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Author(s): Pipat Soisook , Sara Bumrungsri , Chutamas Satasook , Vu Dinh Thong , Si Si Hla Bu , David L. Harrison , and Paul J. J. Bates
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A taxonomic review of *Rhinolophus stheno* and *R. malayanus* (Chiroptera: Rhinolophidae) from continental Southeast Asia: an evaluation of echolocation call frequency in discriminating between cryptic species

Pipat Soisook[1], Sara Bumrungsri[1], Chutamas Satasook[1], Vu Dinh Thong[2], Si Si Hla Bu[3], David L. Harrison[4], and Paul J. J. Bates[4, 5]

[1]*Department of Biology, Faculty of Science, Prince of Songkla University, Hat Yai, Songkla, Thailand 90112*
[2]*Institute for Ecology and Biological Resources (IEBR), Vietnamese Academy of Science and Technology, 18 Hoang Quac Viet Road, Cau Giay, Hanoi, Vietnam*
[3]*Department of Zoology, Mandalay University, Mandalay, Myanmar*
[4]*Harrison Institute, Centre for Systematics and Biodiversity Research, Bowerwood House, St. Botolph's Road, Sevenoaks, Kent, TN13 3AQ, United Kingdom*
[5]*Corresponding author: E-mail: harrisoninstitute@btopenworld.com*

The taxon *Rhinolophus microglobosus* is elevated to specific rank on the basis of clearly defined morphometric and acoustic characters which differentiate it from *Rhinolophus stheno*. It is recorded from Cambodia for the first time. *Rhinolophus malayanus* exhibits considerable geographical variation in echolocation calls, with apparently two phonic types: a northern population with lower frequency calls and a predominantly southern population with higher frequencies. However, this acoustic divergence is not reflected in any morphometric divergence, and the taxonomic status of the two phonic populations remains unclear. Discriminating characters of all three species are given, together with distribution data and short ecological summaries. The value of echolocation as an indicator of cryptic species and the zoogeographical implications of the study are briefly discussed.

Key words: *Rhinolophus microglobosus*, *R. malayanus*, *R. stheno*, taxonomy, echolocation, zoogeography, Southeast Asia

Introduction

Rhinolophus malayanus Bonhote (1903) and *R. stheno* Andersen (1905) are generally considered to be two closely related species and are usually included in the same species group of the Rhinolophidae (Andersen, 1905; Tate and Archbold, 1939; Corbet and Hill, 1992; Csorba *et al*., 2003); although for contrary views see Bogdanowicz (1992) and Guillén Servent *et al*. (2003). In terms of morphometrics, some authors have found it difficult to distinguish between the two taxa (McFarlane and Blood, 1986), whilst others have published a range of discriminating characters (Lekagul and McNeely, 1977; Corbet and Hill, 1992; Robinson, 1995; Bates *et al*., 2000, 2004). However, as Csorba *et al*. (2003) pointed out that there has been little agreement between the authors as to the reliability of each so-called diagnostic feature. Meanwhile, the subspecific characters of *R. stheno* were discussed in some detail by Csorba and Jenkins (1998), who described a new subspecies, *R. stheno microglobosus*, whilst those of *R. malayanus*, with the exception of a few comments by Bates *et al*. (2004), have been largely ignored. The acoustic characters of the two taxa are also virtually unknown, although some data are available in Robinson (1996), Francis and Habersetzer (1998) and Kingston *et al.* (2000).

The idea for the current study came from observed differences of up to 10 kHz in the hand held frequencies of acoustic calls of both *R. stheno* (sensu Csorba *et al*., 2003) and *R. malayanus* from northern and southern Thailand. Previous studies in Asia had suggested that acoustic data are a useful tool to identify cryptic species (Francis and Habersetzer, 1998; Francis *et al.*, 1999*b*; Kingston *et al.*, 2001; Thabah *et al*., 2006). This study sought to determine if differences in echolocation were consistent, had distinctive geographical patterns, and were congruent with observable, discriminating, morphometric characters.

Materials and Methods

Between May 2006 and September 2007, a series of bat surveys was conducted throughout Thailand. Bats were captured using four banks harp traps (Francis, 1989) and mist nets set across forest trails or at the entrance to caves. Hand nets were used within caves. A number of bats was collected as voucher specimens and preserved in 70% ethanol. Skulls were extracted and cleaned.

One hundred and thirty-three specimens of *R. stheno* (sensu Csorba *et al.*, 2003) were examined, including 102 specimens from Thailand held in the collections of the Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University (PSU-M); the Thailand Institute of Science and Technology Research (TISTR); Chiangdao Wildlife Research Station (CD) and the Thailand National Museum of Natural History (THNHM). In addition, five specimens from Myanmar (Harrison Institute, HZM); two from Cambodia (HZM); 14 from Vietnam (Vu Dinh Thong's collection and the Natural History Museum, London (BMNH)) and eight from Malaysia (BMNH and Senckenberg Forschungsinstitut und Naturmuseum (SMF)) were also studied. One hundred and six specimens of *R. malayanus* were examined including 81 from Thailand (PSU(NHM) and BMNH); 15 from Myanmar (HZM); one from Lao PDR (HZM); four from Vietnam (HZM and BMNH) and five from Malaysia (BMNH). Specimen localities are shown in Figs. 1 and 2 and the list of specimens examined is included in the Appendix.

Study Areas

Field surveys were conducted in the following localities:
1. Chiang Mai Province: field surveys took place in October 2006 in Chiangdao district (Fig. 3a). The area comprises mountains and scattered outcrops of limestone surrounded by cultivated flood plains. The natural vegetation is hill evergreen forest and mixed deciduous forest. Bats were captured from two sites: (1) Mae Ja cave in Pha Dang National Park (formerly Chiangdao National Park) (19º31'N, 98º50'E) [loc. G5, Fig. 1], which is the roost of *Rhinolophus stheno microglobosus*, *R. pusillus*, *R. coelophyllus* and *Miniopterus magnator*, (2) Pha Daeng cave in Sri Lanna National Park (19º20'N, 99º01'E) [loc. M16, Fig. 2] where *R. malayanus*, *R. pusillus*, *Hipposideros cineraceus* and *H. halophyllus* were collected.
2. Tak Province: a survey took place on 14 November 2006 at Manora cave (16º46'N, 98º39'E; 604 m a.s.l) [loc. G7, Fig. 1] in Mae Sot district. The cave is in a limestone hill surrounded by bamboo forest. Elsewhere the vegetation includes mixed deciduous and deciduous dipterocarp forest. Some 10,000 bats, primarily *Miniopterus medius*, were observed roosting in the second of two chambers. The other species were *Rhinolophus stheno microglobosus*, *R. coelophyllus*, and *Hipposideros larvatus.*
3. Loei Province: a survey took place in September 2007 in Phu Suan Sai National Park (Fig. 3b) in northern Na Haeo district (centre on 17°31'N, 101°30'E) [loc. G8, Fig. 1]. The area is mainly mountainous with a highest peak of 1,408 m a.s.l. The vegetation comprises lower montane, moist evergreen, dry evergreen, mixed deciduous and some dry dipterocarp forest (National Park, Wildlife and Plant Conservation Department, 2006). Eleven species were captured in harp traps set across trails: *Rhinolophus stheno microglobosus*, *R. affinis*, *R. lepidus*, *R. pusillus*, *Hipposideros larvatus*, *H. pomona*, *Miniopterus pusillus*, *Tylonycteris pachypus*, *Kerivoula hardwickii*, *K. kachinensis* and *K. titania.*
4. Petchabun Province: a field survey took place in September 2007 in Nam Nao cave (16°57'N, 101°30'E) [loc. G10, Fig. 1 and loc. M22, Fig. 2] in Nam Nao National Park, which is situated in the Petchabun Range. The Park's vegetation includes grassland and deciduous dipterocarp, mixed deciduous, dry evergreen, and pine forest. The cave is in a limestone mountain and comprises a large complex cavern with a subterranean stream. Twelve bat species were found: *Rhinolophus malayanus*, *R. stheno microglobosus*, *R. thomasi*, *R. affinis*, *R. pusillus*, *R. marshalli*, *R. luctus*, *R. pearsoni*, *Aselliscus stoliczkanus*, *Hipposideros pomona*, *H. armiger*, and *H. lylei.*
5. Kalasin and Mukdahan Province: a survey took place in September 2007 at Phu Pha San (16º38.6'N, 104º22'E) [loc. M31, Fig. 2] in Phu Sithan Wildlife Sanctuary, which is located on the southern part of the Phu Pan Range. The vegetation comprises mixed deciduous forest on the sandstone foothills, with dry evergreen and deciduous dipterocarp forest on the flattened summits. Two harp traps were set across a forest trail at 417 m a.s.l. *Rhinolophus malayanus* and *R. pusillus* were captured.
6. Ubon Ratchathani Province: a survey took place in September 2007 in Pha Taem National Park (Fig. 3d), which is located on the west bank of the Mekong River. The area is characterised by rugged sandstone mountains. There were two survey sites. (1) Camp ground (15º24'N, 105º30'E), [loc. M32, Fig. 2], the area is covered by deciduous dipterocarp forest with bamboo groves. Harp traps were set across a forest trail and five species were captured: *Rhinolophus malayanus*, *R. shameli*, *R. pusillus*, *Hipposideros larvatus* and *H. pomona*. (2) Patihan cave (15º35'N, 105º34'E) [also loc. M32, Fig. 2] is a large sandstone cavern, which is covered by a small patch of dry evergreen forest and surrounded by dwarf deciduous dipterocarp forest. *R. malayanus*, *R. shameli*, *H. pomona*, *H. larvatus* and *H. galeritus* were collected.
7. Nakhon Ratchasima Province: a survey took place in January 2007 at the Wang Nam Khieo Forestry Training Camp, Pak Thong Chai district (14º28'N, 101º56'E) [loc. M30, Fig. 2]. The underlying geology is sandstone and seven bat species were captured in two harp traps set across a forest trail in dry evergreen forest near a botanical garden: *Rhinolophus malayanus*, *R. coelophyllus*, *Hipposideros bicolor*, *H. larvatus*, *Myotis muricola*, *Cynopterus sphinx* and *Macroglossus sobrinus.*
8. Lop Buri Province: a survey took place in January 2007 at three sites on the east bank of the Chao Phraya River. The area is characterised by flood and alluvial plains and series of isolated limestone outcrops. (1) Ma Tok cave (14º54'N, 100º29'E) [loc. M27, Fig. 2] in Khao Samorkhon limestone outcrop, Ta Wung district (Fig. 3c). The outcrop is covered by secondary forest and surrounded by rice fields and small villages. *Rhinolophus malayanus* and *R. pusillus* were caught in a harp trap set above the cave entrance. *R. malayanus*, *R. coelophyllus*, *R. pusillus* and *Hipposideros halophyllus* were captured in a separate trap set across a trail which runs between the foothills and a rice field (14º54'N, 100º30'E). (2) Wat Tham Suea Leung (14º49'N, 100º47'E) [loc. M28, Fig. 2] is situated in a rugged limestone mountain, which is covered with mixed deciduous forest and bamboo groves. It is surrounded by rice and corn fields and villages. A harp trap was set between bamboo groves at the base of the hill and *R. malayanus* and *H. larvatus* were collected. (3) Khao Don Dueng (15º09'N, 100º37'E) [loc. G13, Fig. 1 and loc. M26, Fig. 2] in Ban Mi district is a large limestone outcrop surrounded by mixed deciduous forest and

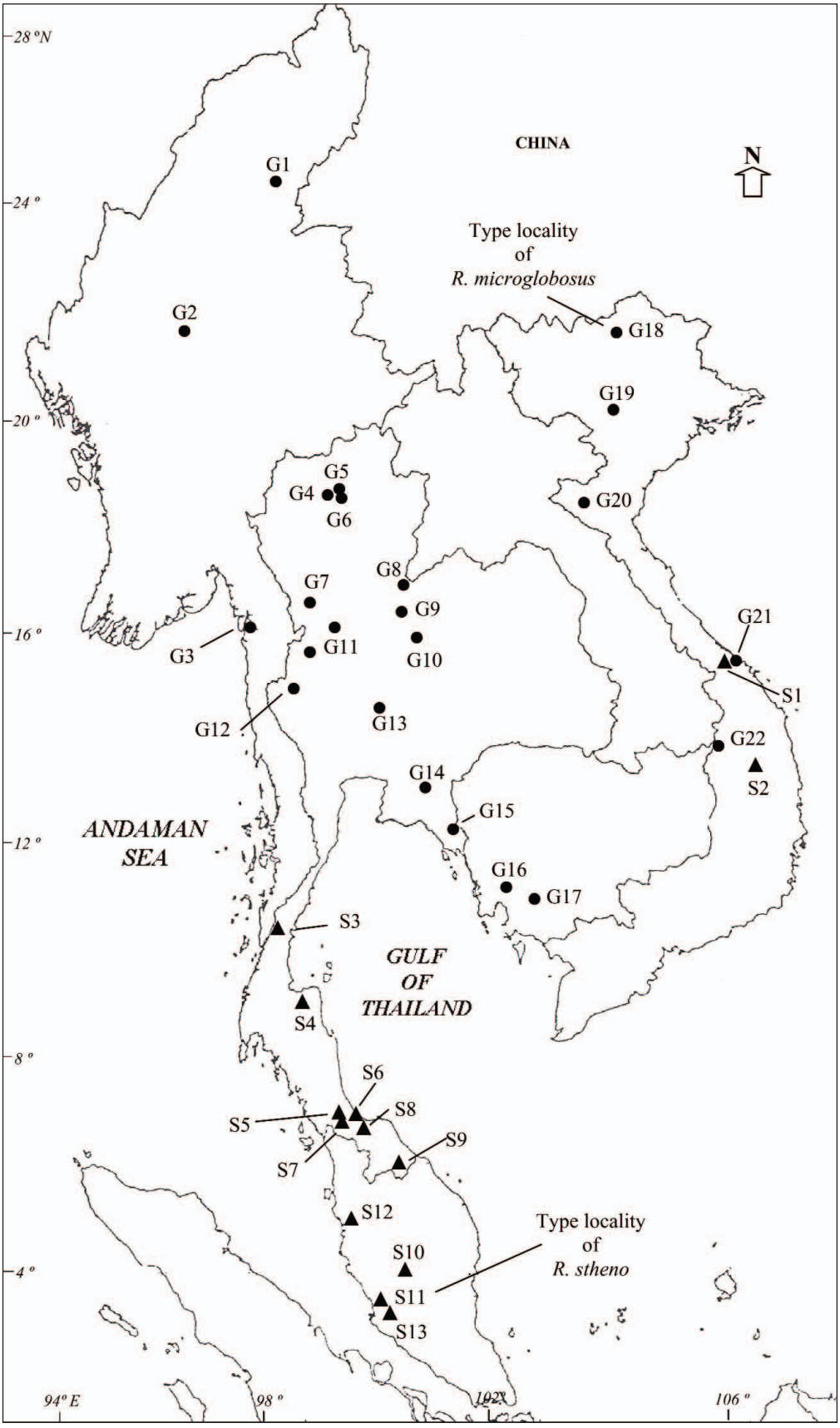

FIG. 1. Localities of *R. microglobosus* (circles) and *R. stheno* (triangles). Locality information and specimen numbers are included in the Appendix

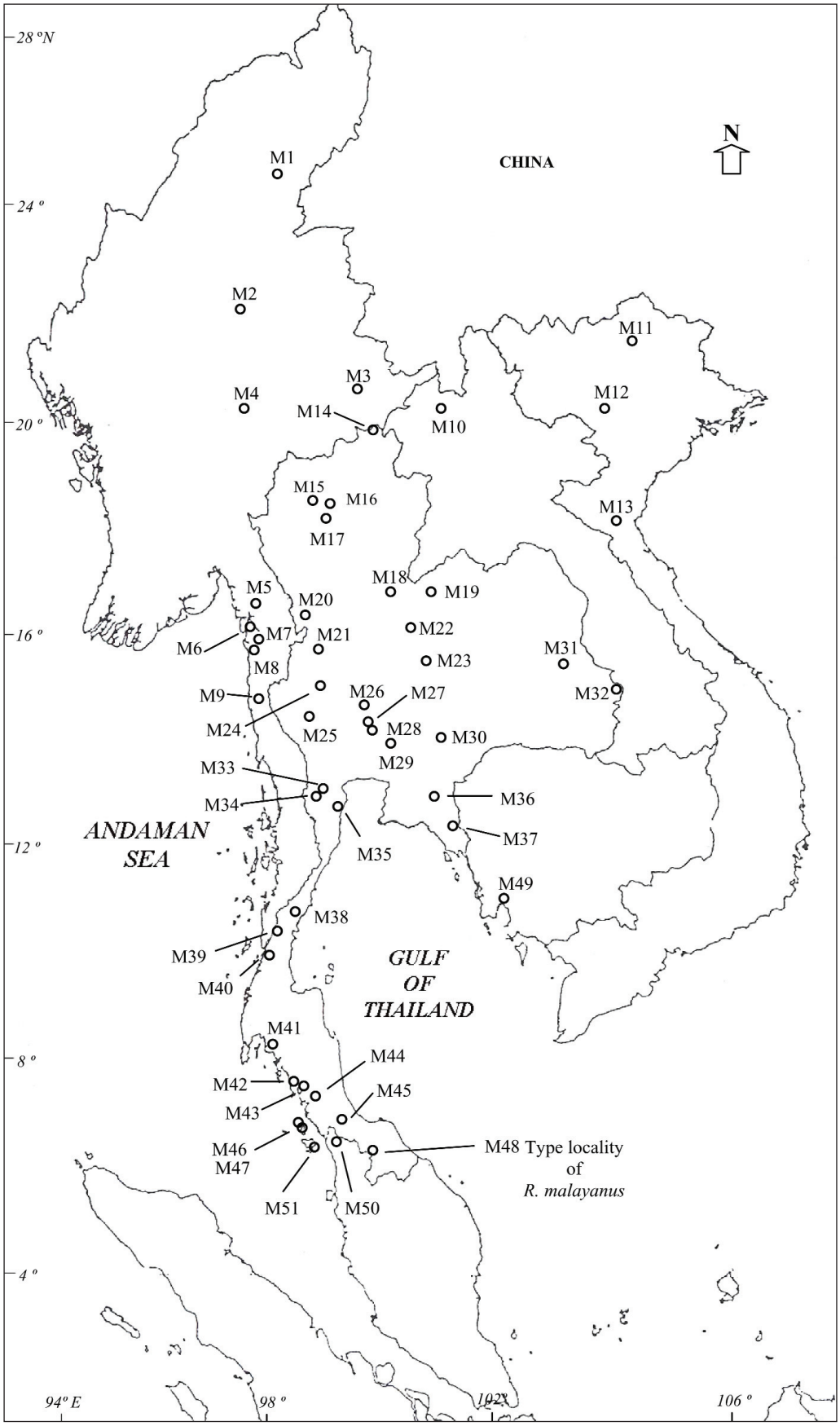

FIG. 2. Localities of *R. malayanus*. Locality information and specimen numbers are included in the Appendix

villages. Three harp traps were set across trails and eight species were captured: *R. malayanus*, *R. stheno microglobosus*, *R. pusillus*, *R. coelophyllus*, *H. pomona*, *H. halophyllus*, *H. cineraceus*, and *H. larvatus*.

9. Sara Buri Province: a survey took place in January 2007 at Wat Tham Phra Phothisat, Tab Kwang (14º34'N, 101º08'E) [loc. M29, Fig. 2], which is in a large limestone outcrop and comprises a complex of caves and caverns (Fig. 3e). It is surrounded by a patch of mixed deciduous forest with bamboo. Two harp traps were set at the base of the hill across a forest trail that leads to the caves and six species were found: *Rhinolophus malayanus*, *R. pearsoni*, *R. coelophyllus*, *R. thomasi*, *Myotis siligorensis* and *Tylonycteris pachypus.*

10. Ratchaburi province: a survey in February 2007 took place at two sites in Photharam district. (1) Khao Bin cave (13º35'N, 99º40'E) [loc. M34, Fig. 2] is a complex of caves, now used for tourism, which is situated in a large limestone outcrop, surrounded by mixed deciduous forest and villages. A harp trap was set at the main entrance to the cave and another between groves of bamboo. Four species were captured: *Rhinolophus malayanus*, *R. thomasi*, *H. cineraceus* and *H. pomona.* (2) Khao Nom Tai (13º42'N, 99º45'E) [loc. M33, Fig. 2] is a large cavern in a limestone outcrop. It is in a township and surrounded by a narrow strip of mixed deciduous forest. Two harp traps were set across a trail which runs around the outcrop, near bamboo groves. Five species were collected: *R. malayanus*, *R. pusillus*, *R. coelophyllus*, *R. thomasi* and *H. larvatus.*

11. Pet Buri Province: a survey took place in February 2007 at Khao Yoi Hill (13º14'N, 99º49'E) [loc. M35, Fig. 2] in Khao Yoi district. Khao Yoi Hill is a large, steeply-scarped limestone outcrop, which contains a complex of caves, modified for tourism and surrounded by local roads and patches of mixed deciduous forest. Eight species were captured in harp traps: *Rhinolophus malayanus*, *R. coelophyllus*, *R. pusillus*, *Hipposideros bicolor*, *H. halophyllus*, *H. cineraceus*, *H. larvatus* and *Myotis siligorensis.*

12. Chumporn Province: surveys took place in October 2006 and January 2007 at Silawan cave (10º41'N, 99º14'E) [loc. M38, Fig. 2] in Pathiu district. The cave is in a limestone outcrop surrounded by deciduous forest and agricultural land, including pineapple and rubber plantations. Nine species were captured: *Rhinolophus malayanus*, *R. lepidus*, *H. armiger*, *H. cineraceus*, *H. bicolor*, *H. larvatus*, *H. galeritus*, *Emballonura monticola*, *Myotis siligorensis* and *Tylonycteris pachypus.*

13. Ranong Province: a survey took place in January 2007 at Knaddai cave (19º21'N, 98º43'E) [loc. S3, Fig. 1 and loc. M39, Fig. 2] in La Oun district in the 'Isthmus of Kra' (Fig. 3f). The cave is in a limestone outcrop and surrounded by mixed deciduous forest and a public park. Seven species were present: *Rhinolophus malayanus*, *R. stheno*, *R. affinis*, *Hipposideros galeritus*, *H. armiger*, *H. lekaguli*, *Megaderma spasma*, *Myotis siligorensis* and *Eonycteris spelaea.*

14. Krabi Province: a short survey was conducted in the area of Sang Phet cave (8º09'N, 98º53'E) [loc. M41, Fig. 2] in Khao Phanom district in September 2006. The area is characterised by rugged limestone mountains, mixed deciduous forest, and agricultural plains, including palm and rubber plantations. Four species were captured: *Rhinolophus malayanus*, *R. coelophyllus*, *Hipposideros bicolor* and *H. turpis.*

15. Satun Province: a survey took place in June 2006 at two sites in Manang district. (1) Chet Kot cave (7°05'N, 99°53'E) [loc. M43, Fig. 2] is situated in a limestone outcrop surrounded by villages and rubber plantations. A harp trap was set across a road which led to the cave entrance. Five species were captured: *Rhinolophus malayanus*, *R. affinis*, *Hipposideros bicolor*, *H. armiger* and *H. larvatus.* (2) Wang Saithong waterfall (7°05'N, 99°54'E) [loc. M44, Fig. 2] is in limestone and surrounded by moist evergreen forest and human habitation. Two harp traps were set across a forest trail and four species were collected: *R. malayanus*, *H. bicolor*, *H. armiger* and *Nycteris tragata.*

16. Songkla Province: surveys took place between March and December 2006 at three sites in Hat Yai and Rattaphum district. (1) Khao Rak Kiat cave complex (7º04'N, 100º15'E) [loc. S5, Fig. 1] is in a limestone outcrop, and surrounded by a township, paddy fields and a narrow strip of secondary forest, dominated by *Cassia siamensis.* Five species were collected in two harp traps: *Rhinolophus stheno*, *R. affinis*, *Hipposideros bicolor* and *Miniopterus medius.* (2) Boripat waterfall (7º01'N, 100º08'E) [loc. S6, Fig. 1] is in lowland evergreen and mixed deciduous forest, fruit orchards and a village. One harp trap was set across a forest trail and another next to a bridge that crosses a stream. Nine species were found: *R. stheno*, *R. affinis*, *R. pusillus*, *R. robinsoni*, *H. larvatus*, *H. bicolor*, *H. cineraceus*, *Myotis horsfieldii* and *Hesperoptenus blanfordi.* (3) Khao Tieb cave (6º60'N, 100º17'E) [loc. S7, Fig. 1] is situated in a small limestone outcrop surrounded by a rubber plantation. Four species were found: *R. stheno*, *R. affinis*, *R. lepidus* and *Miniopterus pusillus.* (4) Ma Kling waterfall (7º02'N, 100º12'E) [loc. M45, Fig. 2] in a limestone area. Two harp traps were set across forest trails and a mist net in the transition zone between mixed deciduous forest and a rubber plantation. Eight species were captured: *R. malayanus*, *R. stheno* (although no specimens taken), *R. robinsoni*, *H. larvatus*, *Kerivoula hardwickii*, *Cynopterus sphinx*, *C. brachyotis*, and *Megaerops ecaudatus.* Echolocation calls of *R. malayanus* and *R. stheno* were recorded.

Measurements

Measurements were taken with a digital caliper, following Bates and Harrison (1997) and Csorba *et al.* (2003). They included: FA: forearm length, from the extremity of the elbow to the extremity of the carpus with the wings folded; EAR: ear length, from the lower border of the external auditory meatus to the tip of the pinna; HB: head and body length, from the tip of the snout to the base of the tail, dorsally; TAIL: tail length, from the tip of the tail to its base adjacent to the anus; TIBIA: length of tibia, from the knee joint to the ankle; HF: from the extremity of the heel behind the os calcis to the extremity of the longest digit, not including the claws; 5MT: fifth metacarpal, from the extremity of the carpus to the distal extremity of the metacarpal; 4MT, 3MT: as above but for the fourth and third metacarpals respectively; 3D1P: first phalanx of the third digit, taken from the proximal to the distal extremity of the phalanx; 3D2P: second phalanx of the third digit, taken from the proximal to the distal extremity of the phalanx; NL: noseleaf width, taken across the outer borders; GTL: greatest length of skull, taken from the tip of the premaxillae to the lambda; CCL: condylo-canine length, from an exoccipital condyle to the anterior alveolus of a canine; SL: skull length, taken from the occiput to the anterior part of the canine; ZB: zygomatic breadth, the greatest width of the skull across the zygomatic arches; BB: breadth of braincase, taken at the posterior roots of the zygomatic arches; MW: mastoid width, the greatest distance across the mastoid region; PC: post orbital constriction, taken at the narrowest point; C–M^3:

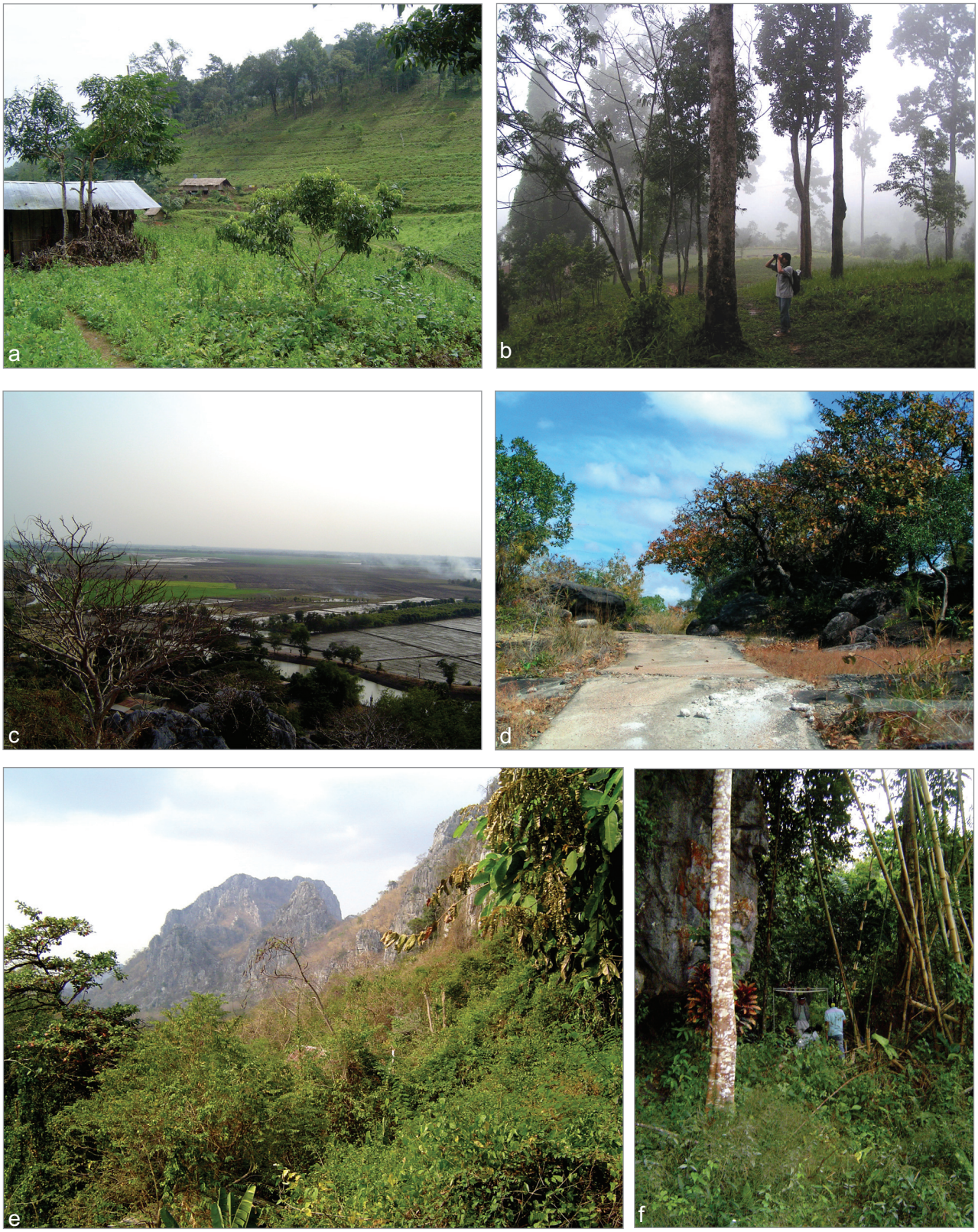

FIG. 3. Habitats of *R. malayanus*, *R. stheno* and *R. microglobosus*: a — agricultural area which surrounds an isolated limestone outcrop in Chiangdao District [loc. G5, Fig. 1]; b — hill evergreen forest in Phu Suan Sai NP, Loei [loc. G8, Fig. 1]; c — Khao Samorkhon limestone outcrop in Lop Buri, which is surrounded by paddy fields [loc. M27, Fig. 2]; d — dwarf-deciduous dipterocarp forest on sandstone mountain of Pha Taem National Park, Ubon Ratchathani [loc. M32, Fig. 2]; e — limestone mountain in Sara Buri Province [loc. M29, Fig. 2]; and f — limestone outcrop which surrounded by mixed deciduous forest in Ranong, peninsula Thailand [loc. S3, Fig. 1 and loc. M39, Fig. 2]

maxillary toothrow length, from the most anterior part of the upper canine to the back of the crown of the third upper molar; M^3–M^3: posterior palatal width, taken across the outer borders of the posterior upper molar; C^1–C^1: anterior palatal width, taken across the outer boarder of the upper canine; C–M_3: mandibular toothrow length, from the most anterior part of the lower canine to the back of the crown of the third lower molar; M: mandible length, from the most posterior part of the condyle to the most anterior part of the first lower incisors; ALSW (after Csorba *et al.*, 2003: figure iv): greatest rostral width, taken across the anterior lateral swellings (chambers), in dorsal view; AMSW (after Csorba *et al.*, 2003: figure iv): greatest width across the anterior median swellings (chambers) of the rostrum, in dorsal view. Body mass (W) was recorded using a Pesola 50 g scale and is given in grams. Drawings were prepared by PS with a camera lucida and a stereo microscope.

Echolocation Call Recordings and Analysis

Calls were recorded from individual hand held bats (hand held frequency, FMaxE), unless otherwise stated. This was to avoid the effect of the Doppler shift compensation (Table 1). A Pettersson D-240X ultrasound detector (in 10x time-expansion mode) was connected to a digital iRiver iHP-120 Multi-Codec Jukebox recorder. Calls were transferred to a laptop computer to determine the frequency of maximum energy (kHz) using the Power spectrum in BatSound Pro 3.31 (Pettersson Elektronik, AB). A sampling frequency of 44.10 kHz was used and produced a spectrogram using 1024 samples Fast Fourier Transform (FFT) with Hanning window. The CF portions of 10 calls from each individual were analysed. The echolocation calls of *R. malayanus* were recorded from throughout Thailand (87 specimens) and Cambodia (four specimens). In addition, the echolocation data of three specimens from Myanmar were received from Sébastien Puechmaille. In *R. stheno* (sensu Csorba *et al.*, 2003), the echolocation calls were also recorded from throughout Thailand (66 specimens). Additional data from Myanmar (four specimens) were also received from Sébastien Puechmaille. Statistical comparison between the frequency of calls for male and female specimens was conducted using a two way ANOVA.

Results

Echolocation

Echolocation calls were recorded at 42 localities in Thailand and Cambodia. At ten localities, the hand held frequency of males and females were compared (Table 1). No significant variation in frequency between the sexes was found in all three taxa (two-way ANOVA, $F_{1, 148} = 0.125$, $P = 0.725$).

In *R. stheno* (sensu Corbet and Hill, 1992), there was well marked geographical variation in acoustic characters (Fig. 4). All specimens from peninsular Thailand had a hand held frequency of between 85 and 88 kHz. In *R. stheno microglobosus*, north of the peninsular Thailand, the frequency was 92 to 101 kHz. There was no overlap in the frequency between

Table 1. Comparison of acoustic calls between males and females of *R. malayanus*, *R. stheno* and *R. microglobosus*. Locality codes (M, S and G) are linked to Figs. 1 and 2, and the Appendix. The mean, SD, minimum and maximum are given. Sample sizes are in brackets

Locality	Hand held frequencies (kHz)		Hand release frequencies (kHz)	
	♂♂	♀♀	♂♂	♀♀
	R. malayanus			
Nam Nao NP., Petchabun; loc. M22	76.8, 76.8	78.4 ± 1.0	–	76.9
	[2]	(77.7–79.6) [3]	–	[1]
Pha Taem NP., Ubon Ratchathani; loc. M32	82.7 ± 0.7	83.2 ± 0.6	81.3 ± 0.5	81.3 ± 0.9
	(82.0–83.3) [4]	(82.3–84.2) [13]	(80.7–81.7) [3]	(79.9–83.2) [12]
Phra Phothisat cave, Sara Buri; loc. M29	80.4	80.4	–	–
	(78.6–81.6) [7]	(80.0–80.7) [3]	–	–
Knaddai cave, Ranong; loc. M39	88.1 ± 0.6	89.3 ± 1.2	–	–
	(87.7–88.8) [5]	(87.7–90.7) [4]	–	–
Ma Kling waterfall, Songkla; loc. M45	87.2 ± 0.9	88 ± 0.4	85.3 ± 1.1	85.9 ± 0.7
	(85.4–88.2) [7]	(87.5–88.3) [3]	(83.7–86.6) [6]	(85.1–86.3) [3]
	R. stheno			
Knaddai cave, Ranong; loc. S3	88.1 ± 0.2	88.2, 88.2	85.9	–
	(87.7–88.2) [7]	[2]	[1]	–
Boripat Waterfall, Songkla; loc. S6	86.5 ± 0.4	86.1 ± 0.7	–	–
	(85.9–86.8) [4]	(85.4–86.3) [5]	–	–
Ma Kling waterfall, Songkla	86.3	86.3, 86.6	84.6	86.1, 86.2
	[1]	[2]	[1]	[2]
	R. microglobosus			
Mae Ja cave, Chiang Mai; loc. G5	94.7 ± 0.4	94.6 ± 0.2	–	–
	(94.1–95.0) [5]	(94.5–95.0) [5]	–	–
Phu Suan Sai NP., Loei; loc. G8	100.3	98.9 ± 1.2	–	98.8
	[1]	(97.7–99.6) [5]	–	[1]

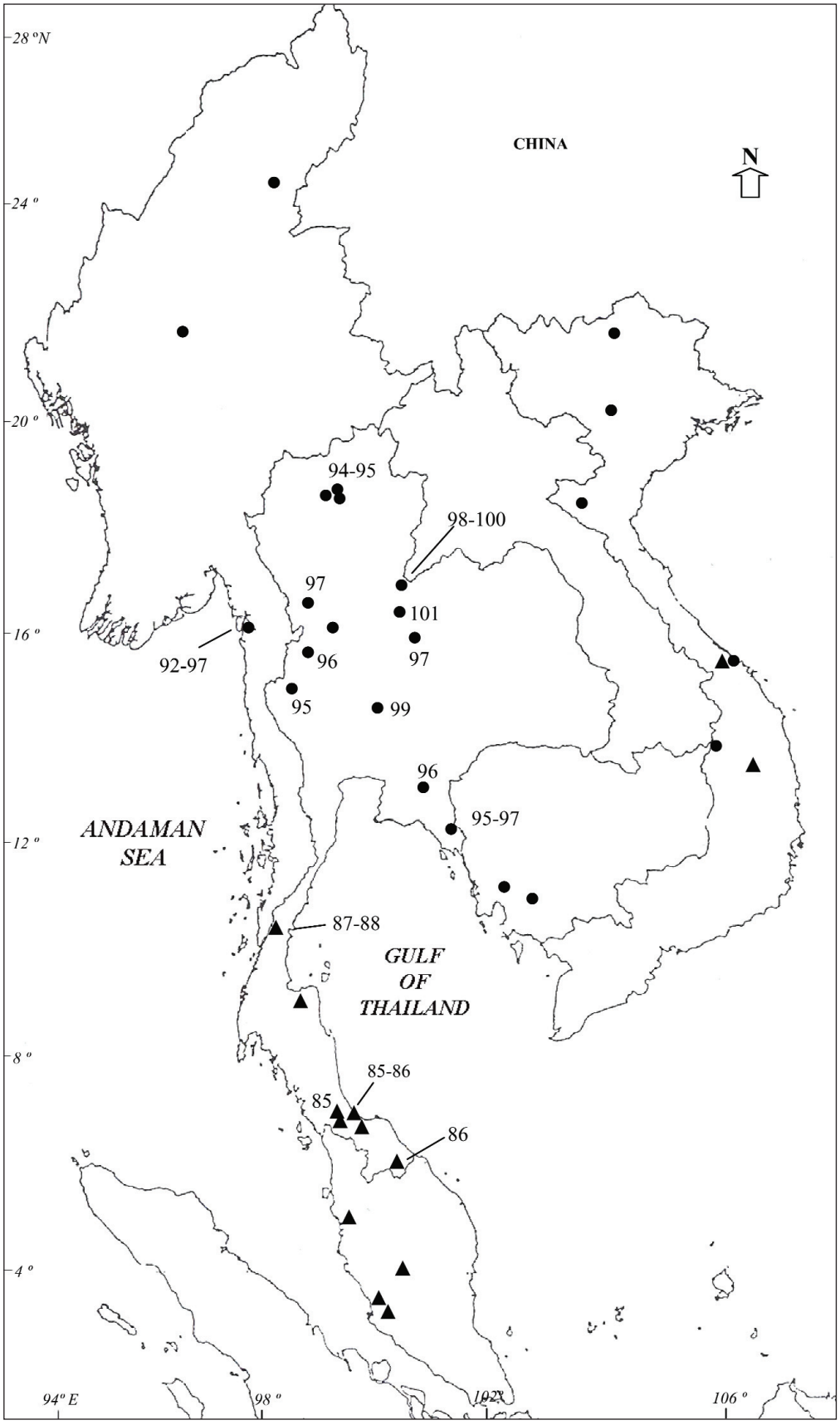

FIG. 4. Echolocation call frequencies (in kHz) of *R. microglobosus* (circles) and *R. stheno* (triangles). Locality information is included in the Appendix

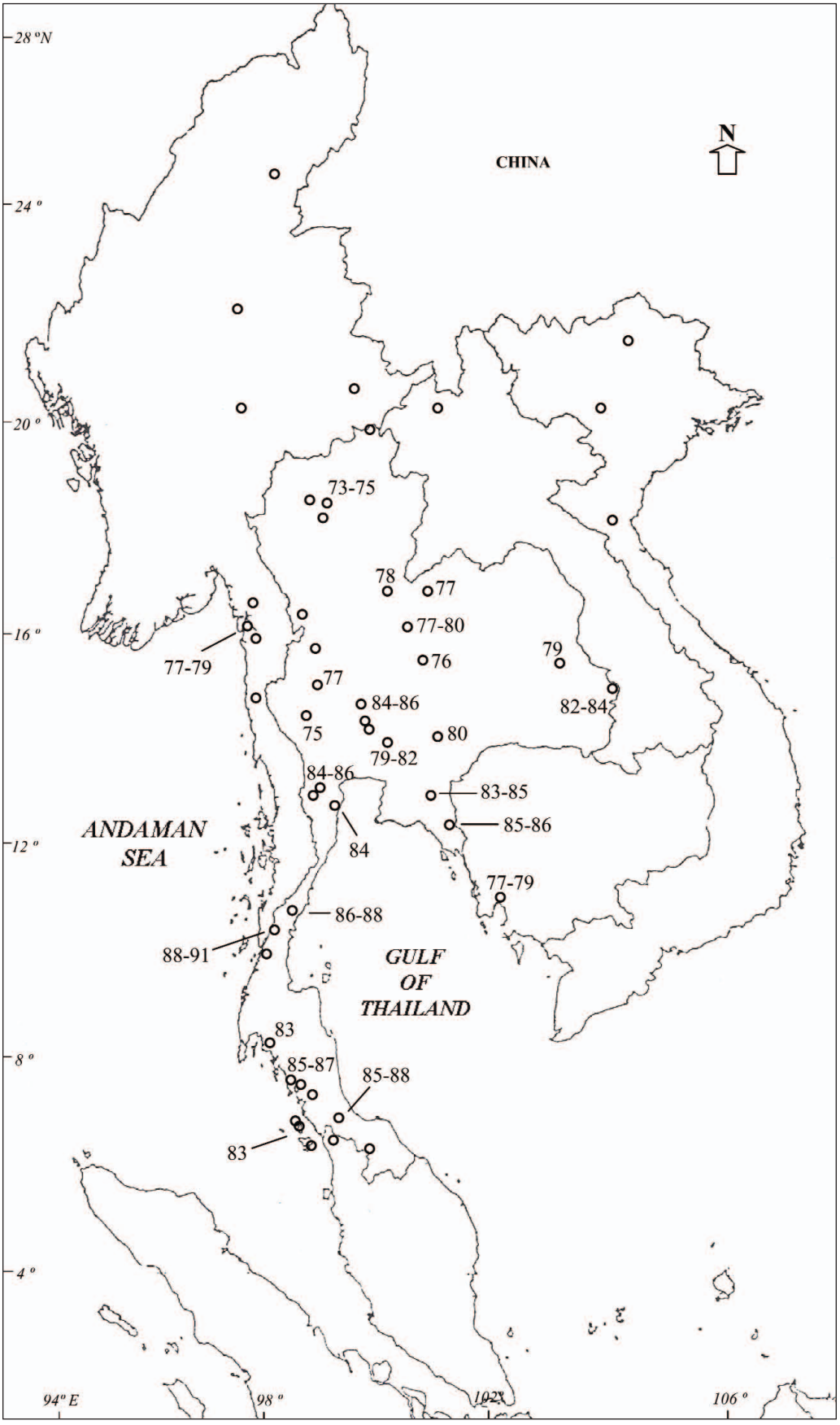

FIG. 5. Echolocation call frequencies (in kHz) of *R. malayanus*. Locality information is included in the Appendix

the two geographically separated populations. In *R. malayanus*, there was also geographical variation in call frequency (Fig. 5). All individuals in peninsular Thailand have a hand held frequency of between 83 and 91 kHz. In northern Thailand, north of latitude 16°N, all frequencies were between 73 and 80 kHz. In the zone between 12° and 16°N (and Cambodia), two distinct populations, with two different phonic types, appeared to be present. One population has a hand held frequency of 75 to 82 kHz and another of 82 to 86 kHz. Although individuals exhibiting these different frequencies were not found at the same site, they were found in populations that were close to one another, for example M25 (75 kHz) and M26 (84–86 kHz) are 166 km apart.

As a diagnostic character, echolocation calls cannot be used to differentiate between *R. stheno* and *R. malayanus* (Figs. 4 and 5) in peninsular Thailand. However, in Thailand north of the peninsula and potentially in southeast Myanmar and Cambodia (although data in these latter areas are still scarce), it is apparent that both phonic types of *R. malayanus* are distinguishable from *R. s. microglobosus* (sensu Csorba *et al.*, 2003).

Morphometrics

As with echolocation, metric data generally supported the division of *R. stheno* (sensu Csorba *et al.*, 2003) into two populations. Specimens from peninsular Thailand and Malaysia averaged larger in 28 of the 29 external and cranio-dental measurements as compared to *R. stheno microglobosus* from north of latitude 12°N ($P < 0.01$) (Tables 2 and 3). The exception was tail length. Differences in size between the larger southern and smaller northern populations were also reflected in a difference in the morphology of the rostrum. All specimens of *R. stheno* in peninsular Thailand and Malaysia have well developed anterior median rostral chambers (swellings), contrasting strongly with the less inflated posterior chambers (Fig. 6a). In 54 of 56 specimens examined from north of the Isthmus of Kra, the rostrum is less well developed anteriorly (Fig. 6b). The exceptions to this general rule are two specimens from two localities in central Vietnam, Bach Ma National Park (loc. G21, S1, Fig. 1) and Kon Ka Kinh (loc. S2, Fig. 1), in which, despite their geographical location, the rostra and cranial size are similar to those from the peninsular. At Bach Ma N.P., a specimen of the northern form (less developed rostrum and smaller skull) was also found. In terms of morphology, it appears that within the study area, the range of *R. s. stheno* is disjunct with the primary population in southern Thailand and peninsular Malaysia and a secondary, apparently isolated population in central Vietnam. This latter population overlaps with that of *R. s. microglobosus* (sensu Csorba *et al.*, 2003).

TABLE 2. External measurements (in mm) of *R. malayanus, R. stheno* and *R. microglobosus* (specimens listed in the Appendix) including the length of forearm (FA); ear (EAR); head and body (HB); tail (TAIL); tibia (TIBIA); hind foot (HF); the fifth, fourth and third metacarpal (5MT, 4MT and 3MT); first and second phalange of the third digit (3D1P, 3D2P) and their ratio (3D1P/3D2P); noseleaf width (NL). Body mass (W) is in g. Peak frequency at maximum energy (FmaxE: hand held) in kHz. For male and female specimens, the mean, ± SD, minimum and maximum are given. Sample sizes are in brackets

Species and sex	FA	EAR	HB	TAIL	TIBIA	HF	5MT	4MT
R. stheno (♂♂)	45.2 ± 1.1	17.7 ± 1.1	51.8 ± 3.1	17.4 ± 1.9	21.3 ± 0.6	9.2 ± 0.5	35.3 ± 1.03	4.7 ± 0.8
	43.2–48.1	15.4–19.5	45.5–56.8	12.9–21.4	20.4–22.7	8.2–9.9	33.3–37.5	33.2–36.3
	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]
R. stheno (♀♀)	45.2 ± 1.0	17.1 ± 1.0	50.3 ± 3.0	17.3 ± 1.5	20.9 ± 0.6	8.9 ± 0.6	35.1 ± 0.8	34.8 ± 0.9
	43.5–46.6	15.1–18.9	45.7–55.4	13.7–19.1	19.8–21.9	7.5–10.0	33.6–36.4	33.2–36.5
	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]
R. microglobosus (♂♂)	44.0 ± 1.2	15.1 ± 0.9	44.7 ± 4.3	18.1 ± 1.8	20.8 ± 1.1	8.0 ± 0.6	34.2 ± 1.0	33.9 ± 1.0
	41.4–46.3	13.2–17.3	39.9–60.1	14.5–22.4	17.9–22.8	6.0–9.0	32.1–36.2	32.4–36.0
	[37]	[37]	[37]	[37]	[32]	[37]	[32]	[32]
R. microglobosus (♀♀)	43.8 ± 1.2	15.9 ± 1.0	43.1 ± 2.0	18.7 ± 1.2	20.6 ± 0.7	8.3 ± 0.5	33.8 ± 1.1	33.5 ± 0.9
	41.7–45.5	14.5–17.6	39.9–46.4	17.1–22.0	19.4–21.8	7.4–9.5	32.3–35.8	32.3–35.4
	[16]	[16]	[16]	[16]	[15]	[16]	[15]	[15]
R. malayanus (♂♂)	41.0 ± 1.1	16.4 ± 1.1	46.4 ± 4.0	21.5 ± 2.0	17.2 ± 0.6	7.2 ± 0.6	31.1 ± 0.8	31.7 ± 1.0
	38.8–43.4	12.7–19.3	37.4–55.8	17.7–26.0	15.4–18.6	5.8–9.6	29.6–32.9	28.6–33.7
	[64]	[64]	[64]	[64]	[63]	[64]	[63]	[63]
R. malayanus (♀♀)	40.9 ± 1.2	16.2 ± 0.8	45.8 ± 4.1	21.4 ± 2.4	16.8 ± 0.8	7.2 ± 0.7	31.0 ± 1.1	31.5 ± 1.0
	38.2–44.0	14.1–17.9	36.1–55.2	15.0–26.9	15.5–19.2	6.1–9.6	28.1–33.3	29.4–33.8
	[35]	[35]	[35]	[35]	[35]	[35]	[35]	[35]

In *R. malayanus*, although there was some geographical variation in size, for example larger specimens were seen at Nagamuak cave (loc. M8, Fig. 2) in southeast Myanmar, at Pha Daeng cave (loc. M16, Fig. 2) in northwest Thailand and at Lub Lae cave (loc. M24, Fig. 2) in western Thailand, there did not appear to be any particular pattern to this variability. In addition, there were some differences in rostral morphology, with for example, specimens from Ranong, southern Thailand (loc. M39, Fig. 2) having relatively uninflated anterior rostral chambers (Fig. 6d). However, acoustic, metric and morphological data are not congruent and there is no obvious geographical pattern, although in general lower frequency calls were associated with those specimens that were larger and had the broadest noseleaves (Fig. 7).

In terms of interspecific variation, the data highlighted a number of morphometric characters that can distinguish *R. malayanus* from the other two taxa. The sella of *R. malayanus* is larger with a squared off, rather than rounded tip (Fig. 8c). The median septum is noticeably narrower than that of *R. s. stheno* and *R. s. microglobosus* (Fig. 9). In the wing, the second phalanx of the third digit is relatively short, usually < 1.5 times the length of the first phalanx (Table 2). In *R. stheno* (sensu Csorba *et al.*, 2003, which includes *microglobosus*), it is equal to or exceeds 1.5. The tail of *R. malayanus* is longer than those of *stheno* and *microglobosus* but the tibia is shorter and the foot averages smaller. The skull of *R. malayanus* averages smaller than both the other taxa. It is shorter and narrower and with shorter upper and lower toothrows. However, the postorbital constriction is distinctly broader. The rostrum has more developed posterior chambers (swellings), which leads to a less stepped rostral profile, when viewed laterally (Fig. 6).

Systematic Section

The results indicate that there are at least three distinct taxa present within the study area. Specimens of *R. s. stheno* from the Thai-Malay peninsula compare favourably, in terms of external, cranial and dental morphology with the holotype of *R. stheno* Andersen, 1905, which was described from western peninsular Malaysia. Two specimens from south-central Vietnam are also provisionally referred to this taxon, although further morphometric, molecular and acoustic studies with additional material would be of considerable interest. Similarly, specimens from Thailand north of the peninsula, southeastern and eastern Myanmar, Cambodia and northern and central Vietnam agree closely with the holotype of *R. s. microglobosus* Csorba and Jenkins, 1998.

Since there are morphometric characters that are constant throughout their respective ranges that clearly discriminate between *stheno* and *microglobosus*, including in the apparent zone of overlap in central Vietnam and since, where known, there is also a significant difference in the echolocation call, the taxon *microglobosus*, previously treated as a subspecies, is here recognised as a distinct species, *R. microglobosus.*

In the case of *R. malayanus*, the taxonomic conclusions are less clear cut. In terms of echolocation,

TABLE 2. Continued

Species and sex	3MT	3D1P	3D2P	3D2P/3D1P	NL	W	FMaxE
R. stheno (♂♂)	33.5 ± 0.8	13.2 ± 0.5	22.5 ± 0.8	1.7 ± 0.1	8.1 ± 0.5	7.8 ± 0.9	86.8 ± 1.1
	32.0–35.7	12.2–14.3	20.9–24.2	1.6–1.9	7.4–9.0	6.9–10.0	85.0–88.2
	[21]	[21]	[21]	[21]	[19]	[18]	[18]
R. stheno (♀♀)	33.5 ± 0.8	13.1 ± 0.4	21.9 ± 0.9	1.7 ± 0.1	8.1 ± 0.5	7.6 ± 0.4	86.5 ± 1.0
	31.9–34.3	12.3–13.6	20.3–23.1	1.6–1.8	7.4–8.7	6.9–8.0	85.3–88.2
	[14]	[14]	[14]	[14]	[14]	[12]	[12]
R. microglobosus (♂♂)	32.5 ± 1.0	13.0 ± 0.6	21.4 ± 1.0	1.7 ± 0.1	7.6 ± 0.5	6.1 ± 1.0	96.2 ± 1.4
	30.3–34.7	12.0–14.0	18.8–22.7	1.5–1.8	6.8–8.4	5.0–9.0	94.1–100.7
	[32]	[32]	[32]	[31]	[29]	[23]	[23]
R. microglobosus (♀♀)	32.0 ± 1.0	12.9 ± 0.4	21.2 ± 1.0	1.6 ± 0.1	7.6 ± 0.4	6.3 ± 0.6	96.1 ± 1.1
	30.3–34.1	12.4–13.6	19.5–22.7	1.5–1.8	7.0–8.4	5.1–6.7	94.5–97.4
	[15]	[15]	[15]	[15]	[12]	[6]	[5]
R. malayanus (♂♂)	31.1 ± 0.8	12.0 ± 0.5	17.2 ± 1.0	1.4 ± 0.1	7.8 ± 0.5	6.4 ± 0.9	82.9 ± 4.4
	29.2–33.0	11.0–13.3	14.3–19.3	1.2–1.4	6.9–9.0	5.0–9.7	73.1–88.8
	[63]	[63]	[63]	[63]	[51]	[57]	[49]
R. malayanus (♀♀)	30.7 ± 1.0	11.8 ± 0.5	17.3 ± 0.8	1.5 ± 0.1	7.6 ± 0.3	5.8 ± 0.6	84.8 ± 3.0
	28.2–33.0	10.5–12.9	15.5–18.8	1.4–1.6	7.0–8.4	4.5–6.8	79.5–90.7
	[35]	[35]	[35]	[35]	[28]	[28]	[22]

TABLE 3. Cranial and dental measurements (in mm) of *R. malayanus*, *R. stheno* and *R. microglobosus* (specimens listed in the Appendix) including greatest length of skull (GTL); condylocanine length (CCL); skull length (SL); zygomatic breadth (ZB); breadth of braincase (BB); mastoid width (MW); postorbital constriction (PC); upper toothrow length ($C–M^3$); palatal width ($M^3–M^3$); anterior palatal width ($C^1–C^1$); lower toothrow length ($C–M_3$); mandible length (M); rostral width (across anterior lateral swellings (chambers) (ALSW); width across anterior median rostral swellings (chambers) (AMSW). For male and female specimens, the mean ± SD, minimum and maximum are given. Sample sizes in are brackets. * — measurements of the holotype

Species and sex	GTL	CCL	SL	ZB	BB	MW	PC	$C–M^3$	$M^3–M^3$	$C^1–C^1$	$C–M_3$	M	ALSW	AMSW
*R. stheno**	19.7	16.7	19.4	9.4	8.4	9.4	1.6	7.5	7.3	4.9	7.8	12.8	5.0	4.3
R. stheno (♂♂)	20.6 ± 0.4	17.3 ± 0.3	19.7 ± 0.2	9.7 ± 0.2	8.6 ± 0.2	9.4 ± 0.2	1.8 ± 0.1	7.6 ± 0.1	7.4 ± 0.1	5.0 ± 0.1	8.1 ± 0.2	13.3 ± 0.2	5.3 ± 0.1	4.4 ± 0.2
	19.5–21.3	16.9–18.3	19.3–20.4	9.2–10.0	8.3–8.9	8.8–9.7	1.6–2.0	7.4–8.1	7.1–7.6	4.7–5.3	7.8–8.3	12.9–13.7	5.1–5.5	4.1–4.6
	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]	[21]
R. stheno (♀♀)	20.4 ± 0.3	17.1 ± 0.2	19.4 ± 0.3	9.5 ± 0.1	8.4 ± 0.3	9.4 ± 0.2	1.8 ± 0.2	7.5 ± 0.1	7.3 ± 0.2	4.9 ± 0.2	7.9 ± 0.1	13.1 ± 0.2	5.1 ± 0.1	4.3 ± 0.1
	19.9–20.9	16.7–17.5	19.0–19.9	9.3–9.8	8.0–8.9	9.1–9.6	1.4–2.0	7.2–7.7	7.0–7.6	4.4–5.1	7.7–8.2	12.8–13.5	4.8–5.3	4.1–4.6
	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]	[14]
*R. microglobosus**	20.0	16.8	19.4	9.0	7.9	9.1	1.7	7.3	6.7	4.7	7.5	13.0	5.0	3.9
R. microglobosus (♂♂)	19.4 ± 0.4	16.2 ± 0.3	18.6 ± 0.3	9.0 ± 0.1	7.9 ± 0.1	8.9 ± 0.1	1.7 ± 0.1	7.1 ± 0.1	6.9 ± 0.2	4.5 ± 0.1	7.5 ± 0.1	12.3 ± 0.2	4.9 ± 0.1	3.8 ± 0.1
	18.5–20.1	15.7–16.8	18.0–19.2	8.6–9.3	7.5–8.2	8.7–9.1	1.4–2.0	6.8–7.3	6.6–7.1	4.2–4.9	7.2–7.8	11.7–12.7	4.7–5.3	3.4–4.0
	[38]	[39]	[38]	[38]	[38]	[38]	[38]	[38]	[38]	[38]	[38]	[36]	[38]	[38]
R. microglobosus (♀♀)	19.2 ± 0.4	15.9 ± 0.3	18.3 ± 0.3	8.8 ± 0.2	7.8 ± 0.1	8.8 ± 0.2	1.7 ± 0.1	6.9 ± 0.1	6.7 ± 0.2	4.5 ± 0.1	7.3 ± 0.1	12.2 ± 0.1	4.8 ± 0.1	3.7 ± 0.1
	18.3–19.8	15.1–16.7	17.8–18.7	8.5–9.1	7.6–8.1	8.6–9.1	1.5–1.9	6.6–7.2	6.5–7.0	4.3–4.8	7.0–7.5	12.0–12.5	4.7–4.9	3.5–4.0
	[16]	[18]	[16]	[16]	[16]	[16]	[16]	[16]	[16]	[16]	[16]	[16]	[16]	[16]
*R. malayanus**	17.9	15.4	17.6	8.9	7.7	8.2	2.6	6.8	6.9	4.3	7.0	11.6	5.2	4.3
R. malayanus (♂♂)	18.8 ± 0.5	15.8 ± 0.4	17.8 ± 0.4	8.8 ± 0.2	7.6 ± 0.2	8.4 ± 0.2	2.5 ± 0.1	6.9 ± 0.2	6.5 ± 0.2	4.3 ± 0.2	7.3 ± 0.2	12.2 ± 0.3	5.3 ± 0.1	4.2 ± 0.2
	17.9–20.2	15.1–16.7	17.1–19.0	8.2–9.6	6.8–8.3	8.0–8.7	2.1–2.8	6.5–7.3	5.8–7.0	3.5–4.7	6.6–7.9	11.5–12.9	5.0–5.5	3.9–4.7
	[57]	[66]	[59]	[59]	[60]	[59]	[60]	[60]	[59]	[60]	[59]	[58]	[60]	[60]
R. malayanus (♀♀)	18.4 ± 0.6	15.4 ± 0.4	17.5 ± 0.4	8.6 ± 0.3	7.4 ± 0.2	8.3 ± 20.0	2.5 ± 0.1	6.7 ± 0.2	6.5 ± 0.4	4.2 ± 0.2	7.1 ± 0.2	11.9 ± 0.3	5.1 ± 0.1	4.1 ± 0.2
	17.1–19.5	14.6–16.4	16.6–18.5	8.1–9.2	7.0–7.9	7.8–8.8	2.1–2.7	6.3–7.1	5.6–8.7	3.7–4.6	6.7–7.5	11.1–12.8	4.8–5.4	3.9–4.5
	[31]	[46]	[36]	[36]	[36]	[35]	[35]	[36]	[35]	[33]	[36]	[36]	[36]	[36]

there is circumstantial evidence that suggests there are two separate, phonic populations present in continental Southeast Asia between the latitudes of 12° and 16°N. However, as noted above, in terms of morphometrics there is no strong evidence to support this conclusion. In the absence of any supporting molecular data, it is here considered that *R. malayanus* should continue to be considered as a monotypic species, albeit one that exhibits two distinct phonic types.

All information provided below is based on data collected for this current project unless otherwise stated.

Rhinolophus stheno Andersen, 1905
Lesser brown horseshoe bat

R. stheno Andersen 1905: 91; Selangor, Malaysia

Description and Taxonomic Notes

External characters

This is a medium size horseshoe bat with a forearm length of 43.2–48.1 mm (Table 2). The tail is short and averages shorter than the tibia. In the wing, the fifth metacarpal is subequal or slightly longer than the fourth; the third is the shortest. The second phalanx of the third digit is long, 1.7 (1.6–1.9) times the length of the first phalanx. The wings are usually attached between 1 and 3 mm above the ankles. The ears are not greatly enlarged (Fig. 9a and 9b). The outer ring of the horseshoe is dark in comparison to the paler area around the nostrils; a supplementary noseleaf is clearly present. The connecting process is rounded. The sella is narrow, parallel sided or slightly concave in the mid-part and with a rounded tip (Fig. 8a). The lancet is long and broadly triangular. The median septum is broad (Fig. 9b). The hairs on the upperpart of the body are greyish to reddish-brown, the underparts essentially the same but usually much paler.

Cranial and dental characters

The skull has a condylo-canine length of 16.7–18.3 mm. The zygomatic width is equal to or only slightly exceeds the mastoid width (Table 3). The post orbital constriction is narrow, usually < 2.0 mm.

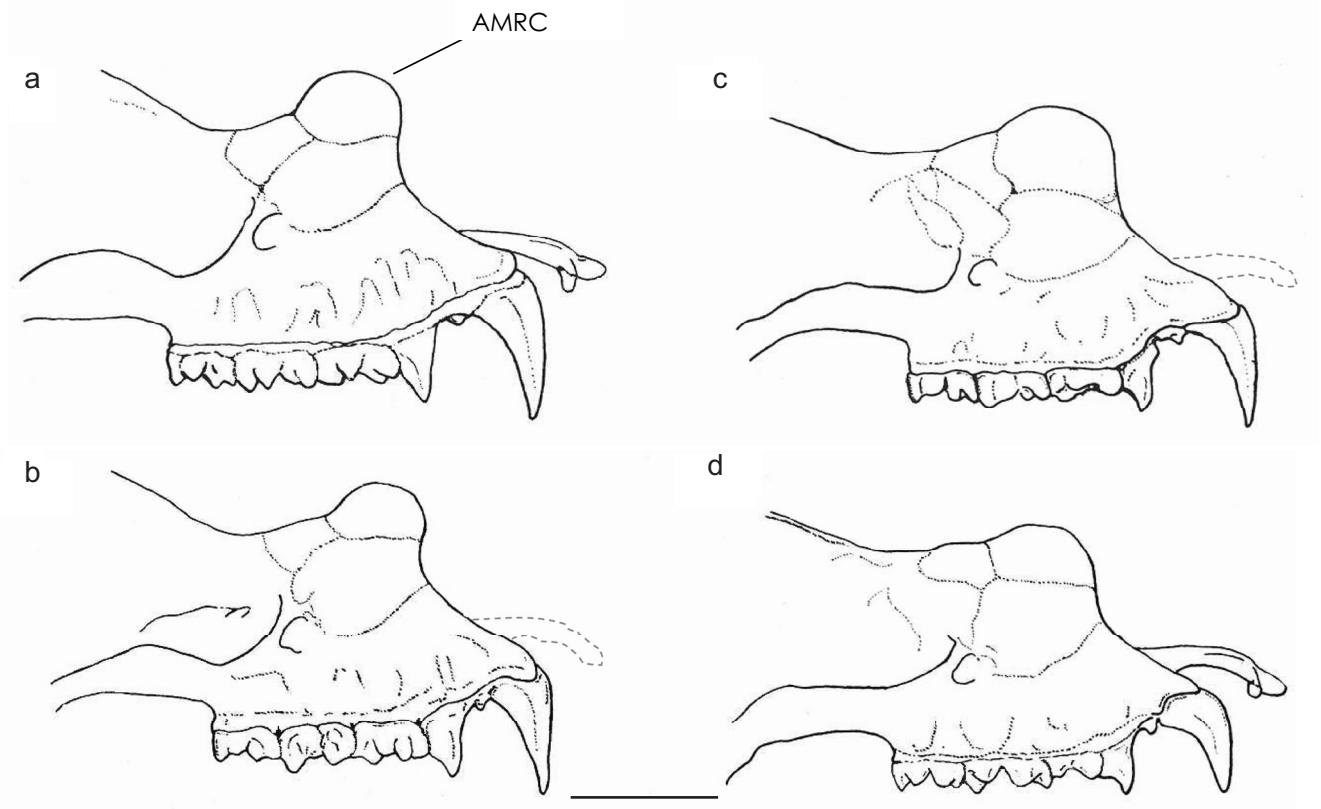

FIG. 6. Lateral view of anterior part of skulls (AMRC: anterior median rostral chamber). a — *R. stheno* (♂PSU-M06.44), Khao Tieb cave, Songkla [loc. S7, Fig. 1]; b — *R. microglobosus* (♂PSU-M06.95), Mae Ja cave, Chiang Mai [loc. G5, Fig. 1]; c — *R. malayanus* (♂PSU-M06.90), Pha Dang cave, Chiang Mai [loc. M16, Fig. 2]; d — *R. malayanus* (♂PSU-M07.61) from Knaddai cave, Ranong [loc. M39, Fig. 2]. Scale = 3 mm

The anterior median rostral chambers are distinctly elevated above the posterior ones (Fig. 6a). The small first upper premolar (P^2) is situated in the toothrow. The first (P_2) and the third (P_4) lower premolars are in contact, the second (P_3) is extruded.

Echolocation

Based on this study, the hand held frequency of individuals from peninsular Thailand is between 85–88 kHz (Fig. 4). According to Kingston *et al.* (2000), in Malaysia, it is 86 kHz.

Ecological notes

In Thailand, *R. stheno* was found in limestone karst areas, although this could reflect collecting bias. Within these areas it was collected in caves, mixed deciduous and lowland evergreen forest, agricultural areas and rubber plantations. In peninsular Malaysia, it was netted in hill forest (Kingston *et al.*, 2006) and also found in Batu Cave (SMF specimen). Pregnant females were collected in March in Thailand and from March to May in Malaysia, where lactating females were found from May to

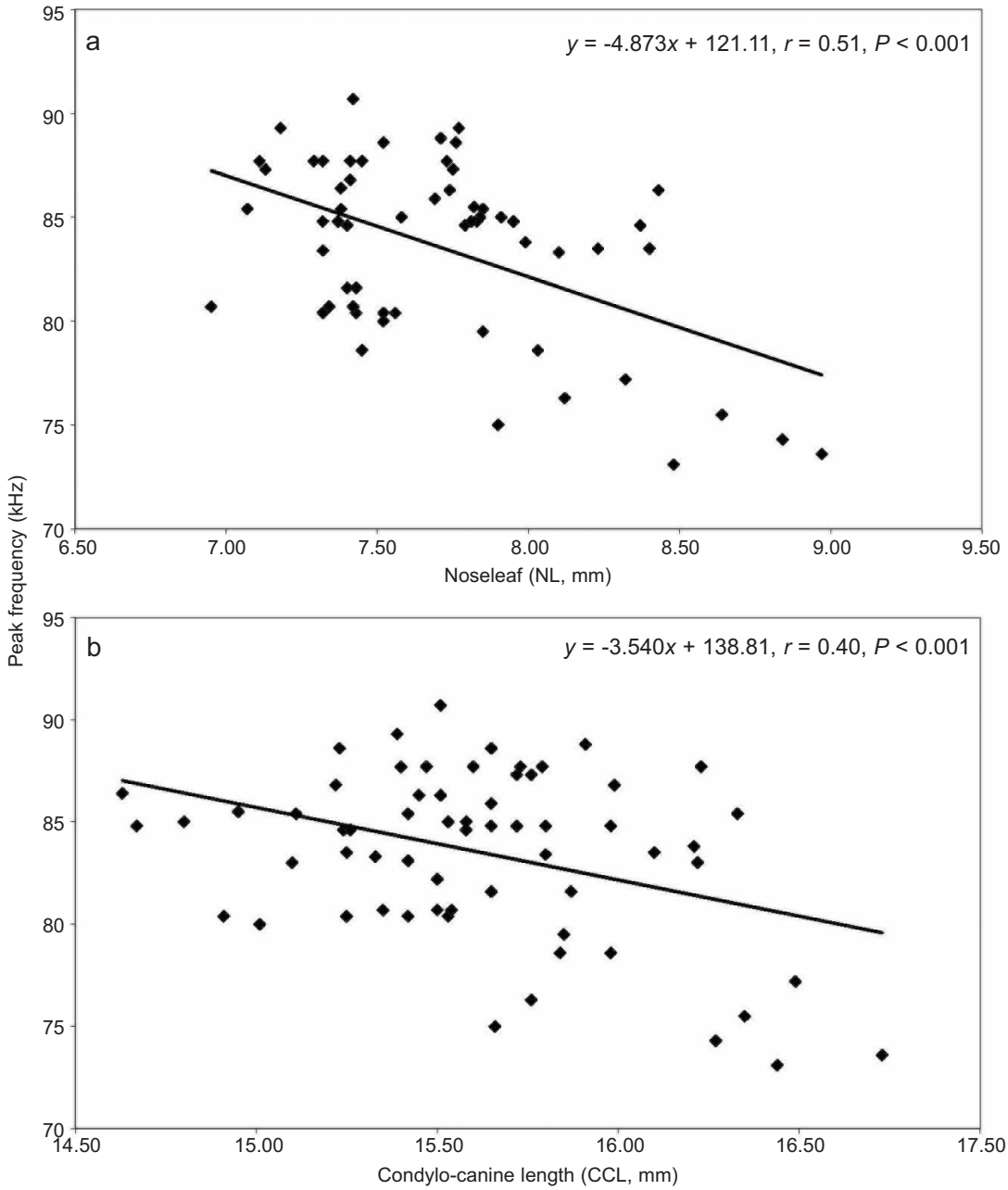

FIG. 7. Relationship between: a — noseleaf width and echolocation call frequency (n = 59), and b — condylo-canine length and echolocation call frequency (n = 64) of *R. malayanus*

July (Kingston *et al.*, 2006). In Vietnam, it co-exists with *R. microglobosus* in Bach Ma National Park in the Annamite Mountains and was found at 1,700 m a.s.l. on a mountain ridge in pristine montane forest at Kon Ka Kinh. In Thailand, it shares its roosts with a range of species (see Method section).

Distribution and conservation status

As here understood, it is restricted to the Thai-Malaysian peninsula and central Vietnam (Fig. 1: for details of localities see the Appendix). In addition, specimens from Sumatra and Java listed in Csorba *et al.* (2003) are also probably referable to this species. It is listed as 'Lower risk: least concern' by Hutson *et al.* (2001), Simmons (2005) and Boitani *et al.* (2006) based on the taxonomic understanding of Corbet and Hill (1992).

Rhinolophus microglobosus Csorba and Jenkins, 1998
Indo-Chinese lesser brown horseshoe bat

R. stheno microglobosus Csorba and Jenkins 1998: 208; Na Hang Nature Reserve, Tuyen Quang Province, Vietnam

Emended Diagnosis

The skull, with a condylo-canine length of 15.1–16.8 mm, is narrow, with a zygomatic breadth of 8.5–9.3 mm (Table 3). The anterior median chambers of the rostrum are narrow (3.4–4.0 mm) and elevated in comparison to the posterior chambers but not greatly inflated (Fig. 6).

Description and Taxonomic Notes

External characters

This species generally resembles *R. stheno* but averages smaller (except for tail length), with a forearm length of 41.4–46.3 mm (Table 2). In the wing, the fifth metacarpal is subequal with the fourth; the third is the shortest. The second phalanx of the third digit is long, 1.6 (1.5–1.8) times the length of the first phalanx. The wings are mostly attached between 1–3 mm above the ankles or occasionally at the ankles. The ears are not greatly enlarged (Fig. 9c). The horseshoe is narrower than that of *R. stheno*; a supplementary noseleaf is clearly present. As with *R. stheno*, the outer ring of the horseshoe is dark in comparison to the paler area around the nostrils. The connecting process is rounded; the lancet tall, triangular and straight-sided. The sella is similar to that of *R. stheno* (Fig 8b). In the pelage, the upper parts are greyish to yellowish-brown, the underparts pale brown.

Cranial and dental characters

The skull, with a condylo-canine length of 15.1–16.8 mm, averages smaller than that of *R. stheno*, although the holotype of *microglobosus* is a particularly large individual (Table 3). The zygomatic width is about equal to or only slightly exceeds the mastoid width; it is distinctly narrower than that of *R. stheno*. The post orbital constriction is usually < 2.0 mm. The anterior median rostral chambers are elevated in comparison to the posterior chambers (Fig. 6b), but are less inflated and narrower than those of *R. stheno*; the frontal depression is shallower. The small first upper premolar (P^2) is situated in the toothrow. The first (P_2) and the third (P_4) lower premolars are in contact, the second (P_3) is extruded.

Echolocation

Based on this study, a hand held frequency of between 94–101 kHz was recorded from Thailand north of Isthmus of Kra (12°N) (Fig. 4). Previously, Robinson *et al.* (1995) had reported 85–95 kHz from western Thailand based on a heterodyning QMC Mini Bat Detector. In Myanmar, frequencies

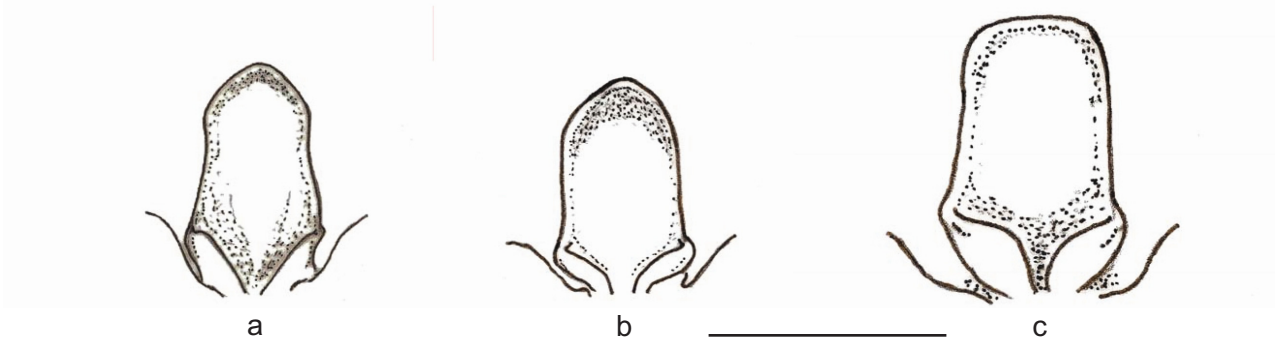

FIG. 8. Shape of sella. a — *R. stheno* (♂PSU-M07.46), Khao Tieb cave, Songkla; b — *R. microglobosus* (♂PSU-M06.27), Thung Slang Luang, Pitsanulok; c — *R. malayanus* (♂PSU-M07.44), Wat Tham Phra Phothisat, Sara Buri. Scale = 3 mm

FIG. 9. Face, ears and noseleaf of *R. stheno* (a and b); *R. microglobosus* (c, d) and *R. malayanus* (e, f). MS: median septum. Not to scale

of 92–97 kHz (S. Puechmaille, personal communication) and 101.5–101.7 kHz (Khin Mie Mie, 2004) have been recorded, and in Lao PDR, 95 kHz by C. M. Francis (personal communication).

Ecological notes

In Thailand, it was collected in the areas of limestone karst and lowland to hill evergreen forest (for further details see Methods section). Previously, a colony of approximately 1,200 individuals was found in western Thailand and torpid individuals were seen roosting during the day in July (Robinson *et al.*, 1995). In Myanmar, it was collected from the same caves as *R. malayanus* and *Aselliscus stoliczkanus* (Bates *et al.*, 2004). In Vietnam, it was found in an area of relatively undisturbed forest in Pu Mat (Hendrichsen *et al.*, 2001). In central Thailand, a pregnant female was collected in late February and lactating females in May.

Distribution and conservation status

As here understood, *R. microglobosus* is known from Thailand north of Isthmus of Kra (12°N), Myanmar, south Cambodia, north and central Vietnam, Lao PDR (Francis *et al.*, 1999*a*; Csorba *et al.*, 2003) and Yunnan, south-west China (Zhang *et al.*, 2005). This is the first record from Cambodia. A list of specimens is included in the Appendix. Its conservation status has not been assessed separately by the IUCN but only in conjunction with *R. stheno.*

Rhinolophus malayanus Bonhote, 1903
Malayan horseshoe bat

R. malayanus Bonhote 1903: 15; Biserat, Jalor, Thailand

Description and Taxonomic Notes

External characters

Rhinolophus malayanus is a small horseshoe bat with the forearm length of 38.2–44.0 mm (Table 2). The tail averages longer than that of *R. stheno* and *R. microglobosus* but the tibiae are considerably shorter. The wings are usually attached at the ankles or occasionally at the base of the metatarsals. The third, fourth and fifth metacarpals are almost the same length. The second phalanx of the third digit is short in comparison to *R. stheno* and *R. microglobosus*; it is 1.4 (1.2–1.6) times the length of the first phalanx. The ears are not greatly enlarged (Fig. 9e). The horseshoe (6.9–9.0 mm) is intermediate in width between that of *R. stheno* and *R. microglobosus*, and the secondary noseleaf is clearly present. In contrast to *R. stheno* and *R. microglobosus*, the outer ring of the horseshoe is not dark but pale, almost similar to the area around the nostrils (Fig. 9f). The connecting process is broadly rounded. The sella is relatively wide, almost parallel sided and with the tip broadly rounded (Fig. 8c). The lancet is triangular. The pelage is uniformly brown to reddish brown, paler on the belly.

Cranial and dental characters

The skull, with a condylo-canine length of 14.6–16.7 mm, averages smaller than that of *R. stheno* and *R. microglobosus* (Table 3). The zygomata slightly exceed the width of the mastoids and the post orbital constriction is broader than that of the other two taxa, usually exceeding 2.0 mm. The rostral chambers (swellings) are inflated, with the anterior median chambers usually extending down the side of the rostrum (Fig. 6c). The posterior chambers are more inflated than those of *R. stheno* and *R. microglobosus* ensuring that the anterior chambers look less abruptly elevated in lateral profile. The small first upper premolar (P^2) is situated in the toothrow. The second lower premolar (P_3) is slightly extruded or external to the toothrow.

Echolocation

Based on the current study, the hand held frequency shows considerable geographical variation. In peninsular Thailand, it is between 83 and 91 kHz (south of 12°N); in northern Thailand, north of latitude 16°N, all frequencies are between 73 and 80 kHz and in the zone between 12° and 16°N, in Thailand and Cambodia, two distinct populations, with two different phonic types, appear to be present. One population has a hand held frequency of 82 to 86 kHz and another of 75 to 82 kHz. Previously Robinson *et al.* (1995) and Robinson (1996) had recorded 75 kHz from western Thailand. In Myanmar, 76–79 kHz were recorded by Khin Mie Mie (2004) and S. Puechmaille (personal communication) and in Lao PDR, 75 kHz by C. M. Francis (personal communication).

Ecological notes

In Thailand, it was primarily collected in areas of limestone karst, where it roosted in caves and in sandstone mountains. Vegetation types included lowland mixed deciduous forest, hill evergreen forest and highly disturbed dry dipterocarp forest. It was also collected in agricultural areas, including rubber plantations. Its altitudinal range was 5 to 1,400 m a.s.l. In western Thailand, approximately 3,000 individuals were located roosting in a cave.

Torpid individuals were found roosting by day in July (Robinson *et al.*, 1995). In Cambodia, pregnant individuals were found in late February in lowland secondary evergreen forest. In Vietnam, it was also collected in limestone karsts areas (V. D. Thong, personal communication). In Myanmar, it was recorded in limestone outcrops, agricultural land and forest (Bates *et al.*, 2001). It was also found in heavily degraded forest and banana plantations in Lao PDR (Robinson and Webber, 1998).

Distribution and conservation status. It is known from Thailand, eastern Myanmar, Lao PDR, southern Cambodia, north Vietnam and the north of Malaysia (Appendix). Further records from Lao PDR are included in Francis *et al.* (1999*a*). Considered 'Lower risk: least concern' by Hutson *et al*. (2001), Simmons (2005) and Boitani *et al.* (2006). It was classified as 'Potentially at risk in Lao PDR' (Francis *et al*., 1999*a*).

Discussion

In general, the project gave conflicting views about the efficacy of using acoustic data alone to identify possible cryptic species. Initial echolocation studies of *R. stheno* (sensu Csorba *et al.*, 2003) from throughout continental and peninsular Thailand suggested the possible presence of two species on the basis of an average of 10 kHz difference in hand held frequency. In the case of *R. stheno*, this was confirmed by a suite of morphometric characters. However, in the case of *R. malayanus*, a similar divergence of 10 kHz between northern and southern populations is not considered here to represent specific divergence. Morphometric data gave no support to any division and it would appear that phonic differentiation and morphometric differentiation are not congruent in this taxon. This tends to support the view of Thabah *et al*. (2006) who suggested that drifts in call frequency resulting from geographical separation may theoretically lead to divergence in acoustic communication without concomitant changes in morphology. Subsequent studies of molecular data (already being undertaken at the Prince of Songkla University) will be of great interest to determine the extent of genetic differentiation of the two populations.

No difference was found between the echolocation calls of the two sexes. This is in contrast to the study of *Rhinolophus rouxii* by Neuweiler *et al*. (1987) but is comparable to similar findings observed by Heller and Helversen (1989) for other taxa. As might be predicted from many previous studies (Robinson, 1996; Francis and Habersetzer, 1998; Zhang *et al.*, 2000), *R. stheno*, with its larger body size has a lower hand held frequency call than the smaller *R. microglobosus.* In *R. malayanus*, there was a modest correlation between animal size, including noseleaf width and skull length, and call frequency (Fig. 7).

In contrast to *R. stheno* and *R. microglobosus*, individuals of *R. malayanus* with higher frequency calls were located in the central and southern part of the range and those with lower frequencies in central and northern part. This is contrary to what might be expected since normally, high relative humidity attenuates high frequency sound more than lower frequencies (Griffin, 1971; Hartely, 1989; Guillén *et al.*, 2000) and therefore it would be expected that the lower frequencies should be found in the more humid Thai-Malay peninsula, as is the case with *R. stheno.* Here it is possible that in *R. malayanus* foraging habitat may be a controlling factor. In less-cluttered microhabitats, bats use lower frequency calls to increase their detection ranges; higher call frequencies are better suited for foraging in background cluttered and highly cluttered space (Schnitzler and Kalko, 1998; Kingston *et al.*, 2001). Such cluttered spaces are typical of the under-storey of tropical rain forests and therefore it is possible that differences in frequency in *R. malayanus* may reflect microhabitat preferences. Alternatively, it may reflect random cultural drift in two isolated populations.

It has long been recognized that Thailand is subdivided into two zoogeographic subregions with the Indochinese subregion to the north and the Sundaic subregion to the south (Lekagul and McNeely, 1977; Corbet and Hill, 1992) with a transition zone in the Isthmus of Kra. Distribution patterns corresponding to this division have been observed in a range of biota including rodents (Mein and Ginsburg, 1997), insects (Corbet, 1941), reptiles (Inger and Voris, 2001) and plants (Woodruff, 2003). Initially, Wallace (1876) had placed the transition zone at 13–14°N, whereas Wells (1976) fixed the avifaunal transition zone at about 10°30'N, in the Isthmus of Kra. Subsequently, Hughes *et al*. (2003), based on forest birds, found a highly significant transition zone at 11–12°N, in the north of the peninsula.

The distribution patterns of the three species were of considerable interest since they strongly support the existing concepts of a subregional division. *R. microglobosus* is restricted to the Indochinese subregion and is not found further south in

the Thai-Malay peninsula. In contrast, *R. stheno* is primarily restricted to the peninsula (and elsewhere in the Sundaic subregion), but also appears to have a small isolated population in a mountain range in central Vietnam. This high mountain range, which is part of Annamite Mountains, is covered by evergreen forest and runs west-east from Laotian border to the east coast of Vietnam, and forms a biogeographical boundary between northern and southern Vietnam. It is the wettest part of Vietnam (Tordoff *et al.*, 2004). The presence of this latter population seems analogous to the situation in the freshwater prawn *Macrobrachium rosenbergii*, in which closely related populations are reported from peninsular Thailand and southern Vietnam (Bruyn *et al.*, 2005). In the case of *R. malayanus*, the phonic type with an echolocation call of between 73 and 82 kHz is entirely restricted to the Indochinese subregion, whereas the 82 to 90 kHz phonic type has a Sundaic distribution but also appears to have spread north into south-central Thailand and Cambodia.

Since molecular data are currently in the process of being analysed, it is perhaps inappropriate to speculate about possible vicariance events, or the time scales involved, that may have led to the speciation of *R. stheno* and *R. microglobosus*. However, it is known that frequent changes in global climates during the Pleistocene (and previous to that in the Pliocene and Miocene) had significant effects on both the vegetation and sea levels of the Indo-Malay peninsula. At times, the evergreen rain forest was restricted to a small number of refugia, whilst changes in sea level both exposed vast areas of the Sundaic shelf or led to inundations of the Isthmus of Kra (Woodruff, 2003; Bruyn *et al.*, 2005).

Today, the transition zone at 11–12° is characterized by a change from seasonal evergreen rain forest to mixed moist deciduous forest (Woodruff, 2003). Vegetation apart, there is no other clearly defined barrier to the movement of bat taxa and yet it seems to represent a barrier to the southern expansion of *R. microglobosus* and to the 73 and 82 kHz phonic type of *R. malayanus.* It would be of considerable interest to determine if other bat taxa have a similar distribution with such clearly defined Indochinese or Sundaic affinities. It would also be of interest to collect acoustic data from south-central Vietnam to ascertain the hand held frequencies of *R. stheno* and *R. microglobosus* at Bach Ma NP. and ascertain whether they correspond closely to those from these respective taxa elsewhere in their range.

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APPENDIX

Specimen localities and their geographical coordinates

Rhinolophus stheno

VIETNAM: S1 — Bach Ma NP., (16º12'N, 107.45'E): field no. T44 (IEBR); S2 — Kon Ka Kinh, Gai Lai, (14.19'N, 108.24'E): HZM.1.32327.

THAILAND: S3 — Knaddai Cave, La Oun, Ranong, (10º01'N, 98º50'E): PSU-M07.79–87; S4 — Khao Wong Cave, Klong Panom, Surat Thani, (approx. 8º50'N, 98º48'E): field no. SW00179, 00182 (TISTR); S5 — Khao Rak Kiat, Rattaphum, Songkla, (7º04'N, 100°15'E): PSU-M06.24, 06.107–109; S6 — Boripat, Rattaphum, Songkla, (7º01'N, 100º08'E): PSU-M06.52, 06.54–55, 06.58–59; S7 — Khao Tiab Cave, Hat Yai, Songkla, (6º59'N, 100º17'E): PSU-M06.42–47; S8 — Ton Nga Chang, Songkla, (6°55'N, 100º17'E): PSU-M05.44, 06.31; S9 — Bala, Hala-Bala, Narathiwat, (5º 48'N, 101º 49'E): PSU-M05.46.

MALAYSIA: S10 — Gunong Benom, Pahang, (approx 3°35'N, 102°15'E): BMNH 1967.1492, 1967.1533–34; S11 — Selangor, (Type locality of *R. stheno*) (3º30'N, 101º30'E): BMNH 1898.3.13.1, SMF 83.843; S12 — Maxwell's Hill, Taiping, Perak, (approx. 4º54'N, 100º42'E): SMF 88.436; S13 — Batu Cave, Kuala Lumpur (3º14'N, 101º41'E): SMF 91.116, 91.117

R. microglobosus

MYANMAR: G1 — Nanti Hill Forest, Bhamo Township, Kachin State, (24°34'N, 97°07'E): field no. MS6, HZM.6.35967; G2 — Sanite cave No.2, Wetwun Village, Pyin Ooo Lwin, Shan State, (22º06'N, 96º37'E): HZM.4.35114; G3 — Indian Single Rock Temple Cave, Mon State, (16º19'N, 97º43'E): field no. H21 (HZM)

THAILAND: G4 — Khimee Cave, Chiangdao, Chiang Mai, (19º21'N, 98º43'E): CD-B-0047–49, 0054–55, 0057, 0070; G5 — Mae Ja Cave, Chiangdao, Chiang Mai, (19º31'N, 98º50'E): PSU-M05.93, 06.94–98; G6 — Mae Pong Cave, Chiang Dao, Chiang Mai, (19º33'N, 98º 42'E): PSU-M05.59; G7 — Manora Cave, Mae Sot, Tak, (16º46'N, 98º39'E): PSU-M06.105–106; G8 — Phu Suan Sai NP., Na Haeo, Loei, (17°30'N, 100°57'E): PSU-M07.295–296; G9 — Thung Slang Luang, Nhong Mae Na, Pitsanulok, (16º 34'N, 100º 52'E): PSU-M06.27; G10 — Nam Nao Cave, Nam Nao, Petchabun, (16°57'N, 101°30'E): PSU-M07.297; G11 — East Thung Yai, Tak, (15°42N, 99°01E): THNHM 12–14; G12 — Kao Roi Rai Cave, Sangkla Buri, Kanchanaburi, (15º 07'N, 98º28'E): PSU-M05.127; G13 — Khao Don Dueng, Ban Mi, Lop Buri, (15º08'N, 100º36'E): PSU-M07.163; G14 — Bo-tong, Ang Runai, Chacherngsao, (13º11'N, 101º44'E): PSU-M05.128–137; G15 — Makok, Phliu, Chantaburi, (12º35'N, 102º15'E): PSU-M05.138–143.

CAMBODIA: G16 — Chumnoap-Areng, (11º38'N, 103º34'E): HZM.7.36484; G17 — Kirirom NP., Kompong Spev., (11º 20'N, 104º03'E): HZM.3.34173.

VIETNAM: G18 — Na Hang, (Type locality of *R. microglobosus*) (between 22º16' and 22º31'N, 105º22' and 105º29'E): BMNH 1997.360 [holotype], 1997.359, 1997.361; G19 — Xuan Son NP., (21º06'N, 104º57'E): IEBR35; G20 — Thac Kem Ridge Top, Pu Mat, (18.58'N, 104.46'E): HZM.4.32376; G21 — Bach Ma NP., (16º12'N, 07.45'E): field no. B 026 (IEBR); G22 — Chu Mom Ray National Park, (14º28'N, 107º47'E): field no. T43 (IEBR).

R. malayanus

MYANMAR: M1 — Nanti Hill Forest, Bhamo Township, Kachin State, (24°34'N, 97°07'E): HZM.17.35969; M2 — Pauk Inlay cave, Pyaung Gaung, Shan state, (22°28'N, 96°59'E): HZM.12.35122, 14.35124; M3 — Tonetar Cave, Tonetar Village, (21°19'N, 99°17'E): HZM.19.36073; M4 — Montawa Cave, Taunggyi Township, Shan State, (20°45'N, 97°01'E): HZM 11.35108; M5 — Bayint Nyi Cave, Kayin State,

(16º58’N, 97º30’E): HZM. 16.35293, H24; M6 — Yathay Payan Cave, Hpa-an Township, (16º32’N, 97º34’E): HZM 6.34144; M7 — Sadden Sin Cave, (16°31’N, 97°49’E): HZM .7.34145, 8.34875, 10.34041; M8 — Nagamuak Cave, Mon State (16°19’N, 97°42’E): HZM.9.34990; M9 — Taung Thit Mine, Ohn Un Kwin, Dawei Dist. Thaninthary, (14°36’N, 97°59’E): HZM.18.35970.

LAO PDR: M10 — Tham Omar Kok, Lao PDR (20º41’N, 101º11’E): HZM.20.37754.

VIETNAM: M11 — Ba Be NP., Cho Ra District, Crobang, (22º32’N, 105º07’E): BMNH 1997.319; M12 — Xuan Son NP., (21º06’N, 104º57’E): field no. T23 (IEBR); M13 — Thac Kem Ridge Top, Pu Mat, (18.58’N, 104.46’E): HZM.12.35122, 14. 35124.

THAILAND: M14 — Ban San Ko Pui, Mae Sai, Chiang Rai, (20º25’N, 99º53’E): TISTR 54-5181; M15 — Khimee Cave, Chiangdao, Chiang Mai, (19º21’N, 98º43’E): CD-B-0039, 0052–53; M16 — Pha Daeng Cave, Sri Lan Na, Chiang Mai, (19º20’N, 99º01’E): PSU-M06.90–93; M17 — Ban Huai Kaeo, San Sai, Chiang Mai, (18º51’N, 99º03’E): field no. 184 (TISTR); M18 — Phu mieng-Phu thong, Pitsanulok, (17º19’N, 100º 39’ E): PSU-M06.29; M19 — Nam Tob, Phu Luang, Loei, (17º15’N, 101º35’E): PSU-M05.60; M20 — Khao Pha Wo, Mae Sot, Tak, (approx. 16º47’N, 98º50’E): 54-5436 (TISTR); M21 — East Thung Yai, Tak, (15°42’N, 99°01’E): PSU-M05.49; M22 — Nam Nao Cave, Nam Nao, Petchabun, (16°57’N, 101°30’E): PSU-M07.290–292, 07.297; M23 — Thung Kamang, Chaiyaphum, (16º23’N, 101º 33’E): PSU-M06.28; M24 — Lub Lae Cave, Ban Rai, Uthai Thani, (15º03’N, 99º28’E): PSU-M07.168–169; M25 — Pisut cave, Sri Nakarind, Kanchanaburi, (14º30’N, 99º00’E): PSU-M05.51; M26 — Khao Don Dueng, Ban Mi, Lop Buri, (15º08’N, 100º36’E): PSU-M07.162, 07.64-167; M27 — Ma Tok Cave, Khao Samorkhon, Ta Wung, Lop Buri, (14º54’N, 100º29’E): PSU-M07.52; M28 — Suea Luang Cave, Koktum, Muang, Lop Buri, (14º49’N, 100º47’E): PSU-M07.53–54; M29 — Wat Tham Phra Phothisat, Tab Kwang, Kang Koi, Sara Buri, (14º34’N, 101º08’E): PSU-M07.42–51; M30 — Sakaerat, Pak Thong Chai, Nakhonratchasima, (14º28’N, 101º56’E): 54-5681, 54-5682 (TISTR), PSU-M07.55; M31 — Phu Pha San, Phu Sithan WS., Kham Cha-I, Mukdahan, (16º38.6’N, 104º22’E): PSU-M07.293; M32 — Patiharn Cave, Pha Taem, Ubon Ratchathani, (15º35’N, 105º34’E): PSU-M05.16, 05.61; M33 — Khao Nom Tai, Photharam, Ratcha Buri (13º42’N, 99º45’E): PSU-M07.70–73; M34 — Khao Bin Cave, Chom Bung, Ratcha Buri, (13º35’N, 99º40’E): PSU-M07.74–75; M35 — Khao Yoi Hill, Pet Buri, (13º14’N, 99º49’E): PSU-M07.76–78; M36 — Bo-tong, Ang Runai, Chacherngsao, (13º11’N, 101º44’E): PSU-M05.144, 05.146–148; M37 — Makok, Phliu, Chantaburi, (12º35’N, 102º15’E): PSU-M05.145, 05.149–153; M38 — Silawan Cave, Pathiu, Chumporn, (10º41’N, 99º14’E): PSU-M07.56–60; M39 — Knaddai Cave, La Oun, Ranong, (10º01’N, 98º50’E): PSU-M07.61–69; M40 — Ban Bang Non, Ranong, (approx. 9º60’N, 98º39’E): TISTR 54-5971; M41 — Sang Phet Cave, Phanom, Krabi, (8º09’N, 98º53’E): PSU-M06.41; M42 — Ban Wang Bla Chan, Muang, Satun, (approx. 6º35’N, 100º04’E): BMNH 78.2295; M43 — Chet Kot Cave, Manang, Satun, (07°05’N, 99°54’E): PSU-M06.13–16; M44 — Wang Saithong waterfall, Manang, Satun, (07°05’N, 99°54’E): PSU-M06.12; M45 — Ma Kling waterfall, Rattaphum, Songkla, (7º02’N, 100º12’E): PSU-M07.155, 07.157; M46 — Ao Son-Ao Chak, Tarutao, Satun, (6º39’N, 99º38’E): PSU-M05.54; M47 — Talo-wow, Tarutao, Satun, (6º36’N, 99º41’E): PSU-M05.50, 05.52, 05.54, 06.30; M48 — Biserat, Jalor, (Type locality of *R. malayanus*) (not located): BMNH 1903.2.6.83 [holotype], 1908.2.5.24.

CAMBODIA: M49 — Bortum Sakor, Koh Kong, (11º04’N, 103º20’E): field no. 3634T, 3635T, 3638T (Frontier Cambodia).

MALAYSIA: M50 — Wang Tangga, Kaki Bukit, Kangkar, Perlis, (6º39’N, 100º12’E): BMNH 1968.812; M51 — Kisap Forest Reserve, Palau, Langkawi, (6º23’N, 99º52’E): BMNH 1968.813–816.