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# A reassessment of the taxonomic status and distribution of the subspecies of *Lyroderma lyra* (Chiroptera: Megadermatidae)

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**Abstract**

*Lyroderma lyra* is one of the six currently recognised species of the family Megadermatidae. Previous studies have suggested subspecific division within *L. lyra*, wherein the nominate subspecies is predominantly distributed in South Asia, and the other subspecies, *L. lyra sinense* is occurring in southern China and Southeast Asia. Based on the congruent results of comparative morphology of skulls and bacula, as well as phylogenetic tree reconstructions – the first ones including both subspecies and incorporating the most extensive geographic sampling of "*sinense*" to date – using *co1* and *cytb* sequences, we have elevated the Southeast Asian subspecies to a distinct species status, *Lyroderma sinense*.

**Keywords**

false vampire – *Megaderma* – morphometrics – phylogenetics – South Asia – Southeast Asia

## Introduction

The false vampires, belonging to the family Megadermatidae, are restricted to the tropics and subtropics of the Old World (Wilson & Mittermeier, 2019). Members of the family are characterized externally by a rounded anterior noseleaf, well-developed, simple and erect posterior noseleaf, large oval ears joined above the forehead, forked tragus, and well-developed interfemoral membrane but no

bony tail (Bates & Harrison, 1997; Wilson & Mittermeier, 2019). Cranially, the premaxillae are essentially absent, and the nasals are greatly reduced; and dentally, the lack of upper incisors and the strongly bifid upper canines are the defining characteristics of the family (Soisook et al., 2015; Wilson & Mittermeier, 2019).

Six genera are currently recognised, each containing one extant species, namely *Lavia frons* (distributed in sub-Saharan Africa), *Cardioderma cor* (East Africa), *Macroderma gigas* (Australia), *Megaderma spasma* (Southeast Asia), *Eudiscoderma thongareeae* (Peninsular Thailand), and *Lyroderma lyra* (South and Southeast Asia) (American Society of Mammalogists (ASM), 2024; Simmons & Cirranello, 2024; Volleth et al., 2021; Wilson & Mittermeier, 2019).

*Lyroderma* Peters, 1872 was generally treated as a subgenus of *Megaderma* Geoffroy, 1810; but recent phylogenetic reconstructions using various markers (Eick et al., 2005; Kanuch et al., 2015; Soisook et al., 2015) consequently separated *Lyroderma* and *Megaderma* as full genera. Soisook et al. (2015) provided a comprehensive overview of the taxonomic-nomenclatural history of Megadermatidae; for a short summary of the changes, see table 1.

Within *Lyroderma* two subspecies are currently recognised; the nominal form is widespread in South Asia, from Afghanistan to Bangladesh, whereas *L. lyra sinense* (originally described as *sinensis* but changed into *sinense* for gender agreement) is found in Southeast Asia, from South China to Peninsular Malaysia (Singh & Sharma, 2023; Soisook et al., 2015; Wilson & Mittermeier, 2019), but the exact distributional limits are not clear. The Myanmar (formerly Burma) population of *Lyroderma* was first regarded as belonging to the taxon "*lyra*" by Sinha (1980), albeit

TABLE 1 Nomenclatural history of the genera *Megaderma* and *Lyroderma*

| **Geoffroy (1810)** | **Andersen & Wroughton (1907)** | **Ellerman & Morrison (1951)** | **Corbet & Hill (1992)** | **Simmons (2005)** | **Francis (2019)** | **Simmons & Cirranello (2024)** |
|---|---|---|---|---|---|---|
| *Megaderma* | *Eucheira** | *Megaderma* | *Megaderma* (*Lyroderma*) | *Megaderma* (*Lyroderma*) | *Lyroderma* | *Lyroderma* |
| *lyra* | *lyra* | *lyra* | *lyra* | *lyra* | *lyra* | *lyra* |
| | *lyra* | *lyra* | *lyra* | *lyra* | *lyra* | *lyra* |
| | *caurina* | *caurina* | *sinensis* | *sinensis* | *sinense* | *sinense* |
| | *sinensis* | *sinensis* | | | | |
| | *Megaderma* | | *Megaderma* (*Megaderma*) | *Megaderma* (*Megaderma*) | *Megaderma* | *Megaderma* |
| *spasma* | *spasma* | *spasma* | *spasma* | *spasma* | *spasma* | *spasma* |
| *trifolium* | *carimatae* | | | | | |
| | *natunae* | | | | | |

* According to Andersen and Wroughton (1907) *Eucheira* Hodgson, 1847 antedates the name *Lyroderma* Peters, 1872; however, *Eucheira* Hodgson, 1847 is preoccupied by *Eucheira* Westwood, 1834 (a Lepidoptera) (see Miller, 1907).

that his arguments are debatable. He considered the skull size as the only difference between "*lyra*" and "*sinense*" [*sinense* being the larger taxon] but noted that "Indian examples have smaller skulls than those from Burma" (Sinha, 1980).

The taxon *sinense* was described by Andersen & Wroughton (1907) as a new species in the genus *Eucheira* based on two skins and skulls collected from Xiamen, Fujian Province and Shantou, Guangdong Province, South China (Andersen & Wroughton, 1907). The authors distinguished the new species from *E. lyra* on the basis of size and certain cranial traits (skull length of *sinense* is between 29.3–32.0 mm, the prenasal notch narrower, rounded posteriorly; vs. skull length between 27.8–29 mm, and the prenasal notch posteriorly wider, flattened in *lyra*) (Andersen & Wroughton, 1907). Sanborn (1933) published a study of bats from China, in which he measured 35 specimens of *E. sinensis* collected in western Sichuan, China, and 6 specimens collected in Fujian. Investigating if the two populations under study may represent two distinct forms, based on the external and craniodental measurements taken by him, he finally concluded that these two populations cannot be distinguished neither based on size nor on the observed slight color differences. Despite the limitations of his study (Sanborn, 1933), without further explanation he listed *sinense* as a subspecies of *L. lyra*, the view that is widely accepted by subsequent authors (Bates & Harrison, 1997; Corbet & Hill, 1991; Csorba & Topál, 1994; Ellerman & Morrison-Scott, 1951; Lekagul & McNeely, 1977; Sanborn, 1933; Simmons, 2005; Simmons & Cirranello, 2024; Wei, 2023; Wilson & Mittermeier, 2019; Wilson & Reeder, 2005).

The karyology of the two subspecies has been studied, and they share the same karyotype (Wu & Harada, 2006). Nevertheless, the obvious morphological differences between the two subspecies (summarised by Csorba & Topál, 1994) have never been tested by molecular biological methods. In this study, we applied an integrative taxonomic approach, including analyses of morphological data and mtDNA sequences based on the most comprehensive taxonomic samplings to investigate the taxonomic status of *L. lyra lyra* and *L. lyra sinense*.

## Methods

### *Specimens examined*

For morphological comparison and partly for multivariate statistics, seventy-one specimens of *L. lyra* and eleven specimens of *Megaderma spasma* – the other common, widely distributed and frequently sympatric Asian false vampire species – were used. The specimens are housed in the following collections: GZHU – School of Life Sciences, Guangzhou University, Guangdong, China, HNHM – Hungarian Natural History Museum, Budapest, Hungary, HUNNU – Hunan Normal University, Changsha, Hunan, China, NENU – Northeast Normal University, Changchun, Jilin, China, NHMUK – Natural History Museum, London, United Kingdom, PSUZC – Prince of Songkla University Zoological Collection, Hat Yai, Thailand, SCAF – Sichuan Academy of Forestry, Chengdu, Sichuan, China, SMNH – Slovenian Museum of

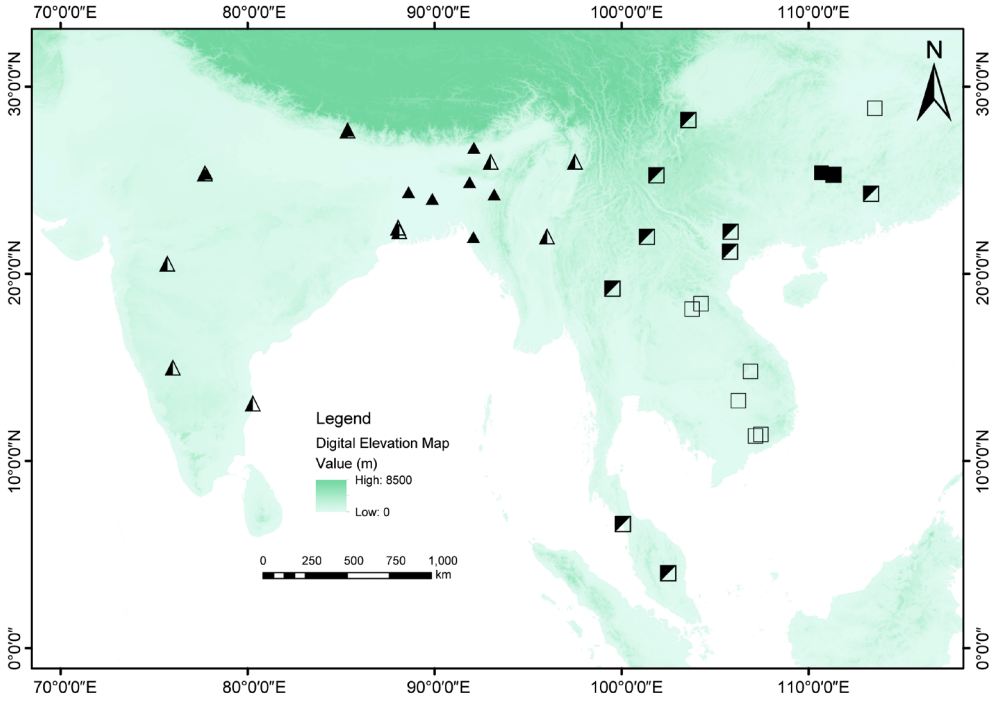



FIGURE 1 Geographic distribution of the Indian false vampire bat *Lyroderma lyra* (triangles) and Greater false vampire bat *Lyroderma sinense* (squares) and samples analysed in the present paper. Full symbols: both morphological and genetic data were used; empty symbols: only molecular data were available; half-full symbols: only morphological information was used. Some symbols represent multiple specimens from the same locality.

Natural History, Ljubljana, Slovenia, UKMMZ – Universiti Kebangsaan Malaysia, Muzium Zoologi, Bangi, Malaysia, ZSI Pune – Western Regional Centre, Zoological Survey of India, Pune and ZSI Shillong – North Eastern Regional Centre, Zoological Survey of India, Shillong. The distribution map of the sampling points is shown in fig. 1.

*Lyroderma lyra lyra*: BANGLADESH: HNHM-28234, ♀; HNHM-28235, ♀; HNHM-28237, ♀; HNHM-28238, ♀; HNHM-28239, ♀; HNHM-28241, ♂; INDIA, ASSAM: ZSI-VMERS-384, sex unknown; ZSI-VMERS-429, ♀; INDIA, KARNATAKA: HNHM-93.11.1., ♀; HNHM-93.11.2., ♂; INDIA, MADHYA PRADESH: ZSI-CZRC-V-6175, ♀; ZSI-CZRC-V-6176, ♀; ZSI-CZRC-V-6179, ♀; INDIA, MAHARASHTRA: HNHM-92.79.1., sex unknown; HNHM-92.79.2., sex unknown; HNHM-92.78.2., ♂; HNHM-92.78.5., ♀; INDIA, MANIPUR: ZSI-VMERS-429, ♂; INDIA, TAMIL NADU: HNHM-93.13.2., ♀; HNHM-93.13.3., ♀; INDIA, WEST BENGAL: HNHM-93.10.1., ♂; HNHM-93.10.2., ♀; HNHM-93.10.3., ♀; HNHM-92.76.1., ♀; HNHM-92.76.2., ♂; HNHM-92.76.3., ♂; NEPAL: HNHM-98.5.2., ♂; HNHM-95.48.1., ♂; HNHM-95.48.2., ♂.

*Lyroderma lyra sinense*: CAMBODIA: HNHM-23746, ♂; CHINA, SICHUAN: SCAF-LDS-000, ♂; SCAF-LDS-001, ♀; SCAF-LDS-002, ♀; SCAF-LDS-003, ♂; SCAF-LDS-004, ♂;

SCAF-LDS-005, ♀; SCAF-LDS-006, ♂; SCAF-LDS-007, ♂; SCAF-LDS-009, ♂; SCAF-LDS-010, ♂; SCAF-LDS-011, ♀; CHINA, GUANGDONG: GZHU-01091, ♂; GZHU-99058, sex unknown; GZHU-99059, ♀; GZHU-99152, ♀; CHINA, GUANGXI: NENU-GX181022, ♂; CHINA, HUNAN: HUNNU-JY01, ♂; HUNNU-JY02, ♂; HUNNU-JY03, ♀; NENU-JY-19-02, ♀; NENU-JY-19-03, ♀; NENU-JY-19-04, ♀; NENU-HUN-10-32, ♀; CHINA, YUNNAN: NENU-YN-08-121, ♂; SMNH, not registered, sex unknown; MALAYSIA: UKMMZ-m1505, ♀; THAILAND: PSUZC-05.214, ♂; THAILAND, PENINSULAR: PSUZC-2014.159, ♀; VIETNAM: HNHM-2007.27.10., ♀; HNHM-95.49.1., ♂; HNHM-95.49.2., ♂; HNHM-95.49.3., ♀; HNHM-95.49.4., ♂; HNHM-95.49.5., ♂; HNHM-98.90.35., ♀; HNHM-98.90.37, sex unknown.

*Lyroderma lyra* ssp: MYANMAR: NHMUK-ZD1950.425, ♂; NHMUK-ZD1950.426, ♀; NHMUK-ZD1950.427, ♂; NHMUK-ZD1950.428, ♂; NHMUK-ZD1950.429, ♂; NHMUK-ZD1950.430, ♀; NHMUK-ZD1921.2.1.43, ♀; NHMUK-ZD1921.2.1.44, ♀.

*Megaderma spasma*: CAMBODIA: HNHM-2005.81.40, ♀; HNHM-2006.34.35, sex unknown, HNHM-2005.81.34, ♂; HNHM-2011.1.13, ♀; MALAYSIA, PENINSULAR: HNHM-95.47.1, ♀; HNHM-95.47.2, ♂; MALAYSIA, SARAWAK: HNHM-26465, ♂; VIETNAM: HNHM-2010.42.6, ♂; THAILAND, PENINSULAR: PSUZC-07.267, ♂; PSUZC-07.5, ♀; PSUZC-06.119, ♂.

## Measurements and morphometric analysis

We took one external (forearm length) and 13 craniodental measurements, following Bates and Harrison (1997); definitions are shown in table 2. The external measurements were taken in the field, the cranial and dental ones were measured under a stereomicroscope by digital vernier calliper to the nearest 0.01 mm. Measurements were recorded from adult specimens only.

Previous studies have indicated that the forearm of female individuals of *L. l. lyra* is longer than that of male individuals (Sinha, 1980). The results of the independent samples *t*-test show that the forearm length of female individuals of *L. l. sinense* is significantly longer than that of male individuals ($T = -3.525$, $p = 0.002$). Since the craniodental parameters did not meet the homogeneity of variances, we employed the Mann-Whitney *U* test to ascertain whether there were significant differences in the craniodental parameters between male and female individuals of *L. l. sinense* and *L. l. lyra* (Nachar, 2008). The skull length (GLS) and width (ZYW) of female *L. l. sinense* are significantly greater than those of male *L. l. sinense*, henceforth, the analysis of craniodental parameters was conducted separately for the two sexes. We employed 9 craniodental measurements of 58 specimens (a subset of the morphologically studied museum materials), with 29 individuals each for females and males (tables 3 and 4), to perform principal component analysis (PCA) and linear discriminant analysis (LDA). To reduce the potential influence of skewed distributions or outliers, we performed logarithmic transformation on the data before conducting PCA and LDA analyses. The results showed that the PCA and LDA outcomes before and after logarithmic transformation were similar. The analyses were carried out using R 4.3.1 (R Core Team, 2024), incorporating methods like

TABLE 2 Description of cranial, mandibular, and external dimensions and their abbreviations

| Measurements | Acronyms | Descriptions |
|---|---|---|
| Forearm length | FA | From the elbow to the distal end of the forearm including carpals |
| Greatest length of skull | GLS | From the apex of the upper internal incisors to the occiput |
| Condylo-canine length | CCL | From the anterior surface of the upper canines to a line connecting the occipital condyles |
| Interorbital breadth | IOB | Least breadth between the orbits |
| Zygomatic width | ZYW | Greatest breadth across the outer margins of the zygomatic arches |
| Mastoid width | MAW | Greatest breadth across the mastoid region |
| Braincase width | BCW | Greatest breadth of the globular part of the braincase |
| Braincase height | BCH | Braincase height posteriorly to the auditory bullae |
| Maxillary canine outer width | CCW | Distance between outer margins of C1 |
| Width of upper molars | M3M3W | Maximum distance between the bases of the outer edges of the third posterior molars on each maxillary side |
| Maxillary toothrow length | CM3L | Maximum length from the anterior margin of the maxillary canine to the posterior margin of the base of the last molar on the same side |
| Mandible length | MANL | The length from the most anterior edge of the mandible (excluding incisors) to the most posterior edge of the mandible |
| Mandibular toothrow length | cm3L | Maximum length from the anterior edge of the mandibular canine to the final edge of the last molar |
| Mandibular molariform toothrow length | m1m3L | Distance from the anterior edge of the m1 alveolus to the posterior edge of the m3 alveolus of the mandibular posterior molar |

the Mann-Whitney *U* Test. Visualization of the results was accomplished using the ggord, ggplot2, plot and factoextra packages in R 4.3.1 (R Core Team, 2024). To assess the suitability of the data for use in PCA, we utilized Kaiser-Meyer-Olkin (KMO) test and the Bartlett's test of sphericity focusing on the skull dataset. The Kaiser-Meyer Olkin measure of sampling adequacy (KMO) was greater than 0.5 and the Bartlett's test of sphericity was significant ($p < 0.001$), indicating that the data was suitable for PCA (Maskey et al., 2018). Missing data were filled with average values.

TABLE 3 Selected measurements (mm) of male group *L. sinense*, *L. lyra* and *M. spasma*, and vector correlation loadings with original variables of principal components (PC1 and PC2) and discriminant functions (DF1 and DF2) for selected samples of male group *L. l. sinense*, *L. l. lyra and M. spasma*. See Table 2 for variable abbreviations.

| Meareplsurements | *L. l. sinense* | *L. l. lyra* | *M. spasma* | PC1 | PC2 | DF1 | DF2 | *p*-value |
|---|---|---|---|---|---|---|---|---|
| GLS | 30.63(29.92–31.96)16 | 28.85(28.1–29.68)8 | 24.93(23.36–25.61)5 | −0.34 | 0.12 | −0.68 | 0.34 | < 0.001 |
| CCL | 27.43(26.54–28.55)16 | 25.53(24.77–26)8 | 21.65(20.47–22.62)5 | −0.34 | 0.12 | 1.55 | 0.01 | < 0.001 |
| IOB | 5.52(5.28–5.69)16 | 4.83(4.63–4.93)8 | 3.78(3.6–4.14)5 | −0.34 | 0.13 | 5.59 | 1.37 | < 0.001 |
| ZYW | 17.02(16.42–17.51)16 | 16.57(16.29–17.04)8 | 13.81(12.71–14.23)5 | −0.34 | 0.22 | 0.78 | −0.83 | 0.003 |
| MAW | 13.28(12.82–13.63)16 | 12.59(12.38–12.93)8 | 10.91(10.35–11.2)5 | −0.34 | 0.19 | 0.57 | 1.00 | < 0.001 |
| BCW | 12.64(12.37–13)16 | 12.32(11.86–12.49)8 | 10.55(9.83–10.79)5 | −0.34 | 0.21 | −1.07 | −2.06 | 0.001 |
| BCH | 12.64(12.37–13)16 | 10.24(10.04–10.45)8 | 8.85(7.92–9.43) | – | – | – | – | < 0.001 |
| CCW | 6.42(6.01–8.6)16 | 5.67(5.46–5.87)8 | 5.18(4.86–5.46)5 | −0.28 | −0.81 | −0.52 | 4.50 | < 0.001 |
| M3M3W | 10.31(9.67–12.37)16 | 9.90(9.41–10.11)8 | 8.27(7.81–8.81)5 | −0.32 | −0.41 | 0.39 | −4.43 | 0.016 |
| CM3L | 11.91(11.48–12.48)16 | 11.23(11.03–11.45)8 | 9.63(9.05–10.21)5 | −0.35 | 0.06 | −0.40 | 1.30 | < 0.001 |
| MANL | 21.46(20.5–22.54)16 | 19.69(18.95–20.28)8 | 16.99(15.77–17.59)5 | – | – | – | – | < 0.001 |
| cm3L | 12.96(12.52–13.41)16 | 12.22(11.96–12.6)8 | 10.70(9.97–11.26)5 | – | – | – | – | < 0.001 |
| m1m3L | 7.80(7.57–8.56)16 | 7.36(7.15–7.54)8 | 6.42(6.03–6.7)5 | – | – | – | – | < 0.001 |

TABLE 4 Selected measurements (mm) of female group *L. sinense*, *L. lyra* and *M. spasma*, and vector correlation loadings with original variables of principal components (PC1 and PC2) and discriminant functions (DF1 and DF2) for selected samples of female group *L. l. sinense*, *L. l. lyra and M. spasma*. See Table 2 for variable abbreviations.

| Measurements | *L. l. sinense* | *L. l. lyra* | *M. spasma* | PC1 | PC2 | DF1 | DF2 | *p*-value |
|---|---|---|---|---|---|---|---|---|
| GLS | 30.96(30.18–31.73)17 | 28.80(28–29.55)8 | 25.10(24.12–25.8)4 | −0.34 | −0.12 | −0.55 | −0.51 | < 0.001 |
| CCL | 27.58(26.39–28.5)17 | 25.56(24.93–26.21)8 | 22.25(21.35–22.89)4 | −0.34 | −0.06 | −0.05 | −3.52 | < 0.001 |
| IOB | 5.55(5.26–6.09)17 | 4.89(4.78–5.07)8 | 3.64(3.34–3.96)4 | −0.33 | −0.30 | −2.92 | −1.89 | < 0.001 |
| ZYW | 17.40(16.82–18.09)17 | 16.61(16.32–16.9)8 | 13.84(12.87–14.29)4 | −0.34 | 0.25 | 0.90 | 1.56 | < 0.001 |
| MAW | 13.49(12.86–13.92)17 | 12.73(12.38–13.17)8 | 10.97(10.57–11.37)4 | −0.33 | 0.20 | −2.16 | 0.81 | < 0.001 |
| BCW | 12.86(12.37–13.28)17 | 12.40(11.95–12.68)8 | 10.45(10.05–10.65)4 | −0.34 | 0.30 | −0.55 | 3.58 | < 0.001 |
| BCH | 11.22(10.66–12.07)17 | 10.24(10.1–10.38)8 | 8.55(8.37–8.81)4 | | | | | < 0.001 |
| CCW | 6.35(6.09–6.72)17 | 5.71(5.53–5.89)8 | 5.09(4.94–5.39)4 | −0.32 | −0.76 | 0.55 | −4.84 | < 0.001 |
| M3M3W | 10.45(9.93–11.01)17 | 10.08(9.92–10.24)8 | 8.19(8.03–8.4)4 | −0.33 | 0.30 | −1.79 | 4.01 | < 0.001 |
| CM3L | 11.86(11.45–12.44)17 | 11.32(11.04–11.59)8 | 9.74(9.45–10.02)4 | −0.33 | 0.16 | −0.40 | 3.41 | < 0.001 |
| MANL | 21.57(20.47–22.63)17 | 19.66(19.29–20.07)8 | 17.17(16.49–17.7)4 | | | | | < 0.001 |
| cm3L | 13.03(12.24–13.63)17 | 12.21(11.88–12.43)8 | 10.65(10.42–11.02)4 | | | | | < 0.001 |
| m1m3L | 7.83(7.53–8.3)17 | 7.39(7.26–7.51)8 | 6.49(6.24–6.74)4 | | | | | < 0.001 |

### *Baculum*

Preparation and preservation of the penial bone followed that of Friley (1947). The baculum was drawn, and its maximum length was measured using a Mitutoyo digital calliper to the nearest 0.01 mm under a stereomicroscope.

### *Phylogenetic inference*

Total genomic DNA was extracted with DNeasy Blood & Tissue Kit (Qiagen, Germany) according to the instructions of the manufacturer from ethanol-preserved tissue samples of 18 *Lyroderma* specimens forming part of the genetic resources' collections of HNHM, HUNNU, NENU, ZSI Pune and ZSI Shillong.

For phylogenetic analysis, the mitochondrial cytochrome oxidase c subunit I (*CO1*, 657 bp) and the cytochrome b gene (*cytb*, 1140 bp) were amplified with the primers C1L705/UtyrLA (Hassanin et al., 2012) and Molcit-F/Cytb-H (Ibáñez et al., 2006; Weyeneth et al., 2008), respectively. PCR reactions were performed in 50 µl using 1 µl (ca. 20 ng) of genomic DNA, 1-1 µl of the primers (10 mM), 40.25 µl of nuclease-free water, 1.5 µl of dNTP, 5 µl of DreamTaq Green Buffer (Thermo Scientific, USA) and 0.25 µl of DreamTaq DNA Polymerase (Thermo Scientific, USA). Laboratory works were done in-country for respective specimens housed in a particular museum. The *CO1* and *cytb* sequences were aligned with related taxa with MEGA7 (Kumar et al., 2016). The newly generated sequences were compared with 43 *CO1* (including 6 outgroups) and 14 *cytb* (including 6 outgroups) gene sequences of false vampires downloaded from the National Center for Biotechnology Information (NCBI) GenBank (supplementary table S3).

The phylogenetic analysis was performed using the maximum likelihood (ML) method, in the software MEGA7. To evaluate nodal support, we computed a nonparametric bootstrap using 1000 replicates. Additionally, the genetic distance (*p*-distance) of *CO1* and *cytb* genes was calculated by Bootstrap method using MEGA7.

## Results

### *Morphology and multivariate statistics*

We could not establish any statistically significant difference (paired samples *T*-test, $F = 1.134$, $p = 0.295$) between *L. l. sinense* (67.76 ± 1.06 mm) and *L. l. lyra* (67.3 ± 1.55 mm) with respect to forearm length (FA).

The Mann-Whitney *U* Test was used to compare thirteen cranial parameters of males and females between two subspecies. The results showed significant sex differences in all cranial parameters of *L. l. lyra* and *L. l. sinense*. On average, within the same sex, the skull of *L. l. sinense* is longer and wider than that of *L. l. lyra* (tables 3 and 4, fig. 2, supplementary figs. S1 and S2) despite that overlapping values in all measurements were observed. However, in line with the observations of (Andersen & Wroughton, 1907), the anatomy of the interorbital region and the prenasal notch showed clear differences between the two taxa (see details in the Introduction and in fig. 2).

The first principal component (PC1) accounted for more than 93.00% of the total craniometric variation and represents the size of the upper jaw of the skull (figs. 3A and 4A). Along the PC1 axis, there is

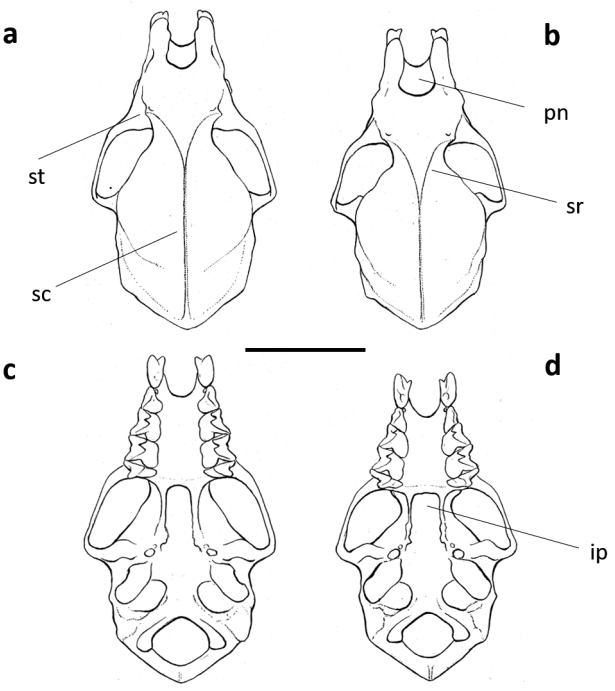



FIGURE 2 The dorsal and ventral views of the skulls of *L. sinense* (HNHM 98.90.35.) from Bac Thai, Vietnam (a, c), and *L. lyra* (HNHM 92.77.1.) from West Bengal, India (b, d). st = supraorbital tubercle; sc = sagittal crest; pn = prenasal notch; sr = supraorbital ridge; ip = interpterygoid. Scale = 10 mm

no overlap between the groups of male *M. spasma* and *L. l. lyra*, or between *M. spasma* and *L. l. sinense*; these groups show some overlap along PC2 between *M. spasma* and *L. l. lyra*, or between *M. spasma* and *L. l. sinense* (2.44%). However, male *L. l. lyra* and *L. l. sinense* exhibit overlap along both PC1 and PC2. Along the PC1 axis, there is no overlap among female *M. spasma*, *L. l. lyra*, and *L. l. sinense*; however, on the PC2 axis, all three groups show overlap (2.07%). For both male and female groups, the factor loadings show that the loadings for the first PC are very close, while on the second PC, the factor loadings for CCW and M3M3W are higher than those of the other samples, indicating that they are the most useful discriminant factors; following these, the next important discriminant factors include BCW, ZYW, and IOB (tables 3 and 4, figs. 3B and 4B). The factor loadings of other PCs are shown in supplementary tables S1 and S2. The LDA of craniodental measurements shows that in LD1, there is no overlap among the three species for both males (89.67%) and females (80.41%), whereas in LD2, there is some overlap among the three species in males, and only between *L. l. sinense* and *M. spasma* in females (figs. 3C and 4C). In males, some parameters associated with the length or width of the skull and maxilla

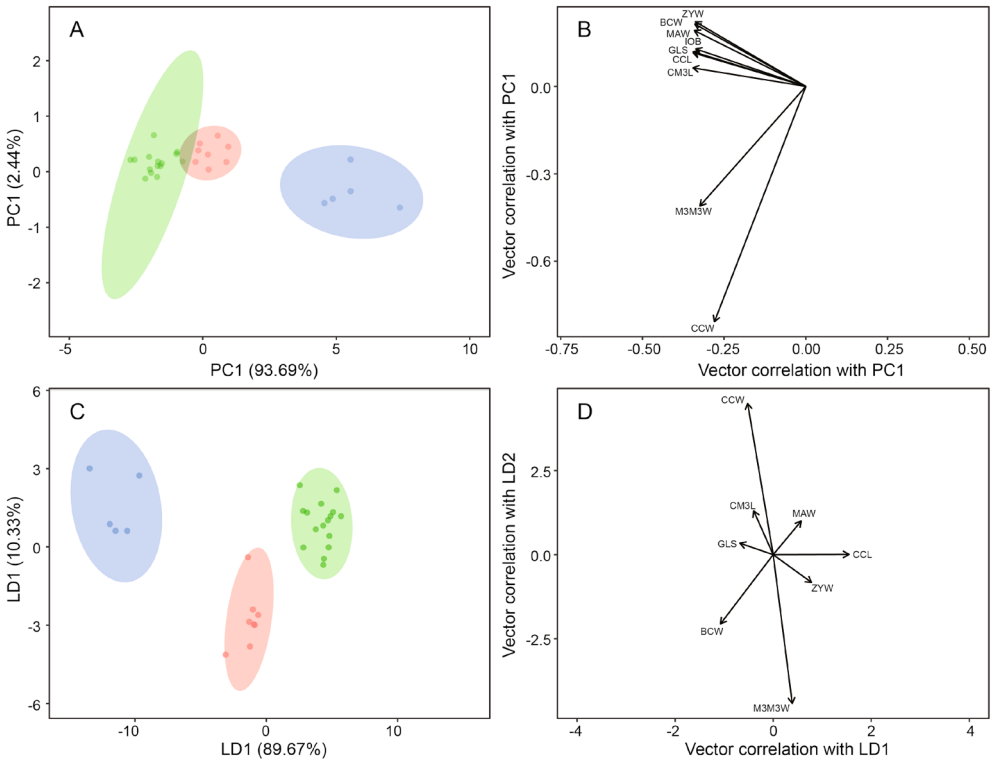



FIGURE 3 Two-dimensional PCA and vector correlation (A, B) and two-dimensional LDA and vector correlation (C, D) of cranial measurements for male *Lyroderma sinense* (green dots), *Lyroderma lyra* (red dots) and *Megaderma spasma* (blue dots). The range of the axes of A and B, C and D are different.

(IOB, CCL, BCW, GLS) are most helpful in distinguishing these three groups (fig. 3D, table 3). In females, however, some parameters related to the width of the skull and maxilla (IOB, MAW, M3M3W, ZYW) are most effective in differentiating these three groups (fig. 4D, table 4).

The baculum of both *L. l. sinense* and *L. l. lyra* consists of two separate, stick-like bones only partially connected with ligaments; the penis bones of *L. l.* sinense are distinctly longer than those of *L. l. lyra*, (1.01 mm vs. 0.69–0.72 mm) and straight (vs. distinctly bent dorsoventrally in *L. l. lyra*) (fig. 5).

### *Phylogenetic reconstructions*

The newly obtained sequences included *COI* and *cytb* sequences for eight *L. l. sinense*, 10 *L. l. lyra*, and one *M. spasma*. All novel sequences were deposited in the NCBI GenBank and registered under the accession numbers PQ615380-PQ615394 and PQ619736-PQ619752.

The ML phylogenetic tree constructed based on *COI* and *Cytb* sequences revealed similar phylogenetic relationships, with *L. l. sinense* being closely related to and forming a sister clade with *L. l. lyra*, while *M. spasma* grouped with species of other genera within the Megadermatidae family,

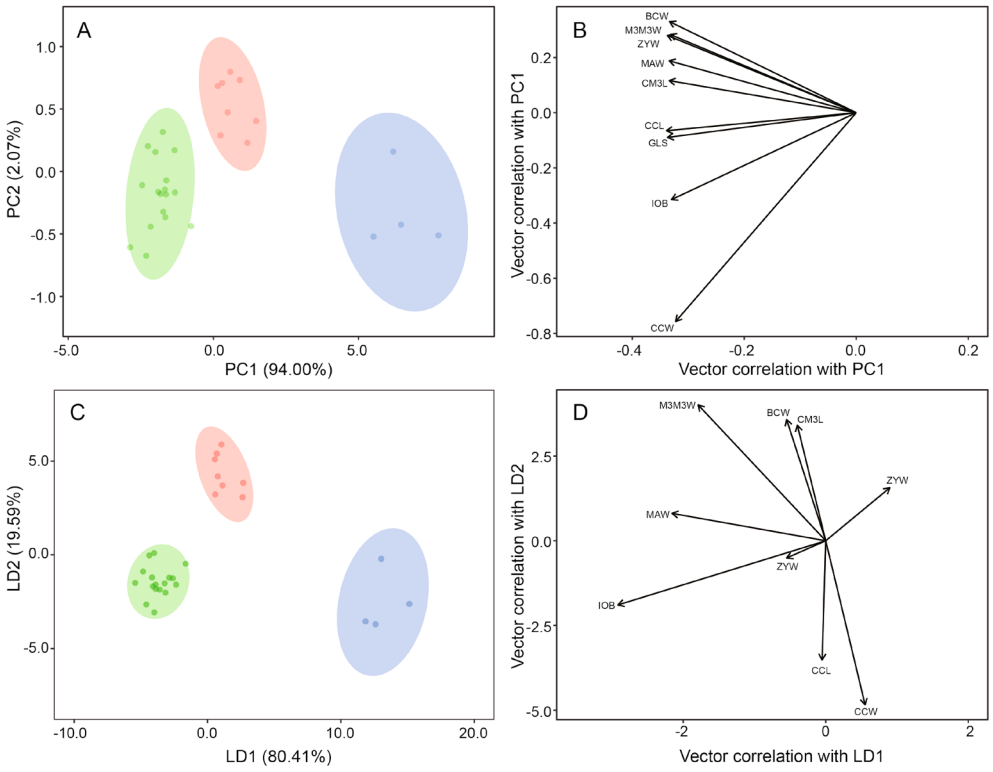



FIGURE 4 Two-dimensional PCA and vector correlation (A, B) and two-dimensional LDA and vector correlation (C, D) of cranial measurements for female *Lyroderma sinense* (green dots), *Lyroderma lyra* (red dots) and *Megaderma spasma* (blue dots). The range of the axes of A and B, C and D are different.

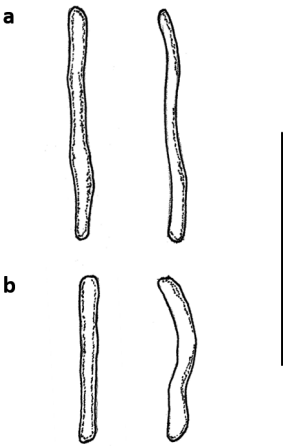



FIGURE 5
The dorsal (left) and lateral (right) views of the baculum of (a) *L. sinense* (HNHM 95.49.4.) from Bac Thai, Vietnam; and (b) *L. lyra* (HNHM 92.78.1.) from Maharasthra, India. Scale = 1 mm

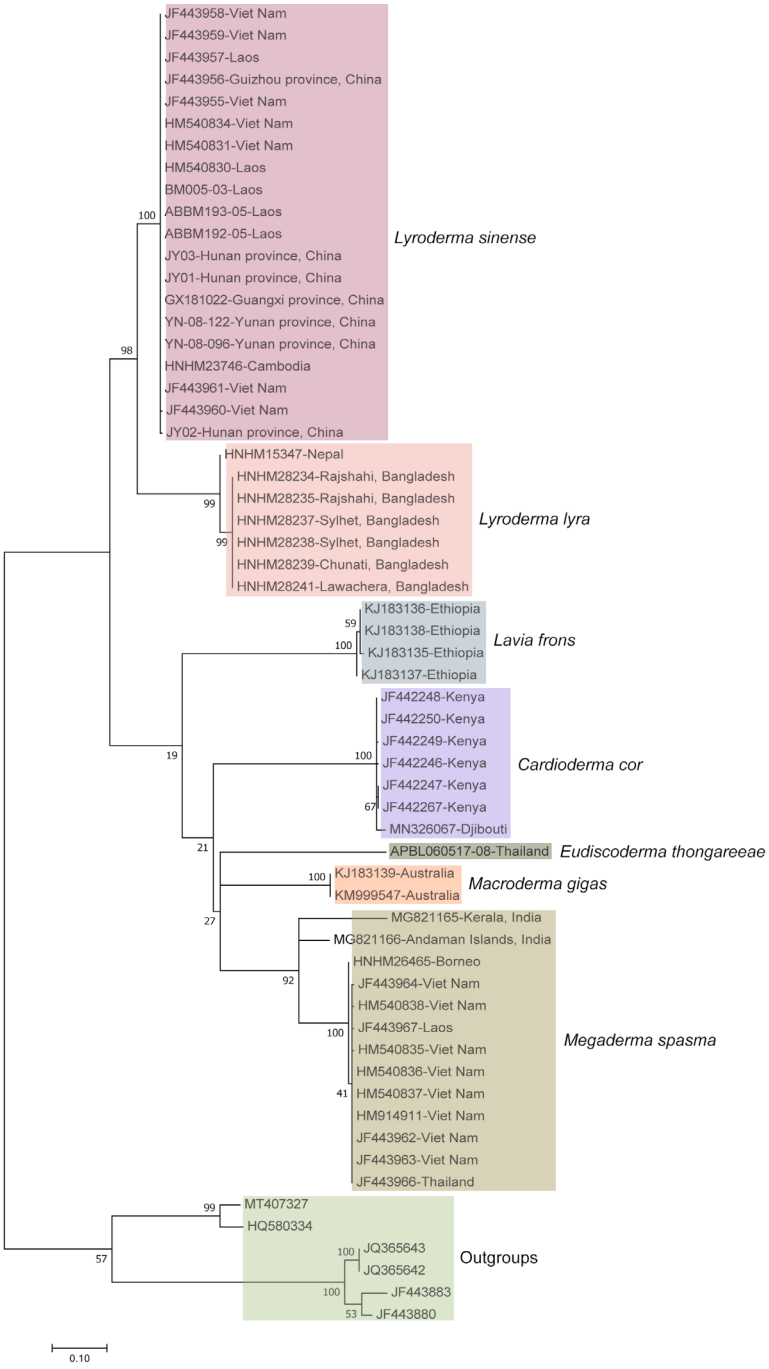



FIGURE 6 Phylogenetic tree resulting from the Maximum Likelihood analysis of *co1* sequences of species of Megadermatidae, numbers indicate nodal support, the outgroup genes were derived from species of the genera *Hipposideros* and *Rhinolophus*.

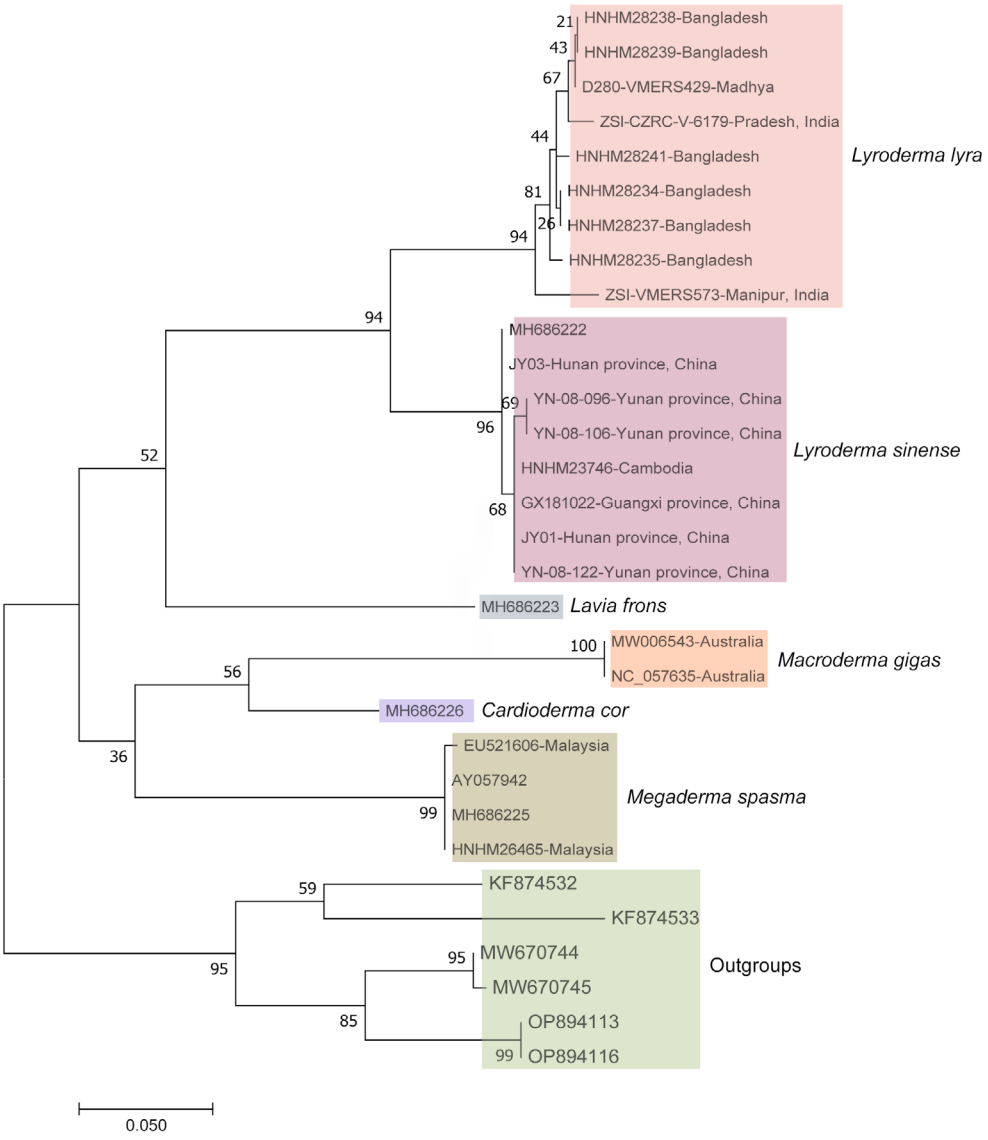



FIGURE 7 Phylogenetic tree resulting from the Maximum Likelihood analysis of *cytb* sequence of species of Megadermatidae, numbers indicate nodal support, the outgroup genes were derived from species of the genera *Hipposideros* and *Rhinolophus*.

despite the low nodal support for this phylogeny and branching events (figs. 6 and 7, supplementary fig. S3). The average *p*-distance between *L. l. sinense* and *L. l. lyra* for *COI* is 12.61%, and for *Cytb*, it is 9.86%, which is much lower than the average *p*-distances for the two mitochondrial genes between *Lyroderma* and *Megaderma* (both are higher than 17%; tables 5 and 6).

TABLE 5 Average *p*-distance within Megadermatidae based on *COI* sequences. Boldface value indicates the distance between *Lyroderma sinense* and *Lyroderma lyra*.

| | Taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|---|
| 1 | *Lyroderma sinense* | – | | | | | | |
| 2 | *Lyroderma lyra* | **0.1261** | – | | | | | |
| 3 | *Eudiscoderma thongareeae* | 0.1715 | 0.2006 | – | | | | |
| 4 | *Megaderma spasma* | 0.1886 | 0.1988 | 0.1692 | – | | | |
| 5 | *Lavia frons* | 0.1937 | 0.1968 | 0.1968 | 0.1914 | – | | |
| 6 | *Cardioderma cor* | 0.1829 | 0.2032 | 0.1957 | 0.1857 | 0.1911 | – | |
| 7 | *Macroderma gigas* | 0.1818 | 0.1890 | 0.1864 | 0.1700 | 0.1830 | 0.1960 | – |

TABLE 6 Average *p*-distance genetic distance within Megadermatidae based on *cytb* sequences. Boldface value indicates the distance between *Lyroderma sinense* and *Lyroderma lyra*.

| | Taxa | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| 1 | *Lyroderma sinense* | – | | | | | |
| 2 | *Lyroderma lyra* | **0.0986** | – | | | | |
| 3 | *Megaderma spasma* | 0.1843 | 0.1796 | – | | | |
| 4 | *Lavia frons* | 0.1670 | 0.1683 | 0.1836 | – | | |
| 5 | *Cardioderma cor* | 0.1711 | 0.1680 | 0.1603 | 0.1754 | – | |
| 6 | *Macroderma gigas* | 0.1671 | 0.1717 | 0.1718 | 0.1816 | 0.1693 | – |

## Discussion

Although there have been variable amounts of overlap among all the measured craniodental characters, we observed significant differences between the two previously recognized subspecies of *L. lyra*. The results of the PCA of the nine craniodental measurements showed slight overlap between *L. l. sinense* and *L. l. lyra* males, whereas the results of the LDA showed no overlap in LD1 between male and female *L. l. sinense*, *L. l. lyra*, and *M. spasma*.

The morphological diversity of the mammalian baculum is subject to direct selection as a result of their role in copulation (Rakotondramanana & Goodman, 2017; Stockley, 2012), and the total length of the baculum of adult individuals is considered a diagnostic criterion for species characterization (Douangboubpha et al., 2010; Latorre, 2023; Soisook et al., 2015; Srinivasulu et al., 2020; Thomas, 1915; Vercillo & Ragni, 2011). The length of the baculum of a *Lyroderma* collected in Thailand was about 1 mm (Soisook

et al., 2015), whereas the bacular length of an Indian specimen was about 0.5 mm (Srinivasulu et al., 2020), which is similar to our results. The bacular differences among different genera of Megadermatidae are significant, which supports that bacular features play an important role in the classification of Megadermatidae (Soisook et al., 2015). The difference in baculum length between the two taxa, but the similarity in structure, supports the idea that *L. sinense* and *L. lyra* are two separate, but closely related species.

The phylogenetic reconstructions using *co1* and *cytb* gene sequences, consequently placed all *Lyroderma* samples into a single clade, sister to a clade containing all other genera. This result is consistent with other recent phylogenies and supports the validity of *Lyroderma* as a separate genus (Eick et al., 2005; Kanuch et al., 2015; Soisook et al., 2015).

Phylogenetic analyses also evidenced that *L. lyra* is divided into two independent clades, and the genetic distances between the *co1* and *cytb* gene fragments were more than 12% and nearly 10% between *L. lyra lyra* and *L. lyra sinense*, respectively. In line with the widely accepted view (Bradle & Baker, 2001) this magnitude of genetic distance is considered to indicate specific distinctiveness rather than subspecific status. The congruent results of the morphological, morphometric, and molecular analyses in the present study strongly support the view of Andersen and Wroughton (1907) that the genus *Lyroderma* consists of two species, *L. lyra* and *L. sinense*.

The critical evaluation of previous works, based on craniodental measurements and the structure of the interorbital region, helped us to clarify the taxonomic status of the populations in Afghanistan and Pakistan where neither directly comparable museum specimens nor molecular data were available from. Shahbaz et al. (2020) reported the species from Jhelum, Punjab, Pakistan, and as it can be judged from the poor-quality photographs, on the bases of the shape of the interorbital region, anterior narial emargination and the interpterygoid region (fig. 1), the population is more likely to represents *L. lyra* (Shahbaz et al., 2020). Benda and Gaisler (2015) provided IOB measurements (the trait which proved to be a reliable distinguishing character between "*lyra*" and "*sinense*", see fig. 1 and table 3) of three Afghani specimens (range 4.66–4.79 mm). Both above publications concur with the view of previous authors (Bates & Harrison, 1997; Corbet & Hill, 1992; Khajuria, 1980; Srinivasulu & Srinivasulu, 2012), that the westernmost populations of *Lyroderma* belongs to *L. lyra*.

The Myanmar specimens held in the collection of NHMUK (probably these are the same individuals as listed by Sinha) exceed the size limits of "*lyra*" given by Sinha (1980) (see the upper mensural extremes of *L. lyra* given in table 3), but the morphology of the interorbital region, narial emargination, and the interpterygoid region, indeed, clearly defines these specimens as *L. lyra* (fig. 1).

## Conclusion

The present study is the first which included both former subspecies of *L. lyra* in a phylogenetic framework and used the widest geographic sampling of the taxon "*sinense*" so far. We have found significant

differences in cranial and dental measurements, and in the size of the bacula of the taxa "*lyra*" and "*sinense*". These data were corroborated by multivariate statistical analyses (PCA and LDA) and by phylogenetic tree reconstructions based on mitochondrial markers. This integrative approach provides solid evidence that the two former subspecies represent separate species, *L. lyra* and *L. sinense*. Additionally, our results also supported that the westernmost and Myanmar populations of *Lyroderma* belongs to *L. lyra*. To sum up, *L. sinense* is distributed in southern China, Thailand, Laos, Vietnam, Cambodia, and Malaysia, whereas *L. lyra* occurs from Afghanistan to Myanmar (fig. 1). As the presence of *L. lyra* can be assumed in east Myanmar, future studies should involve the collection of more samples from that country and from the surrounding areas, to reveal the phylogenetic affinities of the Myanmar populations and to determine the precise distribution boundaries of the two species.

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**Author contributions**

Feng: conceptualization, methodology, formal analysis, writing – original draft, visualization; Győrössy: data curation, methodology, formal analysis, writing – review & editing; Portela Miquez: resources, writing – review & editing; Kokkini: resources, writing – review & editing; Görföl: writing – review and editing, supervision, funding acquisition; Ali Khan: resources, funding acquisition; Saikia: resources, writing – review and editing; Talmale: resources; Yu: resources; Liu: resources; Jiang: writing – review and editing, supervision, funding acquisition; Csorba: conceptualization, resources, writing – review and editing, supervision, funding acquisition.

**Conflict of interest**

The authors have no conflicts of interest to declare.

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## Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.27718839.

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