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Source: Acta Chiropterologica, 5(1) : 31-48

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/001.005.0103

Acta Chiropterologica, 5(1): 31–48, 2003
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

A new species of the *Hipposideros pratti* group (Chiroptera, Hipposideridae) from Lao PDR and Vietnam

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A new species of *Hipposideros* belonging to the *H. pratti* group is described. The species has been identified from a fairly restricted area in central Lao PDR and adjacent Vietnam, in South East Asia. The species is a large leaf-nosed bat, mid-way in size between the two other species known from the group, *H. lylei* and *H. pratti*, and its skull is significantly different in shape compared to the other two species. The new species roosts at least partially in caves in areas of degraded mixed deciduous and semi-evergreen forest as well as in areas of undisturbed semi-evergreen forest. The known distribution of all three species appears be allopatric, however, many areas within the region remain to be surveyed and so subsequent survey work may show the species to be sympatric.

Key words: *Hipposideros pratti* group, *Hipposideros lylei*, *Hipposideros* sp. nov., Lao PDR, Vietnam

INTRODUCTION

In October 1993 Lao Peoples Democratic Republic (PDR) formally declared 18 National Biodiversity Conservation Areas (NBCA), along with a further 11 recommended areas (Berkmuller *et al*., 1995). This provided an impetus for extensive biodiversity survey work in the country, to evaluate the existing selection of NBCAs, and to help set priorities for future management activity. Prior to this, few wildlife surveys had been conducted in the country, especially for small mammals.

Small mammal surveys by MFR, with support from World Wildlife Fund for Nature (WWF) and the Forest Management and Conservation Project (FOMACOP), Department of Forestry, Lao PDR, and by CMF, with support from the Wildlife Conservation Society (WCS), have resulted in many new species distribution records for Lao PDR and the discovery of several undescribed species (Robinson, 1998, 1999; Smith *et al*., 1998; Francis, 1999; Francis *et al*., 1999*a*, 1999*b*; Robinson and Webber, 2000; Jenkins and Robinson, 2002). As a further result of this work, examination of material from Lao PDR and nearby Vietnam has revealed a new species of *Hipposideros* belonging to the *H. pratti* group, formerly considered to contain two species, *H. pratti*

Thomas, 1891 and *H. lylei* Thomas, 1913 (see Hill, 1963). This third species is described below and compared with the other species in the group.

Material and Methods

Field Survey

MFR and CMF independently carried out surveys for bats in several localities throughout central and southern Lao PDR. Bats were captured with a variety of methods, but most frequently using four-bank harp traps (Francis, 1989) set across trails in the forest, over small stream beds, alongside limestone cliffs or across the entrance of a cave. Bats were also caught with mist-nets set across streams or small rivers, or in other areas, and a few bats were caught by hand in roosts. In addition MFR located bat roosts by searching hollow logs and trees, overhangs on riverbanks, and caves and fissures in rocky outcrops. All roosts were searched for bats, including the remains of dead ones.

The locations from which the undescribed species were obtained are presented below. Further specimens, from Vietnam, were located at the Harrison Institute, Sevenoaks, Kent, British Isles, whilst examining species of *Hipposideros* in their collection. These specimens had previously been assigned to either *H. lylei* or *H. pratti* (Hendrichsen *et al*., 2001).

Measurements

All cranial measurements (including those of *H. lylei* and *H. pratti* used for comparisons) were taken by MFR using dial callipers, with a resolution of 0.01 mm (accuracy ±0.02 mm). All dental measurements were taken across the crowns, unless otherwise stated. The number of specimens measured is given in parentheses. Measurements of the baculum were taken by PDJ using a micrometer eyepiece and microscope measuring stage. Bacular terminology follows Topál (1975) and Zubaid and Davison (1987).

Skull measurements were taken as follows: condylocanine length — from exoccipital condyle to anterior alveolus of canine; condylobasal length — from exoccipital condyle to anterior edge of premaxillary; greatest skull length — from posterior edge of skull to anterior edge of premaxillary; least interorbital width — the narrowest width across the interorbital region; rostal width — maximum width posterior to anteorbital bar; rostal height — perpendicular to M^2; anteorbital foramen height — maximum dorsoventral height; zygomatic width — greatest width across the zygomatic arches; jugal process height — from base of zygomatic arch; mastoid breadth — greatest width at mastoid processes; braincase width — across posterior roots of zygomatic arches; external width across canines — greatest width across upper canines at alveoli; upper toothrow length — anterior of the upper canine to posterior of M^3; external width across molars — greatest width across third upper molars (M^3–M^3); lower toothrow length — from anterior of the upper canine to posterior of M_3; mandible length — from condyle to anterior of I_1 at alveolus; ramus length — from condyle to anterior of I_1 at alveolus.

Statistical Analysis

The average dimensions are expressed as geometric means, whose precision is given by the 95% confidence intervals (CI) for these estimates. The between-species and sex differences in skull and noseleaf measurements were analysed using a two-level, nested ANOVA implemented with Stata's (version 7, Stata Corporation, Texas), 'anova' command. 'Specimen level' effects (i.e., main effects of species and sex) were tested against the between-specimen sum of squares, while 'measurement level' effects (i.e., interactions between dimension and species or sex) were tested against the residual sum of squares. A third level, 'location', nested within species, was introduced to test whether the new species lies outside the variation expected between different geographical locations. All P-values were derived from the appropriate F-test of the sum of squares for the term concerned.

The new species was compared separately to *H. lylei* and *H. pratti*, with respect to cranial and noseleaf measurements. The baseline analysis, which included all the data, not controlling for locality or sex, was modified in three ways by: (i) omitting both noseleaf measurements in order to examine cranial size difference between the species (noseleaf measurements distort this because they are not closely related to other measurements and some of the data, especially for *H. pratti*, are ill-balanced with respect to these variables), (ii) controlling for sex, (iii) allowing for location.

Confidence intervals for the difference in skull size between species were calculated from the Huber-White variance estimator implemented using the 'robust' and 'cluster' options provided by Stata's 'anova' command. The model used to obtain these estimates included terms for the first order effects of sex, dimension and species and the interaction between sex and dimension, but not the interaction between dimension and species.

Measurements were all transformed by taking the logarithm for analysis so that additive effects on the analysis scale correspond to proportional (or multiplicative) differences between measurements. As expected, the variance of untransformed measurements increased with the mean, but the relationship between variance and mean was not proportional and the logarithmic transformation overcompensates for it. Consequently a weighted analysis was applied with weights derived from the reciprocal of estimates of the within-specimen variance. Fitting the relationship between predicted value and residual variance from an unweighted model derived this variance estimate (i.e., a two-step, re-weighted analysis). The variance of noseleaf measurements did not fit the same pattern as the other measurements. Soft tissue of the nose structure is likely to be related to echolocation frequency (Bogdanowicz, 1992; Robinson, 1996) and may have been altered by preservation. For these measurements weights were derived from the residual variance itself, rather than the value predicted from the fitted relationship. Plots of residuals versus predicted values and normal scores (not shown) indicate that this procedure results in normally distributed residuals with constant variance.

Ultrasound Recordings

Echolocation calls were recorded from hand held bats, shortly after capture. An Ultrasound Advice S-25 bat detector was used to pick up calls and a Portable Sound Processor (PUSP) digitised the signal and replayed it with a 20-fold time expansion. The transformed signal was then recorded using a Sony Professional Walkman (WM D6C). Recorded calls were analysed using digital sound processing software (Sona PC) on a Pentium-based PC. The constant frequency (CF) component was determined by measuring each individual call from a computer display that had a resolution of 512 steps of Fourier Transform within a frequency bandwidth of 172 kHz.

Abbreviations Used for Institutes

AMNH — American Museum of Natural History, New York, USA; BMNH — The Natural History Museum, London, British Isles; FMNH — The Field Museum, Chicago, USA; HZM — Harrison Institute, formerly the Harrison Zoological Museum, Sevenoaks, Kent, British Isles; RMNH — Rijksmuseum van Natuurlijke Historie, Leiden, Holland; ROM — Royal Ontario Museum, Toronto, Canada; SMF — Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany; TISTR — Thailand Institute of Scientific and Technological Research, Bangkok, Thailand; USNM — Smithsonian Institution, Washington D.C., USA.

Systematic Description

Hipposideros scutinares sp. nov.

Holotype

SMF 88.023 (Field No. CMF 960430.36), adult ♂ (Fig. 1), body in alcohol, skull and baculum extracted, collected by CMF on 30 April 1996 as part of a WCS survey.

Type locality

Ban Khankeo (formerly known as Ban Phahôm), along the upper Nam Hinboun, Bolikhamsai Province, Khammouan Limestone NBCA, Lao PDR, 17°58’N, 104°49’E.

Paratypes

SMF 88.024 (Field No. CMF 960425.2), adult ♀, body in alcohol, skull extracted, collected by CMF on 25 April 1996 during a WCS survey; caught on the Nakai Plateau, west of Nam Theun, in the catchment of the Nam Nyalong, near the escarpment, Nakai-Nam Theun NBCA, Bolikhamsai Province, Lao PDR, 17°53’N, 104°50’E.

Fifteen incomplete skulls, some with mandibular rami, collected by MFR, as part of surveys with WWF and FOMACOP, in the Khammouan Limestone NBCA, Lao PDR: BM(NH) 1998.947–952, 1998.954–955, 1998.957, 1998.959–1998.963 (Field Nos. 203/98–208/98, 210/98, 211/98, 213/98, 250/98–252/98, 290/98, 391/98) on 28 January 1998 from Tam Thea, Hinboun District, Bolikhamsai Province, 18°08’54”N, 104°30’57”E; BM(NH) 1998.956 (Field No. 212/98) on 1 February 1998 from Tam Pha Muang, Ban Tonglom, Hinboun District, Bolikhamsai Province, 18°00’30”N, 104°40’50”E; BM(NH) 1998.953 (Field No. 209/98) on

23 January 1998 from Tam Dan Jar, Gnommalat District, Khammouan Province, 17°33’35”N, 104°56’50”E and BM(NH) 1998.958 (Field No. 214/98) on 14 January 1998 from Tam Jungvung, near Ban Pontong/Mauang, Thakhek District, Khammouan Province, 17°33’40”N, 104°50’15”E.

Other material

Four specimens have been collected from Vietnam. HZM 2.32600, adult ♂ and HZM 4.32602, adult ♀, bodies in alcohol, skulls extracted, were collected by D. Hendrichsen on 8 July and 8 August 1998, respectively, at Hang En Cave (Lam Hang Ou Cave), Phong Nha Nature Reserve, Quang Binh Province, Vietnam, 17°26’N, 106°18’E. HZM 1.32599, adult ♂ and HZM 3.32601, adult ♀, bodies in alcohol, skulls extracted, collected by D. Hendrichsen on 3 and 4 August, respectively, at Hang Lon Cave, Ke Bang Forest, Quang Binh Province, Vietnam, 17°39’N, 105°59’E.

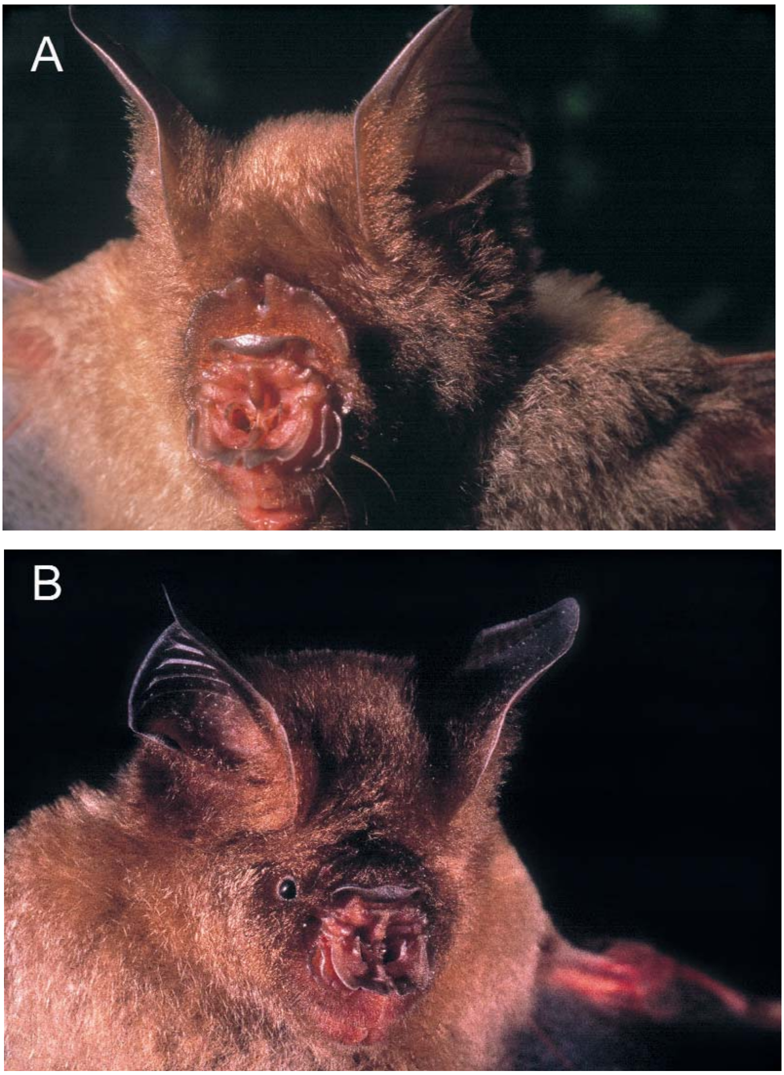

FIG. 1. *Hipposideros scutinares*, (A) ♂ (SMF 88.023, holotype) and (B) ♀ (SMF 88024)

Diagnosis

A large leaf-nosed bat belonging to the *H. pratti* group, forearm length of 77.9–82.7 mm (n = 6), condylocanine length 26.49–27.86 mm (8), with a fleshy outgrowth behind the posterior noseleaf as in other members of the *H. pratti* group. The lateral margins of the anterior and posterior noseleaves are connected (Fig. 2). The depth of the median emargination of the anterior noseleaf is 1.00–1.35 mm (6). Intermediate in skull size between *H. lylei* and *H. pratti*. Frontal region of cranium inflated with moderate dorsolateral depressions; anteroventral wall of the orbit strongly inflated; anteorbital foramen large, height 1.50–2.17 mm (19); zygoma with large jugal process; anterodorsal vomer spine low anteriorly, high posteriorly; posterodorsal vomer spine forms a concave vertical midline strut recessed within the narial chamber; slight discontinuity between sphenoid and narial chamber; first upper premolar (P^2) small, not or barely visible in buccal view. Baculum with broad basal portion, distinct hook-shaped proximal processes, the ventral lobe approximately twice as long as the dorsal lobe; distal region of shaft broad with long, ventrally projecting apical processes. The species has echolocation calls with a CF component of 63.6 kHz (2).

Description

A large Old World leaf-nosed bat of the *H. pratti* group (Hill, 1963; Corbet and Hill, 1992); forearm length 77.9–82.7 mm (6), tail length 50.4–59.3 mm (6), ear length 27.6–29.4 mm (6), hind foot length 15.0 –18.8 mm (6). Ears are large, broad and bluntly pointed with their posterior margins slightly concave below the tip. They are haired for one third of their length and have no antitragal modification. The anterior noseleaf is 9.55–10.49 mm (6) wide, with a median emargination 1.0–1.35 mm (6) in depth. Two lateral supplementary leaflets are present. The lateral margins of the anterior and posterior noseleaves are connected. Behind the true posterior noseleaf is a transverse fleshy lobated prominence, positioned on each side of the opening of the frontal sac, resembling a supplementary posterior noseleaf, prominent in males, but

FIG. 2. The noseleaf structure from top to bottom: *H. scutinares* (SMF 88.023, holotype, ♂), *H. lylei* (HZM 5.32603, ♂), and *H. pratti* (AMNH 47987, ♀). Scale = 1 mm

which may be small or rudimentary in females and immatures (Figs. 1 and 2). Although the noseleaf structure of both males and females shows little variation, there does appear to be sexual dimorphism; in males, the transverse prominence (located behind the true noseleaf) of the Lao PDR type specimen (SMF 88.023) and two from Vietnam (HZM 2.32600, 1.32599) were 6.55, 6.95 and 14.17 mm high, respectively. In comparison three females, two from Vietnam (HZM 4.32602, 3.32601) and one from Lao PDR (SMF 88.024) were 2.69, 3.26 and 4.2 mm high, respectively.

The dorsal pelage is brown/ginger (orange-red) at its base, followed by a buff central band, then brown tips, with a degree of frosting. Epaulets lack brown tips and frosting. The ventral pelage is reddish/brown at its base with buff tips.

The skull is moderately large, with a low, broad rostrum, poorly defined supraorbital ridges, narrow interorbital region and well-developed sagittal crest (Figs. 3 and 4; and Table 1 for dimensions). The anterodorsal rostral eminences are slightly inflated; the frontal is inflated, especially in the supraorbital region, with a slight depression in the midline and marked dorsolateral depressions. The anteorbital foramen is large, roofed by a long, slender bar and the underlying anteroventral wall of the orbit is strongly inflated (Fig. 5); zygoma with large jugal process (see Figs. 4 and 5). In narial view the vomer is narrow anteriorly at the junction with the premaxillae, moderately broad posteriorly, with an anterodorsal midline spine which is low anteriorly, high posterodorsally; anterior foramen small, in same plane as vomer (Fig. 6). In mesopterygoid view a spine arises from the posterodorsal region of the vomer and anterior to the internal palatal border forming a concave vertical midline strut recessed within the narial chamber; in most specimens a low spine continues from the midline strut and traverses the roof of the narial chamber, although this spine is lacking in the postpalatal region in some specimens; there is a slight discontinuity from the sphenoid into the narial chamber. The sphenoidal region is slightly inflated with a narrow midline depression. The basisphenoid is concave, particularly anteriorly, and moderately broad. Cochleae small, their width approximately equal to their distance apart. Dentition as described for the *H. pratti* group (Hill, 1963), but the upper canine (C^1) and upper second premolar (P^4) are in contact or nearly so; first upper premolar (P^2) barely visible in buccal view and below the level of the cingula of C^1 and P^4 in labial view.

The baculum is asymetrical (Fig. 7); total length 1.9 mm, maximum basal width 0.8 mm. Basal cone broad with well-defined dorsal and ventral proximal processes, slight emarginations evident on dorsal and ventral processes; in lateral view proximal processes distinctly hook-shaped, the ventral lobe twice as long as the dorsal lobe; shaft moderately broad, dorsoventrally compressed, convex dorsally, concave ventrally with a marked depression ventrally; shaft constricted towards apex, distal region broad with long, ventrally projecting apical processes, right apical process more curved and longer than the left.

Ultrasound

Both individuals captured by CMF (SMF 88023 and 88024) had echolocation calls with a CF component of 63.6 kHz.

Etymology

Named the ‘shield-nosed bat’ from the Latin *scutum* (= shield) and *nares* (= nostrils), for the resemblance to a shield of the transverse fleshy lobated prominence behind the true posterior noseleaf.

Comparative material

See Appendix.

TABLE 1. Comparative measurements (in mm) of *H. scutinares*, *H. lylei* and *H. pratti*. The 95% confidence interval ($CI_{95\%}$) for the mean is based on the standard error of mean of logarithm of measurements, and shows precision of the geometric mean

Character	*H. scutinares*			*H. lylei*			*H. pratti*		
	n	Geometric mean ($CI_{95\%}$)	Range	*n*	Geometric mean ($CI_{95\%}$)	Range	*n*	Geometric mean ($CI_{95\%}$)	Range
Condylocanine length	8	27.1 (26.8–27.4)	26.49–27.86	64	25.5 (25.4–25.6)	24.15–26.51	16	29.0 (28.7–29.3)	27.76–29.95
Condylobasal length	6	27.5 (26.9–28.1)	26.81–28.41	52	26.1 (26.0–26.2)	25.16–27.00	8	29.2 (28.8–29.7)	28.29–30.30
Greatest skull length	6	30.6 (30.0–31.3)	29.78–31.58	51	29.1 (28.9–29.2)	28.21–30.18	7	32.4 (31.9–33.0)	31.37–33.48
Least interorbital width	15	4.5 (4.4–4.6)	4.31–4.97	74	4.3 (4.3–4.3)	3.94–4.82	16	4.4 (4.3–4.5)	4.15–4.71
Rostal width	18	10.0 (9.9–10.2)	9.65–10.70	74	9.5 (9.4–9.5)	8.92–10.07	16	10.0 (9.9–10.1)	9.74–10.31
Rostal height	18	6.6 (6.5–6.7)	6.31–9.93	74	6.2 (6.1–6.2)	5.69–6.68	16	7.7 (7.6–7.8)	7.43–7.90
Anteorbital foramen height	19	1.8 (1.7–1.9)	1.50–2.17	76	1.1 (1.0–1.1)	0.67–1.44	16	1.5 (1.4–1.5)	1.17–1.81
Zygomatic width	11	16.5 (16.2–16.7)	15.95–17.06	60	15.5 (15.4–15.6)	14.51–16.25	16	17.8 (17.6–18.1)	17.01–18.74
Jugal process height	13	2.8 (2.7–2.9)	2.48–3.03	66	2.3 (2.3–2.4)	1.69–2.85	16	2.7 (2.5–2.8)	2.30–3.03
Mastoid breadth	9	14.7 (14.5–15.0)	14.39–15.33	64	14.0 (13.9–14.0)	13.02–14.60	16	15.7 (15.6–15.8)	15.41–16.16
Braincase width	10	11.8 (11.7–12.0)	11.50–12.28	67	11.1 (10.4–11.8)	10.85–12.19	16	12.3 (12.1–12.5)	11.41–12.92
External width across canines	17	7.8 (7.6–7.9)	7.28–8.27	73	7.1 (7.0–7.2)	6.44–7.90	16	8.5 (8.4–8.6)	8.06–8.79
Upper toothrow length	11	11.8 (11.7–12.0)	11.47–12.28	71	11.2 (11.1–11.2)	10.40–11.88	16	12.5 (12.4–12.6)	12.10–12.76
External width across molars	14	10.9 (10.7–11.0)	10.43–11.41	72	10.6 (10.5–10.6)	10.05–11.20	16	11.8 (11.7–12.0)	11.36–12.23
Lower toothrow length	8	12.7 (12.5–12.9)	12.35–12.98	69	12.0 (12.0–12.1)	11.44–12.72	16	13.7 (13.6–13.9)	13.21–14.03
Mandible length from condyle	6	20.1 (19.8–20.4)	9.63–20.61	60	19.2 (19.1–19.3)	18.24–20.56	7	21.9 (21.3–22.4)	20.41–22.60
Ramus length from condyle	10	20.9 (20.6–21.1)	20.08–21.30	61	19.5 (19.3–19.6)	17.82–20.40	15	22.7 (22.4–23.0)	21.25–23.33
Noseleaf width	6	10.0 (9.7–10.3)	9.55–10.49	6	8.9 (8.7–9.1)	8.82–9.23	6	9.0 (8.6–9.4)	8.29–9.68
Noseleaf emargination depth	6	1.2 (1.1–1.3)	1.00–1.35	6	1.9 (1.7–2.2)	1.53–2.28	11	0.9 (0.8–1.0)	0.63–1.11

FIG. 3. Dorsal (A) and ventral views (B) of the crania from left to right of *H. scutinares* (SMF 88.024), *H. lylei* (BM(NH) 1913.4.18.3), and *H. pratti* (BM(NH) 1891.5.11.1). Scale = 1 mm

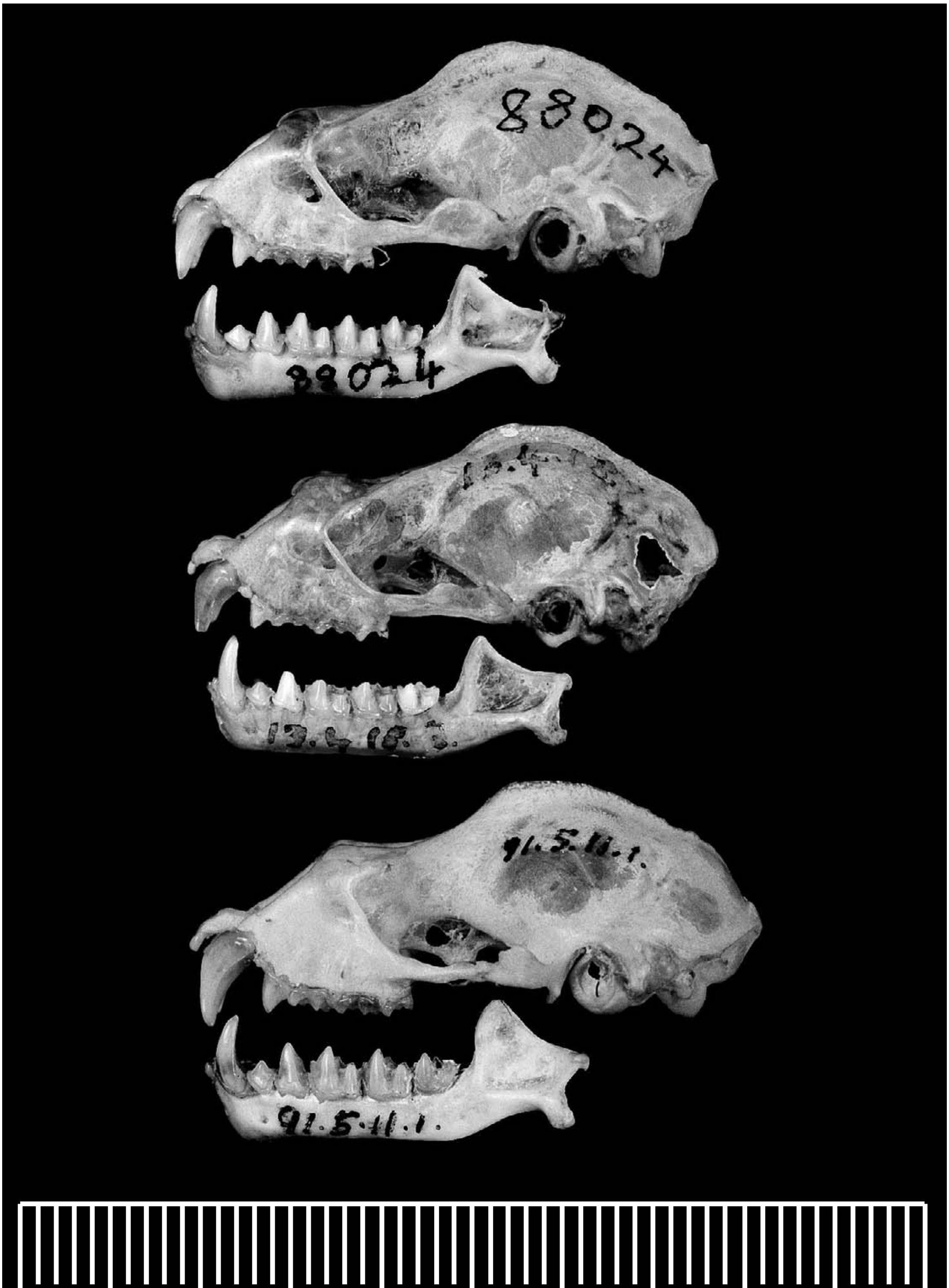

FIG. 4. Lateral view of the skulls from top to bottom of *H. scutinares* (SMF 88.024), *H. lylei* (BM(NH) 1913.4.18.3), and *H. pratti* (BM(NH) 1891.5.11.1). Scale = 1 mm

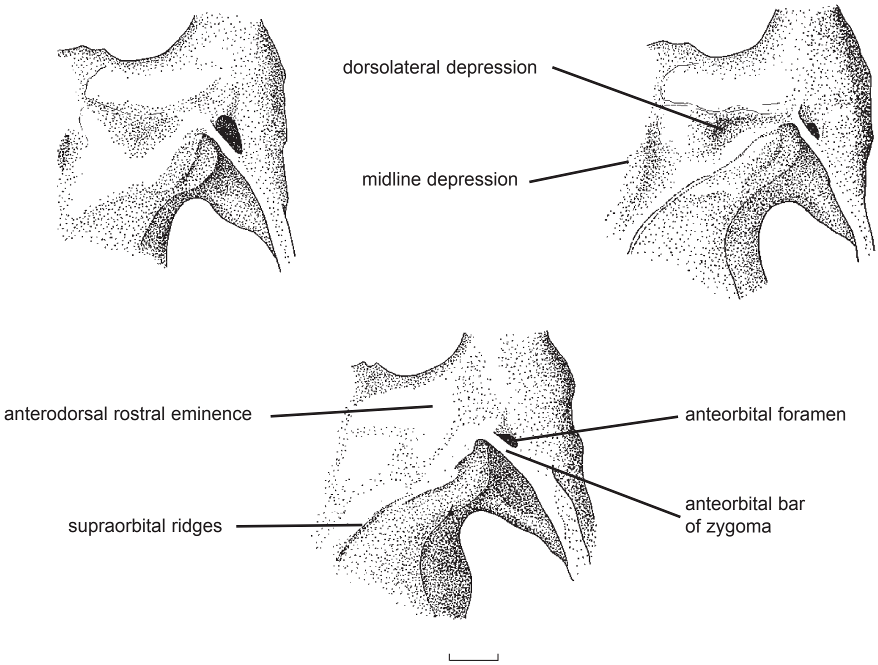

FIG. 5. Dorsal view of right half of the rostrum from top row left *H. scutinares* (SMF 88.023), right *H. lylei* (BM(NH) 13.4.18.3), and below *H. pratti* (BM(NH) 91.5.11.1). Scale = 1 mm

DISCUSSION

Comparison with Other Taxa

The new species has a forearm measurement that ranges from 77.9–82.7 mm (6), similar in size to both *H. lylei* and *H. pratti*, being 73.0–84.0 mm (15) (Robinson *et al*., 1995; Robinson and Smith, 1997) and 79.3–89.5 mm (23) (Allen, 1938; G. Jones, pers. com.), respectively. However, ANOVA (Table 2) confirms that the cranial

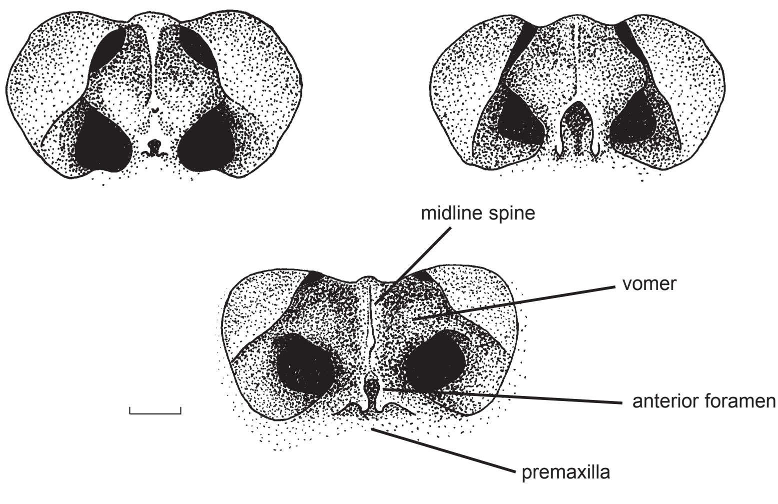

FIG. 6. Narial view of vomer, top row left *H. scutinares* (SMF 88.023), right *H. lylei* (BM(NH) 13.4.18.3), and below *H. pratti* (BM(NH) 91.5.11.1). Scale = 1 mm

and noseleaf measurements of the new species are, on average, significantly larger than *H. lylei* and a little smaller than *H. pratti*. These differences are more obvious after removing the noseleaf measurements from the analysis, when the mean skull size of *H. scutinares* is seen to be 5.4% ($CI_{95\%}$ 3.3–7.5%) larger than that of *H. lylei* and 5.9% ($CI_{95\%}$ 3.5–8.2%) smaller than that of *H. pratti*. The condylocanine length and zygomatic width of the new species range from 26.49 to 27.86 (8) and from 15.95 to 17.06 mm (11), respectively. This is in comparison to 24.15 to 26.51 (64) and 14.51 to 16.25 mm (60), respectively, for *H. lylei* and 27.76 to 29.95 (16) and 17.01 to 18.74 mm (16), respectively, for *H. pratti* (Table 1).

When the interaction between dimensions and species is added to the ANOVA model (the 'dim × species' term in Table 2) it becomes apparent that the relative sizes of the measured dimensions of both *H. lylei* and *H. pratti* differ significantly from those of the new species, i.e., their skulls differ in shape as well as size. When compared to both *H. lylei* and *H. pratti* the height of the anteorbital foramen and jugal process are both larger than expected in the new species, yet in comparison to the shape of *H. lylei* skulls, the width across the canines and molars are, respectively, relatively larger and smaller than expected. When compared with *H. pratti* skulls the interorbital and rostal widths are greater, whereas the rostal height is less than expected.

Controlling for sex does not much affect the results of the ANOVA. Measurements varied only weakly with locality and none of the significant differences observed above were lost when allowance was made for variation between localities. In the case of *H. pratti* versus *H. scutinares* analysis,

TABLE 2. Results of ANOVA comparing *H. scutinares* with *H. lylei* and *H. pratti*. This analysis employs nested, random effects models. The overall difference in size between the species is fitted by the 'Species' terms. In the basic model and variants (i) and (ii) the *F*-statistics for this term compares the sum of squares explained by the difference in size between the species with that for the variation in size between individual specimens. In variant (iii) there is an additional level, 'location', between species and individual. In this case the *F*-statistics derives from a comparison of the difference between species and variation between locations. The 'dim × species' interaction term is fitted to test whether there is an additional difference between the species over and above a simple enlargement or reduction of all dimensions by a fixed factor. In all models the *F*-statistics for this term is derived from a comparison of the sums of squares due by the interaction and the residual variation

Type of analysis	versus *H. lylei*			versus *H. pratti*		
	F	*d.f.*	*P*	*F*	*d.f.*	*P*
Basic analysis						
species	12.85	1, 96	0.001	0.25	1, 43	ns
dim × species	25.42	18, 1217	0.000	21.05	18, 392	0.000
(i) Dropping noseleaf						
species	58.64	1, 93	0.000	7.23	1, 33	0.011
dim × species	25.62	16, 1200	0.000	23.66	16, 377	0.000
(ii) Controlling for sex						
species	14.83	1, 69	0.001	0.01	1, 24	ns
sex	2.49	1, 69	ns	1.35	1, 24	ns
dim × species	11.75	18, 1017	0.000	10.77	18, 286	0.000
(iii) Allowing for locality						
species	12.87	1, 18	0.002	0.58	1, 5	ns
locality	0.56	18, 78	ns	0.40	5, 37	ns
dim × species	2.29	18, 247	0.003	4.50	18, 80	0.000

there were too few localities to obtain a good estimate of their variability.

Morphologically the new species possesses the common features of the *H. pratti* group (see Hill, 1963) as described above. Although the species is clearly distinct from both *H. pratti* and *H. lylei,* it has characteristics similar to one or other species as well as features midway between the two. The lateral margins of the anterior and posterior noseleaf are connected, similar to *H. lylei*, but in contrast to *H. pratti*, where they are not continuous. The depth of the median emargination of the anterior noseleaf, 1.00 –1.35 mm (6), is mid-way between that exhibited by *H. lylei*, which is deep, 1.53–2.28 mm (6), and *H. pratti*, which is shallow, 0.64–1.11 mm (11). The noseleaf width of *H. scutinares* ranges from 9.55–10.49 mm (6) in comparison to *H. lylei* 8.82–9.23 mm (4) and *H. pratti* 8.29–9.68 mm (6).

The anterodorsal rostral eminences of *H. scutinares* are more inflated than those of *H. pratti* (Fig. 5); the midline frontal depression and dorsolateral depressions present in *H. scutinares* are more prominent in *H. lylei*, but scarcely evident in *H. pratti*; the supraorbital region is inflated in *H. scutinares* and *H. lylei*, but only slightly in *H. pratti*; supraorbital ridges are poorly defined in *H. scutinares*, present in *H. pratti*, but well marked in *H. lylei*. The anteroventral orbital wall behind the anteorbital bar is strongly inflated in *H. scutinares*, slightly inflated in *H. lylei* and scarcely inflated in *H. pratti*. The anteorbital foramen of *H. scutinares* is larger than in *H. lylei* or *H. pratti* and the anteorbital bar is longer than that of *H. lylei*, longer and more slender than in *H. pratti* (height of anteorbital foramen 1.50–2.17 mm (19) in *H. scutinares*, 0.67–1.44 mm (75) in *H. lylei* and 1.17 –1.75 mm (16) in *H. pratti*).

The vomer of *H. scutinares* differs from that of the other species; in narial view the vomer of *H. lylei* is narrow, and flat, the midline spine is very low anteriorly and the anterior foramen large, lying in the same plane as the vomer (Fig. 6); in *H. pratti* the vomer is broad with a pronounced, steep-sided midline spine, rising steeply from the anterior foramen, which is near vertical to the plane of the vomer. In mesopterygoid view the spine on the posterodorsal surface of the vomer is present in *H. lylei*, but the vertical strut is absent, the spine is very low or absent on the roof of the narial chamber and the roof of the narial chamber and sphenoid merge smoothly. In *H. pratti* the spine on the posterior surface of the vomer and the floor of the palate just anterior to the palatal border forms a vertical midline strut, which is considerably more pronounced than in *H. scutinares*, as is the mid-dorsal spine traversing the roof of the narial chamber and the abrupt discontinuity between the sphenoid and narial chamber, evident only as a slight step in *H. scutinares*. The sphenoidal bridge of both *H. scutinares* and *H. lylei* is wider than that of *H. pratti*. The basisphenoid is more concave in *H. scutinares* than in *H. lylei* and *H. pratti*. The second upper premolar is extruded from the toothrow in all three species, but is smaller in *H. scutinares* than *H. lylei* or *H. pratti*; C and P^4 of *H. lylei* and *H. pratti* are usually separate and P^2 is readily visible in buccal view in *H. lylei*, but not in *H. pratti*.

The morphology of the baculum of *H. scutinares* is similar to that of *H. lylei* (see Fig. 7; Zubaid and Davison, 1987) and, to a lesser degree, *H. armiger* Hodgson, 1835 (e.g., Topál, 1975; Zubaid and Davison, 1987) and *H. turpis* Bangs, 1901 (see Yoshiyuki, 1989); it also bears some resemblance to that of *H. pratti*, but differs from most other species of *Hipposideros* in which the baculum has been examined to date. The shaft of the baculum of *H. scutinares* is broader and shorter than that of *H. lylei* and the proximal process consists of separate

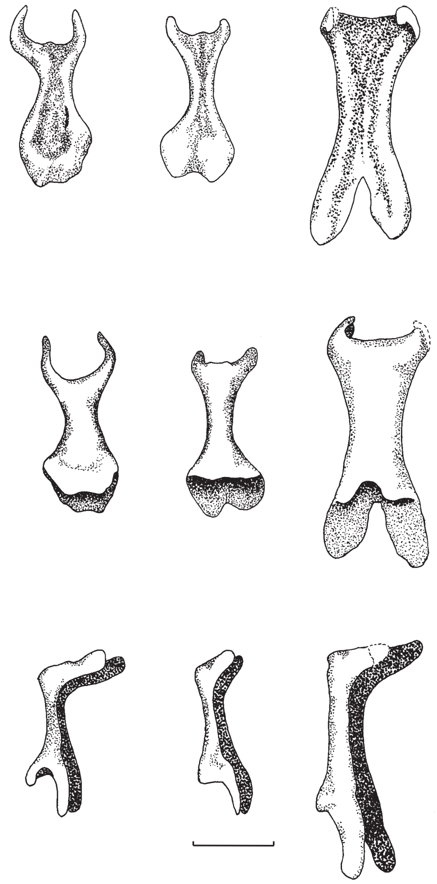

FIG. 7. Bacula from left to right of *H. scutinares* (SMF 88.023), *H. lylei* (BM(NH) 1964.831) and *H. pratti* (FMNH 38920). Top row: ventral view; middle row: dorsal view; bottom row: lateral view. Scale = 1 mm

dorsal and ventral lobes forming a hook-shaped structure, unlike *H. lylei* which has a shelflike dorsal region and shorter ventral lobe, apparently similar to the condition in *H. armiger* figured by Topál (1975). The proximal process of the baculum of *H. pratti* differs in that the small dorsal lobes form a short shelf with two long ventral lobes. The long apical processes of the baculum of *H. scutinares* differ from the much shorter processes of *H. lylei* and *H. pratti*. The baculum of *H. scutinares* is similar in size (total length 1.9 mm; basal width 0.8 mm) to that of *H. lylei* (total length 1.8 mm; basal width 0.8 mm) and *H. armiger* (total length 1.86–2.08 mm; basal width 0.55–0.63 mm — see Topál, 1975), larger than that of *H. turpis* (greatest length 1.4 mm), but markedly smaller than that of *H. pratti* (total length 2.4 mm; basal width 1.0 mm).

Individuals of *H. scutinares* (SMF 88023 and 88024) captured by CMF had echolocation calls with a CF component of 63.6 (2) kHz. In contrast, Robinson (1996), using a heterodyne detector, recorded *H. lylei* in Thailand, echolocating at 70–75 kHz, whereas G. Jones (pers. com.), using a time expansion detector, at Bian Fu Cave, Xixia countryside, Henan Province, PDR China, recorded *H. pratti* calls with a CF component of 61.0–61.9 (6) kHz.

Habitat

Hipposideros scutinares is thought to roost at least partially in caves, similar to both *H. lylei* and *H. pratti* (Allen, 1938; Lekagul and McNeely, 1977; Robinson *et al*., 1995; Robinson and Smith, 1997). Twenty of the 21 specimens were found in or close to limestone caves. In Lao PDR an adult male and female were captured by CMF in harp traps, set across a small stagnant stream bed and along the edge of a limestone cliff, respectively, in evergreen forest at an altitude of 160 m above sea level (a.s.l.). In addition, fifteen incomplete skulls were recovered by MFR from limestone caves in Lao PDR at altitudes of 150–160 m a.s.l. Caves at Tam Thea and Tam Jungvung were on the edge of a limestone karst, at the base of which was degraded mixed deciduous forest, with scrub and bamboo. The low-lying areas away from the karst had been cleared for the cultivation of paddy rice. Tam Dan Jar was on the edge of a massive limestone karst adjacent to a valley area of less than 2 km^2. The habitat was dense, relatively undisturbed, semi-evergreen forest, although some larger trees had been removed and small areas were starting to be cleared. Within the central plain of the valley were two areas of grassland totalling approximately 18 ha. Tam Pha Muang was a cave surrounded by mostly rice paddy and heavily degraded semi-evergreen forest and scrub, adjacent to the Hinboun River. The four specimens from Vietnam were also found in caves.

Distribution

Hipposideros lylei and *H. pratti* have relatively widespread distributions in South East Asia, with records of *H. lylei* from Malaysia, Thailand, Myanmar (formerly Burma), Vietnam and PDR China, and *H. pratti* from Vietnam and PDR China (Fig. 8, see also Appendix). *Hipposideros scutinares* has been recorded from eight localities, six within central Lao PDR and two from

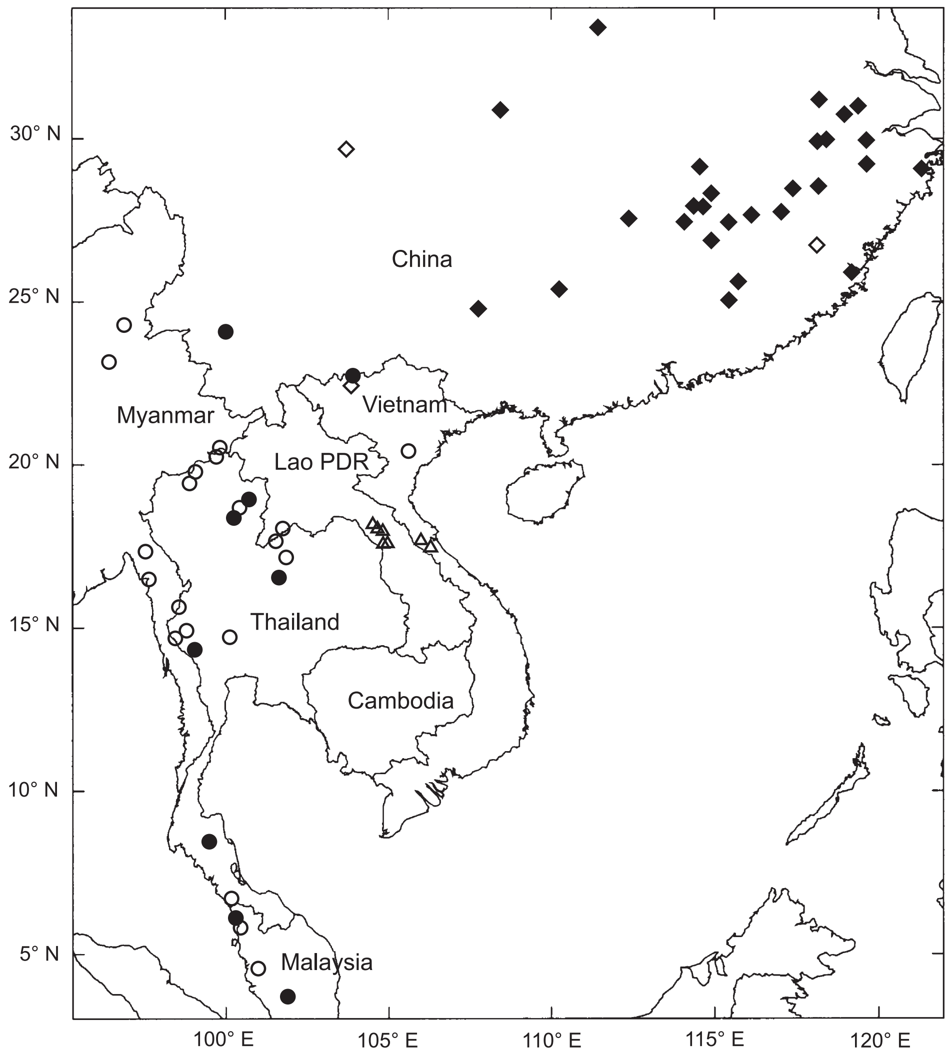

FIG. 8. The known distribution of *H. scutinares* (triangles), *H. pratti* (diamonds), and *H. lylei* (circles) in South East Asia. Hollow symbols represent localities from which specimens have been examined, whereas localities with black symbols have not been examined

adjacent Vietnam, all from a fairly restricted area. The known distribution of all three species; *H. scutinares*, *H. lylei* and *H. pratti*, is mostly allopatric (Fig. 8), with the exception of Vietnamese records by Kruskop (2000*a*, 2000*b*) and single records of *H. lylei* and *H. pratti* from northern Vietnam. Although Kruskop's (2000*a*, 2000*b*) specimens were collected from Ke Bang, Quang Binh, the same locality as some of the paratype specimens of *H. scutinares*, they have not been examined in the light of current knowledge and may therefore represent *H. scutinares*. In addition, many areas within the region remain to be surveyed and so subsequent survey work may show the species to be sympatric.

Acknowledgements

We would like to thank the staff of WWF-Thailand, the WCS-Lao office, the Lao PDR Department of Forestry (DoF) and FOMACOP, for permission to work in Lao PDR and for organising the field work projects of MFR and CMF, in particular Bouahong Phanthanousy (National Project Director, FOMACOP), Bouaphanh Phantavong (Deputy National Project Director, FOMACOP), Bruce Jefferies (FOMACOP), Robert Mather and Robert Steinmetz (WWF-Thailand) and Bill Robichaud (WCS-Lao). We would also like to thank Bruce Jefferies for overseeing the export of MFR's specimens. We are very grateful to Maurice Webber who collaborated with MFR in the field, and Nik Aspey and Khamkhoun Khounboline who assisted CMF on the 1996 field work. Assistance to MFR in the field was also gratefully received from Thongphanh Ratanalangsy (Khammouan Limestone and Dong Phu Vieng NBCA Co-ordinator), Sinnasone Seangchantharong (Field Manager for Khammouan Limestone NBCA), Chainoi Sisomphone (DoF) and Nousine Latvylay (driver for FOMACOP in Savannakhet). The headmen and villagers from Pontong, Muang, Mouangkhai, Louang, Vieng, Kengkhot, Thamtem and Tonglom provided excellent field support and companionship, and without them MFR's project would not have been possible.

MFR's field work was funded by the Global Environment Facility (GEF) through the World Bank to the Government of Lao PDR, via a contract with Burapha Development Consultants, sub-contracted to WWF-Thailand. CMF's field work was funded by the WCS.

We would like to thank Nivesh Nadee, TISTR, Sara Bumrungsri, Prince of Songkla University, Thailand, Dieter Kock, SMF, Paul Bates, HZM, Bruce Patterson and John Phelps, FMNH, Bob Randall, AMNH, and Daw Tin New, Khin Maung Swe and Si Si Hla Bu, University of Yangon, Myanmar, for access to, and the loan of specimens. Wiesław Bogdanowicz, Polish Academy of Sciences, Sue McLaren, Carnegie Museum of Natural History, USA, Judith Chupasko, Museum of Comparative Zoology, Harvard University, USA, Chris Smeenk, RMNH, Michi Schulenberg, The Field Museum Chicago, USA, Christopher Norris and Bob Randall, AMNH, USA, Susan Woodward, ROM, Gabor Csorba, Hungarian Natural History Museum, Linda Gordon, Smithsonian Institute, USA and Gareth Jones, University of Bristol, British Isles and Joe Walston, WCS, Cambodia provided valuable information and records of *H. pratti* and *H. lylei*. Dai Qiang, Institute of Zoology, Chinese Academy of Science, Bejing, kindly translated locations of *H. pratti* from Chinese papers and Anait Nalbandian, NHM similarly translated Russian papers. We are very grateful to Joerg Habersetzer, Forschungsinstitut Senckenberg, Germany, for analysing sound recordings made by CMF and to Angela Smith for her valuable contribution to the manuscript.

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Received 02 December 2002, accepted 21 March 2003

Appendix

Records of *Hipposideros lylei* and *H. pratti* obtained from museum records and published sources. Additional locality data added by the authors is indicated in square brackets. Those specimens that have been examined are presented in italics

Hipposideros lylei

CHINA — West Yunnan, Lin-Tsang Area, [23°53'N, 100°01'E] (Lu *et al*., 1965).

MALAYSIA — Pahang, Bentong, Bukit Chintamani, [03°36'N, 101°57'E]: FMNH 64101; Perak, Gunong Gajah, Gua Sanding, [04°31'N, 101°03'E]: *HZM 1.7447, 2.7448*; Perlis, Kaki Bukit, Wang Tangga, [06°39'N, 100°12'E]: *BM(NH) 1964.832, 1964.831*, ROM 38695; Kedah, Kedah Peak, [05°45'N, 100°30'E]: *BM(NH) 1964.1192*; Kedah, Gunong Keriang (5 km W of Alor Star [Setar]), [06°05'N, 100°23'E]: SMF 44656; Kedah, Gunong Keriang (3 miles W of Alor Star [Setar]), [06°05'N, 100°23'E]: *AMNH 235579–235581*.

MYANMAR — Kachin State, Shwego Township, U Daung Taung, near Sinken Village, 24°08'N, 96°58'E: *C8-University of Yangon*; Shan [North Shan States], Pyaunggaung, [23°00'N, 96°28'E]: FMNH 82673–82676; North Shan [States], Pyaunggaung, [23°00'N, 96°28'E]: *BM(NH) 21.1.17.136–21.1.17.147*; Karen State, Pa–an Township, Weibyan Cave, 17°13'N, 97°37'E: *HZM 6.34237*, *HZM–H10 (field no.)*; Mon State, Hnidon Hill, 16°23'N, 97°44'E: *HZM–H20 (field no.)*.

THAILAND — Chaiyaphum Prov., Khon San, Ban Nam Thip, Huai Yang, 16°27'N, 101°40'E (Yenbutra and Felten, 1986); Chaiyaphum Prov., Khon San, Tham Yai Ban Yen, 16°27'N, 101°40'E (Yenbutra and Felten, 1986); Chaiyaphum Prov., Khon San, Thambon Tung Luei Lai, 16°27'N, 101°40'E (Yenbutra and Felten, 1986); Chiang Mai Province, Ban Tham Tap Tao (25km SSW of Fang), 19°42'N, 99°07'E, (Yenbutra and Felten, 1986): SMF 52527–52536; *TISTR 54-2202, 54-2203*; Chiang Mai Prov., Chiang Dao, Tam Chang Dao, 19°23'N, 98°56'E (Yenbutra and Felten, 1986*): TISTR 54-1907–54-1909, 54-2105–54-2110, 54-2112–54-2118, 54-2120–54-2123, 54-2125, 54-2126; BM(NH) 13.4.18.3* (type specimen); Chiang Rai Prov., Mae Chan, [20°11'N, 99°46'E]: *TISTR 54-3259*; Chiang Rai Prov., Mae Sai, Tam Pum, 20°20'N, 99°52'E (Yenbutra and Felten, 1986): *TISTR 54-3316*; Kanchanaburi [Province], Tra Khanun [Tha Khanun], Hinlaem [Ban Hin Laem, 14°42'N, 98°35'E]: USNM 296854–296859; Kanchanaburi Province, Sai Yok, Sai Yok Waterfall, 14°25'N, 98°55'E (Yenbutra and Felten, 1986); Kanchanaburi Province, Thung Yai Wildlife Sanctuary, Ban Jagae Guard Station, [15°28'N, 98°38'E]: *BM(NH) 2000.655* (Robinson *et al.*, 1995); Kanchanaburi Prov., Thung Yai Wildlife Sanctuary, Lum Khao Ngu Guard Station, [14°55'N, 98°48'E] (*Robinson et al.,1995*); Loei Prov., Amphoe Chiang Khan, Ban Pha Baen, Tam Pha Baen, 17°56'N, 101°47'E (*Robinson and Smith, 1997*); Loei Prov., Amphoe Mung, Tambon Nagor, Wat Tam Pha Phu, 17°34'N, 101°42'E (*Robinson and Smith, 1997*); Loei Prov., Ban Nong Hin, Wat Tam Maho Lan, 17°06'N, 101°53'E: *BM(NH) 1996.149–1996.159*; Nakhon Si Thammarat Province, Chawang, Khlong Chan Dee, 08°23'N, 99°33'E (Yenbutra and Felten, 1986); Nan Province, Muang Nan, Tham Song Satang, 18°50'N, 100°45'E (Yenbutra and Felten, 1986); Nan Prov., Mauang Nan, Nan, (18°47'N, 100°47'E, Yenbutra and Felten, 1986): SMF 52514–52519; Nan Prov., Sa, Ban Pha Hang, 18°35'N, 100°31'E (Yenbutra and Felten, 1986): *TISTR 54-1829, 54-1837, 54-1838, 54-1842, 54-2127, 54-2129, 54-2134–54-2140; BM(NH) 1978.2340, 1978.2341*; Phrae Prov., Rong Kwang, (18°23'N, 100°19'E, Yenbutra and Felten, 1986): SMF 52520–52526, 52632; Saraburi Prov., Kaeng Khoi, Phu Nam Tok, Tap Kwang, 14°35'N, 100°08'E (Yenbutra and Felten, 1986), *TISTR 54-1967, 54-1968, 54-2133*.

VIETNAM — Cuc Phuong National Park (Cave of Early Man), Ninh Binh Province, 20°18'N, 105°38'E: *HZM 5.32603*; Cuc Phuong National Park, Ninh Binh Province, 20°19'N, 105°37'E: *HZM 2.30541*.

Hipposideros pratti

CHINA — Anhui, Fanchang, [31°04'N, 118°12'E] (Liang and Dong, 1984); Anhui, Guangde, [30°53'N, 119°25'E] (Liang and Dong, 1984); Anhui, Ningguo, [30°37'N, 118°58'E] (Liang and Dong, 1984); Anhui, Shexian, [29°52'N, 118°26'E] (Liang and Dong, 1984); Anhui, Xiuning, [29°47'N, 118°10'E] (Liang and Dong, 1984); [Fujian], Yenping [Yenping-fu], 26°37'N, 118°10'E: MCZ 20147, 20148, 20278, 20279, 24948, 24949; [Fujian, Yenping-fu], Fukien Prov., Yenping, [26°37'N, 118°10'E]: *AMNH 44639–44643, 47972, 47974–47978, 47986, 47987, 47989, 56948, 56952, 56957, 56958, 57162, 57165, 57167, 60197, 60198, 60200, 60201, 60203, 60205, 60207, 60210*; Fujian Prov., Yenping-fu, [26°37'N, 118°10'E]: USNM 238796, 238800–238803, 238805–238808, 238810, 238812, 238814, 238816, 238818, 238903, 238944, 238950, 238954; [Fujian], Fukien, Yenping [Yenping-fu], Hsi Yuan Keng, 26°37'N, 118°10'E: RMNH 33155; Fujian, Jianyang Pref., Nanping (Yenping Fu), 26°37'N, 118°10'E: FMNH 33891;

Fujian, Jianyang Pref, Nanping (Yenping Fu), Hsi Yuan Keng, 26°37'N, 118°10'E: FMNH 33885–33890; [Fujian], Futsing [25°43'N, 119°22'E], (Allen, 1938); Guangxi, Guilin, [25°16'N, 110°16'E] (Lu, 1987); Guangxi, Hecki, [24°41'N, 107°52'E] (Lu, 1987); Henan, Xixia Countryside, Bian Fu Cave, [33°17'N, 111°28'E] G. Jones (pers. comm.); Hunan (Hunan – Kiangsi border, Hunan – Jiangxi Provincial border), Changshow Kai, 27°28'N, 112°25'E: USNM 240185–240189, 240238–240243; [Jiangxi, Guangfeng], Kiangs, Kwangfeng, 28°26'N, 118°12'E: CM 92147, 92148; Jiangxi, Yiyang, [28°22'N, 117°25'E] (Chen *et al*., 1987); Jiangxi, Qianshan, [27°21'N, 114°07'E] (Chen *et al*., 1987); Jiangxi, Yichun, [27°49'N, 114°24'E] (Chen *et al*., 1987); Jiangxi, Shanggao, [28°15'N, 114°55'E] (Chen *et al*., 1987); Jiangxi, Fenyi, [27°48'N, 114°40'E] (Chen *et al*., 1987); Jiangxi, Xiushui, [29°01'N, 114°34'E] (Chen *et al*., 1987); Jiangxi, Huichang, [25°31'N, 115°45'E] (Chen *et al*., 1989); Jiangxi, Yongfeng, [27°19'N, 115°27'E] (Chen *et al*., 1989); Jiangxi, Zixi, [27°41'N, 117°04'E] (Chen *et al*., 1989); Jiangxi, Xunwa, [24°56'N, 115°28'E] (Chen *et al*., 1989); Jiangxi, Taike, [26°48'N, 114°55'E] (Chen *et al*., 1989); Jiangxi, Yihuang, [27°33'N, 116°10'E] (Chen *et al*., 1989); [Sichuan], Szechwan, Kia-ting-fu, [29°34'N, 103°43'E]: *BM 91.5.11.1* (Type specimen); [Sichuan Prov., Chongqing Municipality], Szechwan, Wanhsien, [30°49'N, 108°20'E] (Allen, 1938); Zhejiang, Jinhua, [29°07'N, 119°39'E] Wen *et al*., 1981); Zhejiang, Tonglu, [29°49'N, 119°40'E] Wen *et al*., 1981); [Zhejiang], Chekiang, Tung-lu, 28°57'N, 121°15'E: MCZ 24240–24242, 24247, 24248.

VIETNAM — Tonkin, Chapa, [22°21'N, 103°52'E]: *BM 33.4.1.69*; MCZ 33512, 33513; FMNH 34756, 34757, 38913–38919, *38920*, 38921–38930; Lao Cai, Sa Pa District, Chapa, [22°30'N, 104°00'E]: USNM 260110, 260111.