



Solving the taxonomic identity of *Hipposideros cineraceus sensu lato* (Chiroptera: Hipposideridae) in the Thai-Malay Peninsula, with the description of a new species

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Abstract

A new species of small *Hipposideros* in the *bicolor* group is described based on specimens from Thailand and Malaysia. It can be distinguished from other small *Hipposideros* in Southeast Asia by a combination of external, craniodental, and bacular morphology, as well as echolocation call frequency. The new species has a distinct rounded swelling on the internarial septum of the noseleaf, with a forearm length of 35.3–42.6 mm, greatest skull length of 15.94–17.90 mm, and a call frequency of maximum energy of 132.3–144.0 kHz. Although clearly different in morphology, the new species forms a sister clade with *H. kunzi* and *H. bicolor* in the phylogenetic trees based on mitochondrial DNA. In addition, this study reports echolocation and genetic data, with a confirmed record of *H. einnaythu* from Thailand for the first time. The new species most closely resembles *H. einnaythu*. However, it differs in the details of the noseleaf and craniodental morphology, and it has a genetic distance of 9.6% and 10.4% based on mitochondrial COI and ND2, respectively. It is currently documented from five localities: two in peninsular Thailand, at Hala Forest in Yala Province, and Phru To Daeng Swamp Forest in Narathiwat Province, one from peninsular Malaysia at Krau Wildlife Reserve in Pahang, and another two in Sabah, Malaysian Borneo at Gunung Kinabalu, and near Madai Caves. However, it is likely that many previous records of “*H. cineraceus*” from Borneo refer to this species. Most records of the species are from lowland evergreen rainforest, though one record from Sabah was at 1800m. The roosting sites for this new species are currently unknown. Future research with a combination of data such as genetics, echolocation and morphology would be necessary to further determine the species geographic distribution in Southeast Asia.

Key words: Chiroptera, Hipposideridae, Malaysia, new species, phylogeny, Southeast Asia, taxonomy, Thailand

Introduction

The family Hipposideridae, the Old-World leaf-nosed bats or roundleaf bats, contains seven living genera and 90 species. They inhabit tropical and subtropical regions of Africa and associated islands, the Middle East, through the Indian subcontinent, Asia, and Oceania (Monadjem *et al.*, 2019). The most diverse genus in the family is *Hipposideros*, with 73 species currently recognised (Simmons and Cirranello, 2022). The genus has been classified into nine species groups (*sensu* Corbet and Hill, 1992; Monadjem *et al.*, 2019). One of these, the *Hipposideros bicolor* group, includes 35 species with at least 25 reported from Southeast Asia. They present a significant taxonomic challenge due to the limited morphological variation among species (Francis *et al.*, 2010; Murray *et al.*, 2012; 2018; Monadjem *et al.*, 2019).

In Southeast Asia, the identification of *Hipposideros bicolor* (Temminck, 1834), *H. cineraceus* Blyth, 1853, *H. gentilis* K. Andersen, 1918 (now considered distinct from *pomona* K. Andersen, 1918 which is restricted to southern India; see Srinivasulu and Srinivasulu 2018), and *H. ater* Templeton, 1848 has caused much confusion. Douangboubpha *et al.* (2010) demonstrated the morphological and acoustic differences among these species and recognised a previously unnamed taxon, labelled informally “*H. bicolor*-142”, as *H. atrox* K. Andersen, 1918 based on morphology. Douangboubpha *et al.* (2011) subsequently raised the taxon *nicobarulae* Miller, 1902 from a subspecies of *ater* to a distinct species, restricted the range of true *H. ater* to India and Sri Lanka, and described a new species *H. einnaythu* from Myanmar. However, the taxon referred to *H. atrox* by Douangboubpha *et al.* (2010) has subsequently been revised and named as a new species *H. kunzi* by Murray *et al.* (2018), with the name *atrox* considered a junior synonym of *H. bicolor*.

Murray *et al.* (2018), as well as previous studies (Kingston *et al.*, 2006; Francis, 2008; Murray *et al.*, 2012), suggested that specimens currently included in *H. cineraceus* in peninsular Malaysia represent at least two distinct species, provisionally labelled *H. cineraceus*-A and *H. cineraceus*-B. Murray *et al.* (2012; 2018) published a molecular phylogeny of the *Hipposideros bicolor* group based on mitochondrial ND2 and nuclear RAG1 markers. It showed that *H. cineraceus*-B forms a sister clade with *H. bicolor* and *H. kunzi*. However, the appropriate name for the so-called *H. cineraceus*-A and *H. cineraceus*-B forms remained unclear, particularly determining which is typical *cineraceus* (*sensu stricto*) and what species name should be assigned to the other.

A series of bat surveys in Thailand and Myanmar (2014–2021), with a particular focus on the lowland rainforest of peninsular Thailand, increased the number of specimens and data of many individuals from the *H. bicolor* group from the region. This new material facilitated a more integrative review based on better comparative material. These analyses found that *H. cineraceus*-A was distributed through much of mainland Southeast Asia, including specimens from northern Myanmar, and hence appears to represent true *H. cineraceus*, though we were unable to examine the type (see below) and hence label it as *H. cf. cineraceus*. In contrast, *H. cineraceus*-B was detected only in the southern Thai-Malay peninsula and Borneo and does not match any existing names. It is therefore described here as a new species. We also confirmed the presence of *H. einnaythu* in Thailand and obtained additional information on its echolocation calls and phylogenetic relationships.

Materials and methods

Specimens examined

Specimens of the *H. bicolor* group in the Princess Maha Chakri Sirindhorn Natural History Museum [PSUZC-MM; uncatalogued PS], Prince of Songkla University (PSU), Thailand, including those analysed and reported in Douangboubpha *et al.* (2010; 2011), were examined. Additional specimens were also included from the Museum of Zoology, Universiti Kebangsaan Malaysia [DWNP; uncatalogued TK], peninsular Malaysia (UKMMZ); Indonesian Institute of Sciences [MZB], Indonesia (LIPI); Harrison Institute [HZM], UK; Natural History Museum, London [BMNH], UK; Doñana Biological Station [EBD], Spain; Senckenberg Research Institute and Natural History Museum [SEN; CMF], Germany; Hungarian Natural History Museum [HNH], Hungary; Royal Ontario Museum [ROM], Canada (Fig. 1; see list of comparative specimens in Appendix 1).

Field surveys

Fieldwork was undertaken between 2014 and 2021. Bats were captured with four-bank harp traps (modified from

Francis, 1989) and mist nets set across forest trails and streams in forest areas, or at cave entrances in several sites throughout Thailand (Fig. 2). These include *Chiang Mai Province*: Chiang Dao Wildlife Research Station; *Kanchanaburi Province*: Our Land Conservation Effort; Mahidol University, Sai Yok Campus; *Phetchaburi Province*: Kaeng Krachan National Park; *Ratchaburi Province*: Khao Bin Cave; *Songkhla Province*: Kuan Khao Wang Forest Park, Boripat Waterfall, Than Khiri Community Forest; *Phatthalung Province*: Khao Pu Khao Ya National Park; Sumano Cave; *Narathiwat Province*: Bala Forest; Hala Forest; Phru To Deang Swamp Forest.

Bats were provisionally identified to species in the field following Francis (2019). Sex, age, and reproductive status were determined following Racey (2009). Selected individuals were collected as museum vouchers and deposited in the mammal collection of the Princess Maha Chakri Sirindhorn Natural History Museum (PSUNHM), Prince of Songkla University (PSU), Hat Yai, Thailand.

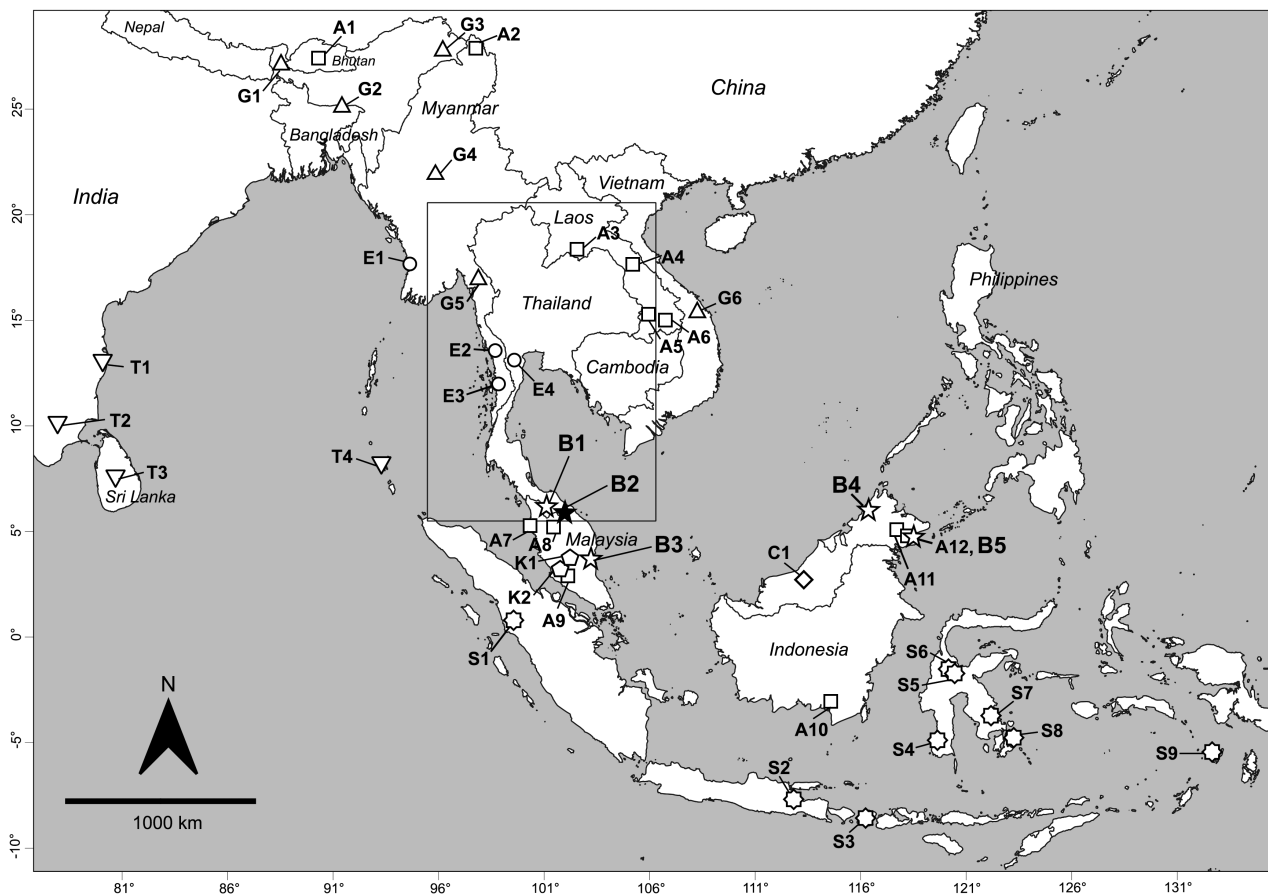


FIGURE 1. Locality map of specimens included in this study: *H. cineraceus*-A (A, squares), *H. kingstonae* sp. nov. (B, stars), *H. bicolor* (C, diamonds), *H. einnaythu* (E, circles), *H. gentilis* (G, triangles), *H. kunzi* (K, pentagons), *H. cf. saevus* (S, eight-pointed stars), and *H. ater* (T, inverted triangles). Black symbols represent specimens from recent field surveys; open symbols represent specimens examined in museum collections. A1: Bhutan; A2: Kachin, Myanmar; A3: Vientiane, Laos; A4: Khammouane, Laos; A5: Champassak, Laos; A6: Attapeu, Laos; A7: Penang, Malaysia; A8: Temengor Forest Reserve, Malaysia; A9: Kuala Lumpur, Malaysia; A10: Bandjarmasin, Indonesia; A11: Segarong Cave, Sabah, Malaysia; A12: Madai Cave, Sabah, Malaysia; B1: Hala Forest, Yala; B2: Phru To Daeng, Narathiwat; B3: Krau Wildlife Reserve, Pahang, Malaysia; B4: Gunung Kinabalu, Sabah, Malaysia; B5: Madai Cave, Sabah, Malaysia; C1: Sarawak, Malaysia; E1: Kan Thar Yar Beach, Rakhine, Myanmar; E2: Kyauk Taung Cave, Tanintharyi, Myanmar; E3: Lenya, Tanintharyi, Myanmar; E4: Kaeng Krachan National Park, Phetchaburi; G1: Darjeeling, West, Bengal, India; G2: Cherrapunji, Meghalaya, India; G3: Mishmi Hills, India; G4: Phy Taw Aye Cave, Pyin Oo Lwin, Mandalay, Myanmar; G5: Nagamauk Cave, Mon State, Myanmar; G6: Tam Trà, Quảng Nam, Vietnam; K1: Pahang, Malaysia; K2: Selangor, Malaysia; S1: West Sumatra, Indonesia; S2: Java Timūra, Indonesia; S3: Lombok, West Nusa Tenggara, Indonesia; S4: Goa Rumbia, Sulawesi, Indonesia; S5: Badangkaia, Sulawesi, Indonesia; S6: Gimpoe or Bada, Sulawesi, Indonesia; S7: Kendari, Sulawesi, Indonesia; S8: Kakenauwe Forest, Sulawesi, Indonesia; S9: Kai Island, Indonesia; T1: Tirunelveli, Tamil Nadu, India; T2: Sarah Tucker College, Tamil Nadu, India; T3: Rattota, Sri Lanka; T4: Katchal Island, Andaman and Nicobar Islands, India. Full list of specimens is in Appendix 1. Area within rectangle is shown in more detail in Figure 2.

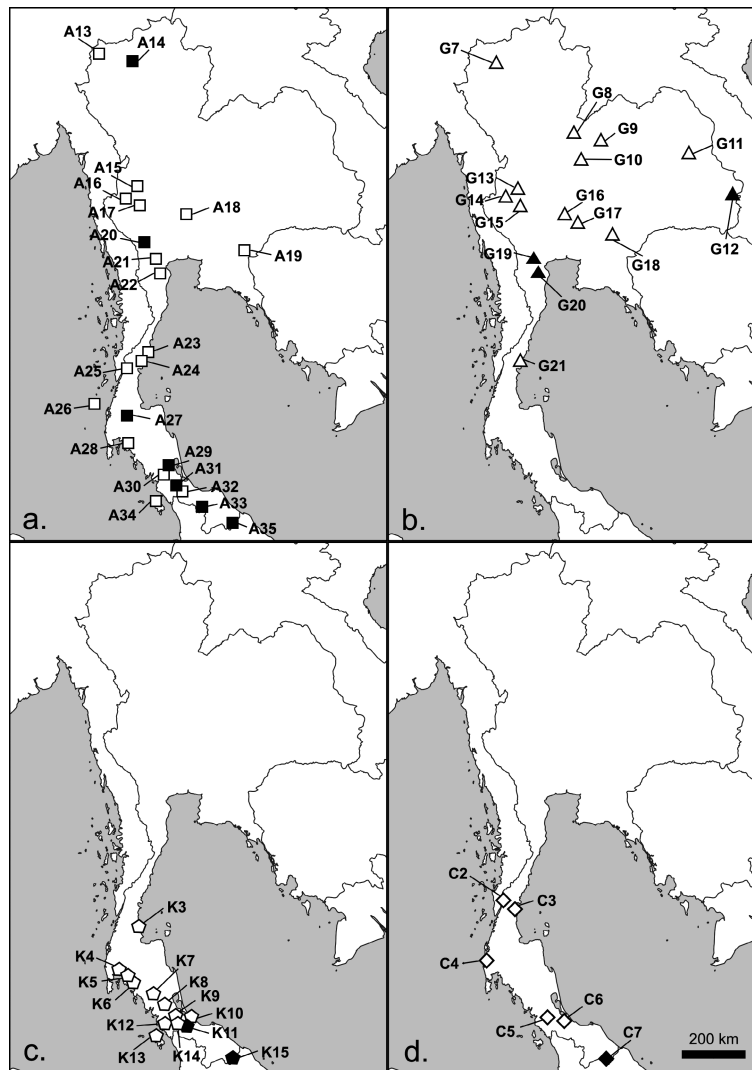


FIGURE 2. Localities within Thailand of (a) *H. cineraceus*-A (A, square symbols), (b) *H. gentilis* (G, triangle symbol), (c) *H. kunzi* (K, pentagon symbol) and (d) *H. bicolor* (C, diamond symbol) examined in this study. Black symbols represent specimens from field surveys; open symbols represent specimens examined in museum collections (a) A13: Pha Dang Cave, Chiang Mai; A14: Chiang Dao, Chiang Mai; A15: Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani; A16: Thung Yai Naresuan Wildlife Sanctuary, Tak; A17: Lop Lae Cave, Uthai Thani; A18: Khao Don Dueng, Lopburi; A19: Wat Khao Singto, Sa Kaeo; A20: Mahidol University Kanchanaburi Campus, Kanchanaburi; A21: Khao Bin Cave, Ratchaburi; A22: Khao Yoi Cave, Phetchaburi; A23: Silawan Cave, Chumphon; A24: Khao Kram Cave, Chumphon; A25: Pra Kayang Cave, Ranong; A26: Surin Island, Phang Nga; A27: Ratchaprapha Dam, Surat Thani; A28: Thanbok Koranee National Park, Krabi; A29: Khao Pu Khao Ya National Park, Phatthalung; A30: Khao Chong, Trang; A31: Srisorn Cave, Songkla; A32: Ton Nga Chang Wildlife Station, Songkhla; A33: Sabayoi, Songkhla; A34: Tarutao Island, Satun; and A35: Hala-Bala Forest, Narathiwat. (b) G7: Khi Mee Cave, Chiang Dao, Chiang Mai; G8: Phu Suan Sai National Park, Loei; G9: Phu Luang Wildlife Sanctuary, Loei; G10: Thung Salaeng Luang National Park, Pitsanulok; G11: Pha Pheung Cave, Phu Sithan Wildlife Sanctuary, Kalasin; G12: Pha Taem National Park, Ubon Ratchathani; G13: Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani; G14: Mae-Chan Ta Station, Thung Yai Naresuan Wildlife Sanctuary, Tak; G15: Lop Lae Cave, Uthai Thani; G16: Khao Don Dueng, LopBuri; G17: Mongkutthong Cave, Sara Buri; G18: Wang Nam Khiao, Nakhon Ratchasima; G19: Khao Bin Cave, Ratchaburi; G20: Khao Yoi Cave, Phetchaburi; and G21: Khao Kram Cave, Chumphon. (c) K3: Khao Plu Cave, Chumphon; K4: Koh Mai Pai, Phang Nga; K5: Khao Kanabnam, Krabi; K6: Sangphet Cave, Krabi; K7: Rad Cave, Trang; K8: Ka Chong Waterfall, Trang; K9: Khao Noi Cave, Songkhla; K10: Khao Rub Chang, Songkhla; K11: Srisorn Cave, Songkhla; K12: Wang Sai Thong Waterfall, Satun; K13: Tarutao Island, Satun; K14: Boripat Waterfall, Songkhla; and K15: Bala forest, Narathiwat. (d) C2: Kra Buri River, Ranong; C3: Wat Tham Hui Klang, Chumphon; C4: Lam Pi Waterfall, Phang Nga; C5: Wang Pha, Songkhla; C6: Outaphao Whatershed, Songkhla; and C7: Bala Forest, Narathiwat. Full list of specimens is in Appendix 1.

Measurements

Body mass (W) was measured with a Pesola spring scale (Pesola AG, Switzerland). External characters were measured using a dial calliper to the nearest 0.1 mm, and cranio-dental characters were measured with a digital calliper to the nearest 0.01 mm. The definition of measurements follows Bates and Harrison (1997) and Csorba *et al.* (2003), unless stated otherwise. The measurements are as follows: Forearm length (FA), Head and body length (HB), Ear length (E), Tail length (Tail), Tibia length (TIBIA), Hindfoot length (HF), Greatest length of the skull (GTL), Lambda to upper canine length (SL), Condylar-basal length (CBL), Condylar-canine length (CCL), Mastoid width (MW), Zygomatic breadth (ZB), Breadth of the braincase (BB), Postorbital constriction (PC), Upper toothrow length (C–M3), Anterior palatal width (C1–C1) Posterior palatal width (M3–M3), Lower toothrow length (c–m3), Mandible length (ML), Lateral rostral chambers width (ALSW) and Median rostral chambers width (AMSW). The statistical analysis using the Man-Whitney U-test was calculated by IBM SPSS Statistics Base Ver 22.0 and Principal components analysis (PCA, with correlate matrix) was undertaken by Past3 (Hammer *et al.*, 2001). Bacula were extracted, drawn or photographed under a microscope.

Echolocation call recording and analysis

Echolocation calls were recorded from hand-held and/or hand-released individuals using a Pettersson D-1000X Ultrasound Detector with the sampling rate set at 768 kHz. Calls were analysed with BatSound Pro 4.2 (Pettersson Elektronik, AB). A good signal-to-noise ratio call of each individual was selected for the measurements. The frequency of maximum energy (FmaxE) (in kHz), corresponding to the frequency of the constant frequency element (CF), was measured in the power spectrum.

Genetic samples and analyses

Tissue samples (wing punches and/or liver) were collected either from the field or from museum specimens and stored in absolute ethanol. DNA was extracted with QIAGEN The DNeasy Blood & Tissue Kit. After DNA extraction, three mitochondrial genes were amplified. These include the 509 base pairs (bp) of mitochondrial NADH dehydrogenase (ubiquinone) subunit 2 (ND2) gene using the forward-primer L5758.M (5'GGHTGAGGNGGMCTNAAAYCARC3'), and the reverse-primer H6305.M (5'GGCTTTGAAGGCYCTTGTC3') and PCR reactions started with an initial denaturation at 94 °C for 9 min, followed by strand denaturation at 94 °C (30 s), annealing at 59–48 °C (45 s), and primer extension at 72 °C (1 min) repeated for 35 cycles followed by a final extension at 72 °C for 7 min (Murray *et al.*, 2012). A 657 bp fragment of cytochrome c oxidase subunit I (COI) gene was amplified with the forward-primer VF1d (5'TTCTCAACCAACCACAARGAYATYGG3'), and the reverse-primer VR1d (5'TAGACTTCTGGGTGGCCRAARAAYCA3'). PCR reactions started with strand denaturation at 94 °C for 1 min, followed at 94 °C (30 s), 50 °C (40 s) and 72 °C (1 min) repeated for 5 cycles, 94 °C (30 s), 55 °C (40 s) and 72 °C (1 min) repeated for 35 cycles and followed by the final elongation steps at 72 °C for 10 min (Lim *et al.*, 2016). The entire (1140 bp) mitochondrial cytochrome b (CytB) gene was amplified using forward-primer Molcit-F (5'AATGACATGAAAATCACCGTTGT3') and reverse-primer CytB-H (5'CTTTTCTGGTTTACAAGACCAG3'). PCR reaction condition started with an initial denaturation at 94 °C (5 min), followed at 94 °C (60 s), 48 °C (60 s) and 72 °C (60 s) repeated 35 cycles and final elongation was 5 min at 72 °C (Soisook *et al.*, 2017). Each reaction for ND2, COI and CytB genes was carried out in total volume 25 µl containing 3 µl of DNA template, 12.5 µl of Qiagen Toptaq Master mix, 2.5 µl of Coral load, 0.5 µl of each Primer and water. Amplified DNA fragments were run on 1.5% agarose gel. Cycle sequencing reactions were labelled with Big Dye® terminator (v3.1, Applied Biosystems), purified with BigDye XTermination® Purification Kit and run on an ABI 3100 automated Genetic Analyzer (Applied Biosystems).

Sequences of other hipposiderids which are available in the Barcode of Life Database (BOLD) and GenBank, as well as a few previously unpublished sequences from one of us (AGS), were included in the analyses, together with *Rhinolophus affinis* as an outgroup (see Appendix 2). Sequences were aligned with MEGAX. Phylogenetic analyses using Maximum Likelihood approach were performed in CIPRESS with RAxML-HPC2 on XSEDE Tool. The Bayesian inference was analysed with the HKY+G+I model for five million generations in MrBayes ver. 3.2 (Ronquist *et al.*, 2012). The phylogenetic trees were visualised and annotated in FigTree ver. 1.4.4 (available from <http://tree.bio.ed.ac.uk>). Genetic distances between taxa were calculated using Kimura-2-parameter (K2P) in MEGAX.

Systematic description

Hipposideros kingstonae sp. nov.

Figs. 3–6, 9; Tables 1–2

[= *H. cineraceus*-B (Kingston *et al.*, 2006; Murray *et al.*, 2012; 2018)]

Holotype. PSUZC-MM2014.164 (field number PS140903.2), adult male, body in alcohol, skull and baculum extracted, collected on 3 September 2014, by Sunate Karapan, Puchit Saekong and Pipat Soisook.

Full measurements (in mm) of the holotype are as follows; FA: 38.4, HB: 40.2, E: 14.2, Tail: 25.9, TIBIA: 16.7, HF: 6.81, GTL: 16.35, SL: 16.13, CBL: 14.54, CCL:13.94, ZB: 8.20, BB: 7.66, MW: 8.50, PC: 2.75, C–M3: 5.54, C1–C1: 3.25, M3–M3: 5.83, c–m3: 5.88, ML: 9.62, ALSW: 4.18, AMSW: 2.19.

Type locality. Phru To Daeng Peat Swamp Forest (=Sirindhorn Peat Swamp Forest), Princess Sirindhorn Wildlife Sanctuary, Narathiwat Province, Thailand, 6°4' N, 101°58' E, 170 m a.sl. The specimen was collected in a harp trap in combination with a mist net set along a boardwalk in the swamp forest.

Paratypes. *Thailand*—PSUZC-MM2022.2 (field number PS211113.5), adult male ♂, body in alcohol, skull and baculum extracted, collected on 13 November 2021 by Sunate Karapan, Phutita Wongwaiyut and Pipat Soisook from the same area as the holotype but in a different spot, near the edge of the forest (6°4.3' N, 101°57.8' E). It was caught in an 18 m-long mist net along a boardwalk by the edge of the swamp. PSUZC-MM2022.1 (field number BL160219.1), adult female, body in alcohol, skull extracted, collected by Puchit Saekong and Sunate Karapan from the same locality as the holotype on 19 February 2016.

Referred specimens. *Thailand*—PSUZC-MM2014.165 (field number PS140830.2), adult female, body in alcohol, skull extracted, collected from Border Police Base, Bang Lang Dam, Hala-Bala Wildlife Sanctuary, Yala Province, 6°4' N, 101°17' E, 22 m a.s.l., on 30 August 2014, by Sunate Karapan, Puchit Saekong and Pipat Soisook. *Malaysia*—Uncatalogued specimen field number TK020622.10, adult female, body in alcohol, skull extracted, collected from Lubuk Baung, Krau Wildlife Reserve, Pahang, peninsular Malaysia, on 22 June 2002, by Juliana Senawi. This specimen was caught in a four-bank harp trap set across a forest trail in lowland dipterocarp forest. DWNP-M-1996-07-29-05653 (field number TK960729.1), adult male, body in alcohol, skull extracted, collected from Kuala Lompat, Krau Wildlife Reserve, Pahang, peninsular Malaysia, on 29 July 1996 by Tigga Kingston. This specimen was caught in a four-bank harp trap in a lowland dipterocarp forest trail. DWNP-M-1996-05-12-05654 (field number TK960519.1), adult male, body in alcohol, skull and baculum extracted, collected from Kuala Lompat, Krau Wildlife Reserve, Pahang, peninsular Malaysia on 19 May 1996 by Tigga Kingston. This specimen was caught in a four-bank harp trap in a lowland dipterocarp forest trail. SMF83823 (field number CMF920706-01), immature male, collected from Krau Wildlife Reserve, Pahang, peninsular Malaysia on 5 July 1992 by Charles M. Francis. EBD 23565 (field number 960523n05), adult female, EBD 23561 (field number 960523n06) and EBD 23560 (field number 969523n33), adult males, previously identified as *H. cf. cineraceus*, caught together with 6 other individuals (3 female, 3 male) in a four-bank harp trap set in a lowland forest trail about ~150 m from the entrance of Madai Caves, Sabah by Antonio Guillén-Servent and Charles M. Francis. EBD 23821 (field number 960604n01), adult female, previously identified as *H. cf. cineraceus*, caught in a mist-net set in the understory of the lower montane forest near the park headquarters in Gunung Kinabalu National Park, Sabah by Antonio Guillén-Servent.

Diagnosis. This is a small *Hipposideros* with a FA of 35.3–42.6 mm and GTL of 15.94–17.90 mm. The sides of the anterior part of the noseleaf are slightly concave; the anterior border has a deep V-shaped median notch and is somewhat angular in appearance. The internarial septum is large, rounded, and distinctly swollen from the middle to the top. The lateral leaflet is absent. The dorsal pelage is dark brown, with the individual hairs creamy-white from the base to the mid-part. The ventral pelage is orange-brown; the hairs are dark brown at the tip, and paler at base. The baculum is very small, 0.5 mm in length, with short but distinct distal prongs. The constant frequency (CF) element of the echolocation call is 141.0–144.0 kHz in the Thai-Malay Peninsula individuals and 132.3–141.4 kHz in the Bornean individuals.

Etymology. The species is named in honour of Tigga Kingston, who as the chair and founder of the Southeast Asian Bat Conservation Research Unit (SEABCRU), spearheads the global bat research community in understanding diversity and promoting bat conservation.

Description. *Hipposideros kingstonae* sp. nov. is a small hipposiderid with a forearm length of 35.3–42.6 mm (Table 1). The body mass is 4.9–7.0 g (n=4), with three male specimens at 4.9–5.6 g, and one female at 7.0 g. The ear is rounded with a pointed tip, and a height of 14.0–18.7 mm; it has short brown hairs along the inner sides. The tail is relatively short (21.5–30.0 mm) in comparison to the head and body length (40.2–49.0 mm). The hindfoot is shorter than half of the tibia in length, 5.0–7.1 mm versus 14.7–17.9 mm, respectively.

The noseleaf is without a lateral supplementary leaflet (Fig. 3). The anterior leaf is dark brown, slightly concave on both lateral borders. The anterior border (bottom edges) has an angular appearance and is separated by a deep groove in the middle. The internarial septum is large, rounded, and distinctly swollen from the middle to the top. The intermediate leaf is relatively broad and sparsely haired. The male specimens have a well-defined frontal sac behind the posterior leaf. The dorsal pelage is dark brown (Fig. 3), with the base to the middle of the hairs creamy white. The ventral pelage is orange brown to dark brown at the hair tips, and paler at the bases. The baculum is very short, 0.5 mm in length (n=3) (Fig. 4a). The shaft is narrow and straight in dorsal and ventral view, with a rounded base and bifid tip. In lateral view, it is slightly curved from the middle towards the base.

The skull is elongate, with a mean greatest length of the skull (GTL) of 16.29 mm (15.94–17.90 mm), a skull length (SL) of 16.13 mm (15.73–17.79 mm) and a condylocanine length (CCL) of 14.00 mm (13.56–15.94 mm) (Table 2). The mastoid width (MW) is 8.32 mm (8.07–8.50 mm). This slightly exceeds the zygomatic breadth (ZB), which is 8.01 mm (7.79–8.26 mm). In lateral view, the nasal swelling is well-developed, and the sagittal crest is clearly defined particularly on the anterior part of the braincase (Fig. 5a). The anterior median swellings are rounded, with the AMSW 3.07 mm (1.99–4.28 mm) in width. The frontal depression is shallow when viewed from either the side or the top (Fig. 5a). The postorbital constriction (PC) is 2.62 mm (2.40–2.91 mm). The zygomata are narrow with an angular process projecting upwards in the mid-part of the jugal bone (Fig. 5a). The upper canine (C1) is large, about twice the height of the second upper premolar (P4). The crown area of the P4 is about two-thirds that of the C1 (Fig. 6a). The first upper premolar is very small and fully extruded, so that the C1 and P4 are in contact. The upper toothrow length (C–M3) is 5.41 mm (5.12–5.81 mm). The lower toothrow length (c–m3) is 5.67 mm (5.05–6.28 mm) and the mandible length (ML) is 9.64 mm (9.22–10.92 mm) (Table 2). The lower canine (c1) has an elongated postero-basal heel (Fig. 6a). The c1 is twice the height of the second lower premolar (p4). The p4 is rounded and subequal to that of the c1 in crown area. The first lower premolar (p2) is short and only about half the height of (p4) (Fig. 5a).

Echolocation. The echolocation call of *H. kingstonae* sp. nov. is a typical CF-FM signal. In three individuals recorded from Thailand, the frequency of maximum energy (FmaxE), corresponding to the frequency of the constant element (CF), is 142.4 kHz (141.0–143.4 kHz; n=3). In peninsular Malaysia, the FmaxE from Krau Wildlife Reserve is 144.0 kHz (n=1), whereas in Malaysian Borneo, the FmaxE of the bats from the Madai caves was 138.4 kHz (136.6–141.4 kHz; n=5 individuals) for males and 137.7 kHz (137.4–138.2 kHz; n=4 individuals) for females, while the female from Gunung Kinabalu had a FmaxE of 132.3 kHz.

Genetics. The phylogenetic trees based on mitochondrial COI reveal that the new species clusters with *H. kunzi* and *H. bicolor* (Fig. 7), with a genetic distance of 2.3% and 4.9%, respectively (see Appendix 3). Although clustered as a subclade of the new species, the Sabah population is only 0.3% different from the specimens from the Thai-Malay Peninsula (Fig. 7; Appendix 3), and no significant difference in morphology were observed. The new species is not closely related to any of other forms currently referred to *H. cineraceus*. The tree topology based on ND2 and CytB is similar (Fig. 8), as previously noted by Murray *et al.* (2012; 2108). The ND2 and partial CytB sequences of 4 specimens from the island of Palawan deposited in the FMNH as *H. ater* (Esselstyn *et al.*, 2012) belong in the clade of the new species, as sister to the Sabah specimens with less than 1% genetic distance from them. The genetic distances between the new species and *H. kunzi* and *H. bicolor*, are 8.0% and 7.3% based on CytB, and 7.3% and 10.5%, respectively, based on ND2. In addition, these two species are clearly different from the new species in terms of morphology (see comparison section below). Morphologically, the new species is similar to *H. einnaythu* (see comparison section below), which is also present in the region (Douangboubpha *et al.*, 2011; Douangboubpha, 2019) but has a genetic distance of 9.6% and 10.4% based on COI and ND2, respectively.

In addition, this study provides, for the first time, genetic data (as well as echolocation—see below) of *H. einnaythu* from Tanintharyi, Myanmar and Thailand. Besides being closely clustered with *H. kunzi*, *H. bicolor* and *H. kingstonae* sp. nov., it also shares a clade with *H. cf. gentilis* (Fig. 7 & 8).

The samples of *H. cf. cineraceus* and *H. cf. gentilis* appeared to be paraphyletic based on mitochondrial COI analyses (Fig. 7), as well as ND2 and CytB (Fig. 8), and suggest multiple cryptic taxa (Francis *et al.*, 2010; Murray *et al.*, 2012; 2018). However, recent analyses of nuclear markers suggested that they are monophyletic,



FIGURE 3. External appearance, ear and noseleaf of *H. kingstonae* sp. nov.; (a) ♂PSUZC-MM2014.164 (holotype), from Narathiwat, Thailand; (b–c) ♀PSUZC-MM.2014.165, from Yala, Thailand. Not to scale.

and the appearance of multiple mtDNA clades may be explained by historical introgression (Yuzefovic *et al.*, 2021). This is in line with our analyses of external, craniodental and bacular morphology that show no clear distinction between different genetic clades within either *H. cf. cineraceus* or *H. cf. gentilis*. Although neither the type specimen nor any of *H. cineraceus* (sensu stricto) from India were examined, the specimens from Bhutan and north Myanmar (Fig. 1) included in this study agreed morphologically with specimens of *H. cf. cineraceus* from Thailand and elsewhere in SE Asia.

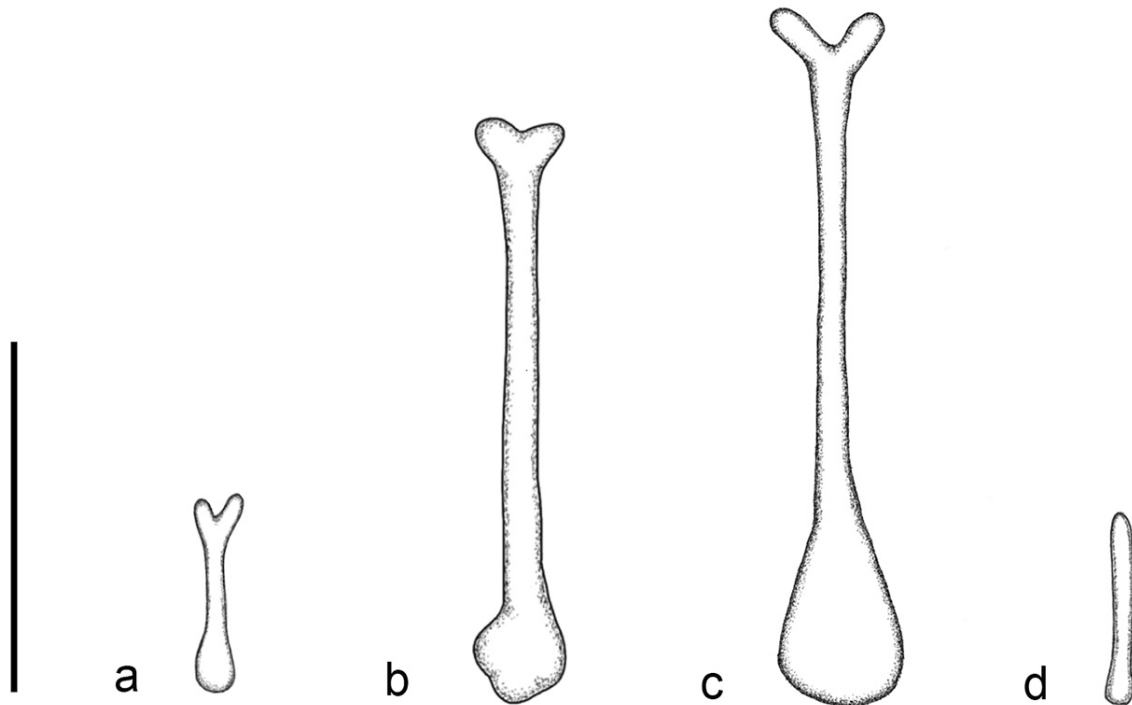


FIGURE 4. Comparison of the baculum between (a) *H. kingstonae* sp. nov., ♂PSUZC-MM2014.164 (holotype), from Narathiwat, Thailand; (b) *H. einnaythu*, ♂PS200120.18, from Phetchaburi, Thailand; (c) *H. cf. cineraceus*, ♂PS200108.13, from Songkhla, Thailand; (d) *H. cf. gentilis*, ♂PSUZC-MM2007.231, from Phetchaburi, Thailand (redrawn from Douangboubpha *et al.*, 2010). Scale=1 mm. Drawing by PW.

Comparison with similar species. *Hipposideros kingstonae* sp. nov., with a mean FA of 39.0 mm and GTL 16.29 mm, is intermediate in size between the smaller *H. cf. cineraceus* (FA 35.3 mm; GTL 15.55 mm) and the larger *H. kunzi* (FA 43.0 mm; GTL 18.05mm), *H. bicolor* (FA 46.3 mm; GTL 18.95 mm) and *H. cf. gentilis* (FA 41.7 mm; GTL 17.82mm) (Tables 1 and 2). However, it can be readily distinguished from these species by the distinct rounded swollen internarial septum (Fig. 9a), which is narrow and parallel-sided in *H. cf. cineraceus* (Fig. 9d), and *H. bicolor* (Fig. 9f), or more or less triangular with a wider base in *H. kunzi* (Fig. 9e). The internarial septum of *H. cf. gentilis* (not illustrated) is less swollen than that of the new species, and it has a distinctly larger ear (mean 21.0 vs 15.0 mm) (see also figure 4e and 4f in Douangboubpha *et al.*, 2010). Acoustically, with a frequency of 141.0–144.0 kHz in the mainland populations and 132.3–138.2 kHz in Borneo, the new species overlaps in FmaxE with *H. kunzi* (mean 142.5 kHz, min–max 135.1–146.7 kHz) (Table 1). However, as mentioned above, they are clearly distinguished by body size and the shape of the internarial septum. As expected, the smaller *H. cf. cineraceus* has an average higher FmaxE (147.9 kHz in Thailand; 149.0 kHz in individuals caught at Madai Caves, Sabah), while the larger *H. bicolor* and *H. cf. gentilis* have a lower FmaxE, 132.0 and 132.8 kHz, respectively (Table 1).

Hipposideros kingstonae sp. nov. most closely resembles *H. einnaythu*, particularly in the shape of the internarial septum (Fig. 9a vs Fig. 9b), forearm length (39.0 vs 40.8 mm) and call frequency (139.0 vs 140.3 kHz) (Table 1). The skull measurements between the two species also overlap considerably, with *H. kingstonae* averaging slightly smaller than *H. einnaythu* in all characters, except the PC that is larger (2.62 vs 2.53 mm, Table 2). However, *H. einnaythu*, has one rudimentary lateral leaflet on each side of the noseleaf, although it can be hardly seen in some individuals, and the baculum of *H. kingstonae* is very small with a distinct bifid tip (Fig. 4a) and only about one-third that of *H. einnaythu* in length (~1.5 mm; Fig. 4b). In addition, as mentioned above, the genetic distance between the two species is 9.6% and 10.4% based on COI and ND2, respectively.

TABLE 1. External measurements (in mm), body mass (in g) and call frequency (FMaxE; in kHz) of *H. kingstonae* **sp. nov.**, *H. einnaythu*, *H. cf. saevus*, *H. cf. cineraceus*, *H. kunzi*, *H. bicolor*, *H. ater*, and *H. cf. gentilis*. See methods for the definition of measurements. Sample size, mean \pm standard deviation (SD) are provided, with min–max in parentheses.

Characters	<i>H. kingstonae</i> sp. nov.		<i>H. einnaythu</i>		<i>H. cf. saevus</i>		<i>H. cf. cineraceus</i>	
	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD
Mass (g)	4	5.8 \pm 0.9 (4.9–7.0)	6	6.1 \pm 0.4 (5.6–6.6)	10	5.1 \pm 0.9 (3.0–6.0)	103	4.1 \pm 0.8 (2.7–6.0)
HB	11	44.8 \pm 2.6 (40.2–49.0)	6	43.3 \pm 1.6 (41.0–45.2)	-	-	85	40.9 \pm 2.8 (34.5–49.0)
FA	11	39.0 \pm 2.1 (35.3–42.6)	7	40.8 \pm 1.1 (39.5–42.2)	7	41.0 \pm 2.9 (36.0–44.3)	108	35.3 \pm 1.5 (32.4–40.0)
E	11	16.2 \pm 1.8 (14.0–18.7)	7	16.1 \pm 1.9 (13.8–19.3)	-	-	93	16.3 \pm 1.4 (13.4–20.2)
Tail	11	26.1 \pm 2.2 (21.5–30.0)	7	26.2 \pm 3.3 (20.0–29.9)	-	-	99	25.0 \pm 2.3 (18.3–29.0)
HF	11	6.3 \pm 0.6 (5.0–7.1)	7	6.1 \pm 0.5 (5.2–7.0)	8	6.4 \pm 0.6 (5.5–7.2)	91	5.3 \pm 0.7 (4.0–7.1)
TIBIA	11	16.7 \pm 0.9 (14.7–17.9)	6	18.5 \pm 1.0 (17.5–20.0)	12	38.6 \pm 1.94 (35.4–43.0)	72	15.2 \pm 0.8 (12.0–17.0)
FmaxE (kHz)	13	139.0 \pm 3.2 (132.3–144.0)	5	140.3 \pm 0.9 (139.0–141.4)	1	142.7	48	147.9 \pm 4.67 (134.8–154.1)

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TABLE 1. (Continued)

Characters	<i>H. kunzi</i>		<i>H. bicolor</i>		<i>H. ater</i>		<i>H. cf. gentilis</i>	
	N	Mean±SD	N	Mean±SD	N	Mean±SD	N	Mean±SD
Mass (g)	38	6.8±1.0 (5.0–9.5)	11	9.1±1.3 (7.5–11.0)	-	-	39	6.1±0.8 (4.9–8.0)
HB	44	49.6±2.8 (44.5–56.0)	12	52.5±2.6 (49.6–56.6)	-	-	49	46.3±3.6 (36.5–53.1)
FA	64	43.0±1.2 (40.4–46.0)	18	46.3±1.6 (42.8–48.8)	9	36.7±1.3 (35.0–38.2)	50	41.7±1.3 (38.4–44.6)
E	59	17.9±1.4 (15.0–22.5)	12	18.7±0.9 (16.8–20.2)	7	15.4±1.4 (13.0–17.2)	50	21.0±1.4 (17.4–24.0)
Tail	59	28.2±2.4 (23.2–33.6)	12	31.4±1.9 (28.4–33.4)	7	22.6±4.3 (18.0–31.0)	50	30.1±1.8 (25.7–35.1)
HF	59	6.7±0.4 (5.7–7.7)	12	6.9±0.5 (6.0–7.9)	7	6.3±0.6 (5.3–7.0)	50	6.7±0.9 (5.1–9.4)
TIBIA	59	18.7±0.8 (17.2–20.9)	12	21.2±0.9 (19.8–22.9)	3	17.1±1.1 (16.4–18.4)	32	18.6±0.9 (17.1–20.2)
FmaxE (kHz)	39	142.5±2.7 (135.1–146.7)	10	132.0±1.9 (129.0–135.0)	-	-	34	132.8±3.8 (127.3–140.2)

TABLE 2. Cranial and dental measurements (in mm) of *H. kingstonae* sp. nov., *H. einnaythu*, *H. cf. cineraceus*, *H. kunzi*, *H. bicolor*, *H. ater*, and *H. cf. gentilis*. See methods for the definition of measurements. Sample size, mean \pm standard deviation (SD) are provided, with min–max in parentheses.

Characters	<i>H. kingstonae</i> sp. nov.		<i>H. einnaythu</i>		<i>H. cf. saevus</i>		<i>H. cf. cineraceus</i>	
	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD
GTL	11	16.29 \pm 0.57 (15.94–17.90)	7	17.16 \pm 0.71 (15.71–17.71)	23	16.96 \pm 0.74 (15.25–18.65)	73	15.55 \pm 0.27 (14.82–16.28)
SL	11	16.13 \pm 0.60 (15.73–17.79)	7	17.04 \pm 0.83 (15.40–17.71)	23	16.74 \pm 0.77 (14.77–18.36)	74	15.48 \pm 0.29 (14.52–16.38)
CBL	11	14.37 \pm 0.67 (13.95–16.30)	7	15.13 \pm 0.60 (13.90–15.64)	22	14.98 \pm 0.90 (12.65–16.98)	73	13.63 \pm 0.38 (12.86–15.83)
CCL	11	14.00 \pm 0.66 (13.56–15.94)	7	14.65 \pm 0.53 (13.57–15.07)	22	14.59 \pm 0.94 (11.77–16.34)	75	13.19 \pm 0.27 (12.56–13.85)
ZB	11	8.01 \pm 0.16 (7.79–8.26)	7	8.30 \pm 0.41 (7.49–8.64)	20	8.23 \pm 0.25 (7.83–8.7)	77	7.40 \pm 0.22 (6.79–7.95)
BB	11	7.49 \pm 0.17 (7.19–7.78)	7	7.92 \pm 0.52 (6.96–8.31)	23	7.65 \pm 0.38 (6.89–7.89)	77	7.07 \pm 0.19 (6.54–7.59)
MW	11	8.32 \pm 0.12 (8.07–8.50)	7	8.61 \pm 0.20 (8.32–8.75)	22	8.51 \pm 0.17 (8.18–8.87)	78	7.79 \pm 0.17 (7.45–8.26)
PC	11	2.62 \pm 0.14 (2.40–2.91)	7	2.53 \pm 0.19 (2.28–2.87)	23	2.76 \pm 0.22 (2.52–3.44)	78	2.57 \pm 0.12 (2.33–2.86)
C-M3	11	5.41 \pm 0.18 (5.12–5.81)	7	5.69 \pm 0.32 (5.05–5.99)	23	5.66 \pm 0.28 (4.71–6.17)	75	5.05 \pm 0.15 (4.65–5.43)
C1-C1	11	3.22 \pm 0.20 (2.88–3.52)	7	3.38 \pm 0.22 (2.95–3.54)	23	3.00 \pm 0.27 (2.05–3.46)	74	2.71 \pm 0.16 (2.25–3.14)
M3-M3	11	5.54 \pm 0.15 (5.32–5.83)	7	5.77 \pm 0.31 (5.20–6.06)	7	5.70 \pm 0.33 (5.19–6.41)	78	5.01 \pm 0.19 (4.59–5.56)
c-m3	11	5.67 \pm 0.32 (5.05–6.28)	7	6.02 \pm 0.37 (5.26–6.33)	23	5.96 \pm 0.31 (5.07–6.61)	77	5.28 \pm 0.23 (4.43–5.88)
ML	11	9.64 \pm 0.45 (9.22–10.92)	7	10.34 \pm 0.60 (9.17–10.83)	19	10.40 \pm 0.54 (8.98–11.49)	75	8.95 \pm 0.27 (8.06–9.70)
ALSW	11	4.29 \pm 0.13 (4.04–4.43)	7	4.37 \pm 0.16 (4.12–4.61)	23	4.27 \pm 0.23 (3.80–4.59)	79	3.96 \pm 0.12 (3.64–4.31)
AMSW	10	3.07 \pm 1.04 (1.99–4.28)	7	2.47 \pm 0.12 (2.16–3.25)	19	2.61 \pm 0.27 (2.29–3.20)	79	2.40 \pm 0.29 (2.01–3.80)

TABLE 2. (Continued)

Characters	<i>H. kunzi</i>		<i>H. bicolor</i>		<i>H. ater</i>		<i>H. cf. gentilis</i>	
	N	Mean±SD	N	Mean±SD	N	Mean±SD	N	Mean±SD
GTL	53	18.05±0.31 (17.28–18.76)	19	18.95±0.25 (18.53–19.54)	14	16.20±0.31 (15.60–16.76)	47	17.82±0.46 (16.73–18.77)
SL	-	-	6	18.38±0.16 (18.12–18.55)	14	15.87±0.31 (15.25–16.39)	47	17.80±0.46 (16.65–18.77)
CBL	53	15.66±0.27 (15.20–16.33)	19	16.62±0.26 (16.26–17.20)	13	14.20±0.33 (13.47–14.73)	47	15.88±0.45 (15.01–16.72)
CCL	54	15.39±0.26 (14.95–16.04)	19	16.24±0.22 (15.98–16.75)	14	13.72±0.29 (13.08–14.28)	48	15.49±0.43 (14.60–16.26)
ZB	54	9.10±0.17 (8.63–9.60)	19	9.19±0.25 (8.64–9.73)	13	8.08±0.16 (7.86–8.37)	48	8.95±0.24 (8.33–9.38)
BB	54	8.23±0.20 (7.70–8.61)	19	8.48±0.25 (8.05–9.08)	14	7.05±0.16 (6.84–7.54)	48	8.33±0.29 (7.55–8.78)
MW	54	9.05±0.12 (8.79–9.30)	19	9.29±0.14 (9.12–9.62)	13	8.32±0.14 (8.10–8.58)	48	8.95±0.18 (8.62–9.35)
PC	54	2.68±0.12 (2.47–3.05)	19	2.95±0.10 (2.81–3.17)	13	2.48±0.12 (2.30–2.74)	48	2.70±0.13 (2.38–2.89)
C-M3	55	6.14±0.12 (5.90–6.46)	19	6.41±0.10 (6.19–6.71)	15	5.29±0.20 (4.72–5.60)	49	6.11±0.20 (5.71–6.46)
C1-C1	55	3.64±0.2 (3.28–3.89)	19	3.56±0.17 (3.24–3.94)	14	3.20±0.16 (2.91–3.38)	49	3.39±0.15 (3.05–3.64)
M3-M3	55	6.16±0.17 (5.38–6.49)	19	6.14±0.13 (5.84–6.37)	15	5.48±0.19 (5.23–5.85)	49	6.10±0.23 (5.66–6.69)
c-m3	54	6.58±0.13 (6.23–6.91)	19	6.83±0.11 (6.65–7.10)	15	5.73±0.22 (5.36–6.09)	49	6.50±0.25 (5.92–7.11)
ML	54	11.28±0.21 (10.72–11.82)	19	11.76±0.20 (11.46–12.17)	13	9.76±0.24 (9.45–10.16)	49	10.93±0.33 (10.18–11.76)
ALSW	54	4.47±0.10 (4.13–4.67)	19	4.79±0.10 (4.56–4.98)	14	4.11±0.08 (3.96–4.28)	48	4.54±0.10 (4.23–4.85)
AMSW	-	-	-	-	12	2.66±0.24 (2.37–3.08)	48	2.41±0.22 (2.05–2.85)

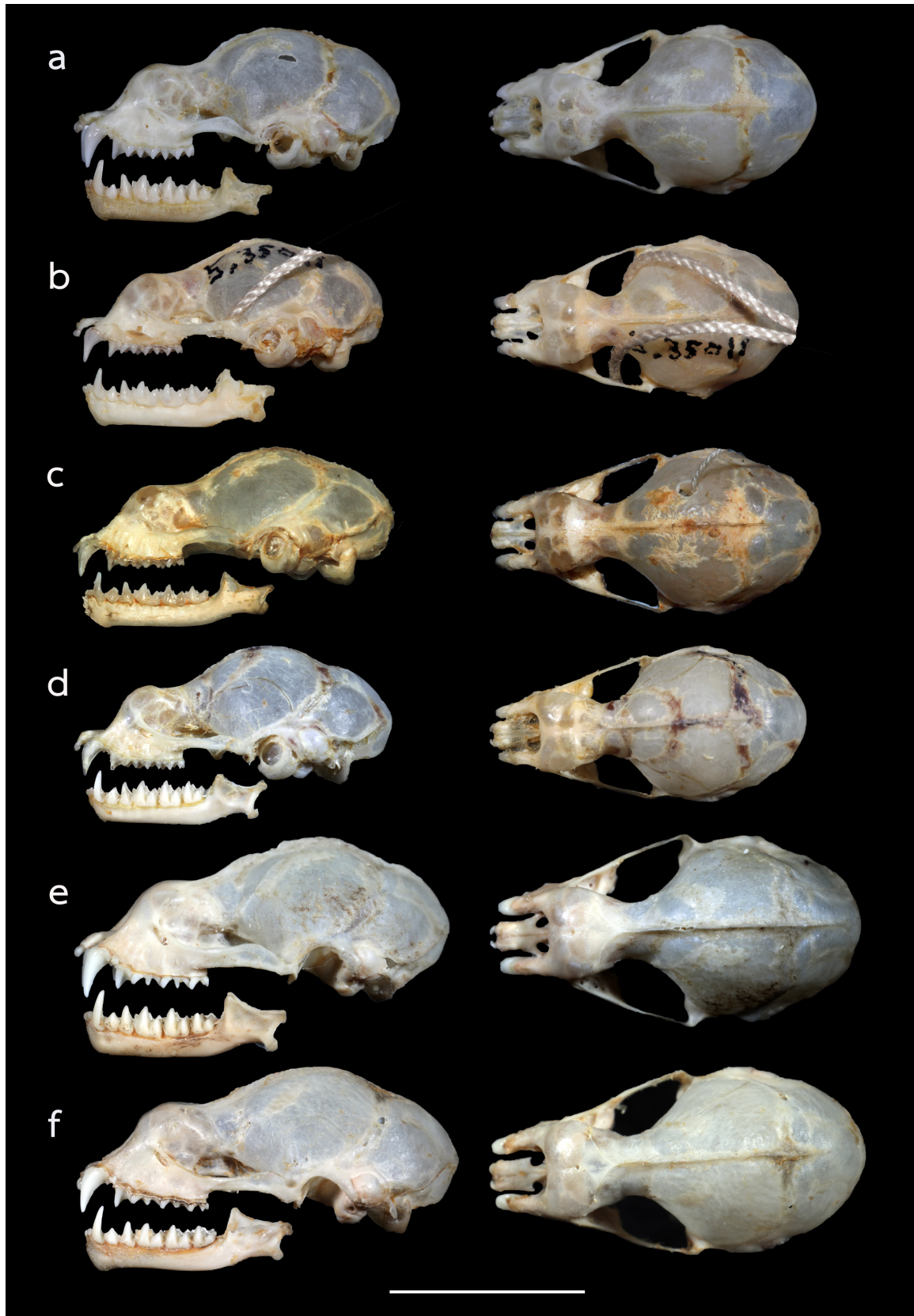


FIGURE 5. Lateral views of skull and mandible (left) and dorsal view (right) of the skull of (a) *H. kingstonae* sp. nov., ♂PSUZC-MM2014.164 (holotype), from Narathiwat, Thailand; (b) *H. einnaythu*, ♀HZM.5.35011 (holotype), from Rakhine, Myanmar; (c) *H. cf. saevus*, ♂BMNH.99.12.4.11 (holotype), from Kei Island, Indonesia; (d) *H. cf. cineraceus*, ♂PSUZC-MM2006.126, from Songkhla, Thailand; (e) *H. kunzi*, ♂PSUZC-MM2005.75, from Narathiwat, Thailand; and (f) *H. bicolor*, ♂PSUZC-MM2005.82, from Narathiwat, Thailand. Scale=10 mm.

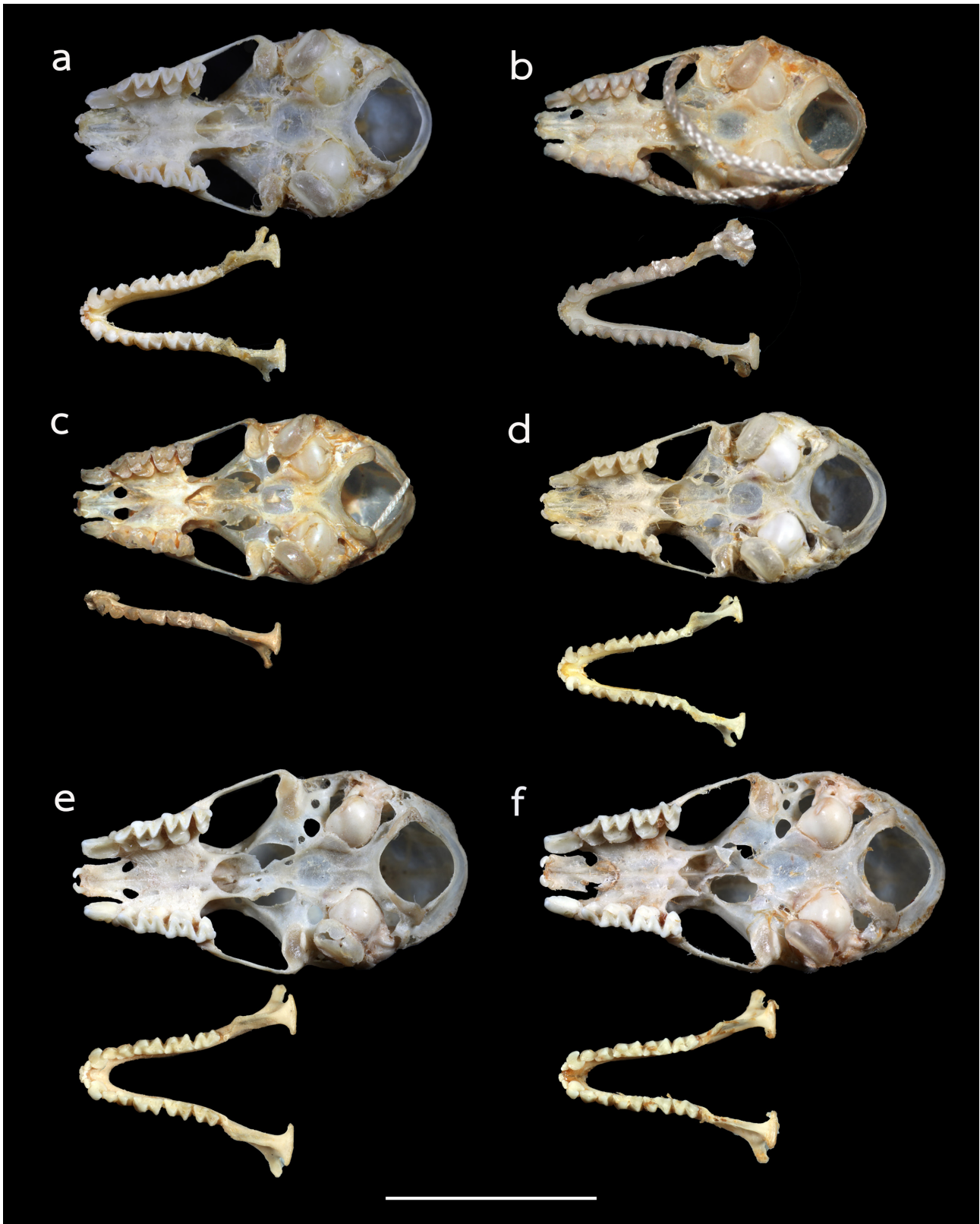


FIGURE 6. Occlusal view of skull and mandible of (a) *Hipposideros kingstonae* **sp. nov.** ♂PSUZC-MM2014.164 (holotype), from Narathiwat, Thailand; (b) *H. einnaythu*, ♀HZM.5.35011 (holotype), from Rakhine, Myanmar; (c) *H. cf. saevus*, ♂BMNH.99.12.4.11 (holotype), from Kei Island, Indonesia; (d) *H. cf. cineraceus*, ♂PSUZC-MM2006.126, from Songkhla, Thailand; (e) *H. kunzi*, ♂PSUZC-MM2005.75, from Narathiwat, Thailand; (f) *H. bicolor*, ♂PSUZC-MM2005.82, from Narathiwat, Thailand. Scale=10 mm.

The availability of recently collected specimens from Thailand and Myanmar allowed for a more comprehensive comparison of both morphology (including bacula) and genetics between *einnaythu* and *ater* (sensu stricto)—which also support the specific distinction of *kingstonae*. The shape of the internarial septum of *ater* is triangular, and the baculum is rather straight, ~1.7 mm in length, without prongs at the tip (see figure 2a and 4a in Douangboubpha *et al.*, 2011).

As *H. ater* (sensu stricto) is currently believed to be restricted to India and Sri Lanka (Douangboubpha *et al.*, 2011), while the taxon *antricola* from the Philippines is most likely quite distinct (Simmons and Cirranello, 2022), the identity of specimens from Indonesia and Sabah (Hill and Francis, 1984) referred to ‘*H. ater*’ and ‘*H. cf. ater*’ is uncertain. The internarial septum of specimens from Java and Sabah (Fig. 9c) is similar to that of *ater* from India but the external and cranial measurements are larger (Table 1 and 2). It is hereby provisionally assigned to ‘*H. cf. saevus* K. Andersen, 1918’. Although a taxonomic revision is needed, nonetheless, it differs from *kingstonae* in the shape of the internarial septum (Fig. 9a vs 9c) and in the shape of the skull.

In the skull, *kingstonae* has well-developed nasal swellings, with a shallow depression behind (Fig. 5a). However, the frontal depression of *einnaythu* is more pronounced, deeper with a well-defined supraorbital ridge (Fig. 5b). In contrast, this part is flat or slight curved upward in the specimens of *H. cf. saevus* (Fig. 5c).

The combination of the forearm length (FA) together with call frequency (FmaxE) can be very useful for provisionally identifying *kingstonae* from other species (Fig. 10). The biplot shows clear groupings, particularly between the new species and smaller species (*H. cf. cineraceus*) and larger species (*H. kunzi*, *H. bicolor* and *H. cf. gentilis*) (Fig. 10). The Principal Components Analysis (PCA) based on 14 cranial and dental measurements of 56 specimens also shows the same pattern of groupings (Fig. 11) and the new species can be distinguished from the species overlapped in size (*H. einnaythu*, *H. ater* and *H. cf. saevus*) by the combination of characters described above.

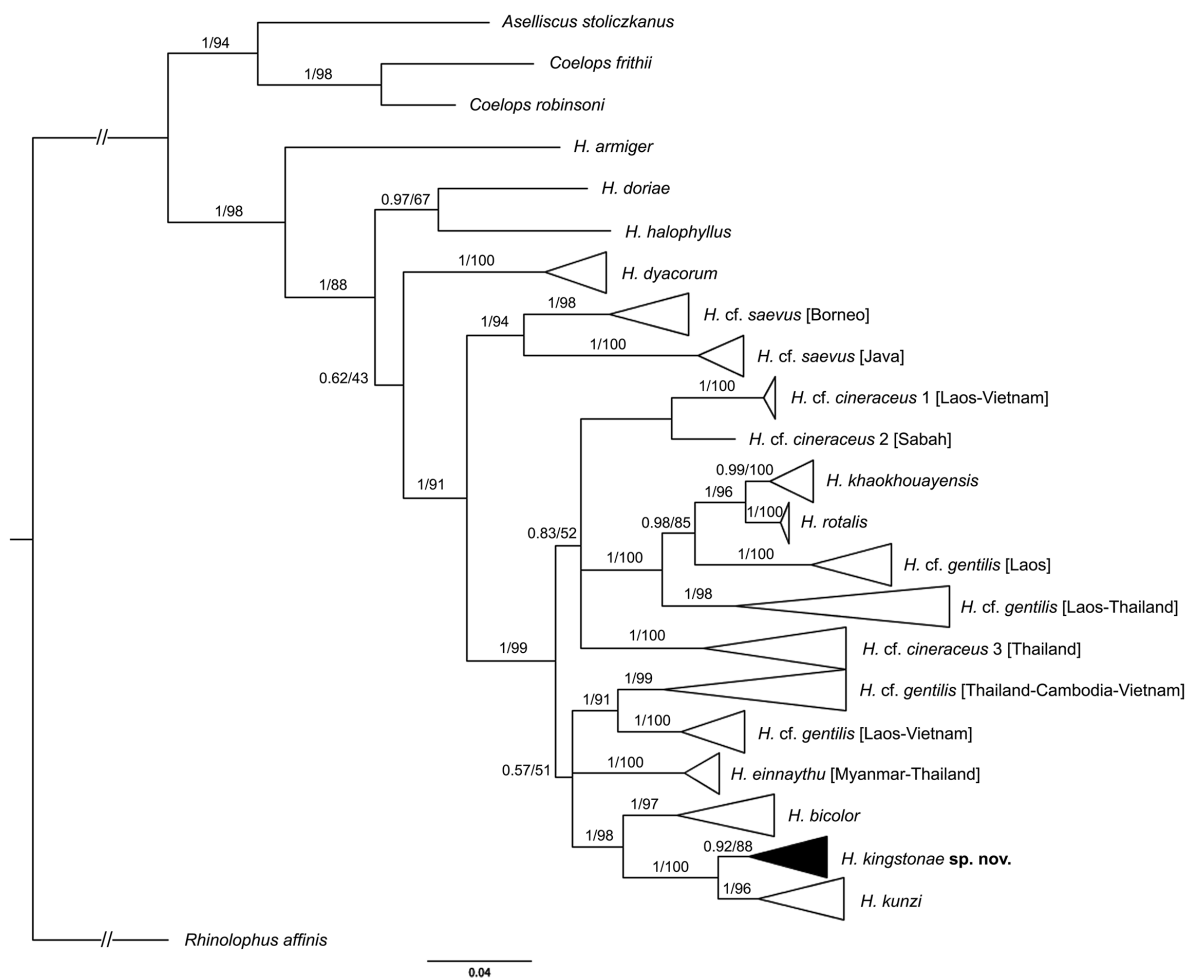


FIGURE 7. Phylogenetic tree based on 195 mitochondrial COI sequences (653 bp) of *Hipposideros* spp. with *Rhinolophus affinis* as an outgroup. The numbers shown on each branch represent Bayesian posterior probability, followed by maximum likelihood bootstrap support values. List of samples used is in Appendix 2.

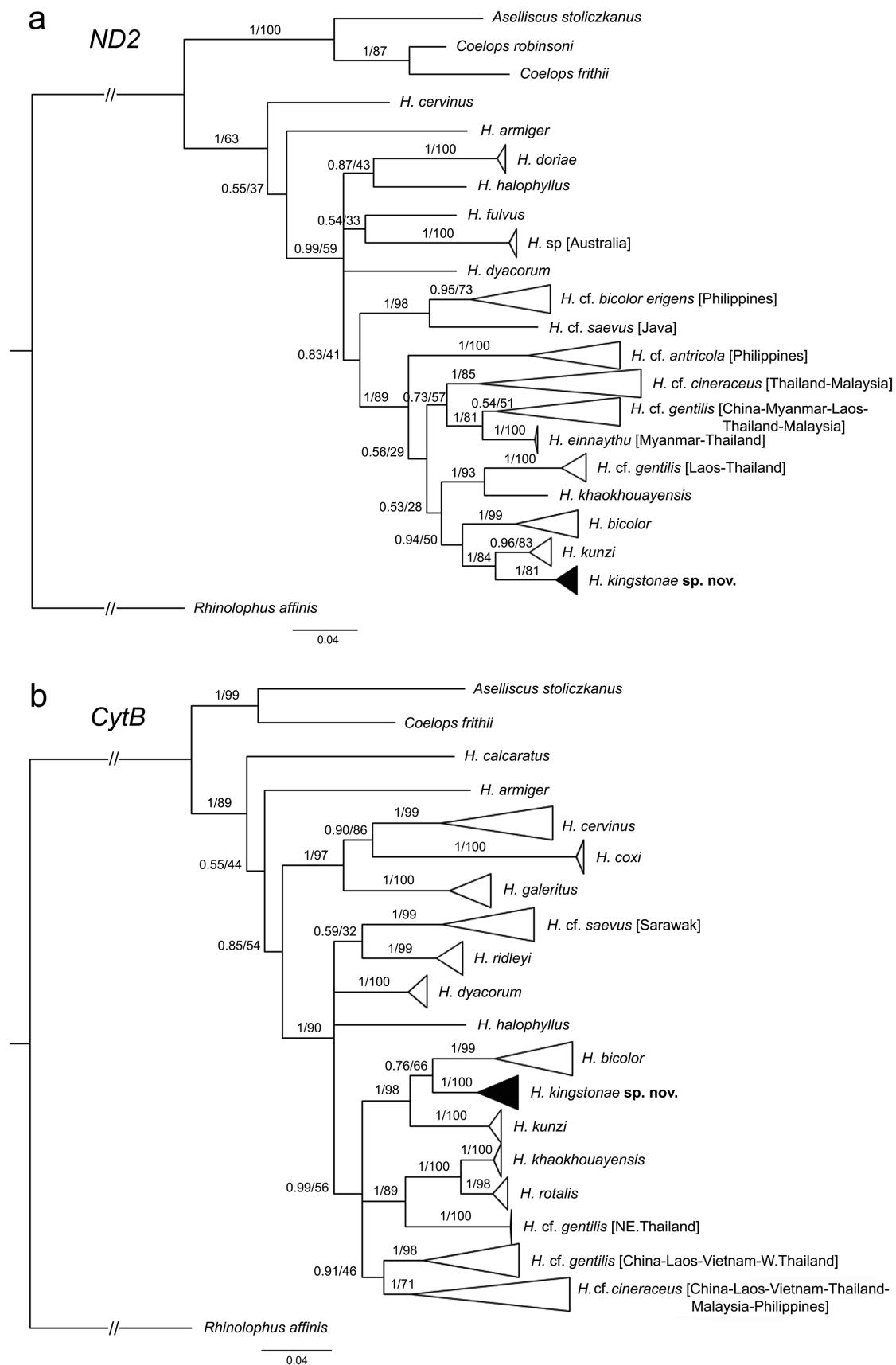


FIGURE 8. Phylogenetic trees based on (a) 146 mitochondrial ND2 sequences (442 bp) and (b) 111 CytB sequences (899 bp) of *Hipposideros* spp. The numbers shown on each branch represent Bayesian posterior probability, followed by maximum likelihood bootstrap support values. List of samples used is in Appendix 2.

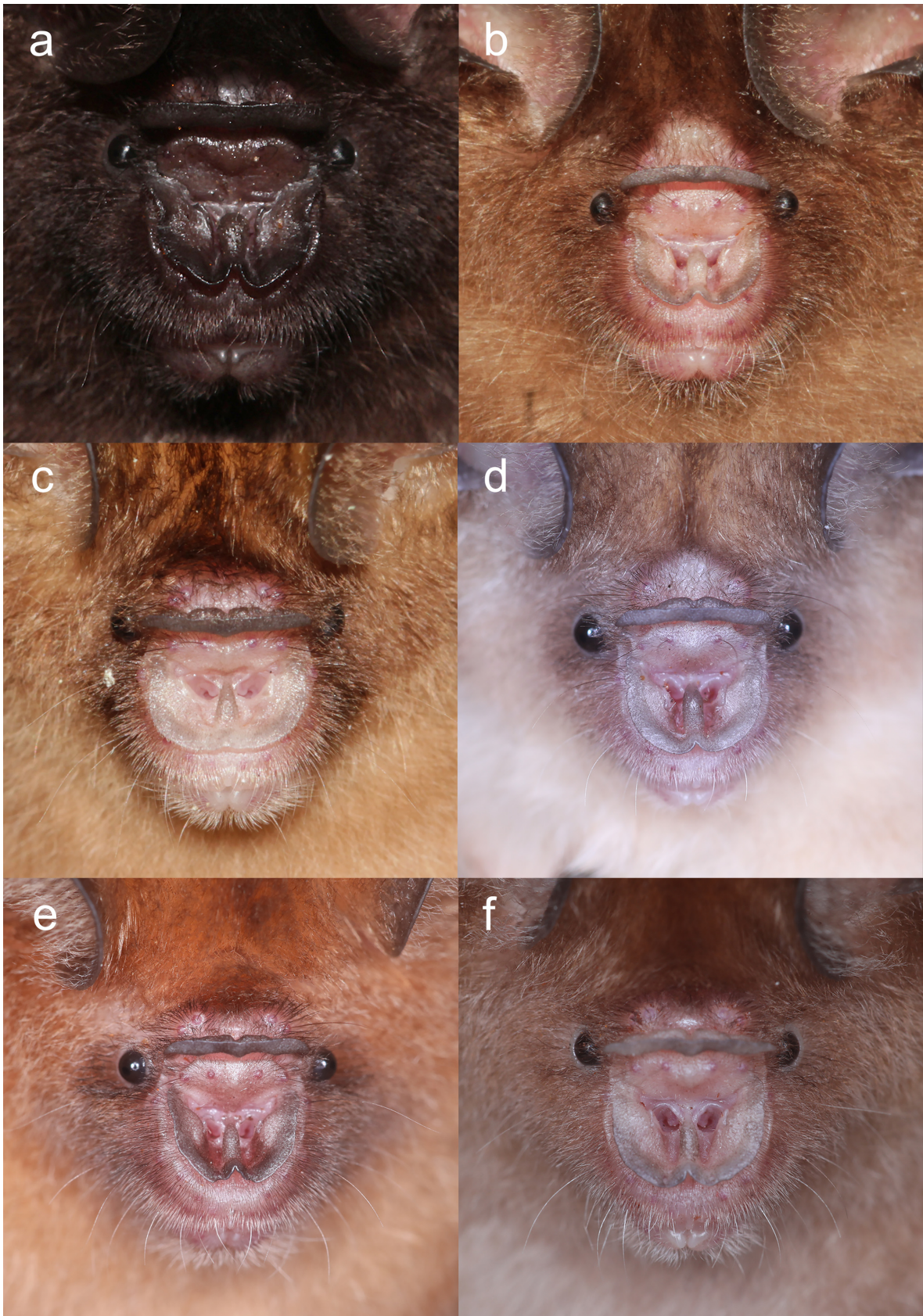


FIGURE 9. Comparison of noseleaf between (a) *H. kingstonae* sp. nov., ♂PSUZC-MM2014.164 (holotype), from Narathiwat, Thailand; (b) *H. einmaythu*, ♂PS150305.11, from Tanintharyi, Myanmar; (c) *H. cf. saevus*, from West Java, Indonesia; (d) *H. cf. cineraceus*, ♂PS180409.3, from Songkhla, Thailand; (e) *H. kunzi*, ♀PS180613.4, from Narathiwat, Thailand; and (f) *H. bicolor*, ♀PS180613.8, from Narathiwat, Thailand. Photographs by PS.

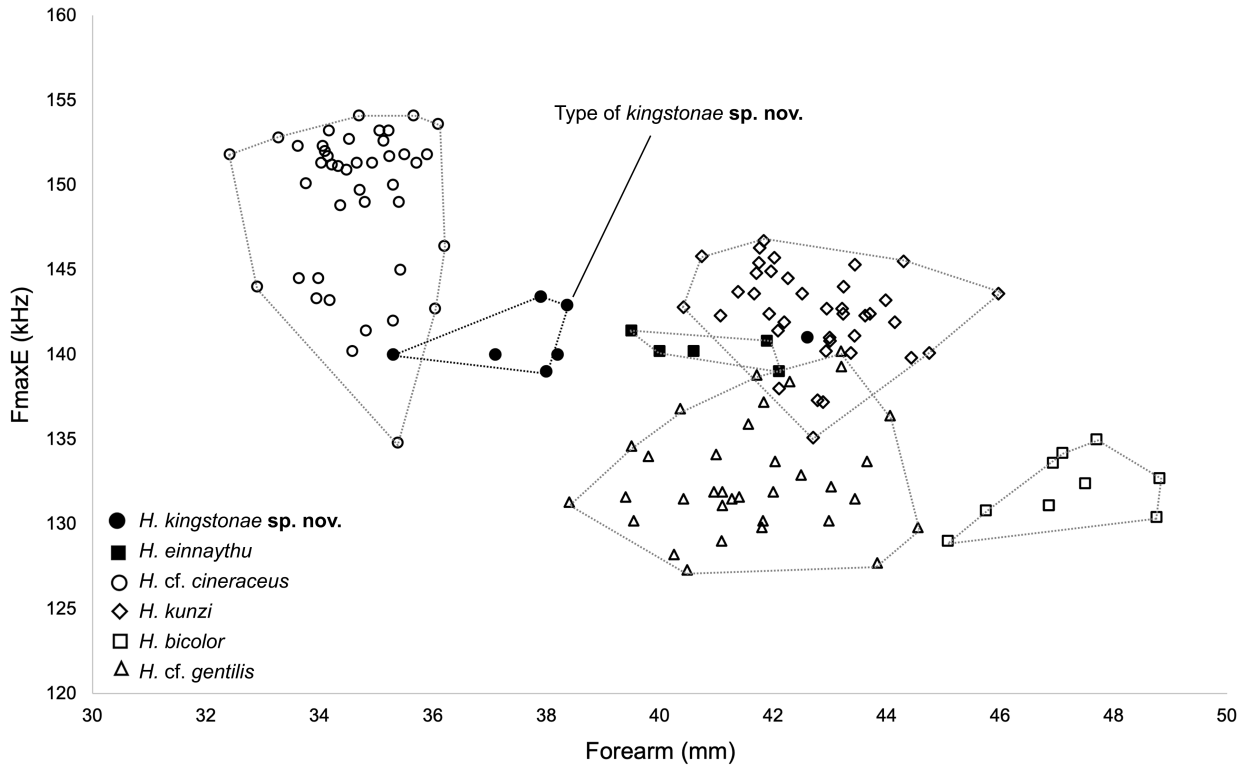


FIGURE 10. Biplot between forearm length (FA) and echolocation frequency (FmaxE) of *H. kingstonae sp. nov.* (dots), *H. einnaythu* (black squares), *H. cf. cineraceus* (open circles), *H. kunzi* (diamonds), *H. bicolor* (squares) and *H. cf. gentilis* (triangles).

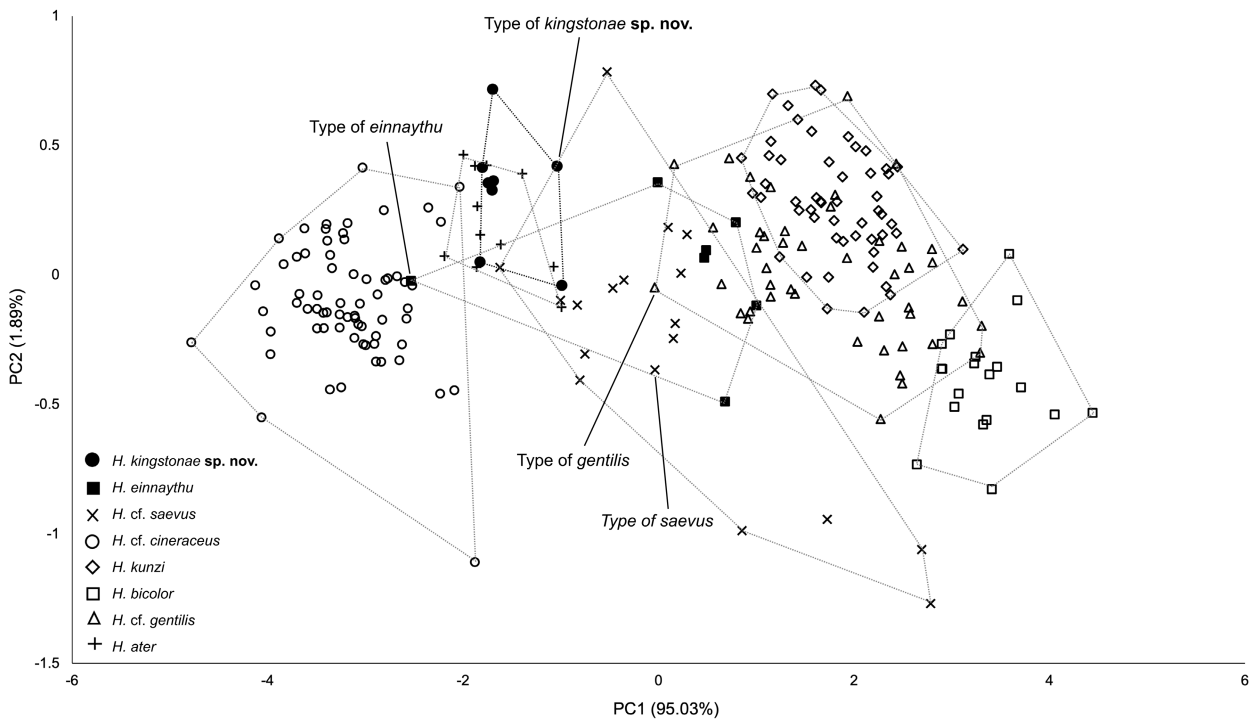


FIGURE 11. Principal component analysis of 11 cranial and dental characters of *H. kingstonae sp. nov.* (dots), *H. einnaythu* (black squares), *H. cf. saevus* (cross symbols), *H. cf. cineraceus* (circles), *H. kunzi* (diamonds), *H. bicolor* (squares), *H. cf. gentilis* (triangles) and *H. ater* (plus symbols). Loading scores are presented in Table 3.

Ecology, distribution and conservation notes. *Hipposideros kingstonae* **sp. nov.** is here documented from five localities, two in the deep south of peninsular Thailand, one in peninsular Malaysia, and two in the Malaysian state of Sabah, on the Borneo island (Fig. 1). The morphology of the noseleaf matches the description of “*H. cineraceus*” in Payne and Francis (1985) suggesting that many previous records from Borneo (including those from Segarong caves and Baturong caves mentioned by Hill and Francis 1984) likely represent the new species. In addition, published DNA sequences from the Philippine island of Palawan are genetically very close to those from Sabah, suggesting that the species is also present on that island, which is so geographically and biogeographically close to Borneo that it was almost connected during the Last Glacial Maximum (Piper *et al.*, 2011). The type series of the new species is from lowland primary rainforest at an elevation between 22 and 170 m a.s.l. In Sabah, 9 individuals of the species were captured in the understory of lowland rainforest near the large cave system of Madai, at 110 m a.s.l. presumably emerging from the caves along with specimens of *H. cf. cineraceus*. One specimen was captured inside the lower montane forest on the slopes of Gunung Kinabalu at 1600 m a.s.l., suggesting it is a forest-restricted bat that forages in forest gaps in the understory or near the edge of the forest. The roosting sites of the species are not known, but several individuals in Sabah were caught near large limestone caves, suggesting it likely roosts in the caves. However, elsewhere, individuals were caught far from known caves and may roost in tree hollows. The current threats to the new species are not known, although loss of habitat due to agriculture, including tree plantations, is a major concern in much of the Thai-Malay Peninsula and Borneo.

TABLE 3. Factor loading scores of the first two components based on cranial and dental measurements of the PCA in Figure 10.

Cranial and Dental characters	PC 1	PC 2
GTL	0.503	-0.174
CBL	0.452	-0.473
CCL	0.465	-0.278
ZB	0.306	0.453
BB	0.241	0.269
MW	0.231	0.268
PC	0.039	-0.070
C-M3	0.212	0.136
C1-C1	0.145	0.369
M3-M3	0.205	0.399
ALSW	0.111	0.036
Eigenvalue	5.94	0.12
% variance	95.03	1.89

Acknowledgements

We would like to thank the Department of National Park, Wildlife and Plant Conservation, Thailand, and the Department of Wildlife and National Parks Peninsular Malaysia (DWNP), Malaysia Economic Planning Unit (UPE: 40/200/19/2781) for the research permits to PS and JS, respectively. We give special thanks to the staff of Halabala Wildlife Research Station for their support and collaboration. We are indebted to Wieslaw Bogdanowicz for his support of the molecular work at the beginning of the study. At PSU, we thank the director, Chutamas Satasook, and staff of Princess Maha Chakri Sirindhorn Natural History Museum, as well as staff of the Division of Biological Science, Faculty of Science, Prince of Songkla University. We thank Sai Sein Lin Oo, Zin Mar Myo, Moe Moe Aung of the Department of Zoology, University of Mandalay, Khin Swe Oo of Myeik University, and Aung Lin and staff of Fauna & Flora International (FFI)—Myanmar Programme, for their help with fieldwork and specimens. We are grateful to Ibnu Maryanto of the Indonesian Institute of Science (LIPI) and Roberto Portela-Miguez of the Natural History Museum, London, UK, and Tshering Dendup from Bhutan, for their permission to examine specimens and share the data. We would like to thank Pachara Promnopwong, Najthamas Mekmuang, Awatsaya Pimsai, Abdulloh Samoh and Sakiya Morlor for their help in field and laboratory works. Bat research in Krau Wildlife Reserve,

Malaysia was supported by National Science Foundation (NSF) USA through Boston University and Texas Tech University. JS was supported by National Science Fund - USA through Texas Tech University (ST-2019-006) and Malaysia Ministry of Higher Education (FRGS/1/2020/WAB11/UKM/02/3). FAAK thank the Economic Planning Unit of the Malaysian Prime Minister's Department (UPE: 40/200/19/1466), Department of Wildlife and National Parks (JPHL&TN(IP):60-4/1.13 Jld 4 (64)), Universiti Malaysia Sarawak, Sarawak Forestry Corporation, Sarawak Forestry Department (NPW.907.4.2-112), and Sabah Parks (TS/PTD/5/4 Jld. 24 (76)) for permission to conduct wildlife research in Malaysia. FAAK was supported by the Malaysian Ministry of Higher Education (FRGS/1/2019/WAB13/UNIMAS/03/2). PW thanks the Development and Promotion of Science and Technology Talents Project (DPST) for their financial support. The bat research of PS was supported by Thailand Research Fund (TRF), grant number DBG6180028, and the Plant Genetic Conservation Project under the initiative of Her Royal Highness Princess Maha Chakri Sirindhorn (RSPG), grant numbers SCI6401002 and SCI600089S.

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<https://doi.org/10.3390/d13050218>

APPENDIX 1. List of specimens examined in this study.

- H. kingstonae* sp. nov.—*Thailand*: ♂PSUZC-MM2014.164 (holotype), ♀PSUZC-MM2022.1, ♂PSUZC-MM2022.2, Phru To Daeng, Narathiwat; ♀PSUZC-MM2014.165, Hala Forest, Yala.—*Malaysia*: ♀TK020622.1, ♂DWNP-M-1996-07-29-05653, ♂DWNP-M-1996-05-12-05654, Krau Wildlife Reserve, Pahang. ♀EBD 23563, ♀EBD 23565, ♀EBD23566, ♂EBD 23560, ♂EBD 23561, ♂EBD 23564, Madai Cave, Sabah. ♀EBD 23821, Gunung Kinabalu National Park.
- H. einnaythu*—*Myanmar*: ♀HZM.5.35011 (holotype), Rakhine; ♀PS150305.1, ♀PS150305.9, ♂PS150305.11, ♂PS150305.15, Tharabwin; ♀PS150309.3, Lenya. —*Thailand*: ♂PS200121.4, Kaeng Krachan National Park, Phetchaburi.
- H. cf. saevus*—*Indonesia*: ♂BMNH.99.12.4.11 (holotype), Kai (=Kei) Island. ♀BMNH37837, West Sumatra; ♀BMNH219391, Badangkaia, Sulawesi; ♂BMNH219398, Gimpoe or Bada, Sulawesi; (unknown sex) MZB M21094, (unknown sex) MZB M21108, Lombok, West Nusa Tenggara; ♂MZB M22927, ♀MZB M22945, ♀MZB M22946, Kakenauwe Forest, Sulawesi; ♂MZB M22938, Kendari, Sulawesi; ♂MZB M24093, ♂MZB M24094, Goa Rumbia, Sulawesi; ♀MZB M28524, Java Timur; ♂MZB M21108, Java.
- H. ater*—*India*: ♂HZM.2.28189, ♂HZM.2.39966, ♀HZM.3.28190, ♀HZM.10.39959, ♀HZM.12.40208, ♀HZM.13.40211, Tamil Nadu; ♂HZM.6.35498, Katchal Island, Nicobar Islands.—*Sri Lanka*: ♀BMNH277245, Rattota; ♀BMNH122163; ♀BMNH277244, ♀BMNH.66.5221, (unknown sex) BMNH.13.2.10.16; ♂BMNH.21.1.17.45; ♂BMNH.21.1.17.54; ♂BMNH.53.7.19.4; ♀BMNH.66.5524, exact locality not known.
- H. cf. cineraceus*—*Laos*: ♀ROM MAM114099, ♂ROM MAM 110559, Attapeu; ♂CMF970524-98, Champassak; ♂HNNH2005.82.48, ♀SEN88025, Khammouane; ♂ROMMAM118430, ♀ROMMAM118431, ♂ROM118043, Vientiane. —*Thailand*: ♀PS201130.1, Chiang Dao, Chiang Mai; ♀PSUZC-MM2006.72, ♀PSUZC-MM2006.73, ♂PSUZC-MM2006.74, ♂PSUZC-MM2006.75, ♂PSUZC-MM2006.76, ♂PSUZC-MM2006.80, ♂PSUZC-MM2006.81, Pha Dang Cave, Chiang

Mai; ♀PSUZYC-MM2005.39, East Thung Yai Wildlife Sanctuary, Tak; ♂PSUZYC-MM2007.192, Lub Lae Cave, Uthai Thani; ♂PSUZYC-MM2008.84, Huai Kha Khaeng, Uthai Thani; ♀PSUZYC-MM2007.184, Khao Singto, Sa Kao; ♂PS211209.4, ♀PS211209.5, ♀PS211209.18, Mahidol University, Kanchanaburi; ♂PS200120.25, Ban Krang, Petchaburi; ♀PSUZYC-MM2007.185, ♂PSUZYC-MM2007.186, ♂PSUZYC-MM2007.187, ♀PSUZYC-MM2007.188, ♀PSUZYC-MM2007.189, ♂PSUZYC-MM2007.190, Khao Don Dueng, Lopburi; ♀PSUZYC-MM2007.23, ♀PSUZYC-MM2007.191, ♀PSUZYC-MM2007.193, Khao Bin Cave, Ratchaburi; ♂PSUZYC-MM2007.9, Silawan Cave, Chumphon; ♂PSUZYC-MM2006.69, ♂PSUZYC-MM2006.84, ♀PSUZYC-MM2006.85, ♀PSUZYC-MM2006.86, ♂PSUZYC-MM2006.88, ♀PSUZYC-MM2006.89, Khao Kram Cave, Chumphon; ♂PSUZYC-MM2007.10, Pra Kayang Cave, Ranong; ♀PS211005.2, Rajjaprabha Dam, Surat Thani; ♂PSUZYC-MM2008.98, Lampi Waterfall, Phang Nga; ♀PSUZYC-MM2008.86, ♂PSUZYC-MM2008.87, ♀PSUZYC-MM2006.16, ♀PSUZYC-MM2006.17, ♀PSUZYC-MM2006.18, Surin Island, Phang Nga; ♀PSUZYC-MM2008.85, Thanbok Koranee National Park, Krabi; ♀PSUZYC-MM2007.8, Khao Chong, Trang; ♂PS190513.2, KhaoPu KhaoYa National Park, Phatthalung; ♂PSUZYC-MM2006.125, ♂PSUZYC-MM2006.126, Ton Nga Chang Wildlife Sanctuary, Songkhla; ♀PSUZYC-MM2005.63, ♀PSUZYC-MM2006.10, ♀PSUZYC-MM2006.144, Khao Rak Kiat Cave, Songkhla; ♀PSUZYC-MM2007.171, ♀PSUZYC-MM2007.172, ♀PSUZYC-MM2007.173, ♀PSUZYC-MM2007.174, ♂PSUZYC-MM2007.175, Khao Noi Cave, Songkhla; ♀PSUZYC-MM2007.194, Rattaphum, Songkhla; ♀PS190311.1, Sabayoi, Songkhla; ♀PS210520.1, Tan Khiri, Sabayoi, Songkhla; ♂PS210603.1, Srisorn Cave, Songkhla; ♀PSUZYC-MM2008.100, ♂PSUZYC-MM2008.120, ♂PSUZYC-MM2009.27, ♂PSUZYC-MM2005.62, ♂PSUZYC-MM2007.177, ♂PSUZYC-MM2007.178, ♂PSUZYC-MM2007.179, ♀PSUZYC-MM2007.180, ♂PSUZYC-MM2007.181, ♀PSUZYC-MM2007.182, Tarutao Island, Satun; ♂PSUZYC-MM2005.76, Sirindhorn Waterfall, Narathiwat. —*Malaysia*: (unknown sex) BMNH.60.3.19.1396, Penang; ♀BMNH.66.4074, Kuala Lumpur; ♀SEN83830, Temengor Forest Reserve; ♂BMNH.83.341, ♂BMNH.83.342, ♀BMNH.83.344, Segarong Cave, Sabah; ♀EBD 23562, Madai Cave, Sabah. —*Indonesia*: (unknown sex) BMNH.10.4.5.150, Bandjarmasin.

H. kunzi—*Thailand*: ♀PSUZYC-MM2007.227, ♂PSUZYC-MM2007.228, ♂PSUZYC-MM2007.229, Khao Plu Cave, Chumphon; ♂PSUZYC-MM2008.90, ♂PS080627.1, ♂PS080627.14, ♂PS080627.21, ♂PS080627.22, Koh Mai Pai, Phang Nga; ♀PSUZYC-MM2007.355, Khao Nan, Nakhon Si Thammarat; ♀PSUZYC-MM2006.37, ♂PSUZYC-MM 2006.38, Sangphet Cave, Krabi; ♀PSUZYC-MM2006.39, ♂PSUZYC-MM2006.40, Khao Kanabnam, Krabi; ♂PSUZYC-MM2008.49, ♂PSUZYC-MM2008.50, ♂PS080326.4, Thanbok Koranee National Park, Krabi; ♂PS190513.3, KhaoPu KhaoYa National Park, Phatthalung; ♂PSUZYC-MM2007.353, ♂PSUZYC-MM2007.354, Khao Chong, Trang; ♂PSUZYC-MM2006.68, ♂PSUZYC-MM2006.197, Rad Cave, Trang; ♂PSUZYC-MM2008.101, ♀PSUZYC-MM2008.102, Ton Nga Chang, Songkhla; ♂PSUZYC-MM2006.32, ♂PSUZYC-MM2006.48, ♀PSUZYC-MM2006.49, ♂PSUZYC-MM2006.50, ♀PSUZYC-MM2006.51, Boripat Waterfall, Songkhla; ♀PSUZYC-MM2006.65, ♂PSUZYC-MM2006.67, ♂PSUZYC-MM2006.194, ♀PSUZYC-MM2006.195, ♀PSUZYC-MM2006.198, ♀PSUZYC-MM2006.199, Khao Noi Cave, Songkhla; ♂PSUZYC-MM2007.235, Khao Rub Chang, Songkhla; ♀PSUZYC-MM2007.205, Ton Making Waterfall, Songkhla; ♀PSUZYC-MM2008.39, ♀PSUZYC-MM2008.43, ♂PSUZYC-MM2005.73, ♂PSUZYC-MM2007.218, ♀PSUZYC-MM2007.219, ♂PSUZYC-MM2007.220, ♀PSUZYC-MM2007.221, Tarutao Island, Satun; ♀PSUZYC-MM2006.20, ♂PSUZYC-MM2006.21, Wang Saithong Waterfall, Satun; ♀PSUZYC-MM2008.12, ♂PSUZYC-MM2008.13, ♀PSUZYC-MM2008.14, ♀PSUZYC-MM2008.15, ♂PSUZYC-MM2008.17, ♂PSUZYC-MM2008.24, ♀PSUZYC-MM2008.26, ♀PSUZYC-MM2008.28, ♂PSUZYC-MM2008.32, Kong Ka lot Cave, Satun; ♀PSUZYC-MM2008.4, ♂PSUZYC-MM2008.8, ♂PSUZYC-MM2008.20, Chet Kot Cave, Satun; ♀PSUZYC-MM2008.105, Preta Island National Park, Satun; ♂PSUZYC-MM2005.42, ♀PSUZYC-MM2005.47, ♂PSUZYC-MM2005.72, ♂PSUZYC-MM2005.75, Bala Forest, Narathiwat. —*Malaysia*: ♀BMNH.67.1601, Pahang; ♂BMNH.83.34, ♂BMNH.83.66, Sabah, Borneo.

H. bicolor major—*Indonesia*: ♂BMNH.66.4.237 (holotype), Enggano I, W Sumatra; *H. bicolor* —*Thailand*: ♀PSUZYC-MM2007.233, ♂PSUZYC-MM2007.232, ♂PSUZYC-MM2007.234, Tham Huay Klang, Chumphon; ♂PSUZYC-MM2008.103, ♀PSUZYC-MM2008.104, Lamnam Kra Buri, Ranong; ♂PSUZYC-MM2008.94, ♀PSUZYC-MM2008.95, Lampi Waterfall, Phang Nga; ♂PSUZYC-MM2008.52, ♀PSUZYC-MM2007.209, Wang Pha, Songkhla; ♀PSUZYC-MM2007.210, Rattaphum, Songkhla; ♀PSUZYC-MM2005.71, ♂PSUZYC-MM2005.82, Bala Forest, Narathiwat. —*Malaysia*: ♀590233, ♂590235, ♂590236, ♂590237, ♀590239, ♀590240, Sarawak.

H. cf. gentilis—*India*: ♂BMNH.23.1.7.1, Mishmi Hills; ♀BMNH.20.11.1.19, Cherrapunji; ♂BMNH.21.1.17.78, Darjeeling. —*Myanmar*: ♂BMNH.93.11.15.2 (holotype), Thaychuya; (unknown sex) BMNH.87.3.4.12, Pegu, ♂PSUZYC-MM2015.7, ♂PS150220.17, ♀PS150220.18, ♂PS150220.21, Phy Taw Aye Cave, Mandalay; ♀PS150224.5, ♂PS150224.22,

♀PS150224.23, Nagamauk cave. —*Vietnam*: ♂SB0508.16, ♀SB0508.17, ♀SB0508.19, Tam Trà, Quảng Nam. —*Thailand*: ♀CDWLSS-B-0002, Chiang Dao, Chiang Mai; ♂PSUZC-MM2008.88, Huai Kha Khaeng Wildlife Sanctuary, Uthai Thani; ♂PSUZC-MM2007.211, ♂PSUZC-MM2007.217, Lub Lae Cave, Uthai Thani; ♀PSUZC-MM2005.74, ♀PSUZC-MM2005.40, East Thung Yai Wildlife Sanctuary, Tak; ♂PSUZC-MM2007.212, ♀PSUZC-MM2007.213, ♀PSUZC-MM2007.215, Khao Don Dueng, Lopburi; ♀PSUZC-MM2007.225, Mongkutthong Cave, Saraburi; ♂PSUZC-MM2007.224, ♂PSUZC-MM2007.226, Wat Tham Rakang, Saraburi; ♂PSUZC-MM2007.230, ♂PSUZC-MM2007.231, Khao Yoi Cave, Phetchaburi; ♂PS200121.11, Keang Kra Chan, Phetchaburi; ♂PSUZC-MM2007.207, ♂PSUZC-MM2007.208, Khao Bin Cave, Ratchaburi; ♂PSUZC-MM2006.63, ♀PSUZC-MM2006.64, ♀PSUZC-MM2006.87, ♂PSUZC-MM2006.196, Khao Kram Cave, Chumphon; ♂PSUZC-MM2006.04, Thung Salaeng Luang National Park; ♂PSUZC-MM2006.08, Phu Soun Sai National Park; ♂PSUZC-MM2005.55, ♀PSUZC-MM2005.56, Phu Luang Wildlife Sanctuary, Loei; ♂PSUZC-MM2006.06, Rha Kor Waterfall, Loei; ♂PSUZC-MM2007.252, Tham Yai Nam Nao Cave, Phetchabun; ♀PSUZC-MM2007.250, ♂PSUZC-MM2007.251, ♀PSUZC-MM2007.254, Pha Phueng Cave, Kalasin; ♀PSUZC-MM2007.222, ♂PSUZC-MM2007.223, Wangnamkheo, Nakhon Ratchasima; ♂PSUZC-MM2007.214, ♀PSUZC-MM2007.216, Khao Singto, Sa Kaeo; ♀PSUZC-MM2007.253, ♀BD070918.7, ♀PP070920.2, Pha Taem National Park, Ubon Ratchatani.

APPENDIX 2. List of samples/specimens included in the genetic analyses, with BOLD and GenBank accession numbers and locations of the samples.

Species	Collection ID/		BOLD/	Genbank accession #		Location
	Original label	Field No.		Process ID	COI	
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	SMF 83823	-	HM540383	-	Malaysia: Pahang
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	EBD 23821	ABBM036-05	HM540386	-	Malaysia: Kinabalu
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	EBD 23561	ABBM033-05	HM540385	-	Malaysia: Sabah
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	EBD 23565	ABBM032-05	HM540384	-	Malaysia: Sabah
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	THK 41702	-	-	JN714761	Malaysia: Pahang
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	CMF920706-01	-	-	-	Malaysia: Pahang
<i>H. kingstonae</i>	<i>H. cf. cineraceus</i>	EBD23564	-	-	-	Malaysia: Madai Cave
<i>H. kingstonae</i>	This paper	PSUZC-MM2022.1	-	QQ533070	-	Thailand: Narathiwat
<i>H. kingstonae</i>	This paper	PSUZC-MM2014.165	-	QQ533071	QQ434822	Thailand: Narathiwat
<i>H. kingstonae</i>	This paper	PSUZC-MM2014.164	-	QQ533072	QQ434823	Thailand: Narathiwat
<i>H. kingstonae</i>	This paper	PSUZC-MM2022.2	-	QQ533069	QQ434821	Thailand: Narathiwat
<i>H. kingstonae</i>	<i>H. ater</i>	FMNH168919	-	-	JQ915226	Philippines: Palawan
<i>H. kingstonae</i>	<i>H. ater</i>	FMNH168920	-	-	JQ915227	Philippines: Palawan
<i>H. kingstonae</i>	<i>H. ater</i>	FMNH168921	-	-	JQ915228	Philippines: Palawan
<i>H. kingstonae</i>	<i>H. ater</i>	FMNH168922	-	-	JQ915229	Philippines: Palawan
<i>H. eimaythi</i>	This paper	PS150305.1	-	QQ533110	QQ434859	Myanmar: Tharabwin
<i>H. eimaythi</i>	This paper	PS150309.3	-	QQ533107	QQ434856	Myanmar: Lenya
<i>H. eimaythi</i>	This paper	PS150305.9	-	QQ533109	QQ434858	Myanmar: Tharabwin
<i>H. eimaythi</i>	This paper	PS150305.11	-	QQ533108	QQ434857	Myanmar: Tharabwin
<i>H. cf. saevus</i>	<i>H. cf. ater</i>	ROM MAM 101946	BM275-03	HM540368	-	Indonesia: Java
<i>H. cf. saevus</i>	<i>H. cf. ater</i>	SMF 83700	BM129-03	HM540367	-	Malaysia: Sabah
<i>H. cf. saevus</i>	<i>H. cf. ater</i>	A01 Ir2Sp01	ABBID012-09	-	-	Indonesia: Java
<i>H. cf. saevus</i>	<i>H. cf. ater</i>	A02 Pr5sp01	ABBID013-09	-	-	Indonesia: Java
<i>H. cf. saevus</i>	<i>H. ater</i>	B10 BB04	ABBID033-09	-	-	Indonesia: Kalimantan
<i>H. cf. saevus</i>	<i>H. ater</i>	B11 BB05	ABBID034-09	-	-	Indonesia: Kalimantan
<i>H. cf. saevus</i>	<i>H. ater</i>	A06 BS42	ABBID017-09	-	-	Indonesia: Kalimantan
<i>H. cf. saevus</i>	<i>H. ater</i>	IRDTBS0012	BIFZA058-17	-	-	Indonesia: Java
<i>H. cf. saevus</i>	<i>H. ater</i>	IRDTB0034	BIFZA031-17	-	-	Indonesia: Java

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APPENDIX 2. (Continued)

Species		Collection ID/		BOLD/		Genbank accession #		Location	
This paper	Original label	Field No.	Process ID	COI	ND2	CytB			
<i>H. cf. saevus</i>	<i>H. ater</i>	IRDTBS0003	BIFZA059-17	-	-	-	-	Indonesia: Java	
<i>H. cf. saevus</i>	<i>H. ater</i>	SEN 83700	-	-	JN714748	-	-	Malaysia: Sabah	
<i>H. cf. saevus</i>	<i>H. ater</i>	MZB 26345	-	-	JN714749	-	-	Malaysia: Sabah	
<i>H. cf. saevus</i>	<i>H. ater</i>	TTU108379	-	-	JQ915281	-	-	Malaysia: Borneo	
<i>H. cf. saevus</i>	<i>H. ater</i>	ROM101946	-	-	JQ915280	-	-	Indonesia: Java	
<i>H. cf. saevus</i>	<i>H. ater</i>	UNIMAS 00729	-	-	-	EF108140	-	Malaysia: Sarawak	
<i>H. cf. saevus</i>	<i>H. ater</i>	UNIMAS 01577	-	-	-	EF108139	-	Malaysia: Sarawak	
<i>H. cf. saevus</i>	<i>H. ater</i>	TK152234	-	-	-	EU521615	-	Malaysia: Sarawak	
<i>H. cf. bicolor erigens</i>	<i>H. bicolor</i> 131	FMNH 180193	-	-	JN714755	-	-	Philippines: Luzon	
<i>H. cf. bicolor erigens</i>	<i>H. bicolor</i> 131	FMNH 202626	-	-	JQ915290	-	-	Philippines	
<i>H. cf. bicolor erigens</i>	<i>H. bicolor</i> 131	FMNH 202627	-	-	JQ915291	-	-	Philippines	
<i>H. cf. bicolor erigens</i>	<i>H. bicolor</i> 131	FMNH 202628	-	-	JQ915292	-	-	Philippines	
<i>H. cf. bicolor erigens</i>	<i>H. bicolor</i> 131	FMNH 202629	-	-	JQ915293	-	-	Philippines	
<i>H. cf. bicolor erigens</i>	<i>H. bicolor</i> 131	FMNH 202630	-	-	JQ915294	-	-	Philippines	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	SB041218-43	ABBTH118-07	-	-	-	-	Thailand: Songkhla	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM 118043	-	JF443886	-	-	-	Laos	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM MAM 118270	-	HM540495	-	-	-	Laos: Houaphanh	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM MAM 118430	-	HM540494	-	-	-	Laos: Vientiane	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	EBD23562	ABBM035-05	HM540488	-	-	-	Malaysia: Sabah	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	INECOL M0078	ABBM377-05	HM540491	-	-	-	Laos: Vientiane	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	EBD24971	ABBM304-05	HM540490	-	-	-	Laos: Houaphanh	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM MAM 118270	ABBM284-05	HM540495	-	-	-	Laos: Houaphanh	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM MAM 110559	ABBM149-05	HM540492	-	-	-	Laos: Attapeu	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ZMMU S-167179	BM660-05	HM540486	-	-	-	Vietnam: Quang Ninh	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM MAM 118430	ABBM373-05	HM540494	-	-	-	Laos: Vientiane	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	CMF970524-98	ABBM215-05	HM540489	-	-	-	Laos: Champasak	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	CMF980125-03	BM043-03	HM540487	-	-	-	Laos: Khammouane	

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		Genbank accession #			Location
		Field No.	BOLD/ Process ID	COI	ND2	CytB	
<i>H. cf. cineraceus</i>	<i>H. cineraceus</i>	ROM MAM 118431	ABBM374-05	HM540493	-	-	Laos: Vientiane
<i>H. cf. cineraceus</i>	This paper	PS170520.2	-	OQ533075	-	-	Thailand: Phatthalung
<i>H. cf. cineraceus</i>	This paper	PS180515.2	-	OQ533077	OQ434824	-	Thailand: Phatthalung
<i>H. cf. cineraceus</i>	This paper	PS180515.3	-	OQ533078	OQ434825	-	Thailand: Phatthalung
<i>H. cf. cineraceus</i>	This paper	PS180515.4	-	-	OQ434826	OQ434787	Thailand: Phatthalung
<i>H. cf. cineraceus</i>	This paper	PS180613.8	-	OQ533081	OQ434844	-	Thailand: Narathiwat
<i>H. cf. cineraceus</i>	This paper	PS181127.2	-	-	OQ434830	-	Thailand: Tak
<i>H. cf. cineraceus</i>	This paper	PS190111.1	-	-	-	OQ434792	Thailand: Ratchaburi
<i>H. cf. cineraceus</i>	This paper	PS190121.6	-	-	-	OQ434788	Thailand: Ratchaburi
<i>H. cf. cineraceus</i>	This paper	PS190121.7	-	-	-	OQ434789	Thailand: Ratchaburi
<i>H. cf. cineraceus</i>	This paper	PS190121.8	-	-	OQ434827	OQ434790	Thailand: Ratchaburi
<i>H. cf. cineraceus</i>	This paper	PS190130.1	-	-	-	OQ434793	Thailand: Ratchaburi
<i>H. cf. cineraceus</i>	This paper	PS190311.1	-	OQ533079	-	-	Thailand
<i>H. cf. cineraceus</i>	This paper	PS190513.2	-	-	OQ434832	OQ434795	Thailand: Phatthalung
<i>H. cf. cineraceus</i>	This paper	PS200120.13	-	OQ533073	-	-	Thailand: Phetchaburi
<i>H. cf. cineraceus</i>	This paper	PS200120.25	-	OQ533074	-	-	Thailand: Phetchaburi
<i>H. cf. cineraceus</i>	This paper	PS210520.1	-	OQ533080	OQ434835	OQ434798	Thailand: Songkhla
<i>H. cf. cineraceus</i>	This paper	PS210603.1	-	-	OQ434836	-	Thailand: Songkhla
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	NIID VN4201B87	-	-	-	KX458067	Vietnam: Phu Tho
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	GX-004	-	-	-	KX467584	China: Guangxi
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	VN3487B57	-	-	-	LC406456	Vietnam: Tuyen Quang
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	VN3473B43	-	-	-	LC406455	Vietnam: Tuyen Quang
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	VN2839B97	-	-	-	LC406454	Vietnam: Quang Tri
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	VN2830B4	-	-	-	LC406453	Vietnam: Quang Tri
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	VN2829B3	-	-	-	LC406452	Vietnam: Quang Tri
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	-	-	-	-	JF320705	Malaysia: Sarawak
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU SVK 185-09	-	HM914964	-	-	Vietnam: Dong Nai

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APPENDIX 2. (Continued)

Species		Collection ID/		BOLD/		Genbank accession #		Location	
This paper	Original label	Field No.	Process ID	COI	ND2	CytB			
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU SVK 184-09	-	HM914963	-	-	Vietnam: Dong Nai		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU SVK 180-09	-	HM914961	-	-	Vietnam: Dong Nai		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU:S-186729	-	JQ365632	-	-	Vietnam: Ba Ria—Vung Tau		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU:S-186728	-	JQ365631	-	-	Vietnam: Ba Ria—Vung Tau		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU:S-186727	-	JQ365630	-	-	Vietnam: Ba Ria—Vung Tau		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU:S-186726	-	JQ365629	-	-	Vietnam: Ba Ria—Vung Tau		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	ZMMU:S-186730	-	JQ365628	-	-	Vietnam: Ba Ria—Vung Tau		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	HZM 3.34873	-	-	JN714764	-	Myanmar: Mon Stage		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	TTU108176	-	-	JQ915297	-	Malaysia		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	152472C	-	-	-	JF320704	Malaysia: Sarawak		
<i>H. cf. cineraceus</i>	<i>H. cf. cineraceus</i>	TK152013	-	-	-	EU521618	Malaysia: Pahang		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SMF 88497	-	HM540382	-	-	Thailand: Krabi		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SMF 88498	-	HM540381	-	-	Thailand: Krabi		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SM040815.53	-	HM540375	-	-	Malaysia: Pahang		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SM040815.67	-	HM540374	-	-	Malaysia: Pahang		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SM040916.1	-	HM540373	-	-	Malaysia: Kelantan		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SM040815.74	-	HM540372	-	-	Malaysia: Pahang		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	THK40684	-	HM540371	-	-	Malaysia: Pahang		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	THK40812	-	HM540370	-	-	Malaysia: Perlis		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	SM040823.26	-	HM540369	-	-	Malaysia: Perlis		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	-	-	-	JN714752	-	Thailand: Krabi		
<i>H. kunzi</i>	<i>H. bicolor</i> 142	THK 40819	-	-	JN714753	-	Malaysia		
<i>H. kunzi</i>	This paper	PS170520.9	-	OQ533076	-	OQ434810	Thailand: Phatthalung		
<i>H. kunzi</i>	This paper	PS170520.10	-	OQ533086	-	OQ434811	Thailand: Phatthalung		
<i>H. kunzi</i>	This paper	PS170520.15	-	OQ533087	-	OQ434812	Thailand: Phatthalung		
<i>H. kunzi</i>	This paper	PS190513.3	-	OQ533088	OQ434845	OQ434813	Thailand: Phatthalung		
<i>H. kunzi</i>	This paper	PS200102.2	-	OQ533082	-	-	Thailand: Trang		

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/ Process ID	Genbank accession #		Location
		Field No.	Field No.		COI	ND2	
This paper							
<i>H. kunzi</i>	This paper	PS200102.3		-	OQ533083	-	Thailand: Trang
<i>H. kunzi</i>	This paper	PS200102.6		-	OQ533084	-	Thailand: Trang
<i>H. kunzi</i>	This paper	PS201103.1		-	OQ533085	-	Thailand: Satun
<i>H. bicolor</i>	<i>H. bicolor</i>	CMF060508.01		ABBTH138-07	-	-	Thailand
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060512-05		ABBTH024-07	-	-	Thailand: Satun
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060512-06		ABBTH026-07	-	-	Thailand: Satun
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060512-10		ABBTH030-07	-	-	Thailand: Satun
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060512-05		ABBTH023-07	-	-	Thailand: Satun
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060514-01		ABBTH040-07	-	-	Thailand: Songkhla
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060511-06		ABBTH005-07	-	-	Thailand: Songkhla
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060512-07		ABBTH027-07	-	-	Thailand: Satun
<i>H. bicolor</i>	<i>H. bicolor</i>	SB060514-05		ABBTH045-07	-	-	Thailand: Songkhla
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM 113119		-	JF443885	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM MAM 113052		-	HM540345	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM MAM 113051		-	HM540344	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM MAM 113017		-	HM540343	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF 83691		-	HM540342	-	Malaysia: Sabah
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF 83913		-	HM540341	-	Malaysia: Sembilan
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF 83910		-	HM540340	-	Malaysia: Sembilan
<i>H. bicolor</i>	<i>H. bicolor</i> 131	MBCRUA.8991		-	HM540339	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.2		-	HM540338	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	THK 41736		-	-	JN714751	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SEN 83691		-	-	JN714754	Malaysia: Sabah
<i>H. bicolor</i>	<i>H. bicolor</i> 131	UNIMAS-TK152015		-	-	JQ915295	Malaysia: Sabah
<i>H. bicolor</i>	<i>H. bicolor</i> 131	AGS970408-03		-	-	-	Thailand: Krabi
<i>H. bicolor</i>	<i>H. bicolor</i> 131	FH02		-	-	-	Malaysia: Sarawak
<i>H. bicolor</i>	<i>H. bicolor</i> 131	LB048		-	-	-	Malaysia: Sarawak

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/ Process ID	Genbank accession #		Location
		Field No.			COI	ND2	
<i>H. bicolor</i>	<i>H. bicolor</i> 131	UNIMAS 01474	-	-	-	EF108143	Malaysia: Sarawak
<i>H. bicolor</i>	<i>H. bicolor</i> 131	UNIMAS 01459	-	-	-	EF108142	Malaysia: Sarawak
<i>H. bicolor</i>	<i>H. bicolor</i> 131	TK152153	-	-	-	EU521616	Malaysia: Sarawak
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF83910	BM454-04	HM540340	-	-	Malaysia: Negeri Sembilan
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF83913	BM455-04	HM540341	-	-	Malaysia: Negeri Sembilan
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF83691	BM150-03	HM540342	-	-	Malaysia: Sabah
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.2	ABBSI003-04	HM540338	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	MBCRUA8991	ABBSI005-04	HM540339	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM MAM 113051	ABRSS332-06	HM540344	-	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM MAM 113052	ABRSS333-06	HM540345	-	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	ROM MAM 113017	BM423-04	HM540343	-	-	Malaysia: Johor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	CMF920702-05	BM452-04	HM540379	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.67	ABBSI011-04	HM540374	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	THK40684	ABBSI008-04	HM540371	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	MBCRUA8989	ABBSI015-04	HM540378	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.74	ABBSI009-04	HM540372	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.53	ABBSI012-04	HM540375	-	-	Malaysia: Pahang
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.16	ABBSI014-04	HM540377	-	-	Malaysia: Perak
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040916.1	ABBSI010-04	HM540373	-	-	Malaysia: Kelantan
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040815.30	ABBSI013-04	HM540376	-	-	Malaysia: Selangor
<i>H. bicolor</i>	<i>H. bicolor</i> 131	CMF940605-03	BM453-04	HM540380	-	-	Malaysia: Negeri Sembilan
<i>H. bicolor</i>	<i>H. bicolor</i> 131	THK40812	ABBSI007-04	HM540370	-	-	Malaysia: Perlis
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SM040823.26	ABBSI006-04	HM540369	-	-	Malaysia: Perlis
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF88497	ABBM050-05	HM540382	-	-	Thailand: Krabi
<i>H. bicolor</i>	<i>H. bicolor</i> 131	SMF88498	ABBM049-05	HM540381	-	-	Thailand: Krabi
<i>H. bicolor</i>	This paper	PS180613.8	-	QQ434844	QQ434809	-	Thailand: Narathiwat
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 166410	-	-	JN714750	-	Philippines: Luzon

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APPENDIX 2. (Continued)

Species		Collection ID/ Field No.	BOLD/ Process ID	Genbank accession #		Location
This paper	Original label			COI	ND2	
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 140667	-	-	JQ915219	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 140669	-	-	JQ915220	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 140670	-	-	JQ915221	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 166410	-	-	JQ915222	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 166411	-	-	JQ915223	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 166412	-	-	JQ915224	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 166413	-	-	JQ915225	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 177463	-	-	JQ915230	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 180192	-	-	JQ915231	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 180277	-	-	JQ915232	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 180278	-	-	JQ915233	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 180279	-	-	JQ915234	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183303	-	-	JQ915235	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183304	-	-	JQ915236	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183305	-	-	JQ915237	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183306	-	-	JQ915238	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183307	-	-	JQ915239	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183309	-	-	JQ915240	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 183310	-	-	JQ915241	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186022	-	-	JQ915242	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186023	-	-	JQ915243	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186024	-	-	JQ915244	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186025	-	-	JQ915245	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186026	-	-	JQ915246	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186027	-	-	JQ915247	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186028	-	-	JQ915248	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186029	-	-	JQ915249	Philippines

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APPENDIX 2. (Continued)

Species		Collection ID/ Field No.	BOLD/ Process ID	Genbank accession #		Location
This paper	Original label			COI	ND2	
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186030	-	-	JQ915250	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186031	-	-	JQ915251	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 186032	-	-	JQ915252	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 190744	-	-	JQ915253	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 194856	-	-	JQ915254	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 194857	-	-	JQ915255	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	FMNH 194858	-	-	JQ915256	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164241	-	-	JQ915257	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164242	-	-	JQ915258	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164243	-	-	JQ915259	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164244	-	-	JQ915260	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164666	-	-	JQ915261	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164710	-	-	JQ915262	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164711	-	-	JQ915263	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164712	-	-	JQ915264	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164713	-	-	JQ915265	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164829	-	-	JQ915266	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164830	-	-	JQ915267	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164831	-	-	JQ915268	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164832	-	-	JQ915269	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164833	-	-	JQ915270	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164834	-	-	JQ915271	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164835	-	-	JQ915272	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164836	-	-	JQ915273	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164837	-	-	JQ915274	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164838	-	-	JQ915275	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164839	-	-	JQ915276	Philippines

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/ Process ID	Genbank accession #			Location
		Field No.			COI	ND2	CytB	
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164840		-	-	JQ915277	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164841		-	-	JQ915278	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	KU164842		-	-	JQ915279	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM459406		-	-	JQ915282	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM573271		-	-	JQ915283	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM573272		-	-	JQ915284	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM573273		-	-	JQ915285	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM573274		-	-	JQ915286	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM573275		-	-	JQ915287	-	Philippines
<i>H. cf. antricola</i>	<i>H. ater</i>	USNM573276		-	-	JQ915288	-	Philippines
<i>H. sp.</i>	<i>H. ater</i>	-		-	-	KM006989	-	Australia
<i>H. sp.</i>	<i>H. ater</i>	-		-	-	KM006991	-	Australia
<i>H. cf. gentilis</i>	This paper	BD181217.19		-	-	OQ434848	OQ434817	Thailand
<i>H. cf. gentilis</i>	This paper	PS150220.7		-	OQ533092	-	OQ434855	Myanmar: Pyin Oo Lwin
<i>H. cf. gentilis</i>	This paper	PS190121.9		-	-	OQ434852	OQ434814	Thailand: Ratchaburi
<i>H. cf. gentilis</i>	This paper	PS190121.10		-	-	OQ434853	OQ434815	Thailand: Ratchaburi
<i>H. cf. gentilis</i>	This paper	PS190121.11		-	-	OQ434854	OQ434816	Thailand: Ratchaburi
<i>H. cf. gentilis</i>	This paper	PS190123.1		-	-	OQ434828	OQ434791	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS190505.12		-	OQ533093	OQ434850	OQ434819	Thailand: Ubon Ratchathani
<i>H. cf. gentilis</i>	This paper	PS200120.14		-	OQ533090	-	-	Thailand: Kaeng Krachan
<i>H. cf. gentilis</i>	This paper	PS200120.11		-	OQ533089	-	-	Thailand: Kaeng Krachan
<i>H. cf. gentilis</i>	This paper	PS200121.4		-	OQ533091	-	-	Thailand: Kaeng Krachan
<i>H. cf. gentilis</i>	This paper	PS211209.9		-	OQ533094	-	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211209.14		-	OQ533095	-	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211210.2		-	OQ533096	-	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211210.3		-	OQ533097	-	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211210.4		-	OQ533098	-	-	Thailand: Kanchanaburi

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/ Process ID	Genbank accession #		Location
		Field No.			COI	ND2	
<i>H. cf. gentilis</i>	This paper	PS211210.11		-	OQ533099	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211210.12		-	OQ533100	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211211.1		-	OQ533101	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211211.2		-	OQ533102	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211211.3		-	OQ533103	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	This paper	PS211211.4		-	OQ533104	-	Thailand: Kanchanaburi
<i>H. cf. gentilis</i>	<i>H. pomona</i>	SB060516.11		ABBTH058-07	-	-	Thailand
<i>H. cf. gentilis</i>	<i>H. pomona</i>	SB060519.08		ABBTH084-07	-	-	Thailand
<i>H. cf. gentilis</i>	<i>H. pomona</i>	SB060520.12		ABBTH104-07	-	-	Thailand
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118171		ABRLA158-06	HM540607	-	Laos: Champasak
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118170		BM160-03	HM540606	-	Laos: Champasak
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118362		ABBM336-05	HM540555	-	Laos: Luang Namtha
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118216		ABBM256-05	HM540598	-	Laos: Houaphanh
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118054		ABRLA066-06	HM540601	-	Laos: Vientiane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118052		BM036-03	HM540597	-	Laos: Vientiane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118021		ABRLA034-06	HM540600	-	Laos: Khammouane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 117895		BM087-03	HM540599	-	Laos: Khammouane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118126		ABRLA130-06	HM540604	-	Laos: Khammouane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118078		ABRLA087-06	HM540602	-	Laos: Khammouane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111339		ABRVN521-06	HM540570	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111393		ABRVN565-06	HM540592	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111394		ABRVN566-06	HM540593	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111403		ABRVN573-06	HM540596	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111343		ABRVN525-06	HM540573	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111345		ABRVN527-06	HM540575	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111357		ABRVN539-06	HM540583	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111392		ABRVN564-06	HM540591	-	Vietnam: Quang Nam

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APPENDIX 2. (Continued)

Species	Collection ID/		Genbank accession #			Location
	Original label	Field No.	BOLD/ Process ID	COI	ND2	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111348	ABRVN530-06	HM540578	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111355	ABRVN537-06	HM540582	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111396	ABRVN568-06	HM540594	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111346	ABRVN528-06	HM540576	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111370	ABRVN548-06	HM540585	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111391	ABRVN563-06	HM540590	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111342	ABRVN524-06	HM540572	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111347	ABRVN529-06	HM540577	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111389	ABRVN561-06	HM540588	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111344	ABRVN526-06	HM540574	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111341	ABRVN523-06	HM540571	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111358	ABRVN540-06	HM540584	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111388	ABRVN560-06	HM540587	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111390	ABRVN562-06	HM540589	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111352	ABRVN534-06	HM540581	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111349	ABRVN531-06	HM540579	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111371	ABRVN549-06	HM540586	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111350	ABRVN532-06	HM540580	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111397	ABRVN569-06	HM540595	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111338	ABRVN520-06	HM540569	-	Vietnam: Quang Nam
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107632	BM328-04	HM540563	-	Vietnam: Tuyen Quang
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107700	ABRVN175-06	HM540564	-	Vietnam: Tuyen Quang
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107660	ABRVN141-06	HM540565	-	Vietnam: Tuyen Quang
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107546	ABRVN040-06	HM540561	-	Vietnam: Vinh Phuc
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107550	ABRVN044-06	HM540558	-	Vietnam: Vinh Phuc
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107549	ABRVN043-06	HM540559	-	Vietnam: Vinh Phuc
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107551	ABRVN046-06	HM540557	-	Vietnam: Vinh Phuc

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/			Genbank accession #		Location
		Field No.		Process ID	COI	ND2	CytB		
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107548		ABRVN042-06	HM540560	-	-	Vietnam: Vinh Phuc	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 107545		ABRVN039-06	HM540562	-	-	Vietnam: Vinh Phuc	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 116072		ABCMA599-07	HM540566	-	-	China: Guangxi	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 116086		ABCMA609-07	HM540568	-	-	China: Guangxi	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 116077		ABCMA601-07	HM540567	-	-	China: Guangxi	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118171		-	HM540607	-	-	Laos: Champasak	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 118170		-	HM540606	-	-	Laos: Champasak	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM MAM 111352		-	HM540581	-	-	Vietnam	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 118478		-	JF443939	-	-	China: Guizhou	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 118538		-	JF443938	-	-	China: Guizhou	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 118549		-	JF443937	-	-	China: Guizhou	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 111340		-	JF443936	-	-	Vietnam: Quang Nam	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 111353		-	JF443935	-	-	Vietnam: Quang Nam	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 107547		-	JF443930	-	-	Vietnam: Vinh Phuc	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM F42523		-	JF443929	-	-	Vietnam: Vinh Phuc	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	HZM19.35121		BM336-03	HM540555	-	-	Myanmar	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	HZM MS16		-	JF443940	-	-	Myanmar: Kachin	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ZMMU SVK 177-09		-	HM914959	-	-	Vietnam: Dong Nai	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ZMMU S-175109		BM618-04	HM540543	-	-	Vietnam: Dong Nai	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ZMMU S-167170		BM659-05	HM540544	-	-	Vietnam: Quang Ninh	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ZMMU S-175403		BM681-05	HM540545	-	-	Vietnam: Kien Giang	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	YU IJM MN3		BM329-03	HM540553	-	-	Myanmar	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	YU IJM MN4		BM330-03	HM540554	-	-	Myanmar	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	YU IJM TA2		ABBM465-05	HM540542	-	-	Myanmar	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	INECOL M0090		ABBM131-05	HM540547	-	-	Laos: Attapeu	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	INECOL M0093		ABBM360-05	HM540551	-	-	Laos: Vientiane	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	INECOL M0094		ABBM375-05	HM540552	-	-	Laos: Vientiane	

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/		Genbank accession #		Location	
		Field No.		Process ID		COI	ND2	CytB	
<i>H. cf. gentilis</i>	<i>H. pomona</i>	EBD25718		ABBM277-05		HM540550	-	-	Laos: Houaphanh
<i>H. cf. gentilis</i>	<i>H. pomona</i>	EBD23515		ABBM237-05		HM540549	-	-	Laos: Vientiane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	CMF970524-31		ABBM210-05		HM540548	-	-	Laos: Champasak
<i>H. cf. gentilis</i>	<i>H. pomona</i>	CMF970502-13		ABBM105-05		HM540546	-	-	Laos: Attapeu
<i>H. cf. gentilis</i>	<i>H. pomona</i>	CMF980122-12		ABRLA163-06		HM540605	-	-	Laos: Khammouane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	EBD 25718		-		HM540550	-	-	Laos: Houaphanh
<i>H. cf. gentilis</i>	<i>H. pomona</i>	EBD 23515		-		HM540549	-	-	Laos: Vientiane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	CMF970524-31		-		HM540548	-	-	Laos: Champasak
<i>H. cf. gentilis</i>	<i>H. pomona</i>	INECOL_M0090		-		HM540547	-	-	Laos: Attapeu
<i>H. cf. gentilis</i>	<i>H. pomona</i>	CMF970502-13		-		HM540546	-	-	Laos: Attapeu
<i>H. cf. gentilis</i>	<i>H. pomona</i>	NHM.OU.CHI.80.2014		-		MG821201	-	-	India: Telangana
<i>H. cf. gentilis</i>	<i>H. pomona</i>	-		-		-	JN714787	-	China: Yunnan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	ROM 118170		-		-	JN714788	-	Laos: Champasak
<i>H. cf. gentilis</i>	<i>H. pomona</i>	HNHM 2005.82.46		-		-	JN714789	-	Laos: Khammouane
<i>H. cf. gentilis</i>	<i>H. pomona</i>	USNM 583861		-		-	JN714790	-	Myanmar: Mon Stage
<i>H. cf. gentilis</i>	<i>H. pomona</i>	THK 41952		-		-	JN714791	-	Malaysia: Perlis
<i>H. cf. gentilis</i>	<i>H. pomona</i>	BS01		-		-	-	KP336274	China: Henan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	DL01		-		-	-	KP336273	China: Henan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	YN01		-		-	-	KJ623705	China: Henan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	HN02		-		-	-	KJ623704	China: Henan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	FJ01		-		-	-	KJ619513	China: Henan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	YN-153		-		-	-	KX467585	China: Yunan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	-		-		-	-	DQ888671	China: Yunan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	3740		-		-	-	KP876550	China: Wuhan
<i>H. cf. gentilis</i>	<i>H. pomona</i>	-		-		-	-	EU434950	China: Guangdong
<i>H. cf. gentilis</i>	<i>H. pomona</i>	NIID VN1982B4		-		-	-	JX912954	Vietnam: Phu Tho
<i>H. cf. gentilis</i>	<i>H. pomona</i>	CMF950116-02		-		-	-	DQ054810	Laos: Bolikhamsai

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APPENDIX 2. (Continued)

Species		Collection ID/		BOLD/		Genbank accession #		Location	
This paper	Original label	Field No.	Process ID	COI	ND2	CytB			
<i>H. fulvus</i>	<i>H. fulvus</i>	HZM 3.28778	-	-	JN714771	-	Sri Lanka: Waulpane		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	AGS980511-13	ABBM381-05	HM540534	-	-	Laos: Vientiane		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	AGS980511-12	ABBM380-05	HM540533	-	-	Laos: Vientiane		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	INECOL M0107	ABBM382-05	HM540535	-	-	Laos: Vientiane		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	ROM 110671	-	JQ599813	-	-	Laos: Tak Leuk		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	INECOL M0107	-	HM540535	-	-	Laos: Vientiane		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	ROM 116791	-	-	JN714778	-	Laos: Vientiane		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	AGS970604-01	-	-	-	DQ054816	Laos: Saisombun		
<i>H. khaokhouayensis</i>	<i>H. khaokhouayensis</i>	AGS980511-14	-	-	-	DQ054815	Laos: Vientiane		
<i>H. halophyllus</i>	<i>H. halophyllus</i>	SM040823	ABBS1019-04	HM540531	-	-	Malaysia: Perlis		
<i>H. halophyllus</i>	<i>H. halophyllus</i>	SM040823.14	-	HM540531	-	-	Malaysia: Perlis		
<i>H. halophyllus</i>	<i>H. halophyllus</i>	THK 22866	-	-	JN714777	-	Malaysia		
<i>H. halophyllus</i>	<i>H. halophyllus</i>	CVVD AG.200700214	-	-	-	JN247005	Thailand		
<i>H. rotalis</i>	<i>H. rotalis</i>	CMF980204-14	-	HM540619	-	-	Laos: Vientiane		
<i>H. rotalis</i>	<i>H. rotalis</i>	CMF980203-34	-	HM540618	-	-	Laos: Vientiane		
<i>H. rotalis</i>	<i>H. rotalis</i>	ROM MAM 106530	-	HM540617	-	-	Laos: Khammouane		
<i>H. rotalis</i>	<i>H. rotalis</i>	INECOL M0096	-	HM540614	-	-	Laos: Vientiane		
<i>H. rotalis</i>	<i>H. rotalis</i>	AGS970602-01	-	-	DQ054814	-	Laos: Saisombun		
<i>H. rotalis</i>	<i>H. rotalis</i>	CMF950124-02	-	-	DQ054813	-	Laos: Bolikhamsai		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	SMF 83828	-	HM540613	-	-	Malaysia: Pahang		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	CMF920706-04	-	HM540612	-	-	Malaysia: Pahang		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	CMF980204-14	-	HM540619	-	-	Laos: Vientiane		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	CMF980203-34	-	HM540618	-	-	Laos: Vientiane		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	ROM MAM 106530	-	HM540617	-	-	Laos: Khammouane		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	INECOL M0096	-	HM540614	-	-	Laos: Vientiane		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	EBD23516	ABBM223-05	HM540615	-	-	Laos: Vientiane		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	INECOL M0095	ABBM359-05	HM540616	-	-	Laos: Vientiane		

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/ Field No.	BOLD/ Process ID	Genbank accession #		CytB	Location
				COI	ND2		
<i>H. ridleyi</i>	<i>H. ridleyi</i>	CMF950702-06	-	-	-	DQ054812	Malaysia: Sabah
<i>H. ridleyi</i>	<i>H. ridleyi</i>	CMF930816-01	-	-	-	DQ054811	Malaysia: Pahang
<i>H. ridleyi</i>	<i>H. ridleyi</i>	153522C	-	-	-	JF320695	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	152505C	-	-	-	JF320694	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	152848C	-	-	-	JF320693	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	TB007	-	-	-	JF320692	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	152821C	-	-	-	JF320691	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	153543C	-	-	-	JF320697	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	EKS001	-	-	-	JF320690	Malaysia: Sarawak
<i>H. ridleyi</i>	<i>H. ridleyi</i>	AGS970602-01	-	-	-	DQ054814	Laos: Saisombun
<i>H. ridleyi</i>	<i>H. ridleyi</i>	AGS970602-01	-	-	-	DQ054814	Laos: Saisombun
<i>H. ridleyi</i>	<i>H. ridleyi</i>	CMF950124-02	-	-	-	DQ054813	Laos: Bolikhamsai
<i>H. cervinus</i>	<i>H. cervinus</i>	ROM MAM 113033	-	-	-	-	Malaysia: Johor
<i>H. cervinus</i>	<i>H. cervinus</i>	ROM MAM 113118	-	-	-	-	Malaysia: Johor
<i>H. cervinus</i>	<i>H. cervinus</i>	SMF 83687	-	-	-	-	Malaysia: Sabah
<i>H. cervinus</i>	<i>H. cervinus</i>	SMF 83683	-	-	-	-	Malaysia: Sabah
<i>H. cervinus</i>	<i>H. cervinus</i>	-	-	-	JN714757	-	Malaysia: Sabah
<i>H. cervinus</i>	<i>H. cervinus</i>	AGS960516-07	-	-	-	DQ054805	Malaysia: Sabah
<i>H. cervinus</i>	<i>H. cervinus</i>	TB004	-	-	-	JF320701	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	152813C	-	-	-	JF320700	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	152413C	-	-	-	JF320699	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	EKS012	-	-	-	JF320698	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	UNIMAS 00788	-	-	-	EF108146	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	UNIMAS 00787	-	-	-	EF108144	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	-	-	-	-	EF108141	Malaysia: Sarawak
<i>H. cervinus</i>	<i>H. cervinus</i>	TK152006	-	-	-	EU521617	Malaysia: Pahang
<i>H. calcaratus</i>	<i>H. calcaratus</i>	TK20093	-	-	-	DQ054806	Papua New Guinea

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/ Process ID	Genbank accession #			Location
		Field No.	Field No.		COI	ND2	CytB	
<i>H. coxi</i>	<i>H. coxi</i>	-	-	-	-	-	-	Malaysia: Sarawak
<i>H. coxi</i>	<i>H. coxi</i>	UNIMAS 00366	-	-	-	-	-	Malaysia: Sarawak
<i>H. coxi</i>	<i>H. coxi</i>	-	-	-	-	-	-	Malaysia: Sarawak
<i>H. coxi</i>	<i>H. coxi</i>	TK152124	-	-	-	-	-	Malaysia: Sarawak
<i>H. dyacorum</i>	<i>H. dyacorum</i>	EBD 23819	ABBM021-05	-	HM540518	-	-	Malaysia: Sabah
<i>H. dyacorum</i>	<i>H. dyacorum</i>	EBD 23558	ABBM019-05	-	HM540517	-	-	Malaysia: Sabah
<i>H. dyacorum</i>	<i>H. dyacorum</i>	EBD 23555	ABBM013-05	-	HM540516	-	-	Malaysia: Sabah
<i>H. dyacorum</i>	<i>H. dyacorum</i>	SM040916.2	ABBSI020-04	-	HM540515	-	-	Malaysia: Kelantan
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL050110-16	ABBTHI31-07	-	-	-	-	Thailand
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL050113-13	ABBTHI23-07	-	-	-	-	Thailand
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL050113-12	ABBTHI24-07	-	-	-	-	Thailand
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL060517-01	ABBTHI59-07	-	-	-	-	Thailand: Narathiwat
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL060517-05	ABBTHI62-07	-	-	-	-	Thailand: Narathiwat
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL060517-02	ABBTHI63-07	-	-	-	-	Thailand: Narathiwat
<i>H. dyacorum</i>	<i>H. dyacorum</i>	APBL060517-03	ABBTHI64-07	-	-	-	-	Thailand: Narathiwat
<i>H. dyacorum</i>	<i>H. dyacorum</i>	THK 40460	-	-	-	JN714770	-	Malaysia: Kelantan
<i>H. dyacorum</i>	<i>H. dyacorum</i>	UNIMAS 00556	-	-	-	-	EF108151	Malaysia: Sarawak
<i>H. dyacorum</i>	<i>H. dyacorum</i>	UNIMAS 00312	-	-	-	-	EF108150	Malaysia: Sabah
<i>H. dyacorum</i>	<i>H. dyacorum</i>	TK152195	-	-	-	-	EU521620	Malaysia: Sarawak
<i>H. doriae</i>	<i>H. doriae</i>	CMF920702-03	-	-	HM540514	-	-	Malaysia: Pahang
<i>H. doriae</i>	<i>H. doriae</i>	MS040527.1	-	-	JN714769	-	-	Malaysia: Sabah
<i>H. doriae</i>	<i>H. doriae</i>	CMF920702-03	BM472-04	-	HM540514	-	-	Malaysia: Pahang
<i>H. doriae</i>	<i>H. doriae</i>	PS180613.7	-	-	-	QQ434847	-	Thailand: Narathiwat
<i>H. galeritus</i>	<i>H. galeritus</i>	ZMMU SVK 152-09	-	-	HM914937	-	-	Vietnam: Dong Nai
<i>H. galeritus</i>	<i>H. galeritus</i>	ZMMU:S-186735	-	-	JQ365637	-	-	Vietnam: Ba Ria—Vung Tau
<i>H. galeritus</i>	<i>H. galeritus</i>	ZMMU:S-186733	-	-	JQ365636	-	-	Vietnam: Ba Ria—Vung Tau
<i>H. galeritus</i>	<i>H. galeritus</i>	ZMMU:S-186732	-	-	JQ365635	-	-	Vietnam: Ba Ria—Vung Tau

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APPENDIX 2. (Continued)

Species	Original label	Collection ID/		BOLD/ Process ID	Genbank accession #			Location
		Field No.			COI	ND2	CytB	
<i>H. galeritus</i>	<i>H. galeritus</i>	ZMMU:S-186731	-	-	JQ365634	-	-	Vietnam: Ba Ria—Vung Tau
<i>H. galeritus</i>	<i>H. galeritus</i>	ZMMU:S-186734	-	-	JQ365633	-	-	Vietnam: Ba Ria—Vung Tau
<i>H. galeritus</i>	<i>H. galeritus</i>	ROM 118173	-	-	JF443887	-	-	Laos
<i>H. galeritus</i>	<i>H. galeritus</i>	CMF980228-77	-	-	HM540530	-	-	Laos: Champasak
<i>H. galeritus</i>	<i>H. galeritus</i>	152844C	-	-	-	JF320709	-	Malaysia: Sarawak
<i>H. galeritus</i>	<i>H. galeritus</i>	152347C	-	-	-	JF320708	-	Malaysia: Sarawak
<i>H. galeritus</i>	<i>H. galeritus</i>	156017C	-	-	-	JF320707	-	Malaysia: Sarawak
<i>H. galeritus</i>	<i>H. galeritus</i>	152459C	-	-	-	JF320706	-	Malaysia: Sarawak
<i>H. galeritus</i>	<i>H. galeritus</i>	TK152131	-	-	-	EU521621	-	Malaysia: Sarawak
<i>H. armiger</i>	<i>H. armiger</i>	SB060518-05	-	ABBTH067-07	-	-	-	Thailand: Loei
<i>H. armiger</i>	<i>H. armiger</i>	THK 8839	-	-	-	JN714747	-	Malaysia: Perlis
<i>Coelops fritihii</i>	<i>Coelops fritihii</i>	SB060516-02	-	ABBTH050-07	-	-	-	Thailand: Loei
<i>Coelops fritihii</i>	<i>Coelops fritihii</i>	SEN 85775	-	-	-	JN714744	-	Laos
<i>Coelops robinsoni</i>	<i>Coelops robinsoni</i>	APBL050119-04	-	ABBTH129-07	-	-	-	Thailand: Narathiwat
<i>Coelops robinsoni</i>	<i>Coelops robinsoni</i>	MBCRU 0051	-	-	-	JN714745	-	Malaysia
<i>Aselliscus stoliczkanus</i>	<i>Aselliscus stoliczkanus</i>	HZM10.35119	-	BM331-03	HM540130	-	-	Myanmar
<i>Aselliscus stoliczkanus</i>	<i>Aselliscus stoliczkanus</i>	SEN 86209	-	-	-	JN714743	-	-
<i>Rhinolophus affinis</i>	<i>Rhinolophus affinis</i>	SB060511-04	-	ABBTH004-07	KY034116	-	-	Thailand: Songkhla
<i>Rhinolophus affinis</i>	<i>Rhinolophus affinis</i>	-	-	-	-	NC_053269	-	-

APPENDIX 3. Estimated genetic divergence (%) between analysed taxa based on mitochondrial COI. Hki: *H. kingstonae* sp. nov. from Thai-Malay Peninsula; Hki2, *H. kingstonae* sp. nov. from Sabah, Malaysia; Hei: *H. einmaythui*; Hci1: *H. cf. cineraceus* from Laos-Vietnam; Hci2: *H. cf. cineraceus* from Sabah; Hci3: *H. cf. cineraceus* from Thailand; Hku: *H. kumzi*; Hbi: *H. bicolor*; Hsa: *H. cf. saevus*; Hge: *H. cf. gentilis*; Hha: *H. halophyllus*; Hkh: *H. khaokhouayensis*; Hdo: *H. doricae*; Hdy: *H. dyacorum*; Hro: *H. rotalis*; Har: *H. armiger*; Ast: *Aselliscus stoliczkanus*; Cro: *Coelops robinsoni*; and Raf: *Rhinolophus affinis*.

	Hki	Hki2	Hei	Hci1	Hci2	Hci3	Hku	Hbi	Hae	Hge	Hha	Hkh	Hdo	Hdy	Hro	Har	Ast	Cro	Raf
Hki	0.00	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.01	0.04	0.03	0.03	0.03	0.02	0.03	0.04	0.03	0.04
Hki2	0.3		0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.01	0.04	0.02	0.03	0.03	0.02	0.03	0.04	0.03	0.04
Hei	9.6	9.2		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.04	0.03	0.03	0.03	0.03	0.04	0.03	0.03	0.03
Hci1	9.7	9.7	11.7		0.02	0.02	0.02	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04
Hci2	12.5	12.1	12.3	7.4		0.02	0.03	0.02	0.03	0.02	0.03	0.02	0.03	0.04	0.02	0.04	0.04	0.03	0.05
Hci3	9.7	9.4	10.1	11.9	12.6		0.02	0.02	0.03	0.02	0.03	0.02	0.03	0.03	0.02	0.03	0.03	0.03	0.03
Hku	2.3	2.0	11.4	11.5	14.5	11.2		0.01	0.03	0.02	0.04	0.03	0.03	0.03	0.03	0.04	0.03	0.03	0.04
Hbi	4.9	4.7	11.4	11.3	12.8	11.3	5.0		0.02	0.01	0.03	0.02	0.03	0.03	0.02	0.03	0.03	0.03	0.04
Hsa	14.6	14.4	16.0	18.0	21.0	17.4	15.7	15.4		0.02	0.03	0.03	0.03	0.02	0.03	0.03	0.04	0.03	0.03
Hge	8.0	7.8	11.0	11.8	13.1	12.3	9.1	9.2	15.9		0.03	0.02	0.03	0.03	0.02	0.03	0.03	0.03	0.04
Hha	21.0	21.3	21.1	18.0	15.4	19.5	23.6	20.8	21.3	20.4		0.03	0.02	0.02	0.04	0.03	0.04	0.03	0.04
Hkh	11.7	11.3	13.8	14.6	8.8	11.4	13.9	12.2	16.0	14.2	18.1		0.03	0.03	0.01	0.04	0.04	0.04	0.04
Hdo	16.7	16.7	17.9	14.2	14.4	17.2	17.6	16.5	19.9	16.9	10.9	18.3		0.03	0.04	0.04	0.03	0.03	0.04
Hdy	14.6	14.5	17.1	18.6	19.8	17.6	15.4	14.5	14.5	17.4	12.3	16.7	12.6		0.03	0.03	0.04	0.03	0.04
Hro	11.1	10.8	14.7	14.6	11.3	13.0	13.3	12.3	16.7	13.6	20.7	4.8	18.6	18.4		0.05	0.04	0.04	0.04
Har	19.4	19.2	23.6	19.6	23.7	21.0	20.2	19.8	19.6	19.8	18.8	25.5	20.1	17.3	27.1		0.04	0.04	0.04
Ast	20.1	20.0	20.7	19.9	22.4	20.0	19.7	20.2	24.3	19.2	22.3	22.5	18.8	21.3	22.2	21.8		0.03	0.04
Cro	19.6	19.5	17.3	20.1	22.8	20.7	18.6	19.4	23.0	19.6	19.8	22.9	20.0	17.0	22.7	23.1	15.5		0.03
Raf	23.7	23.4	20.7	25.7	28.5	20.8	21.9	22.6	22.0	22.9	25.8	22.0	20.6	23.5	20.8	23.7	23.2	21.4	