to-trunk transition. The maximum body width is anterior to that

TABLE 5 Body measurements of *P. nepenthophilus* larvae in mm, rounded to nearest 0.01 mm

ID	Stage	BL	BH	BW	BS	ED	ES	IND	IOD	LFH	MTH	NE	OFW	SN	SS	TAL	TMH	TMW	TTL	UFH	FlapL	FlapW
ZMH A12304 (lot)																						
647P-1	37	6.59	3.26	4.60	X	1.16	1.48	1.48	2.67	0.90	3.50	1.42	0.93	0.15	X	13.09	2.00	2.04	19.68	0.79	2.49	3.12
647P-2	27	5.55	3.74	4.52	X	X	X	X	X	1.06	3.00	0.85	0.54	0.19	X	9.37	1.20	1.05	14.92	0.83	X	X
ZMH A12303 (lot)																						
647F-1	38	6.90	3.33	4.58	3.00	1.20	1.07	1.42	2.83	0.95	3.64	1.53	1.01	0.24	3.90	14.65	1.88	2.06	21.55	1.10	3.28	2.47
647F-2	37	6.75	3.53	4.47	2.74	1.10	1.35	1.42	2.86	0.96	3.66	1.36	0.92	0.16	4.01	13.34	1.89	2.07	20.09	1.05	3.26	2.68
647F-3	35	6.49	3.31	4.54	3.60	0.91	0.88	1.22	2.37	1.03	4.00	0.68	0.90	0.20	2.89	12.95	1.69	2.00	19.44	1.04	2.30	2.51
647F-4	36	6.57	3.47	4.44	2.91	0.93	1.44	1.25	2.24	1.00	3.90	1.23	0.69	0.23	3.66	13.10	1.75	1.95	19.67	1.06	2.20	2.90
647F-5	27	4.24	3.58	4.26	X	X	X	X	X	0.72	2.50	X	X	X	X	10.23	1.22	1.00	14.47	0.67	X	X
647F-6	27	4.62	3.41	4.26	X	X	X	X	X	0.85	2.73	X	X	X	X	9.64	1.15	0.94	14.26	0.73	X	X
647F-7	26	4.74	4.03	4.19	X	X	X	X	X	0.66	2.47	X	X	X	X	10.17	1.21	1.02	14.91	0.59	X	X

Note: Species / Coll. lot in bold. ZMH, Zoological Museum Hamburg; Stages according to Gosner (1960), however, note the limitations of applying this staging table to this species. Some measurements were considered inapplicable (X) due to insufficient development of respective structures. — BL, body length from snout to the point where the axis of the tail myotomes contacts the body wall; BH, max. body height at trunk; BS, spiracle to body end as calculated difference BL-SS; BW, max. body width; ED, eye diameter; ES, eye snout distance, from center of lens to snout tip in lateral view; FlapL, length of posteroventral skin flap; FlapW, width of skin flap; IND, internarial distance (center to center); IOD, interorbital distance, lens center to center; LFH, lower fin height at point of max. tail height; MTH, max. tail height (fins included); MTH, position of point of max. tail height along length of tail in % of tail length; NE, center of naris to center of eye distance (lateral view); OFW, oral field width; SN, distance of naris (center) to snout (lateral view); SS, snout to center of spiracle distance (lateral view); TAL, tail length as calculated TTL-BL; TTL, total length; TMH, max. tail muscle height at body-tail junction, where ventral line of musculature meets trunk contour; TMW, max. tail muscle width; UFH, upper fin height at point of max. tail height. Specimens of lot A12304 have been used for live photography (P, photography). Specimens of lot A12303 were taken as formalin samples (F, Formalin). They all form the same fieldnumber (647).

constriction (where elbows are), approximately half way along the body. Head and trunk are approximately of the same depth in lateral view (Figure 7c). The snout is very short. In lateral view, it is softly rounded, whereas in dorsal view it is almost truncate, except for a medially protruding soft bulge in the contour (Figure 7b). The body is depressed, wider than deep. The spiracle is sinistral; medial spiracular orifice fused to the body wall, free tube absent. The spiracle is directed posteriorly; spiracular position is clearly ventral to mid-body axis. The anal tube runs in the ventral fin and opens sinistrally. A peculiar large discoid flap of skin is present, which we shall term the posteroventral flap. It is confluent medially with the ventral tail fin dorsally and the abdominal skin anteriorly. The posteroventral flap expands ventral to the developing posterior limbs (Figure 7d, g), that are covered by it to the level of the ankles. The posteroventral skin flap and the ventral tail fin form a pocket for each of the limbs. The eye is positioned dorsolaterally; the cornea does not reach the head contour line in dorsal view. The orientation of the eye axes is anterolateral in dorsal view (Figure 7e) suggesting good frontal vision. The naris is much closer to the snout than to the eye; in fact, the naris is positioned almost terminally on the snout in lateral view. The nares are facing anterolaterally, smoothly rimmed, sunken in. A well-developed, unpigmented orbitonasal streak is present (Figure 7e). The tail is only moderately developed. At its base, tail width is approximately 45% of body width and 56% of body height. The dorsal and ventral tail fins begin at the body-tail junction. The fins do not arch, but are mostly parallel along most of the tail until they end in a broadly rounded tail tip. Dorsal and ventral fins are approximately of the same height; maximum height of the tail is approximately one-third of tail length.

Color in life—The general appearance of the tadpoles is dark brown to dark gray dorsally (Figure 7b–c). Although there are slightly darker (e.g., brain case) and lighter areas (e.g., branchial), there is no clear patterning or any markings. The dark brown of the upper sides rapidly dissolves at the ventral aspects of head, trunk, posterior limbs, and tail. The trunk coloration continues onto the upper half of the tail, where it fades posteriorly and ventrally. The pigmentation extends to the base of the dorsal fin, whereas the ventral muscular part and ventral fin are devoid of melanophores. The ventral skin of the tadpoles (including oral field and posteroventral flap) is transparent (Figure 7d, g), only finely pigmented in the peripheral ventral oral and gular regions. Viscera are visible through the ventral skin. The heart and gill regions and in the abdomen the yolk mass appear red and cream, respectively, through the skin. No gut coils are visible. Eye ball (sclera) and iris possess black backgrounds with dense iridophores scattered on them. The iris iridophores shine golden, the pupil itself is framed by a narrow silver ring. The iridophores on the scleral parts of the eye are mostly silvery to bluish. The orbital cavity has an unpigmented area at the origin of the orbitonasal streak (Figure 7c).

Oral disk—The oral orifice is ventral. An oral disk, as in most other tadpoles, is absent. Structures that might represent remnants of a highly reduced oral disk are the very thin lips along the oral orifice and two lateral knobs, or papillae, on each side of the mouth (Figure 7g). The mouth and its surrounding structures are positioned in the anterior part or a circular depression in the ventral gular region. As suggested by observing tadpoles clinging to the pitcher walls, it is possible that this depression functions as a sucker. Keratodonts are absent. Labial Tooth Row Formula: 0/0. Highly reduced keratinized jaw sheaths could be identified as very thin dark lines along the jaws under high magnification. During an observation period of 24 h in a dish for temporary care, no feeding behavior could be observed.

Ontogeny—Although the number of stages examined was limited, some ontogenetic differences could be noted among specimens. The earlier stages in the sample (26–27, Table 5; one specimen in Figure 7b) have more pronounced pear-shaped bodies, a result of their relatively smaller head and relatively larger abdomen. The maximum width is well within the trunk region. The eyes and nares in the four early-stage tadpoles were very small and undifferentiated, possibly non-functional. The posteroventral flap beginning to form at the lower fin and trunk. The early-stage tadpoles, despite being free-swimming and not encapsulated in jelly, appear embryonic in their overall development. The development of the appendages seems accelerated in relation to general somatic differentiation. Because development of hind limbs is crucial for staging in Gosner's (1960) table, the formal stage overestimates overall development in the stages 26–27 examined.

Similar Species—The morphological features of this tadpole, especially the short snout and the very small ventral oral orifice with two pairs of lateral oral papillae, are unique among Bornean species, except for tadpoles of *Philautus macroscelis* (Hertwig et al., 2011). The latter differs (conditions in parentheses) most notably from *P. nepenthophilus*. in coloration (conspicuous scattered bluish-white iridophores), the position of the nares (ventral), the relative size of the eyes (larger), relative body width (less broad), and the posteroventral skin flap (absent).

3.6 | Etymology

The name *nepenthophilus* is composed of two words which refer to the close ecological relationship of this species to the carnivorous plant *Nepenthes mollis*. "Nepentho" stands for *Nepenthes* and "philus" is derived from the ancient Greek word "φίλος" [phílos] that means "which is loved or important." The name is masculine.

3.7 | Type locality

Eastern edge of Church Camp (N 3°55.603200 E 115°30.867600), at 2,115 m a.s.l., about 3.7 km straight line north-east of the summit of Gunung Murud, within the Pulong Tau National Park, Sarawak, Malaysia (Borneo) (Figure 9b, c).

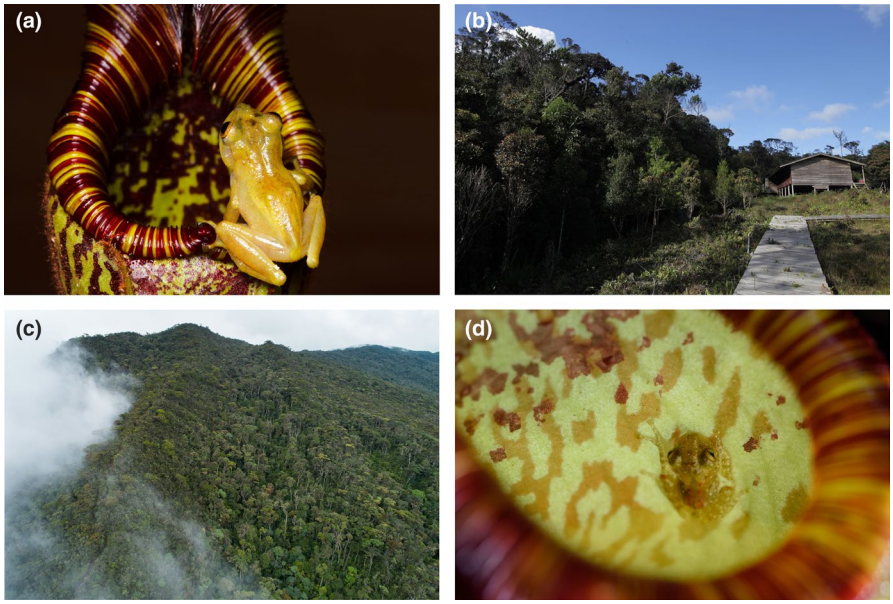

FIGURE 9 (a) Paratype NMBE 1073580 of *Philautus nepenthophilus* on *Nepenthes mollis*. (b) The type locality of *Philautus nepenthophilus* at the edge of Church Camp. (c) View along the Gunung Murud ridge near the type locality Church Camp. (d) A specimen of *Philautus nepenthophilus* hiding in the pitcher of *Nepenthes mollis*

3.8 | Distribution, Habitat, & Ecology

This species is currently only known from the type locality at the Gunung Murud ridge in the Pulong Tau National Park (Figure 9c). A single specimen morphologically similar to *P. nepenthophilus*. was observed and photographed in a pitcher plant (*Nepenthes hurrelliana*, subsequently reduced to synonymy with *N. mollis*) from near Gunung Lumaku, Sabah, Malaysia (108 km north of Gunung Murud) in 1999 (personal observation by C. C. Lee & A. Lamb) (Phillipps, Lamb, & Lee, 2008). A confirmation of the taxonomic status of this population is lacking, because vouchers and tissue samples are not available from that area. All specimens collected or observed so far were found near or around Church Camp, perching at night on or close to *Nepenthes mollis*, usually associated with the aerial (upper) pitchers of the plant, at the edge of montane Kerangas forest (Figure 9a). Males perch and call from the pitchers. Several individuals escaped into the pitchers after being disturbed and dived into the liquid (Figure 9d).

All tadpoles were discovered in pitchers of *Nepenthes mollis*, 2–4 m above the ground. They seemed inactive in the pitcher, resting among bottom debris that had accumulated in the pitcher or at the pitcher wall (Figure 7a). Tadpoles were able to hold position at the pitcher wall suggesting some sort of adhesive mechanism. We observed two markedly different stage groups per pitcher (Figure 7b). This suggests that tadpoles from successive spawning may utilize the same pitcher together. It remains unclear whether or not the tadpoles from the two age classes came from the same female. The tadpoles co-occurred in the same pitcher with an adult. The following anuran species were recorded sympatrically: *Philautus ingeri* (Dring, 1987) and *P. mjobergi*, *Nyctixalus pictus* (Peters, 1871), *Rhacophorus baluensis* (Inger, 1954a), *Pelophryne linanitensis* (Das, 2008) and *P. murudensis* (Das, 2008), *Limnonectes* aff. *kuhlii*, *L. palavanensis* (Boulenger, 1894), and *Leptobrachium montanum* (Fischer, 1885).

4 | DISCUSSION

4.1 | Phylogeny

This study provides a comprehensive phylogenetic analysis of Bornean *Philautus* based on a broad sample of numerous geographic populations. The genus *Philautus* is robustly supported as a natural group (Figure 1, Figures S2-S5). *Philautus nepenthophilus*, described in this study as a distinct species based on an integrative approach considering molecular, morphological, and bioacoustic evidence, represents a separate lineage of *Philautus*, that is the sister taxon to *P. macroscelis*. The taxonomic status of *P. nepenthophilus* as a valid species in accordance with the phylogenetic species concept (Cracraft, 1992), and the unified species concept (de Queiroz, 2007) is justified by the phylogenetic signal in mitochondrial and nuclear markers, by the high uncorrected pairwise genetic distance in the *16S rRNA* gene sequence (6.81-13.76% interspecific vs. 0–0.25% intraspecific), but also by the presence of several autapomorphic characters in external adult and larval morphology and by bioacoustic data (see Diagnosis and Comparison). The sister group relationship to *P. macroscelis* (Hertwig et al., 2011) is not only supported by genetic data, but also by larval characters. The tadpoles of *P. macroscelis* and *P. nepenthophilus* share unique features: short snout, a very small, ventral oral orifice, isolated lateral oral papillae, absence of keratodonts and oral disk, and highly reduced keratinized jaw sheaths.

The phylogenetic relationships of the clade, consisting of *P. nepenthophilus* and *P. macroscelis* and of the remaining early divergent lineages within this genus, *P. tectus* and the *P. hosii* + *P. ingeri* clade, however, could not be resolved robustly and congruently due to at most moderate support values and conflicting topologies of the separate analyses of the different data partions (Figure 1, Figures S2-S5). In previous studies, the *P. hosii* + *P. ingeri* clade represented the first branching lineage (Dehling et al., 2016) or formed the sister clade to *P. tectus* (Chan et al., 2018; Hertwig et al., 2013; Wostl et al., 2017). However, the support values of the early branching events within *Philautus* were consistently low in all previous studies (Chan et al., 2018; Dehling et al., 2016; Hertwig et al., 2011, 2013; Wostl et al., 2017). We interpret the weak support of the affected nodes and the incongruencies between the obtained trees as an indication of a hard polytomy that could probably only be resolved by significantly larger data sets in future studies. Within the monophyletic group comprising the remaining species of *Philautus*, the phylogenetic relationships of *P. davilabangi*, *P. kakipanjang*, *P. larutensis*, and *P. refugii* remain unresolved and conflicting in a comparable manner (see also Dehling et al., 2016; Hertwig et al., 2011, 2013; Wostl et al., 2017).

Apart from the unresolved nodes, our hypothesis concerning the intrageneric phylogenetic relationships of *Philautus* is mainly congruent to results of previous molecular studies (Dehling et al., 2016; Chan et al., 2018; Hertwig et al., 2011; Hertwig et al., 2013; but see Wostl et al., 2017). The traditional intrageneric systematics with formerly recognized species groups (*aurifasciatus*, *hosii*, *tectus*, *vermiculatus* group, respectively) defined by Dring (1987) using external morphological characters (as in Malkmus et al., 2002; Malkmus & Riede, 1996a, 1996b) is not confirmed by the outcomes of our analyses. The characters used for diagnosing these species groups—like the absence or presence of vomerine teeth and nuptial pads, pulsed advertisement call with frequency modulation—are highly variable and homoplastic within *Philautus*.

4.2 | Frog–plant interaction

We observed calling males of *P. nepenthophilus* perching on the pitcher of *Nepenthes mollis* and collected tadpoles, eggs, and empty egg capsules in the fluid of the pitchers (Figures 9a, d, and 7a). Potential food items for tadpoles in the pitchers were insect larvae, detritus, and algae. The reduced mouthparts and small oral orifice, as well as the large intestinal yolk mass seen in each of the larvae examined, however, suggest that the tadpoles of *P. nepenthophilus* are endotrophic and do not feed on matter in the phytotelm pitcher. Given the circumstances of collection and the morphology of the tadpoles, it appears plausible that *P. nepenthophilus* is a montane phytotelm specialist using *Nepenthes* pitchers for reproduction. Whether the use of pitchers of *Nepenthes* is mandatory or whether other phytotelmata could be used if *Nepenthes* pitchers were not available, remains unknown.

The carnivorous pitcher plants of the genus *Nepenthes* are adapted to grow in habitats with nutrient-deficient soils. They use different nutrient acquisition strategies to compensate for the scarcity of essential nutrients, particularly nitrogen and phosphorus, in their substrates, ranging from carnivory by trapping arthropods with their pitchers (jug-shaped leaf organs) to complex mutualism with ants (Bazile et al., 2012) or small mammals (Grafe et al., 2011; Greenwood et al., 2011). Consequentially, the recorded infauna of *Nepenthes* pitchers is quite diverse, including fly and midge larvae, spiders, mites, ants, and crabs, but also small vertebrates like bats and frogs (Beaver, 1979; Clarke, 1997; Das & Haas, 2010; Grafe et al., 2011; Mogi & Yong, 1992; Ng & Lim, 1987; Phillipps et al., 2008; Tan & Ng, 2008).

In frogs including several, phytotelm-breeding evolved several times convergently in different major groups of anurans (Lehtinen et al., 2004). In several genera of the Rhacophoridae, the use of tree holes or bamboo stumps for deposition of eggs and the development of tadpoles has been observed (e.g., Biju et al. 2016; Haas et al., 2012; Inger et al. 2017; Meegaskumbura et al., 2015; Pham et al., 2019; Yang & Chan, 2018). Dover (1928) was the first author who reported breeding by anurans in *Nepenthes ampullaria*, although the species identity of the observed tadpoles remains unclear (Das & Haas, 2010). Subsequently, in several species of microhylids, free-swimming tadpoles that hatch and finish their development in *Nepenthes* pitchers were recorded: *Kalophrynus* "*pleurostigma*" (possibly *K. limbooliati*) (Lim & Ng, 1991, *N. ampullaria*), *Kalophrynus* cf. *heterochirus* (Phillipps et al., 2008, *N. stenophylla*), *Microhyla nepenthicola* (Das & Haas, 2010; Gorin et al., 2020, *N. ampullaria*), and *M. borneensis* (Parker, 1934, *N. ampullaria*). In some species of the genus *Philautus*, for which terrestrial direct development is assumed, deposition and incubation of the eggs in pitchers of *Nepenthes* have been described: *P. aurifasciatus* (Yong et al., 1988, *N. sanguinea*); *P. kerangae* (Dring, 1987, from *N. bicalcarata*), *P. mjobergi* (Smith, 1925, unspecified *Nepenthes*; Phillipps & Lamb, 1988, *N. villosa*), and *P. saueri* (Malkmus et al., 2002, *N. villosa*), unspecified species of *Philautus* (Kiew, 1987, *N. ampullaria*; Clarke, 1997, *N. bicalcarata*; Phillipps et al., 2008, *N. hurrelliana*). In the majority of these anecdotal cases, however, the species assignment of the eggs or larvae was not confirmed unequivocally.

The observed strategy of *P. nepenthophilus* to breed in *Nepenthes* could represent a further case of mutualism (Lam & Tan, 2018, 2019), because frogs and tadpoles provide essential nutrients like nitrogen and phosphorus to the plant. The adult frogs leave their excrements, skin fragments, and egg capsules and the tadpoles produce feces and waste after consuming their yolk in the fluid of the pitchers. In return, the plant offers an exclusive domicile, a permanent water body, and protection in the relatively safe interior of the pitchers for the tadpoles. At higher elevations of the steep Bornean mountains, permanent bodies of water are scarce or indeed absent, despite a high amount of precipitation due to local geomorphological conditions (such as steep inclination and porous soils with only a thin layer of organic substrate). The specific strategy of phytotelm breeding in *Nepenthes* pitchers is beneficial for the anuran larvae as it not only reduces the risk of predation and competition, but also limits the chance of

desiccation or of being washed away. From our observations, it appears that adults and tadpoles of *P. nepenthophilus* are associated solely with the upper pitchers of *N. mollis*, produced by the climbing sections of the host plant. These are held aloft among the supporting vegetation and are morphologically distinct from the lower pitchers which are typically resting on the ground. Whether this is true in all instances of their association, and whether or not upper pitchers are specifically selected for their particular shape, fluid properties, or spatial location, has yet to be determined. In addition, *P. nepenthophilus* has not yet been recorded from any other pitcher plant species despite the presence of four other *Nepenthes* taxa growing in sympatry around Church Camp. Three of these *Nepenthes* (*N. muluensis*, *N. murudensis*, and *N. tentaculata*) have extensive regions of wax crystals lining the inner surface of their upper pitchers, a feature which is much reduced or absent in pitchers of *N. mollis*. This slippery waxy zone is associated with arthropod prey retention and may render the pitcher walls of these species similarly unscalable for amphibians. The fourth sympatric *Nepenthes*, *N. lowii*, has highly specialized upper pitchers designed to facilitate mammal visitation (see below) with their pitchers typically containing a high amount of animal feces and may consequently be unsuitable as a habitat for amphibians. It needs to be tested whether *P. nepenthophilus* is totally dependent on *N. mollis* as a breeding site in the sense of a nepenthebiont (sensu Clarke, 1997), or if this species also accepts other *Nepenthes* species or even opportunistically uses alternative phytotelmata. Furthermore, the degree to which *N. mollis* benefits from the nitrogen input provided by the reproduction of *P. nepenthophilus* remains to be investigated.

A record of mutualism already exists for the ant *Camponotus schmitzi* (myrmecotrophy) and *N. bicalcarata*, a lowland species that grows in the Bornean peat swamp forests (Bazile et al., 2012; Beccari, 1885; Bonhomme et al., 2011). In cases, where *N. bicalcarata* is occupied by *C. schmitzi*, ant-waste-derived nutrition constitutes 42% of the foliar nitrogen (Bazile et al., 2012). Several species of small mammals defaecate in the pitchers of *Nepenthes* when they visit the plants for roosting, resting, or feeding on the nectar provided by the plant. The woolly bat (*Kerivoula hardwickii*) roosts in dead pitchers of *N. bicalcarata* and *N. ampullaria*, but prefers the pitchers of *N. hemsleyana*. The shape of these pitchers makes them an ideal roost for bats; they are easily detected by echolocation, and the waxy texture of the pitchers' inner wall is an excellent insect deterrent, resulting in a pest-free home for the bats. When the bats sleep during the day they defaecate into the pitchers (Grafe et al., 2011; Schöner et al., 2017). *Nepenthes lowii*, *N. macrophylla*, and *N. rajah* are all engaged in a mutualism with the mountain treeshrew, (*Tupaia montana*), and *N. rajah* also with the summit rat (*Rattus baluensis*) (Chin et al., 2010; Clarke et al., 2010; Greenwood et al., 2011). The plants produce modified pitchers that produce copious amounts of sugary exudates that serve as a food source for the mammals. The exudates are only accessible to mammals when they position their hindquarters over the pitcher orifice. Consequentially, the mammals regularly defaecate into the pitchers when they feed on the nectar secretions on the pitchers' lids and provide fecal nitrogen to the plant (Chin et al., 2010; Clarke et al., 2010; Greenwood et al., 2011). Although the basis of this mutualism between plants and frogs in general and the case of *P. nepenthophilus* and *N. mollis* described here for the first time, seems plausible, most aspects of interactions and potential mutual benefits are unclear.

4.3 | Evolution of reproductive biology

The size of the eggs found during the dissection of the females is above-modal size, and the number of eggs is comparatively low for rhacophorid frogs of the same size (Bahir et al., 2005; Gururaja & Ramachandra, 2006; Patil & Kanamadi, 1997). Eggs of *P. kerangae* are much smaller (3.6 mm inside female, 10 mm when froglets hatch) and clutches slightly larger (6–8 eggs per clutch) despite the larger size of the female (SVL 43 mm) (Dring, 1987). Hertwig et al. (2011) found a clutch of three eggs from *P. acutus*, which measured 13 mm in diameter, including the outer jelly. Eggs of a diameter as large as the ones from *P. nepenthophilus* are usually found in frogs with direct development.

The posteroventral skin flap is a unique feature of the *P. nepenthophilus* tadpole (Figure 7g). Due to the limited sample size, we did not want to apply destructive techniques and can only speculate about the function of the skin. In external examination, the skin flap appears without musculature. The flap may be a (passive) device for attaching to the wall of the pitcher or a structure of improved gas exchange by increased skin area. A flap of skin dorsally at the head was reported in the tadpole of *Shismaderma carens* (Charter & MacMurray, 1939) and suggested that it might serve gas exchange purposes. In *P. nepenthophilus*, capillaries are clearly present in the flap, a necessary condition for an organ of gas exchange.

The reduced mouthparts of the tadpoles and very small, ventral oral orifice (Figure 7g), the egg size as well as the large intestinal yolk mass seen in each of the larvae, even in the more advanced stages of *P. nepenthophilus* examined (Figure 7d), suggest that these tadpoles are endotrophic/lecithotrophic and do not feed on matter in the pitcher phytotelm. In *P. macroscelis*, the sister species of *P. nepenthophilus*, the almost completely reduced oral disk, absence of keratinized structures, narrow gill region, and the thick, yellowish intestine indicating a rich load of yolk, were also interpreted as evidence of an endotrophic mode of development (Hertwig et al., 2011). Such combination of morphological characters has been confirmed as evidence of endotrophy by histological examination in different anuran species (e.g., Das & Haas, 2010; McDiarmid & Altig, 1999). In *Philautus*, similar tadpoles were described also for *P. hosii* based on direct observation of the hatching and development of larvae (Inger, 1966). All three species with comparable larval stages belong to the early diverging lineages within this genus.

Anecdotal and unconfirmed observations of lecithotrophic tadpoles exist for *P. kerangae* (Dring, 1987) and *P. mjobergi* (Mjöberg in Smith, 1925). Endotrophic tadpoles are remarkable in *Philautus*,

because most species are believed to use direct aerial development as a reproductive strategy (Chen et al., 2020). The vast majority of rhacophorid tree frogs have free-swimming, ectotrophic tadpoles, but in many species of the genera *Philautus* (Gistel, 1848), *Pseudophilautus* (Laurent, 1943), and *Raorchestes* (Biju et al., 2010) from South and Southeast Asia, direct aerial development was recorded (Alcala & Brown, 1982; Brown & Alcala, 1982; Grosjean et al., 2008; Hertwig et al., 2011, 2014). This mode of reproduction is hypothesized as an adaptation to habitats with few or no permanent bodies of surface water depending on local climatic or geomorphological conditions (Alcala, 1962; Callery et al., 2001; Marmayou et al., 2000; Wells, 2007). However, in *Philautus*, aerial direct development has only been recorded in few species (Hertwig et al., 2012: *P. acutus*; Malkmus et al., 2002: *P. saueri*; Yong et al., 1988: *P. aurifasciatus*). In the vast majority of *Philautus* species, including most representatives from Borneo, however, the effective breeding behavior has actually never been confirmed by direct observations, captive breeding or genetic barcode matching of semaphoronts to each other. The closely related genera *Kurixalus*, *Gracixalus*, and *Nasutixalus* (Chan et al., 2018; Chen et al., 2020) are known to have free-swimming tadpoles (e.g., Biju et al., 2016; Haas et al., 2012; Pham et al., 2019; Yang & Chan, 2018).). The genera in which direct development was confirmed in several species (*Philautus*, *Pseudophilautus*, and *Raorchestes*) have never been supported as a monphyletic group, rather, direct development was confirmed as having convergently evolved in the two separate lineages *Philautus* in Southeast Asia and *Pseudophilautus/Raorchestes* in the western part of the Asian distribution of the Rhacophorinae (Chan et al., 2018; Chen et al., 2020; Hertwig et al., 2013), respectively. Although the basal phylogenetic relationships of *Philautus* have not yet been resolved in this and all previous studies, the new record of endotrophic larvae in *P. nepenthophilus* questions again the hypothesis that direct development was the plesiomorphic condition in this genus (Hertwig et al., 2011; Hertwig et al., 2012; Hertwig et al., 2013; in contrast to Chen et al., 2020). The cases of *P. macroscelis* and *P. nepenthophilus* can be interpreted either as an evolutionary transition from ancestral taxa with tadpoles to more derived taxa with direct development, or in the alternative, less parsimonious scenario, as reversals from ancestral taxa with direct development to free-swimming tadpoles in the *P. nepenthophilus*/*P. macroscelis* clade and eventually independently in *P. hosii*. In order to clarify these open questions, published observations of the reproductive behavior of more *Philautus* species and phylogenetic analyses, that can shed light on the early evolution within that genus, are needed.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available. DNA sequences are available in GenBank at https://www.ncbi.nlm.nih.gov/genbank/, the accession numbers for all sequences used in this study are listed in Appendix 1. References for the sequences obtained from GenBank can be found below. Alignments in fasta file format and the call recording is available in the Data S1 of this original article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Table S1. Partitions of the nuclear (nuDNA), mitochondrial (mtDNA) and combined data set (combDNA) used in Baysian Inference analyses. The search for the best fitting partitioning.

Figure S1. ML Reference tree fromthe*16S rRNA* gene analysis based on 873 bp to confirm species identification and matching of the tadpoles samples. Only robustly supported nodes.

Figure S2. Bayesian Inference (BI) tree from nuclear DNA analysis (nuDNA; *NTF3*, *POMC*; *BDNF*) based on 1,770 bp.

Figure S3. Maximum Likelihood (ML) tree from nuclear DNA analysis (nuDNA; *NTF3*; *POMC*; *BDNF*) based on 1,770 bp.

Figure S4. Bayesian Inference (BI) tree from mitochondrial DNA analysis (mtDNA; *12S-Val-16S*; *CytB*) based on 2,609 bp.

Figure S5. Maximum Likelihood (ML) tree from mitochondrial DNA analysis (mtDNA; *12S-Val-16S*; *CytB*) based on 2,609 bp.

Figure S6. Magnified interorbital of *Philautus nepenthophilus* paratype NMBE 1073588 in preserved condition with visible white keratinous tubercles taken with a calibrated Leica DFC420 camera on a Leica MZ16 Stereomicroscope with motor focus.

Data S1. Audio file of call of *Philautus nepenthophilus*.

Alignment S1. Alignment of partial mitochondrial genes *12S-Val-16S*.

Alignment S2. Alignment of patial nuclear gene BDNF.

Alignment S3. Concatenated alignment of the partial nuclear and partial mitochondrial genes *NTF3*, *POMC BDNF*, *12S-Val-16S*, *CytB*.

Alignment S4. Alignment of partial mitochondrial gene *CytB*.

Alignment S5. Concatenated alignment of the partial mitochondrial genes *12S-Val-16S*, *CytB*.

Alignment S6. Alignment of partial mitochondrial gene *NTF3*.

Alignment S7. Concatenated alignment of the partial nuclear genes *NTF3*, *POMC BDNF*.

Alignment S8. Alignment of partial mitochondrial gene *POMC*.

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APPENDIX 1

Sequences used to calculate the phylogenies and the reference tree for correct species identification in this study. Reference sequences were only used in the reference tree based on the *16S rRNA* gene for the confirmation of species identification, thus no other accession numbers can be found in the table. Location is in Malaysia if no other country is stated. ACD, Arvin Diesmos field series, specimen deposited at the National Museum of the Philippines (PNM); BORN, BORNEENSIS, stored at the Institute for Tropical Biology and Conservation, University Malaysia, Sabah, Malaysia; CAS, California Academy of Sciences, San Francisco, California, US; FM, FMNH, Field Museum Chicago, Chicago, Illinois, USA; KUHE, Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, Japan; LSUHC, La Sierra University, Riverside, California, US; MZB, Museum Zoologicum Bogorinese, Bogor, Java, Indonesia; NMBE, Naturhistorisches Museum der Burgergemeinde Bern, Bern, Switzerland; RMB, Fieldno. by Rafe H. Brown; UNIMAS, Museum of Universiti Malaysia Sarawak, Kota Samarahan, Sarawak, Malaysia; ZMH, Zoological Museum of Hamburg, Germany. References: DD13, Dehling and Dehling (2013); D16, Dehling et al. (2016); DC04, Darst and Cannatella (2004); HA12, Haas et al. (2012); H11, Hertwig et al. (2011); H12, Hertwig et al. (2012); H13, Hertwig et al. (2013); G14, Gonzalez et al. (2014); M11, Meegaskumbura et al. (2011); M14, Matsui et al. (2014); W17, Wostl et al. (2017); WDT02, Wilkinson et al. (2002).

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
Kurixalus appendiculatus									
Kurixalus appendiculatus	NMBE 1056476	Sarawak: Gunung Mulu Natl. Park: Camp 5	H13	KC961248	KC961091	–	KC961189	KC961139	–
	ACD 6322	Philippines: Surigao Island, Surigao Province, Municipality of Del Carmen	G14	–	–	KF933126	–	–	–
Philautus acutirostris									
Ref.P.acutirostris	RMB 589	Philippines: Davao City	DC04	–	AY326059	–	–	–	–
Philautus acutus									
Ref.P.acutus	NMBE 1056431	Sarawak, Gunung Mulu National Park, Camp 3	H12	–	JN705366	–	–	–	–
8898	NMBE 1064022	Sarawak, Gunung Mulu National Park, Camp 3	This study	MW356581		MW356349	MW356502	MW356263	–
09-223	NMBE 1056429	Sarawak, Gunung Mulu National Park	H12, this study	JX091304	JX091301	MW356347	MW356500	MW356261	MW356415
09-224	NMBE 1056430	Sarawak, Gunung Mulu National Park	H12, this study	JX091305	JX091302	MW356348	MW356501	MW356262	MW356416
Philautus amoenus									
Ref.P.amoenus	UNIMAS 8052	Sabah, Gunung Kinabalu Park: Laban Rata Trail	H13	–	KC961076	–	–	–	–
SH-1160	NMBE 1075442	Sabah, Kinabalu National Park, Summit trail	This study	MW356595		MW356360	MW356512	MW356271	MW356428
SH-1161	NMBE 1075443	Sabah, Kinabalu National Park, Summit trail	This study	MW356597		MW356361	MW356515	MW356315	MW356429
SH-1162	NMBE 1075444	Sabah, Kinabalu National Park, Summit trail	This study	MW356596		MW356362	MW356514	MW356272	MW356431
SH-1166	NMBE 1075446	Sabah, Kinabalu National Park, Summit trail	This study	MW356598		MW356363	MW356513	MW356273	MW356430

(Continues)

APPENDIX 1 (Continued)

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
SH-1168	NMBE 1075447	Sabah, Kinabalu National Park, Summit trail	This study	MW356599		MW356364	MW356516	MW356275	MW356432
Philautus aurantium									
Ref.P.aurantium1	FM233226	Sabah, Sipitang District	H13	–	KC961078	–	–	–	–
Ref.P.aurantium2	FMNH233226	not available	unpublished	–	GQ204705	–	–	–	–
Ref.P.aurantium3	UNIMAS 8666	Sabah, Crocker Range National Park	H12	–	JN705367	–	–	–	–
HEP-02669	NMBE 1072612	Sabah, Tawau Hills National Park, Sungei Tawau	This study	MW356582		MW356350	MW356503	MW356264	MW356417
HEP-02670	NMBE 1072613	Sabah, Tawau Hills National Park, Sungei Tawau	This study	MW356583		MW356351	–	MW356269	MW356418
SH-0350	NMBE 1072161	Sabah, Tawau Hills National Park, Mountain Hostel	This study	MW356584		–	MW356505	MW356265	MW356419
SH-1023	NMBE 1075221	Sabah, Kinabalu National Park, Liwagu trail	This study	MW356585		MW356352	MW356504	MW356270	MW356420
SH-1041	NMBE 1075222	Sabah, Kinabalu National Park, Liwagu trail	This study	MW356586		MW356353	MW356508	MW356266	MW356421
SH-1062	NMBE 1075642	Sabah, Kinabalu National Park, Liwagu trail	This study	MW356588		MW356355	MW356506	MW356285	MW356422
SH-1073	NMBE 1075573	Sabah, Kinabalu National Park, Liwagu trail	This study	MW356587		MW356354	MW356510	MW356286	MW356423
SH-1093	NMBE 1075290	Sabah, Kinabalu National Park, Poring, Langanan trail and fall	This study	MW356589		MW356356	MW356509	MW356267	MW356424
SH-1094	NMBE 1075291	Sabah, Kinabalu National Park, Poring, Langanan trail and fall	This study	MW356590		MW356357	MW356507	MW356268	MW356425
Philautus bunitus									
Ref.P.bunitus	UNIMAS 9045	Sabah, Kinabalu National Park, Sayap	H12	–	JN705368	–	–	–	–
8668	NMBE 1063964	Sabah, Crocker Range National Park	This study	MW356591		MW356358	–	–	MW356426
SH-0568	NMBE 1073897	Sarawak, Payeh Maga, high camp, short cut trail	This study	MW356593		–	–	–	–
SH-0570	NMBE 1073899	Sarawak, Payeh Maga, high camp, short cut trail	This study	MW356592		–	–	–	–
Philautus davidlabangi									
Ref.P.davidlabangi1	KUHE: 19594	Sarawak	M14	–	AB847127	–	–	–	–
Ref.P.davidlabangi2	NMBE 1056444	Sarawak, Batang Ai National Park, Hilton Loghouse Resort	H12	–	JN705386	–	–	–	–
Ref.P.davidlabangi3	ZMH A10429	Sarawak, Kubah National Park, Belian Trail	H12	–	JN705387	–	–	–	–
MD09-046	NMBE 1068259	Sarawak, Kubah National Park	This study	MW356666		MW356390	MW356563	MW356342	MW356476

(Continues)

APPENDIX 1 (Continued)

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
MD09-073	NMBE 1068284	Sarawak, Kubah National Park	This study	MW356667		MW356391	MW356564	MW356343	MW356477
Philautus disgregus									
Ref.P.disgregus1	FMNH231141	not available	Unpublished	–	GQ204704	–	–	–	–
Ref.P.disgregus2	FM231141	Sabah, Lahad Datu District	H13	–	KC961077	–	–	–	–
Philautus everetti									
Ref.P.everetti	KU 309610	Philippines: Palawan, Municipality of Brooke's Point: Boundary of Barangay Samarinana and Saubg: Mt. Mantalingahan: Area Pitang	H11	–	JN705377	–	–	–	–
Philautus hosii									
Ref.P.hosii1	NMBE 1057287	Sarawak, Usun Apau National Park	H12	–	JN705384	–	–	–	–
SH-0475	NMBE 1074000	Sarawak, Payeh Maga, big stream below camp 1	This study	MW356637		MW356410	MW356568	MW356300	MW356481
SH-0493	NMBE 1073990	Sarawak, Payeh Maga, big stream below camp 2	This study	MW356641		MW356413	MW356569	MW356301	MW356482
SH-0583	NMBE 1073884	Sarawak, Payeh Maga, old camp 3	This study	MW356638		MW356411	MW356571	MW356302	MW356484
SH-0623	NMBE 1073841	Sarawak, Merarap Hot Spring Lodge	This study	MW356642		MW356414	MW356566	MW356303	MW356483
SH13-106	NMBE 1065969	Sarawak, Paya Maga	This study	MW356636		MW356408	MW356565	MW356298	MW356478
SH13-108	NMBE 1065971	Sarawak, Paya Maga	This study	MW356640		MW356409	MW356567	MW356299	MW356479
SH13-198	NMBE 1066061	Sarawak, Paya Maga	This study	MW356639		MW356412	MW356570	MW356312	MW356480
Philautus ingeri									
Ref.P.ingeri1	NMBE 1056435	Sarawak, Gunung Mulu National Park, Camp 3	H12	–	JN705385	–	–	–	–
Ref.P.ingeri2	FMNH239280	not available	unpublished	–	GQ204706	–	–	–	–
09-249	NMBE 1056435	Sarawak, Gunung Mulu National Park	H12, H13, this study	JN705354	JN705385	–	KC961173	KC961114	MW356485
HJ12-062	NMBE 1061706	Sarawak, Pulong Tau NP, Gunung Murud, Lepo Bunga	This study	MW356643		–	MW356572	MW356305	MW356486
HJ12-065	NMBE 1061677	Sarawak, Pulong Tau NP, Gunung Murud, Lepo Bunga	This study	MW356650		–	MW356573	MW356306	MW356487
HJ12-095	NMBE 1061675	Sarawak, Pulong Tau NP, Gunung Murud, Lepo Bunga	This study	MW356644		–	MW356574	MW356307	MW356488
SH-0693	NMBE 1073776	Sarawak, Pulong Tau NP, Gunung Murud, Lepo Bunga, Trail to Churchcamp	This study	MW356647		–	MW356578	MW356310	MW356492
SH-0703	NMBE 1073758	Sarawak, Pulong Tau NP, Gunung Murud, Lepo Bunga, Trail to Churchcamp	This study	MW356649		–	MW356579	MW356314	MW356493
SH-0717	NMBE 1073744	Sarawak, Pulong Tau NP, Gunung Murud, Lepo Bunga, Trail to Churchcamp	This study	MW356648		–	MW356580	MW356311	MW356494

(Continues)

APPENDIX 1 (Continued)

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
SH13-235	NMBE 1066098	Sarawak, Pulong Tau NP,	This study	MW356651		–	MW356575	MW356308	MW356489
SH13-243	NMBE 1066106	Sarawak, Pulong Tau NP,	This study	MW356645		–	MW356576	MW356309	MW356490
SH13-244	NMBE 1066107	Sarawak, Pulong Tau NP,	This study	MW356646		–	MW356577	MW356313	MW356491
Philautus juliandringi									
Ref.P.juliandringi	NMBE 1056439	Sarawak, Gunung Mulu National Park, Gunung Api	H12	–	JN705378	–	–	–	–
09-064	NMBE 1056438	Sarawak, Gunung Mulu National Park	This study	MW356607		MW356365	MW356523	MW356329	MW356447
Philautus kakipanjang									
Ref.P.kakipanjang2	not stated	Western Sarawak	DD13	–	KF240718	–	–	–	–
AH11-075	NMBE 1065356	Sarawak, Gunung Penrissen	This study	MW356618		MW356377	–	MW356281	MW356452
HH10-328	NMBE 1057558	Sarawak, Borneo Highlands	This study	MW356621		MW356379	–	MW356279	MW356453
HJ12-225	NMBE 1061521	Sarawak, Borneo Highlands Resort, Mount Penrissen	This study	MW356623		MW356380	MW356541	MW356280	MW356456
HJ12-239	NMBE 1061504	Sarawak, Borneo Highlands Resort, Mount Penrissen	This study	MW356622		MW356378	MW356542	MW356282	MW356454
JMD-466	NMBE 1060428	Sarawak, Gunung Gading National Park	This study	MW356619		MW356381	MW356545	MW356284	MW356455
JMD-472	NMBE 1060429	Sarawak, Gunung Gading National Park	This study	MW356620		MW356382	MW356543	MW356283	-
Philautus kerangae									
Ref.P.kerangae1	NMBE 1056437	Sarawak, Gunung Mulu National Park, Mentawai Ranger Station	H13	–	KC961079	–	–	–	–
AH-08-005	NMBE 1063696	Sarawak, Gunung Mulu National Park	This study	MW356594		MW356359	MW356511	MW356295	MW356427
Philautus larutensis									
Ref.P.cf.larutensis	NMBE 1056443	Sarawak, Gunung Mulu National Park, Camp 3	H12	–	JN705381	–	–	–	–
Ref.P.larutensis1	MZB. Amph.26152	Indonesia: Sumatra, Lampung	W17	–	KY435424	–	–	–	–
Ref.P.larutensis2	MZB. Amph.26866	Indonesia: Sumatra, Aceh	W17	–	KY435425	–	–	–	–
Ref.P.larutensis3	LSUHC_8872	Perak	W17	–	KY435426	–	–	–	–
HJ12-018	NMBE 1061456	Sarawak, Gunung Murud, Sungai Bur, Pa Rabata	This study	MW356624		MW356383	MW356534	MW356330	MW356440
HJ12-019	NMBE 1061457	Sarawak, Gunung Murud, Sungai Bur, Pa Rabata	This study	MW356626		MW356384	MW356535	MW356331	MW356441
HJ12-037	NMBE 1061443	Sarawak, Gunung Murud, Sungai Bur, Pa Rabata	This study	MW356627		MW356385	MW356536	MW356332	MW356451

(Continues)

APPENDIX 1 (Continued)

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
SH-0735	NMBE 1073734	Sarawak, Lepo Bunga, stream below camp	This study	MW356629		MW356386	MW356538	MW356334	MW356444
SH-0736	NMBE 1073735	Sarawak, Lepo Bunga, stream below camp	This study	MW356628		MW356387	MW356539	MW356335	MW356445
SH-0737	NMBE 1073736	Sarawak, Lepo Bunga, stream below camp	This study	MW356630		MW356387	MW356540	MW356336	MW356446
SH13-208	NMBE 1066071	Sarawak, Pulong Tau National Park	This study	MW356625		MW356389	MW356537	MW356333	MW356443
Philautus macroscelis									
Ref.P.macroscelis1	NMBE 1056486	Sarawak, Gunung Mulu National Park, Sungai Tapin	H12	–	JN705375	–	–	–	–
SH-0738	NMBE 1073737	Sarawak, Lepo Bunga, stream below camp	This study	MW356654		MW356394	MW356552	MW356289	MW356473
SH-0761	NMBE 1073704	Sarawak, Lepo Bunga, camp and trail to Churchcamp	This study	MW356653		MW356393	MW356553	MW356290	MW356474
SH-0762	NMBE 1073705	Sarawak, Lepo Bunga, camp and trail to Churchcamp	This study	MW356655		MW356395	MW356554	MW356291	MW356475
SH-0983	NMBE 1075643	Sabah, Kinabalu National Park, Silau Silau trail	This study	MW356656		MW356396	MW356555	MW356292	MW356463
SH-0987	NMBE 1075426	Sabah, Kinabalu National Park, Silau Silau trail	This study	MW356657		MW356397	MW356556	MW356293	MW356464
SH13-258	NMBE 1066121	Sarawak, Pulong Tau National Park	This study	MW356652		MW356392	MW356551	MW356288	MW356462
Philautus mjobergi									
Ref.P.mjobergi1	NMBE 1056434	Sarawak, Gunung Mulu National Park, Camp 3	H12	–	JN705380	–	–	–	–
Ref.P.mjobergi2	FMNH 252411	not available	unpublished	–	GQ204708	–	–	–	–
09-211	NMBE 1056446	Sarawak, Gunung Mulu National Park	This study	MW356615		MW356373	MW356532	MW356319	MW356470
09-212	NMBE 1056447	Sarawak, Gunung Mulu National Park	This study	MW356617		MW356374	MW356530	MW356320	MW356471
09-257	NMBE 1056440	Sarawak, Gunung Mulu National Park	This study	MW356613		MW356371	MW356529	MW356317	MW356468
09-258	NMBE 1056441	Sarawak, Gunung Mulu National Park	This study	MW356614		MW356372	MW356531	MW356318	MW356469
09-263	NMBE 1056449	Sarawak, Gunung Mulu National Park	This study	MW356616		MW356375	MW356533	MW356321	MW356472
HJ12-012	NMBE 1061483	Sarawak, Gunung Murud, Sungai Bur, Pa Rabata	This study	MW356612		MW356367	MW356525	MW356325	MW356448
HJ12-022	NMBE 1061460	Sarawak, Gunung Murud, Sungai Bur, Pa Rabata	This study	MW356611		MW356368	MW356526	MW356326	MW356442
HJ12-164	NMBE 1061588	Sarawak, Gunung Murud, Palungan	This study	MW356609		MW356370	MW356527	MW356324	MW356449
HJ12-181	NMBE 1061571	Sarawak, Gunung Murud, Palungan	This study	MW356608		MW356366	MW356524	MW356316	MW356495

(Continues)

APPENDIX 1 (Continued)

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
SH13-334	NMBE 1065915	Sarawak, Kelabit Highlands, Pulong Tau National Park	This study	MW356610		MW356369	MW356544	MW356327	MW356450
Philautus nepenthophilus									
SH13-341	NMBE 1065920	Sarawak, Pulong Tau National Park, Churchcamp	This study	MW356658		MW356398	MW356557	MW356344	MW356465
SH-0768	NMBE 1073711	Sarawak, Pulong Tau National Park, Churchcamp	This study	MW356659		MW356400	MW356558	MW356345	MW356466
SH-0794	NMBE 1073601	Sarawak, Pulong Tau National Park, Churchcamp	This study	MW356660		–	–	–	-
SH-0795	NMBE 1073602	Sarawak, Pulong Tau National Park, Churchcamp	This study	MW356661		MW356399	MW356559	MW356346	MW356467
647	ZHM A12303	Sarawak, Pulong Tau National Park, Churchcamp	This study	–	MW394613	–	–	–	–
E685	ZHM A12303	Sarawak, Pulong Tau National Park, Churchcamp	This study	–	MW394617	–	–	–	–
E686	ZHM A12303	Sarawak, Pulong Tau National Park, Churchcamp	This study	–	MW394615	–	–	–	–
E689	ZHM A12303	Sarawak, Pulong Tau National Park, Churchcamp	This study	–	MW394614	–	–	–	–
E690	ZHM A12303	Sarawak, Pulong Tau National Park, Churchcamp	This study	–	MW394616	–	–	–	–
Philautus nephophilus									
Ref.P.nephophilus	BORN 22666	Sabah, Kinabalu	D16	–	KT445971	–	–	–	–
SH-0982	NMBE 1075644	Sabah, Kinabalu National Park, Silau Silau trail	This study	MW356600		–	MW356517	MW356276	MW356433
SH-0992	NMBE 1075429	Sabah, Kinabalu National Park, Silau Silau trail	This study	MW356601		–	MW356518	MW356277	MW356434
SH-0993	NMBE 1075430	Sabah, Kinabalu National Park, Silau Silau trail	This study	MW356604		–	MW356522	MW356278	MW356435
SH-0998	NMBE 1075431	Sabah, Kinabalu National Park, Silau Silau trail	This study	MW356602		–	MW356519	MW356322	MW356436
SH-1021	NMBE 1075224	Sabah, Kinabalu National Park, Liwagu trail	This study	MW356605		–	MW356520	MW356323	MW356437
SH-1039	NMBE 1075645	Sabah, Kinabalu National Park, Liwagu trail	This study	MW356603		–	MW356521	MW356323	MW356438
Philautus refugii									
Ref.P.refugii1	NMBE 1057544	Sarawak, Borneo Highlands Resort	H12	–	JN705382	–	–	–	–

(Continues)

APPENDIX 1 (Continued)

Name in analysis	Voucher No.	Location	Reference	12S rRNA	16S rRNA	CytB	POMC	BDNF	NTF3
Ref.P.refugii2	ZMH A10415	Sarawak, Kubah National Park, Summit Road	H12	–	JN705383	–	–	–	–
SH-1567	NMBE 1078425	Sarawak, Gunung Gading	This study	MW356631		MW356403	MW356546	MW356337	MW356457
SH-1569	NMBE 1078426	Sarawak, Gunung Gading	This study	MW356632		MW356404	MW356549	MW356341	MW356458
SH-1572	NMBE 1078427	Sarawak, Gunung Gading	This study	MW356633		MW356405	MW356550	MW356338	MW356461
SH-1577	NMBE 1078428	Sarawak, Gunung Gading	This study	MW356634		MW356406	MW356547	MW356340	MW356459
SH-1584	NMBE 1078429	Sarawak, Gunung Gading	This study	MW356635		MW356407	MW356548	MW356339	MW356460
Philautus surdus									
Ref.P.surdus	CAS 219932	not available	WDT02	–	AF458138	–	–	–	–
Philautus tectus									
Ref.P.tectus1	NMBE 1056451	Sarawak, Gunung Mulu National Park, Deer Cave Trail	H12	–	JN705370	–	–	–	–
Ref.P.tectus2	NMBE 1057080	Sarawak, Kubah National Park: Summit Road	H12	–	JN705369	–	–	–	–
09-073	NMBE 1056452	Sarawak, Gunung Mulu National Park	This study	MW356662		–	MW356560	MW356294	MW356496
AH-08-009	NMBE 1063700	Sarawak, Gunung Mulu National Park	This study	MW356663		–	MW356561	MW356295	MW356499
SH13-196	NMBE 1066059	Sarawak, Paya Maga	This study	MW356665		MW356401	–	MW356297	MW356497
SH13-197	NMBE 1066060	Sarawak, Paya Maga	This study	MW356664		MW356402	MW356562	MW356296	MW356498
Philautus umbra									
Ref.P.umbra	NMBE 1056454	Sarawak, Gunung Mulu National Park: Gunung Api	H12	–	JN705379	–	–	–	–
09-066	NMBE 1056453	Sarawak, Gunung Mulu National Park	This study	MW356606		MW356376	MW356528	MW356328	MW356439
Polypedates leucomystax									
Polypedates leucomystax	NMBE 1057524	Sarawak: Borneo Highlands Resort	H13	KC961245	KC961082	–	KC961183	KC961127	–
	FMNH 255296	Laos	M11	–	–	GQ204517	–	–	–
Rhacophorus reinwardtii									
Rhacophorus reinwardtii	NMBE 1056517	Sarawak: Batang Ai Natl. Park: Bebyong Trail	HA12	KC961245	JN377366	–	KC961155	KC961097	–
	FMNH 235034	Malaysia	M11	–	–	GQ204530	–	–	–