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Systematic studies on Southeast Asian bats

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1. INTRODUCTION

1.1 Species diversity and ecological roles of bats

Bats (order Chiroptera) represent the second most specious group of mammals after rodents (order Rodentia) with more than 1,400 species currently recognized. However, this number is increasing as a result of improved sampling techniques, advances in bioacoustic and molecular biological methods and ongoing taxonomic revisions (pl. Csorba *et al.*, 2011; Francis and Eger, 2012; Csorba *et al.*, 2014; Görföl *et al.*, 2014; Csorba *et al.*, 2015). The order Chiroptera is divided into two major suborders: Yinpterochiroptera and Yangochiroptera. The suborder Yinpterochiroptera includes the larger fruit bats (Pteropodidae), which were previously classified as a separate suborder (Macrochiroptera), as well as several smaller groups, such as the horseshoe bats (Rhinolophidae), which were formerly assigned to the Microchiroptera. The second suborder, Yangochiroptera, comprises the remaining bat lineages, including the family Vespertilionidae, which represents the most species-rich family within Chiroptera (Teeling *et al.*, 2005). Due to their exceptional adaptive capacity, bats have colonized a wide range of habitats and display remarkable diversity in body size, coloration, diet and ecological traits. Through their feeding habits, bats play key roles in ecosystem services: insectivorous species act as natural pest controllers in agricultural landscapes, frugivorous and nectar-feeding species contribute to seed dispersal as well as pollination in tropical and subtropical regions, while hematophagous and carnivorous species support the stability of trophic networks (Kunz *et al.*, 2011). Despite their essential ecological roles, many bat species face serious threats to their persistence. Habitat loss and transformation, disturbance of cave- and building-dwelling colonies, intensive agricultural practices and emerging infectious diseases such as white-nose syndrome all contribute to population declines (Blehert *et al.*, 2009; Russo and Ancillotto, 2015). In some cases, drastic population reductions not only threaten global biodiversity but also compromise the long-term stability of the ecosystem services provided by bats.

1.2 Global biodiversity crisis and the vulnerability of tropical mammal fauna

Earth's biota is currently undergoing profound transformations, collectively referred to as the global biodiversity crisis. Extensive habitat loss and fragmentation, intensive land use, overexploitation of natural resources, the spread of invasive species and climate change act synergistically to drive widespread population declines and species extinctions worldwide (Allan *et al.*, 2019). Current extinction rates exceed natural background levels by orders of magnitude, resulting not only in the loss of individual species but also in the disruption of ecosystem functioning and long-term ecological stability (Ceballos *et al.*, 2015).

Biodiversity loss does not affect the regions of Earth uniformly; tropical areas are particularly vulnerable despite harbouring a substantial proportion of global terrestrial species richness. Rapid deforestation, large-scale conversion of natural habitats for agricultural and industrial purposes and expanding infrastructure development in the tropics have drastically reduced both the extent and connectivity of natural habitats within a relatively short time frame. As a consequence, many species experience population isolation and declines leading to an increased risk of local extinctions that may ultimately escalate to global extinction events (Myers *et al.*, 2000; Sodhi *et al.*, 2004).

Tropical mammal assemblages are particularly sensitive to these changes as many species exhibit narrow ecological tolerances or depend on highly specialized habitats. Beyond large mammals, increasing evidence indicates that smaller, more cryptic taxa – including bats – are also experiencing substantial declines, even though these losses are often less conspicuous and more difficult to document (Frick *et al.*, 2020).

One particularly problematic aspect of the biodiversity crisis is that, in tropical regions, the rate of species loss often exceeds the pace of scientific discovery. As a result, numerous species may disappear before their taxonomic status, geographic distribution or ecological roles are ever adequately documented (Mora *et al.*, 2011). This phenomenon, often referred to as "unknown extinction", poses especially serious challenges for conservation planning as incomplete taxonomic and faunistic knowledge complicates the identification of conservation priorities and the development of effective management and protection strategies.

1.3 Biodiversity hotspots and conservation challenges in Southeast Asia

Southeast Asia is one of the most biologically complex and species-rich regions on Earth, yet it is also among the tropical regions' most severely affected areas by the ongoing biodiversity crisis. The rainforests of the region encompass four of the world's 25 biodiversity hotspots, including Indo-Burma, Sundaland, Wallacea and the Philippines (Myers *et al.*, 2000). These areas are characterized by exceptionally high levels of endemism combined with extremely rapid rates of habitat loss, placing them among the most threatened ecosystems worldwide (Myers *et al.*, 2000; Sodhi *et al.*, 2004; Furey *et al.*, 2010). Consequently, documenting and understanding the biodiversity of these regions represents one of the most urgent and important priorities in contemporary basic biological research.

Bats are an important component of this diversity, accounting for nearly one-third of mammal species in Southeast Asia (Kingston, 2010, 2013;

Simmons and Cirranello, 2024). Despite their high diversity and ecological importance, bats remain among the least well-known vertebrate groups in the region in terms of taxonomy, geographic distribution and ecology (Kingston, 2010). Many species are known only from a few specimens or a single locality, while in other cases the presence of morphologically similar, cryptic species complicates accurate species-level identification (Csorba *et al.*, 2011; Srinivasulu *et al.*, 2019). Unfortunately, it has been estimated that ≈40% of regional bat species could become extinct by the end of the 21st century if current rates of deforestation continue (Lane *et al.*, 2006; Kingston 2010; Tuan *et al.*, 2023). In response to this, more comprehensive conservation and taxonomic-systematic studies are urgently needed to improve knowledge regarding patterns of diversity and distribution as well as the natural history of bats in Southeast Asia (Francis *et al.*, 2010; Kingston, 2010, 2013).

1.4 Methodological challenges in bat research in the tropics

Due to their elusive nature, bats pose substantial methodological challenges for faunistic and ecological studies as they are primarily active during the night while often roosting in hidden places during the daytime. Traditional capture methods (mist-nets & harp-traps) are usually suitable for catching bats up to a few meters above ground level. As a result of that, species flying within or above the forest canopy are typically under-represented in ground-based surveys. However, with the exception of most of the Old World fruit bats (Pteropodidae), bats emit high-frequency ultrasonic calls and orient themselves by detecting the returning echoes, a process known as echolocation. This uniqe sensory system allows species to be studied acoustically without trapping and stressing them unnecessarily. These acoustic signals not only play an important role in the life of bats, but are used to orient and hunt in the dark (Jones and Teeling, 2006; Jones and Holderied, 2007).

These signals are also adapted to different environments and resources, as their primary goal is to provide adequate sensitivity at a given foraging site (Jones *et al.*, 2000; Parsons and Jones, 2000; Russo and Jones, 2002; Pfalzer and Kusch, 2003; Schnitzler *et al.*, 2003; Jones and Holderied, 2007). The use of bat detectors is widespread and has a long history in temperate areas (Brigham *et al.*, 2004) and is gradually increasing in Asian countries (Furey *et al.*, 2009a; Phauk *et al.*, 2013; Voigt and Kingston, 2016; Chakravarty *et al.*, 2020; López-Bosch *et al.*, 2021; McArthur and Khan, 2021; Pham *et al.*, 2021; Rai *et al.*, 2021; Raman and Hughes, 2021; Thong *et al.*, 2022). The acoustic characterisation of Asian bats is essential for reliable monitoring and for the identification of species or species groups however, this requires the availability of open-access, regionally representative acoustic reference call databases. Bat echolocation calls exhibit substantial variation not only among species but also within species – being influenced by factors such as sex, age, body size, habitat type, geographic location, flight height and other environmental conditions (Barclay *et al.*, 1999; Jones *et al.*, 2000; O'Farrell *et al.*, 2000; Russo and Jones, 2002; Schnitzler *et al.*, 2003; Sun *et al.*, 2013) – thus, it is crucial that such databases include recordings obtained under a wide range of recording contexts for each taxa. Consequently, species-level acoustic identification can only be considered reliable when it is based on well-documented, open-access regional reference data that lean upon this intra- and interspecific variability. Although several papers have included echolocation parameters of Southeast Asian bat species, comprehensive studies are scarce. Elusive or rare species are often missing from these studies and the call analyses are rarely repeatable as the recordings are not available for further studies.

With 129 bat species currently known (unpublished data), the bat fauna of Vietnam is highly diverse (Kruskop, 2013). Over the last few decades, intensive taxonomic efforts have resulted in the description of nearly 40 bat species as new for science or new record for the country. These include, among others, *Kerivoula titania, Murina eleryi, Mu. beelzebub, Mu. walstoni, Mu. annamitica*, *Myotis ancricola*, *My. annamitica*, *My. annatessae*, *My. indochinensis, My. phanluongi, Hipposideros griffini*) (Csorba *et al.*, 2007; Furey *et al.*, 2009b; Csorba, 2011; Francis and Eger, 2012; Thong *et al.*, 2012; Tu *et al.*, 2018). The first publication containing information on Vietnamese bat echolocation was Borissenko and Kruskop (2003), whereas the first research was published by Furey *et al.* (2009a), who described the calls of 31 bat species occuring in Kim Hy Nature Reserve, northern Vietnam and concluded that acoustic identification of local bat species was feasible. Since then, several studies in other locations of Vietnam have provided information on the call characteristics of additional Vietnamese species (Thong *et al.*, 2011; Thong, 2019; Fukui *et al.*, 2020; Pham *et al.*, 2021; Son *et al.*, 2021; Thong *et al.*, 2022a, 2022b, 2022c; Thong, 2023a, 2023b; Győrössy *et al.*, 2024), however, many questions remain unresolved. Importantly, species-level identification based solely on acoustic data is not always possible and therefore broader taxonomic units, such as genera are often assigned during acoustic surveys. Nevertheless, such information remains highly valuable for conservation decision-making as the detection of a genus composed predominantly of protected or threatened species may, in itself, provide sufficient justification for the implementation of targeted conservation actions.

1.5 The relationship between taxonomy and conservation

Taxonomy and conservation are closely interconnected as conservation decisions are fundamentally based on the accurate identification of species and reliable knowledge of their geographic distributions. The recognition or reinterpretation of a taxon, changes in its taxonomic status, the determination of its distribution range, or the assessments of its population status can all have direct consequences on its conservation assessment, threat category and the design of appropriate conservation strategies (Mace, 2004). Taxonomic uncertainty therefore represents not only a theoretical issue but also a practical challenge, particularly in species-rich yet data-deficient regions such as Southeast Asia.

The taxonomy of bats is a complex and continuously evolving field of research, presenting substantial challenges, particularly in the delimitation of species and subspecies. The description of new species, the elevation of subspecies to species level and the synonymization of taxa previously considered distinct continuously reshape the phylogenetic and systematic framework of the group. Classical morphology-based identification is often challenging as many bat species are morphologically highly similar or differ only in subtle diagnostic characters. The presence of cryptic species, together with pronounced population-level variability, further complicate the clear delineation of species boundaries. Recent field collections and the revision of museum specimens are essential for resolving taxonomic problems, particularly when direct comparisons with type specimens are possible. In many cases however, original species descriptions lack sufficient detail, type specimens have been lost, are in poor condition (e.g. damaged skulls or faded pelage), or are otherwise inaccessible, which complicates the accurate interpretation of certain taxa (Tsang *et al.*, 2015).

Accurate species delimitation is a fundamental requirement for understanding and conserving biological diversity, yet it remains one of the most complex and debated issues in taxonomy. The so-called “species problem” is particularly pronounced in bats, where high species richness, limited morphological differentiation and frequently hidden genetic diversity jointly complicate taxonomic interpretation. The biological species concept emphasizes reproductive isolation; however, this criterion is often not directly testable in wild populations. In contrast, the phylogenetic species concept focuses on the genetic distinctiveness of evolutionary lineages and is well suited for analyses based on molecular data, although it can be sensitive to the geographic scope of sampling and the properties of the genetic markers used (Baker and Bradley, 2006; Hauser, 2009). The morphological species concept is also widely applied, but on its own it is often insufficient for reliably delimiting cryptic species.

The presence of cryptic species in bats is a widely documented phenomenon, particularly in tropical regions, where evolutionary diversification is often rapid while morphological divergence remains limited. In many cases, genetic studies have revealed well-differentiated evolutionary lineages that were previously treated as a single species (Csorba *et al.*, 2011; Kuo *et al.*, 2017; Tu *et al.*, 2018; Kusuminda *et al.*, 2022; Novaes *et al.*, 2023). The recognition of such lineages can substantially alter our understanding of species richness, geographic distributions, and conservation status and may have direct implications for conservation planning. The taxonomic status of subspecies is likewise controversial, as observed differences are often attributable to population-level variability. In many instances, the decision to assign a taxon species or subspecies level remains subjective (Zachos, 2018). Taxonomic interpretation is further complicated by hybridization, which is not uncommon among closely related bat species (Mao *et al.*, 2013; Kruskop and Artyushin, 2021). Gene flow resulting from hybridization can produce transitional or mosaic genetic patterns that further obscure species boundaries, particularly when analyses rely exclusively on mitochondrial markers. In such cases, the contrasting evolutionary dynamics of mitochondrial and nuclear DNA may lead to different – and sometimes conflicting – taxonomic conclusions (Hassanin *et al.*, 2017).

Together, these phenomena constitute the so-called "grey zone of taxonomy", in which neither morphological nor genetic data alone provide an unambiguous basis for deciding whether particular populations should be treated as distinct species or as components of a single taxon. In such cases, robust taxonomic decisions can only be achieved through the combined evaluation of multiple lines of evidence – i.e. by applying integrative taxonomic approaches – along with a critical assessment of the available data (Solari *et al.*, 2019).

1.6 The role of expedition-based research and integrative taxonomy in Southeast Asia

Targeted field expeditions play a crucial role in refining species distribution patterns and resolving taxonomic questions, as many previously undocumented or misidentified taxa can only be revealed through such focused surveys. Hungarian researchers, alongside local specialists, have contributed substantially to the study of Southeast Asian bats over recent decades; however, the shortage of trained taxonomists continues to pose a major obstacle to comprehensive taxonomic revisions. The exceptional species richness of tropical regions, coupled with the frequent occurrence of morphologically similar cryptic taxa, requires highly specialized expertise that, in many cases, cannot be fully replaced even by genetic approaches alone (Tsang *et al.*, 2015). Inaccurate delimitation of taxa may therefore substantially affect research outcomes and, in some cases, lead to false conclusions.

In modern taxonomic research, the integrated use of morphological, acoustic and genetic data (mitochondrial and/or nuclear DNA) has become increasingly important. As no single method is often sufficient for accurate species delimitation, the combined evaluation of evidence from different sources – including ecological information – provides the most reliable results (Will *et al.*, 2005; Mayer *et al.*, 2007). Phylogenetic analyses, in particular, play a key role in the taxonomic assignment of newly collected material and have become a fundamental tool in contemporary taxonomic studies. Over the past two decades, the “Barcoding of Life” project has undergone substantial development, applying nucleotide sequences of the cytochrome c oxidase subunit I (*COI*) gene for species identification (Blaxter, 2004; Hebert and Gregory, 2005). This DNA barcoding approach not only facilitates the recognition of new taxa but also enables the identification of morphologically cryptic species based on genetic data. However, when used in isolation, it is not always sufficient to resolve taxonomic questions conclusively. The project has contributed extensively to the documentation of bat faunas in several regions, including Southeast Asia (Francis *et al.*, 2010) and the Neotropics (Clare *et al.*, 2007).

The application of an integrative taxonomic framework not only enables a more accurate delimitation of species, but also contributes to the reassessment of species’ distribution ranges, the detection of hidden diversity, and the establishment of conservation priorities. This approach is particularly crucial in species-rich yet taxonomically understudied tropical regions, where it plays a key role in improving our understanding of bat diversity.

1.7 Main objectives of the dissertation

Among the studies presented in this dissertation, four primarily aimed to conduct bioacoustic and/or taxonomic revisions of selected groups of Southeast Asian bats, to refine their geographic distributions and to characterize their ecological traits. Particular emphasis was placed on identifying morphological and genetic differences among species and subspecies. Throughout the taxonomic investigations, an integrative approach was applied, combining morphological, genetic, bioacoustic and ecological data in order to draw the most accurate and reliable systematic conclusions possible. In this context, the first study introduces the concept and structure of an open-access bat call database. The importance of such repositories lies in their ability to provide reference calls that support taxonomic identification and improve the reliability of bioacoustic analyses.

In addition, the research aimed to refine the geographic distribution and habitat preferences of the studied taxa, thereby contributing to a better understanding of their conservation status and to the development of more effective conservation strategies. The assessment of genetic differentiation among populations not only informs species delimitation but also contributes to the understanding of evolutionary and biogeographic processes. The objectives of the individual studies were defined within this general framework, taking into account the specific characteristics of each study system and research question.

1.7.1 First study – ChiroVox: the bat call library

Acoustic approaches have several advantages. They can be used without disturbing bats and automatic recorders can be deployed at a given sampling site for several days or months. In addition, multiple recording devices can also simultaneously be used across large areas for comparisons of land use (e.g. Frick, 2013; Gibb *et al*., 2019). However, acoustic methods also have disadvantages. Accurate species identification remains challenging, as many species produce similar echolocation calls, while call parameters may vary both among individuals and across geographic regions (Russo and Voigt, 2016; Rydell *et al.*, 2017; Goerlitz, 2018; Russo *et al.*, 2018). These limitations highlight the need for large, open-access reference databases that document both interspecific and intraspecific variation in echolocation calls, particularly in highly diverse tropical regions.

In the last decade, the number of studies detailing the acoustic parameters of tropical bat calls has increased (e.g. Hughes *et al.*, 2011; Phauk *et al.*, 2013; Zamora-Gutierrez *et al.*, 2016; Hackett *et al.*, 2017; Monadjem *et al.*, 2017; Raman and Hughes, 2021; López-Bosch *et al.*, 2021; McArthur and Khan, 2021). These publications primarily focus on describing acoustic parameters that can be helpful for identifying bats in many cases, but definitions and terminology often differ between studies, which hinders comparisons. In contrast, access to verified reference recordings for species that can then be compared to assess anonymous calls in the same software environment is much more efficient and reliable. The need for such echolocation call libraries has long been suggested (Karine and Kalko, 2001). A number of bat call collections have been published in the last two decades (e.g. Collen, 2012; Zamora-Gutierrez *et al.*, 2020), but only a few are still maintained and even fewer cover large geographic areas.

Recognizing the need for a large and curated call library, we created the ChiroVox database whose purpose is to act as a freely available collection of reference bat calls without geographic or taxonomic restrictions. The database provides a framework for the storage and comparison of bat echolocation recordings, and particular emphasis was placed on including only recordings obtained from reliably identified individuals. Where necessary, species identifications were supported by genetic data, thereby ensuring the taxonomic reliability and reference value of the acoustic material.

1.7.2 Second study – The calls of Vietnamese bats

Acoustic monitoring has appeared as a reliable and standardized method for rapid surveys, but it has to be based on localized (country or province level) acoustic libraries. Therefore, there is an urgent need for bat acoustic studies from many regions of the world. Although several papers have included echolocation parameters of Southeast Asian, and particularly Vietnamese, bat species (Borissenko and Kruskop, 2003; Furey *et al.*, 2009a; Thong *et al.*, 2011; Fukui *et al.*, 2020; Pham *et al.*, 2021; Son *et al.*, 2021; Thong *et al.*, 2022a, 2022b, 2022c; Thong, 2023a, 2023b), comprehensive studies are scarce and are typically restricted to single caves, urban environments or protected areas. Elusive or rare species are often missing from these studies and the call analyses are rarely repeatable as the recordings are not available for further studies.

The goal of our study was to describe and characterize echolocation calls of Vietnamese bats to facilitate research and conservation activities in the wider Southeast Asian region. We ensure repeatability by using open-source software and providing all recordings in the ChiroVox sound database (Görföl *et al.*, 2022), so as to allow comparative analyses and identification of anonymous bat calls.

1.7.3 Third study – First record of *Murina walstoni* (Chiroptera: Vespertilionidae) outside Southeast Asia

Bats represent the most diverse group of mammals in Nepal with 55 species documented across the country, from lowland plains to the Himalayas (Dahal *et al.*, 2024b). Vespertilionidae, is the most specious family with 32 species recorded so far. Prior to 2020, four species of *Murina* were reported from the country (Bates and Harrison, 1997; Acharya *et al.*, 2010; Thapa, 2014). A significant portion of Nepal, including eight protected areas, remains uncharted in terms of bat surveys. Intensive study and exploration of the remaining regions could yield new species discoveries for both the country and the global community (Acharya and Ruedas, 2007; Thapa *et al.*, 2021;

Dahal *et al.*, 2024a, 2024b). Fortunately, the past decade has witnessed a gradual increase in bat research activities. Four new species of bat from various geographical areas of Nepal have been documented over a span of six years (Sharma *et al.*, 2019, 2021; Dahal *et al.*, 2022a, 2022b).

The aim of our study was to improve the knowledge of the bat fauna of Nepal with particular emphasis on the occurence of a species previously not documented from the region. During a field survey, a tube-nosed bat was captured by local researchers which was presumed to belong to *Murina walstoni* (Walston's tube-nosed bat). Our objective was to confirm the species identity based on morphological characters and mitochondrial DNA analyses. Furthermore, this record also contributes to a more accurate understanding of the species' distribution extending its known range to South Asia.

1.7.4 Fourth study – A reassessment of the taxonomic status and distribution of the subspecies of *Lyroderma lyra* (Chiroptera: Megadermatidae)

Lyroderma lyra is one of the six currently recognized species of the family Megadermatidae (false vampire bats). Two subspecies have traditionally been distinguished: the nominal form (*L. lyra lyra*) is widespread in South Asia, from Afghanistan to Bangladesh, whereas *L. lyra sinense* is found in Southeast Asia, from South China to Peninsular Malaysia (Soisook *et al.*, 2015; Wilson and Mittermeier, 2019; Singh and Sharma, 2023), but the exact distributional limits are not clear. Previous studies revealed distinct morphological differences between the two taxa (Andersen and Wroughton, 1907; Csorba and Topál, 1994), but these differences have not been supported by molecular evidence.

The aim of our study was to reassess the taxonomic status of the two subspecies using an integrative taxonomic approach. To this end, we conducted detailed morphological analyses and mitochondrial DNA sequence analyses, including as many specimens and sampling localities as possible in order to evaluate whether the elevation of the two subspecies to species level is justified.

1.7.5 Fifth study – The "grey zone of taxonomy" – The case of the Sikkim Myotis (Chiroptera: Vespertilionidae: *Myotis sicarius*)

During the systematic exploration of Southeast Asian bats, a specimen of *Myotis* was captured in Xuan Lien Nature Reserve (Vietnam), near the Lao border which was morphologically identifiable as *M. sicarius*, a species that was previously known only from a handful of records in montane forests on hill sides and in valleys from Nepal and India, South Asia (Bates and Harrison, 1997; Srinivasulu and Srinivasulu, 2019). Given the biogeographic barriers to dispersal and the possibly of limited gene flow between bats from the two known sampling sites in a distance of over 1700 km, further investigation is required (Slatkin, 1985; Avise, 2000; Castella *et al.*, 2008).

One of the main objectives of our study was to investigate the Vietnamese specimen of *Myotis sicarius* using detailed morphological analyses and genetic approaches based on mitochondrial and nuclear DNA markers. Our aims were to confirm the species identification previously established on the basis of morphological characters, and on the other hand, to explore the phylogenetic relationships between the Vietnamese specimen and the populations previously reported form India and Nepal.

The genus *Myotis* is well known for the occurence of cryptic and pseudocryptic species, as well as for incongruence between morphological and molecular phylogenetic results. Therefore, further comprehensive studies using integrated analyses of multiple datasets are required to confirm the taxonomic status of certain formerly recognized morphological species (Ruedi *et al.*, 2015, 2021; Novaes *et al.*, 2022; Kruskop *et al.*, 2023).

Morphologically, *M. sicarius* closely resembles species of the *montivagus*-complex, especially *M. indochinensis* and *M. annectans* (Son *et al.*, 2013), thus another objective of our study was to investigate the morphological and genetic differences among these taxa. By contrast, a previous phylogenetic study found that this species forms a clade with *M. frater*, *M. bechsteinii* and *M. daubentonii*, and is only distantly related to the *montivagus*-complex (Ruedi *et al.*, 2013), contradicting relationships inferred solely from morphological similarity. Furthermore, the high level of intraspecific variability reported in *Myotis annectans*, particularly in dental characters (Topál, 1970), raises additional taxonomic questions which we aimed to address through the examination of newly collected material from Nepal and Vietnam.

2 MATERIALS AND METHODS

2.1 First study – ChiroVox: the bat call library

ChiroVox was established as an open-access database containing echolocation and social call recordings of bats. Three main sources of sound recordings were available at the start of the project. A considerable part of the information and sound files came from participants of a Data Mobilization Project awarded to the Southeast Asian Bat Conservation Research Unit (SEABCRU) by the Biodiversity Information Fund for Asia (BIFA) and from the collection of the Hungarian Natural History Museum (HNHM). Other sources were individual researchers who wanted to contribute to the project. The quality of the recordings and the metadata (including biodiversity data and recording circumstances) were reviewed by the site administrators and corrected if necessary. The taxonomy of species was checked by experts in the field based on the backbone suggested by Wilson and Mittermeier (2019), with the taxonomic framework of Simmons and Cirranello (2020) applied where necessary. A taxonomic certainty score is required of all submissions. A score goes from 1-5, where 1 indicates greatest uncertainty about the taxonomic identity of the recorded bat. A 5 would be selected if the identification was made by an expert and the animal was studied in the hand and/or there is voucher/genetic data, or the species' calls are unique (like in many cases in temperate zones). All necessary genetic analyses were conducted at the Molecular Taxonomy Laboratory of the Hungarian Natural History Museum, whenever tissue samples were available. Species identification was based on DNA barcoding, using sequences of the mitochondrial cytochrome c oxidase subunit I (*COI*) gene.

Majority of the metadata is in Darwin Core format to be compatible with several other important databases and services. Each recording was assigned a unique identifier (UID), which can be linked to external databases such as the Global Biodiversity Information Facility (GBIF), the National Center for Biotechnology Information (NCBI) GenBank and the Barcode of Life Data System (BOLD). Core metadata included the bat species name, call type, recording method, recording equipment and geographic coordinates.

The sound files and the connected metadata were transferred into the storage and the MySQL database server of the ChiroVox website, respectively. The updated version of the website was developed on the OpenBioMaps platform using HTML, CSS and PHP enabling users to browse, search and download recordings. Tha data were organized by species, geographic region and contributor (recordist), thereby ensuring ease of access and usability.

ChiroVox recordings can be accessed in two ways: (1) Open-access, whereby recordings and their metadata are freely available to the public for viewing and downloading under different Creative Common licenses; (2) Consensual-access, when associated metadata are available to the public and individual recordings can be requested from the contributor(s) on a case-by-case basis. Commercial use of recordings is generally prohibited in ChiroVox, although interested parties may contact the individual data providers to request permission.

2.2 Second study – The calls of Vietnamese bats

To achieve a comprehensive characterization of the echolocation calls of Vietnamese bats, we analyzed recordings collected between 2006 and 2023 from nearly all regions of Vietnam, covering a total of 30 provinces. Fieldwork and acoustic data collection were conducted by Hungarian researchers in collaboration with local partners. Bats were captured using mist nets and/or harp traps and temporarily kept in cloth bags prior to further examination. Whenever conditions allowed, nets were also deployed at canopy level. Captured individuals were preliminarily identified based on morphological characters. The following biological data were recorded: sex, age, forearm length and body mass. In cases where species identification was uncertain, DNA barcoding and comparative morphological analyses with reference specimens were applied. DNA barcoding was carried out at the Molecular Taxonomy Laboratory of the Hungarian Natural History Museum.

Bat calls were recorded under various conditions, including from hand-held individuals, within a flight tent, during hand release or from free-flying bats. For recordings obtained in the flight tent, calls emitted during resting and during flight were distinguished. Different types of bat detectors were used for acoustic recordings, as sampling spanned a long time period during which recording technology continuously evolved and equipment choice also depended on the devices available to researchers. Some older recordings were obtained using a D240x (Pettersson Elektronik AB) or an Echo Meter Touch 1 (Wildlife Acoustics) with a sampling rate of 256 kHz (recording frequencies up to 128 kHz). Consequently, data from high-frequency calling species (e.g. Kerivoulinae) recorded with these devices could not always be used. However, the majority of recordings were made using D980, D1000x, M500 (Pettersson Elektronik AB), SM4BAT-FS detectors (Wildlife Acoustics) and the PCTape system (University of Tübingen). For all recording devices, sampling rates were set to the highest possible values (up to 500 kHz). In some cases, multiple recordings were obtained from the same individual to ensure optimal recording quality.

The free, open-source Sonic Visualiser software (version 4.5.2) (Cannam *et al.*, 2010) was used to measure various call parameters. Standardization was important for our analysis, so we worked with well-defined methods to ensure the data obtained was comparable. Spectrograms were generated using the following settings: FFT (Fast Fourier Transformation) size at 512, 93.75% overlapping, and Hann window. Three consecutive pulses were measured from each individual recording. These "triplets" were selected from the section with the highest signal-to-noise ratio (at least 20 dB over background noise). The parameters we measured were chosen from those most frequently used in literature and suited for species identification (Kingston *et al.*, 1999; Jones *et al.*, 2000; Papadatou *et al.*, 2008; Hughes *et al.*, 2011; Phauk *et al.*, 2013; Barataud, 2015; Hackett *et al.*, 2017; Görföl *et al.*, 2020; López-Bosch *et al.*, 2021; Pham *et al.*, 2021; Zamora-Gutierrez *et al.*, 2021). Thus in general, eight parameters were manually measured from selected pulses depending on their call structure: frequency of maximum energy (FmaxE, kHz), start frequency (SF, kHz), end frequency (EF, kHz), highest frequency (HF, kHz), lowest frequency (LF, kHz), bandwidth (BW, kHz), call duration (D, ms) and inter-pulse interval (IPI, ms). SF and EF values were determined visually. The time parameters (D and IPI) were obtained from oscillograms, SF, EF, HF and LF from sonograms, and BW and FmaxE from power spectra.

Depending on the different structures of the calls, some characteristic parameters were also measured. For example, in the case of the FM-CF-FM (frequency modulated-constant frequency-frequency modulated) and FM-QCF (frequency modulated-quasi-constant frequency) calls, we measured the durations (ms) of the CF and QCF components (DCF & DQCF, respectively) and their frequency values (kHz) (FCF & FQCF, respectively). The number of harmonics (different n-fold frequency components of a given pulse) and the measured harmonics were also recorded. Where multiple call harmonics exhibited sufficient amplitude for measurement, we assessed the same parameters for these additional harmonics alongside the dominant or fundamental (first) harmonic, with the exception of the members of the families Rhinolophidae (horseshoe bats), Hipposideridae (leaf-nosed bats), Emballonuridae (free-tailed bats) and Megadermatidae (false vampire bats), in which the second harmonic consistently contained the maximum energy of the call. For bats producing broadband calls (such as *Myotis* species), the cursor was positioned at the middle of the spectrum when FmaxE was not clearly defined. We calculated mean values and standard deviations of each parameter for each species. All of the recordings and associated metadata are available via ChiroVox (www.chirovox.org) (Görföl *et al.*, 2022).

2.3 Third study – First record of *Murina walstoni* (Chiroptera: Vespertilionidae) outside Southeast Asia

To improve knowledge of the bat fauna of Nepal, local researchers conduct regular field surveys in various regions of the country. In April 2020, sampling was carried out in a forested area located approximately 2 km from the settlement of Tunibote. Mist nets and harp traps were used during the survey. Among the captured individuals was a tube-nosed bat whose identification could not be determined in the field; therefore, it was preserved as a voucher specimen in a museum collection. The specimen was deposited in the Museum of the Central Department of Zoology (CDZ), Tribhuvan University. External, cranial and dental measurements were taken using digital calipers with a precision of 0.01 mm.

A ~3mg pectoral muscle tissue was taken from the voucher specimen and preserved in ethanol. The *COI* sequence obtained from DNA barcoding of the specimen was uploaded to the NCBI GenBank (accession number PQ060030) and subsequently compared with related sequences available in GenBank.

Alignments and calculations of genetic distances were performed using MEGA 11 (Tamura et al. 2021). The analyses of evolutionary divergence between sequences were estimated using the Kimura 2-parameter model (Kimura, 1980), with rate variation among sites modeled by a gamma distribution (shape parameter = 1). The phylogenetic tree was constructed using IQ-TREE (Minh *et al.*, 2020) with the Maximum Likelihood method, employing the HKY + G + I (Hasegawa-Kishino-Yano + Gamma distributed With Invariant Sites) best fit model and bootstrap support with 1,000 replicates.

2.4 Fourth study – A reassessment of the taxonomic status and distribution of the subspecies of *Lyroderma lyra* (Chiroptera: Megadermatidae)

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 examined specimens originated from several museum collections, including those from China, Hungary, the United Kingdom, Thailand, Slovenia, Malaysia and India.

Measurements were recorded from adult specimens only. We took one external (forearm length) and 13 craniodental measurements, following Bates and Harrison (1997). 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. In addition, the bacula (os penis) of male specimens were prepared and preserved following the method of Friley (1947). Variation in baculum morphology is shaped by direct sexual selection, as this structure plays an important role during copulation (Stockley, 2012; Rakotondramanana and Goodman, 2017). The overall length and shape of the baculum in adult individuals can be used as diagnostic characters for species delimitation (Thomas, 1915; Douangboubpha *et al.*, 2010; Vercillo and Ragni, 2011; Soisook *et al.*, 2015; Srinivasulu *et al.*, 2020; Latorre, 2023). Pronounced intergeneric differences in baculum morphology have been documented within the family Megadermatidae, supporting the taxonomic relevance of these characters at the familial level (Soisook *et al.*, 2015). The baculum was illustrated and measured under a microscope using a digital caliper. To test for sexual dimorphism, independent-samples t-tests and Mann–Whitney U tests were applied.

Multivariate statistical analyses were conducted using data from 58 specimens. Principal component analyses (PCA) and linear discriminant analyses (LDA) were applied to explore patterns of morphological variation. To ensure data homogeneity, all variables were log-transformed prior to analysis. Statistical analyses were performed in R version 4.3.1. (R Core Team, 2024).

For the genetic analyses, mitochondrial *COI* and cytochrome b (*cytb*) sequences were examined, obtained from tissue samples of museum specimens. Newly generated sequences were deposited in the NCBI GenBank database under accession numbers PQ615380–PQ615394 and PQ619736–PQ619752. Sequence comparisons were conducted in MEGA7 (Kumar *et al.*, 2016) using additional reference sequences, comprising a total of 43 *COI* and 14 *cytb* sequences. Phylogenetic relationships were inferred using maximum likelihood (ML) analysis with 1,000 bootstrap replicates. Genetic distances were also calculated in MEGA7.

2.5 Fifth study – The "grey zone of taxonomy" – The case of the Sikkim Myotis (Chiroptera: Vespertilionidae: *Myotis sicarius*)

During the study we examined a questionable *Myotis* specimen captured in Vietnam in 2014, as well as three newly captured *Myotis sicarius* individuals from Nepal collected in 2016. A voucher specimen was available for the Vietnamese individual, whereas the three Nepalese specimens were released after external morphological examination and tissue sampling.

For the morphological analysis, external measurements (forearm length) were recorded for the Nepalese specimens, while both external and craniodental measurements were taken for the Vietnamese specimen, using digital calipers with a precision of 0.1 mm and 0.01 mm, respectively. Measurements include only those taken from fully-grown individuals, as indicated by the presence of fully ossified metacarpal-phalangeal joints. The resulting measurements were compared with those of the species' type specimen, as well as with reliably identified Nepalese specimens. In addition, several morphologically similar *Myotis* species were included as comparative material, with particular emphasis on members of the morphologically similar *montivagus* complex (*M. annectans, M. indochinensis*). Data analyses were conducted using the R statistical software (version 4.2.1) (R Core Team, 2018).

Although genetic sequences of most Asian *Myotis* species are available in the GenBank database, inconsistencies are frequently observed, likely resulting from misidentified specimens. In order to obtain the most reliable phylogenetic inference, we sequenced two mitochondrial markers (*COI* and *cytb*) and one nuclear marker (*Rag2*) from our samples. In a second analytical step, three additional nuclear genes (*THY* – thyrotropin, *PRKC1* – protein kinase C Iota, and *ABHD11* – abhydrolase domain-containing protein 11) were also sequenced to further corroborate the phylogenetic relationships inferred from the mitochondrial and *Rag2* data. Laboratory work was conducted at the Molecular Taxonomy Laboratory of the HNHM for the Vietnamese specimen, and at the Center for Molecular Dynamics Nepal for the Nepalese samples. DNA sequencing was performed by Macrogen Europe (Maastricht, the Netherlands). The resulting sequences were deposited in the NCBI GenBank database under accession numbers OR413179, OR413180, and OR413539–OR413554, and subsequently compared with homologous sequences retrieved from GenBank. *COI*, *cytb*, and *Rag2* sequences were aligned together with sequences from other *Myotis* species and several outgroup genera (*Kerivoula*, *Murina*, *Harpiocephalus*) following previous phylogenetic frameworks (Ruedi and Mayer, 2001; Kawai *et al.*, 2003; Stadelmann *et al.*, 2004a, 2004b; Jones *et al.*, 2006; Lack *et al.*, 2010; Ruedi *et al.*, 2012, 2013; Wang *et al.*, 2017), using MAFFT v.7.505 (Katoh and Standley, 2013). Separate phylogenetic trees were reconstructed for each gene using Bayesian inference implemented in MrBayes v.3.2.7a (Ronquist and Huelsenbeck, 2003), with analyses run for 10 million generations and sampling every 1,000 generations. Model parameters were selected using MrModeltest2 v.2.4 (Nylander, 2004). Phylogenetic trees were visualized with iTOL v.3 (Letunic and Bork, 2016). Pairwise genetic distances were calculated under the Kimura two-parameter (K2P) model (Kimura, 1980) using MEGAX v.10.2.6 (Kumar *et al.*, 2018).

3 RESULTS

3.1 First study – ChiroVox: the bat call library

Since its launch in 2022, ChiroVox has grown into the world's largest open-access repository dedicated to bat echolocation and social calls, operating at a global scale. The database currently hosts approximately 5,800 sound recordings representing more than 250 species, covering 16 countries across four continents (Europe, the Americas, Asia, and Africa). To date, over 50 researchers have contributed recordings to the repository. Each recording is accompanied by detailed metadata and a unique identifier (UID), ensuring the reproducibility of acoustic analyses and the traceability of data used in scientific publications.

By the end of 2024, the second version of ChiroVox was completed and is currently in the testing phase. This updated version introduces several major developments aimed at better serving the needs of the research community. The new user management system allows registered users to track their own contributions, upload large datasets efficiently, and individually control the accessibility of their recordings. Expanded metadata options now enable the platform to support a wider range of analytical applications, including the development and validation of automated species identification tools. A newly implemented bulk download function substantially reduces the time required for data access, while an integrated feedback system allows users to add comments to individual recordings, thereby improving data transparency and reliability. In addition, ChiroVox supports GIS-based tools and offers customized data export formats, facilitating interoperability with other platforms and the generation of reports and downstream analyses.

Since its release, the ChiroVox database has been cited by numerous scientific publications for a wide range of research purposes (e.g. Flanders *et al.*, 2022; Tanshi *et al.*, 2022; Alipek *et al.*, 2023; Fundel *et al.*, 2023; Poma-Urey *et al.*, 2023; Kolev *et al.*, 2024; Miller *et al.*, 2024). One of its most important application areas is automated species identification, where reference call libraries have enabled the training and validation of new machine-learning–based classification models (Fundel *et al.*, 2023).

3.2 Second study – The calls of Vietnamese bats

We analyzed a total of 3,438 echolocation pulses in 1,042 recordings manually (in some cases, multiple harmonics were measured). These recordings stemmed from 87 species caught and identified in the field or later through DNA analyses. The bats belong to 28 genera arranged in eight families: Pteropodidae, Megadermatidae, Emballonuridae, Hipposideridae, Rhinolophidae, Molossidae, Miniopteridae and Vespertilionidae and account for 74% of echolocating bat species in Vietnam. Consequently, this research represents a substantial advance in the acoustic characterization of the country’s bat fauna, and, more broadly, of Southeast Asia.

In our study we provide an overview for each family, including the basic characteristics of the calls and species analyzed. Overall, the echolocation calls of the Vietnamese bat fauna exhibit high acoustic diversity, which is consistent with the taxonomic and ecological diversity of the region. The species investigated employ a wide range of call types, spanning from short, broadband frequency-modulated (FM) pulses to long, constant-frequency (CF) and quasi-constant-frequency (QCF) calls. These acoustic parameters closely reflect species-specific habitat preferences, orientation strategies, and foraging behaviour. Species adapted to cluttered forest environments and low-altitude flight, such as members of the genera *Murina* and *Kerivoula*, typically emit short, broadband FM calls with peak energy often between 70 and 140 kHz and highly variable call shapes. These calls are frequently of low intensity and amplitude, which also poses technical challenges for acoustic recording. In contrast, larger-bodied species active in more open habitats (e.g. *Scotophilus* spp.) generally use longer, narrowband QCF calls. The CF calls of the families Hipposideridae and Rhinolophidae, characterised by species-specific dominant frequencies, may in some cases allow reliable acoustic identification. While most families displayed distinct and characteristic call types, the highest level of acoustic diversity was observed within the family Vespertilionidae, where substantial variation occurred in both call structure and frequency ranges.

In addition, particular attention was given to five species for which echolocation calls are described here for the first time. These species are *Glischropus bucephalus*, *Kerivoula depressa*, *Kerivoula dongduongana*, *Myotis laniger* and *Myotis sicarius*. The detailed acoustic characterisation of these taxa contributes to improving call-based identification of Asian bats and supports a more accurate assessment of regional biodiversity.

For each family, we also compiled detailed summary tables presenting the mean values, standard deviations and sample sizes of the measured echolocation parameters for each species. In addition, comparative figures were prepared, illustrating a representative echolocation pulse for every examined species, thereby providing visual support for understanding interspecific differences. For the five species whose echolocation calls are described here for the first time, an additional composite figure is presented, showing a characteristic pulse sequence from each species.

3.3 Third study – First record of *Murina walstoni* (Chiroptera: Vespertilionidae) outside Southeast Asia

The Nepalese specimen is a medium-sized tube-nosed bat based on morphological characters. Although its dorsal pelage is slightly paler than that of Vietnamese and Cambodian individuals, all external as well as craniodental characters are consistent with those of the type specimen of *Murina walstoni*.

According to the phylogenetic tree reconstructions using *COI* gene, the Nepalese specimen formed a monophyletic group with *M. walstoni* samples from Vietnam and Laos, which indicates a close relationship between them. Genetic analysis revealed ~5% (4.6–5.4%) variation in the genetic sequences between South Asian (Nepal) and Southeast Asian (Laos, Vietnam) specimens. *M. suilla*, as the morphologically and phylogenetically closely related species, was also included in this analysis, showing a genetic distance of 12.2–12.8% from the Nepalese *Murina walstoni* specimen. The results therefore confirm that the Nepalese individual can be reliably identified as *Murina walstoni*, providing a new distributional record for the species. This finding is of particular significance, as it extends the known range of the species by approximately 2000 km and currently represents its northernmost and westernmost documented occurrence.

3.4 Fourth study – A reassessment of the taxonomic status and distribution of the subspecies of *Lyroderma lyra* (Chiroptera: Megadermatidae)

We could not establish any statistically significant difference (paired samples T-test, $p=0.295$) between the two subspecies, *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 the 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* despite that overlapping values in all measurements were observed. However, in line with the observations of Andersen and Wroughton (1907), the anatomy of the interorbital region and the prenasal notch showed clear differences between the two taxa.

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. Along the PC1 axis, no overlap was observed between *Megaderma spasma* and the two *Lyroderma* subspecies in either males or females; however, a slight overlap was detected along the PC2 axis. In both males and females, factor loadings indicated that the variables associated with PC1 had very similar contribution patterns. In males, the most important discriminating variables were parameters related to cranial and mandibular length and width, whereas in females, discrimination was driven primarily by width-related measurements.

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*).

The newly obtained sequences included *COI* and *cytb* sequences for eight *L. l. sinense*, 10 *L. l. lyra*, and one *M. spasma*. 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. However, due to generally low nodal support and branching events across the tree, these phylogenetic relationships should be interpreted with caution. 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%). This pattern supports the close phylogenetic relationship between the two Lyroderma lineages, while simultaneously exceeding divergence levels typically associated with subspecific differentiation.

3.5 Fifth study – The "grey zone of taxonomy" – The case of the Sikkim Myotis (Chiroptera: Vespertilionidae: *Myotis sicarius*)

The combination of the external traits mentioned below are typical of the species, and are essentially similar in the three Nepalese, the Vietnamese specimens, and the fluid-preserved holotype of *M. sicarius*. The only notable exception is that the Vietnamese specimen had a developed whitish "pad" at the thumb. Based on the examination of cranial and dental characters, the skull of *Myotis sicarius* proved to be more robust than that of closely related *Myotis* species, with several diagnostic features characteristic of the species being clearly identifiable. The (damaged) skull and dentition of the holotype and a Nepalese specimen agrees well in all important details with the skull of the specimen collected in Vietnam. Overall, the external and cranial morphometric measurements of the Himalayan and Vietnamese specimens were largely congruent, with the only notable difference being the narrower anterior orbital breadth (AOB) observed in the Vietnamese specimen.

Consistent with the morphology-based species identification, our phylogenetic analyses using *cytb* and *COI* sequences indicated that the new material of *M. sicarius* collected from Nepal and Vietnam, and the Nepalese and Indian conspecifics found by previous authors (e.g., Stadelmann *et al.*, 2004b; Chakravarty *et al.*, 2020) group into a well-supported monophyletic lineage (PP=1), which mostly clusters with *M. longicaudatus kaguyae*, *M.*

bechsteinii, *M. frater*, and *M. daubentonii*, and is only distantly related to *M. annectans*. Within *M. sicarius*, both analyses showed that Nepalese bats have low intraspecific variation (K2P distance ≤0.53%) but they differ from the Vietnamese specimen by 8.30–9.78% K2P distances. Within *M. annectans*, three examined specimens including two from Vietnam constituted a clade with very low genetic divergences (K2P≤0.6%).

In relation to results obtained from mtDNA markers, our *Rag2* sequence analysis revealed a similarly distant interrelationship between *M. sicarius* and *M. annectans.* Bats of these two taxa differed from each other by a K2P distance of ca. 1% which is regarded as a potential minimum interspecific distance between accepted species of the genus (Ruedi *et al.*, 2013). Within *M. annectans* low genetic divergence was observed (K2P distances ≤0.44%), whereas within *M. sicarius,* Nepalese and Vietnamese bats exhibited very low genetic divergence (0.088% K2P distance) with only a few heterozygous or transitional positions. Such low genetic divergence was also recovered in the pairwise comparisons of the nucleotide sequences in three other nuclear genes (*ABHD11*, *PRKC1* and *THY*) of the two newly sequenced *M. sicarius* specimens.

4 CONCLUSIONS AND RECOMMENDATIONS

A precise understanding of bat diversity and distribution is fundamental from both taxonomic and conservation perspectives. Modern research approaches, including integrative taxonomy, acoustic investigations and the development of open-access databases, substantially contribute to accurate species identification, the exploration of distribution patterns, and the formulation of effective conservation strategies. The present dissertation is built upon these methodological frameworks and throughout the individual studies we consistently applied the approaches best suited to the specific research questions addressed.

4.1 Bioacoustic research and online acoustic databases

The use of open-access online databases has become almost essential in modern zoological research. Such platforms not only enable rapid access to and comparability of global datasets, but also fundamentally support taxonomic revisions, facilitate conservation decision-making and ensure the reproducibility of scientific studies. One of the major outcomes of my dissertation is the establishment of the ChiroVox bioacoustic database, which has since grown into the world's largest online repository of bat sound recordings and accepts contributions from across the globe. At present, the database hosts nearly 5,800 recordings representing more than 250 species, a substantial proportion of which originate from individuals identified with a high degree of taxonomic certainty. This is particularly important in regions characterised by high species diversity, where species-level identification often requires specialised taxonomic expertise. The identification of free-flying bats can also strongly depend on the recording context of the reference calls. Approximately 75% of the recordings currently available were obtained either from bats recorded in enclosed flight tents or from hand-held individuals, as these conditions allowed for reliable species identification. Recordings from members of the families Hipposideridae and Rhinolophidae are overrepresented in this subset, as their main echolocation parameters (e.g. FCF) remain stable largely independent of the recording environment. Consequently, these calls can serve as reference material for the species-level identification of recordings of unknown origin. At the same time, the database also contains recordings of several species whose call parameters are strongly influenced by recording conditions (Kingston *et al.*, 2003; Siemers, 2004; Russ, 2012); therefore, the use of such data always requires careful consideration of contextual factors. In the future, it would be advisable to encourage researchers to collect as many sound recordings as possible prior to releasing captured individuals, and, where feasible, to obtain tissue samples as well. This approach would facilitate the accumulation of reference recordings that could even more reliably support the species-level identification of free-flying bats. The taxonomic coverage of the library includes nearly half of the ~300 echolocating species that occur in Southeast Asia. Most of these recordings are from bat species that lacked a publicly available recording to date. These include several species recently described such as *Aselliscus dongbacanus*, *Glischropus aquilus*, *Hipposideros kunzi*, *Kerivoula dongduongana*, *Tylonycteris tonkinensis* and *Mirostrellus joffrei*. Several recordings are also available from bats that are yet to be formally described, such as *Phoniscus sp.*, *Submyotodon sp.*. The library may facilitate the identification of less known species resulting in more occurrence records and more complete faunal inventories. It may also lead to the exploration of geographic variations, help to solve complex taxonomic problems and provide insights into the role of echolocation in bat speciation (Kingston and Rossiter, 2004; Ith *et al.*, 2015; Tu *et al.*, 2017). The ChiroVox database is particularly valuable for incorporating acoustic material from poorly studied regions –

such as Africa and the tropical areas of the Americas and South Asia – which are currently underrepresented in existing bioacoustic repositories. To our knowledge, the database already includes recordings from more than 150 echolocating bat species that are not yet available in other online sources. With continued expansion, especially through the active contribution of the bat research community, ChiroVox has the potential to serve as a reliable reference for bioacoustic research and monitoring of bats.

In addition to the development of the online database, our researches placed particular emphasis on the detailed characterization and systematic assessment of the acoustic features of bat species occurring in Southeast Asia. Acoustic identification of bats typically begins with compilation of a library of reference calls from known species within a region, considering potential intraspecific geographic variation. Although some baseline acoustic data are available for Vietnam (e.g., Furey *et al.*, 2009a), a comprehensive call library covering such a large number of distinct (morphologically and/or genetically) species, as included in this study, did not exist for any single country in mainland Asia. We analyzed reference echolocation calls produced by 87 of the 118 echolocating bat species presently known to occur in Vietnam, making this study one of the most comprehensive bioacoustic studies involving Asian bats to date. For several species, we were also able to analyze large datasets of echolocation calls, some of which were very poorly known e.g., *Aselliscus dongbacanus*, *Hypsugo cadornae*, *Kerivoula titania*, *Murina feae*, *Myotis alticraniatus*, *Myotis ater*, however in some cases (e.g., *Hipposideros pratti*, *Miniopterus magnater*, *Miniopterus pusillus*, *Myotis altarium*), the number of investigated calls was limited and the variation in calls recorded for these species may not be sufficiently representative and should be interpreted with caution. We also provide the first description of echolocation calls produced by five species. Every sound recording analyzed can be found in the ChiroVox public sound database (Görföl *et al.*, 2022), hence the calls can be reanalyzed and new parameters can be measured or even studied with a novel identification method. Descriptions of bat echolocation calls are very useful for faunistic surveys, ecological studies, taxonomic research and also in the planning of developments affecting natural habitats (Furey *et al.*, 2009a; Barlow *et al.*, 2015; Stathopoulos *et al.*, 2018). For example, an increasing number of wind farms are being established in Southeast Asia and according to the good practices for environmental impact assessment during the construction and operation phases of these projects, it is recommended to carry out surveys to gather baseline information of local bat populations (Frick *et al.*, 2017; Millon *et al.*, 2018). As wind farms are often sited in open areas where the effectiveness of capture-based methods are inherently limited, acoustic surveys can play an important role in ensuring accurate baselines to be created for subsequent monitoring the health of local bat assemblages (Voigt *et al.*, 2024). In recent years, several software applications, e.g., SonoChiro, Kaleidoscope and BatClassify, have been developed to automatically detect and identify bats from recordings based on large datasets on bat echolocation calls. Although such tools greatly facilitate the processing of bat acoustic data, users have to be cautious when interpreting the results made by the identifiers even in the temperate zone (Rydell *et al.*, 2017), while the tools may be even more imprecise in identifying bat species in regions with high biodiversity. The information presented in our study can aid efforts to overcome this shortcoming and also help to validate the outputs of such software.

4.2 The integration of genetic and morphological data

Although bioacoustic databases play a key role in sound-based species identification, the importance of genetic reference databases cannot be overlooked in bat research – and in zoological studies in general. GenBank is a globally recognized, open-access online reference repository that contains genetic sequences from all major groups of living organisms. During our genetic analyses, all newly generated mitochondrial and nuclear sequences were deposited in this database. By doing so, we contributed to molecular species identification and ensured open access to these data for the wider scientific community. Our work particularly contributed to the expansion and refinement of genetic data available for South and Southeast Asian bats, a region where genetic information for many species has remained incomplete or, in some cases, inaccurate. It is important to emphasize, however, that while GenBank represents a fundamental reference resource, the reliability of its contents is not uniform: sequence entries do not always originate from rigorously verified material, updates are not systematic and misidentifications may occur. Consequently, the use of GenBank data requires careful scrutiny and critical evaluation to ensure accurate species identification.

Genetic analyses represent a particularly valuable tool for identifying taxonomic units that are morphologically similar yet exhibit varying degrees of genetic divergence. Their integration is therefore essential in taxonomic research, whether the aim is to reveal cryptic diversity, reassess taxonomic status, or refine species distribution patterns. In this dissertation, three studies addressed these issues, each focusing on different case studies and consequently requiring distinct methodological approaches. In all cases, the results obtained from the applied methods were critically evaluated, with explicit consideration of their limitations.

For *Murina walstoni*, the examined specimens from South and Southeast Asia show a high degree of morphological uniformity. Phylogenetic tree reconstructions based on the uniparentally inherited barcoding gene sequences, widely accepted in phylogenetic studies of Murininae (Li *et al*., 2024) reveal ~5 % variation between the Nepalese individual and the Southeast Asian specimens of *M. walstoni*. This level of variation, along with the morphological uniformity, supports the idea that all these bats belong to the same species. However, the observed genetic divergence is notable and suggests the presence of distinct lineages within *M. walstoni*. While this finding is intriguing, it would be premature to draw definitive taxonomic conclusions based solely on *COI* data. To confirm and refine this hypothesis, further research is required, including analyses of additional mitochondrial and nuclear genes, as well as bioacoustic investigations. Since its description from Veun Sai protected forest, Ratanakiri, Cambodia, the Walston's tube-nosed bat has been reported from a handful of localities from Thailand, Cambodia, Vietnam and Laos (Csorba *et al*., 2011; Francis and Eger, 2012; Kruskop, 2013; Son *et al*., 2015; Soisook *et al*., 2017; Csorba *et al*., 2020). The present paper therefore represents the westernmost and northernmost record for the species, as well as the first record from South Asia (Francis and Eger, 2012; Soisook *et al*., 2013; Csorba *et al*., 2020). Previously, the species was recorded from dry subtropical deciduous forests (Kruskop, 2013; Csorba *et al*., 2020; Yu *et al*., 2020), and is known to be more tolerant to disturbed habitats than other *Murina* (Francis and Eger, 2012; Csorba *et al*., 2020). Although the present record is from a primary riverine sub-tropical broad-leaved forest, the hills surrounding these habitat patches are dry and the area is heavily disturbed due to logging for fuel, fodder collection, forest fire or overgrazing. The IUCN conservation status of Walston's tube nosed bat is assessed as Data Deficient (DD) due to very little information on its distribution, population status, behaviour, threats and ecology (Csorba *et al.*, 2020). The result presented here adds to the distribution of the species but provide no clarifications of the other aspects, therefore at this point we suggest retaining the IUCN assessment as it is.

In the case of *Lyroderma lyra*, 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 certain cranial and dental measurements (PCA and LDA), and in the size of the bacula. 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 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 *COI* 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 *COI* 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 and 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*. Another objective of our study was to refine the geographic distributions of *Lyroderma lyra* and *L. sinense*. This effort was constrained by the lack of appropriate comparative museum specimens and molecular data from key regions, such as Pakistan and Afghanistan. Consequently, our assessment for these areas relied on a critical evaluation of previous descriptions and the examination of low-resolution photographic material. Specimens from Pakistan reported by Shahbaz *et al.* (2020) were assigned to *Lyroderma lyra* based on morphological characters. Similarly, the interorbital breadth (IOB) measurements of Afghan specimens examined by Benda and Gaisler (2015) (4.66–4.79 mm) are consistent with this taxonomic assignment. Both above publications concur with the view of previous authors (Khajuria, 1980; Corbet and Hill, 1992; Bates and Harrison, 1997; Srinivasulu and Srinivasulu, 2012), that the westernmost populations of *Lyroderma* belongs to *L. lyra*. The Myanmar specimens held in the collection of Natural History Museum of the United Kingdom (NHMUK) exceed the size limits of "*lyra*" given by Sinha (1980), but the morphology of the interorbital region, narial emargination, and the interpterygoid region, indeed, clearly defines these specimens as *L. lyra.* Our results further support that the westernmost and Myanmar populations of *Lyroderma* belong to *L. lyra*. In summary, *L. sinense* occurs in southern China, Thailand, Laos, Vietnam, Cambodia, and Malaysia, whereas the distribution range of *L. lyra* extends from Afghanistan to Myanmar. As *L. lyra* is likely to occur in eastern Myanmar, future studies should prioritize sampling from Myanmar and adjacent regions in order to clarify the phylogenetic relationships of local populations and to more precisely delineate the distributional boundaries between the two species.

In the case of *Myotis sicarius*, our study falls within the so-called "grey zone of taxonomy", where the delimitation of species boundaries represents a particularly complex and challenging process (Roux *et al.*, 2016; Zachos, 2018). A *COI* génre alapozott genetikai vizsgálataink 8-10%-os eltérést mutattak a nepáli és az új vietnámi példányok között, mely érték hasonló a *Myotis* nemzetség több, hagyományosan elfogadott testvérfaj párjai közötti eltérések mértékével (e.g., *M. fimbriatus* vs. *M. pilosus, M. emarginatus* vs. *M. formosus*) (Ruedi *et al.*, 2013). The large geographic distance (which limit their gene flow, even if bats can be strong dispersers) between these samples suggests the existence of two putative reproductively isolated taxonomic units; however, the nuclear gene sequence data and the morphological results are incongruent with this taxonomic inference. In fact, the lack of or low genetic variation in nuDNA markers (0.088%) are attributable to the slower rate of evolution of the nuclear genome (Allio *et al.*, 2017), and speciation is not always accompanied by morphological change, as it was confirmed several bat taxa (e.g. Tu *et al.*, 2015; Kuo *et al.*, 2017; Tu *et al.*, 2017b; Tu *et al.*, 2018; Kruskop *et al.*, 2023). Nevertheless, the observed genetic structure of *M. sicarius* might be explained by sex-biased gene flow with female philopatry and male dispersal (Funk and Omland, 2003). This inference is consistent with previous ecological studies of females of many bat species, especially in case of *Myotis* which are philopatric to their nursery roosts and to their swarming sites (Rivers *et al.*, 2005). Hence, although further examination is needed to confirm the shallow genetic variation of nuDNA genes and only one Vietnamese specimen was studied morphologically, the available data suggest that the split of geographic populations of *M. sicarius* into different taxonomic units is unsupported. *Myotis sicarius* was previously thought to be a montane forest dwelling bat species, endemic to the southern slopes of the Himalayas between 950–1600 m a.s.l. (Srinivasulu and Srinivasulu, 2019). With the new record, the occurrence of this species was extended by 1700 km south-eastwards to the border between Vietnam and Laos; nevertheless, the Vietnamese locality is connected to the southern part of the Himalayas through continuous mountains in North Vietnam, North Laos, North Myanmar, and

South China. The Vietnamese specimen was caught in a mist-net set at the edge of a mixed evergreen secondary forest adjacent to a mosaic of terraced paddy fields, small streams, gardens and houses of Vin village at 717 m a.s.l. However, the area above the sampling site is extending up to the mountain peak (approximately 1500 m a.s.l.) and is covered by less disturbed evergreen forests. Based on our data, it is postulated that *M. sicarius* can adapt to a wider range of habitats than previously known and that the dispersal of individuals among its geographic populations might be less influenced by physical and ecological barriers (Tu *et al.*, 2021). As such, geographic populations of *M. sicarius* are expected to maintain a long-range gene flow even under the impacts of extreme habitat changes during the Pleistocene glacial and interglacial periods and this allowed them to evolve a generalist phenotype to suit a variety of environments throughout its distribution range (Uhrin *et al.*, 2010; Hollander *et al.*, 2014; Tu *et al.*, 2021). Given that *M. sicarius* is a widespread species, its apparent rarity might be due to gaps in survey coverage in Myanmar, Laos, and Northeast India. The increasing intensity of bat research in these regions will therefore undoubtedly document additional bats that so far remain hidden from the eyes of researchers. Based on these and possible further results, the reassessment of the IUCN Red List status (Vulnerable) of the species will be needed, but at this point we suggest retaining it as it is. Our article presents a typical example of the “grey zone of taxonomy”, and highlights the need to use different analytical methods and approaches to clarify taxonomic actions based on dense geographical sampling and voucher specimens.

Overall, the combined interpretation of genetic, morphological, and bioacoustic data has become an indispensable foundation of modern bat taxonomy. The studies presented in this dissertation clearly demonstrate that the assessment of species boundaries, the detection of cryptic diversity, and the reinterpretation of distribution patterns can only be achieved through an integrative approach. Taxonomic reassessments are therefore not merely theoretical exercises but have direct implications for conservation practice. The recognition or revision of species or species complexes can fundamentally influence conservation status assessments, particularly in biologically rich yet data-deficient regions such as Southeast Asia. Owing to its exceptional biodiversity and high vulnerability, the bat fauna of this region warrants continued and focused research attention.

5 NEW SCIENTIFIC RESULTS

My doctoral research is based on five closely interrelated studies that applied a range of modern methodological approaches, from bioacoustic database development to genetic and morphological analyses. Below, I summarize the main scientific results of these investigations.

First study: ChiroVox: the bat call library

The establishment and continuous development of the ChiroVox online, open-access bat sound database represent one of the key outcomes of my doctoral research. The database has grown into the world's largest community-based collection of bat acoustic recordings, currently comprising approximately 5,800 recordings from more than 250 species. It provides an essential resource for acoustic species identification and is particularly valuable for improving knowledge of poorly studied bat faunas in tropical regions.

Second study: The calls of Vietnamese bats

In the second study, we analysed reference echolocation calls of 87 species out of the nearly 120 echolocating bat species occurring in Vietnam.

This represents the most comprehensive bioacoustic study of tropical bats to date and includes the first detailed scientific descriptions of the echolocation calls of five species. All recordings were uploaded to the ChiroVox database, ensuring that the results are openly accessible and can be reanalysed by other researchers.

Third study: First record of *Murina walstoni* (Chiroptera: Vespertilionidae) outside Southeast Asia

Genetic (*COI*) and morphological analyses of a Nepalese specimen confirmed that we documented a new South Asian occurrence of *Murina walstoni*, a species previously known only from Southeast Asia. The analyses revealed approximately 5% genetic divergence between the two populations, indicating a certain degree of genetic structuring; however, due to the pronounced morphological similarity, the Nepalese specimens were assigned to *M. walstoni*. This record extends the known distribution range of the species by approximately 2000 km and represents its currently northernmost and westernmost documented occurrence.

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

In the fourth study, analyses based on *COI* and *cytb* mitochondrial markers combined with morphological data demonstrated that the two previously recognized subspecies of *Lyroderma lyra* (*L. l. lyra* and *L. l. sinense*) in fact represent two distinct species. Based on our results, we were able to refine the geographic distributions of these taxa and conduct a taxonomic revision of these widely distributed and relatively common species.

Fifth study: The "grey zone of taxonomy" – The case of the Sikkim Myotis (Chiroptera: Vespertilionidae: *Myotis sicarius*)

The 8–10% mitochondrial divergence observed between the Vietnamese and Nepalese specimens of *Myotis sicarius*, together with the incongruent results obtained from morphological and nuclear genetic data, provide a clear illustration of the so-called "grey zone of taxonomy". Although these levels of divergence are noteworthy, the currently available evidence does not support treating the geographically distant populations as separate species. The Vietnamese record extends the known distribution of *M. sicarius* by approximately 1,700 km and further suggests that the ecological tolerance of the species may be broader than previously assumed.

6 REFERENCES

1. Acharya, P.R., Adhikari, H., Dahal, S., Thapa, A. & Thapa, S. (eds.) (2010). Bats of Nepal: A field guide. Small Mammals Conservation and Research Foundations (SMCRF). 114 p.
2. Acharya, P.R. & Ruedas, L.A. (2007). The bat fauna of Nepal: A current conspectus. Bat Net Newsletter. Newsletter of the Chiroptera Conservation and Information Network of South Asia CCINSA and the IUCN SSC Chiroptera Specialist Group of South Asia (CSGSA) 8: 16–19.
3. Alipek, S., Maelzer, M., Paumen, Y., Schauer-Weisshahn, H. & Moll, J. (2023). An Efficient Neural Network Design Incorporating Autoencoders for the Classification of Bat Echolocation Sounds. Animals 13, 2560.
4. Allan, J., Watson, J., Di Marco, M., O'Bryan, C., Possingham, H., Atkinson, S., Venter, O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. PLOS Biology 17, e3000158.
5. Allio, R., Donega, S., Galtier, N. & Nabholz, B. (2017). Large variation in the ratio of mitochondrial to nuclear mutation rate across animals: Implications for genetic diversity and the use of mitochondrial DNA as a molecular marker. Molecular Biology and Evolution 34: 2762–2772.
6. Andersen, K. & Wroughton, R.C. (1907). On the bats of the family Megadermatidae. Annals and Magazine of Natural History 19: 129–145.
7. Avise, J.C. (eds.) (2000). Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge, 464 p.
8. Baker, J.R. & Bradley, D.R. (2006). Speciation in Mammals and the Genetic Species Concept. Journal of Mammalogy 87, 643-662.
9. Barataud, M. (eds.) (2015). Acoustic Ecology of European Bats. Species Identification and Studies of Their Habitats and Foraging Behaviour. Biotope Editions, Mèze; National Museum of Natural History, Paris. 340 p.
10. Barclay, R.M., Fullard, J.H. & Jacobs, D.S. (1999). Variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*): Influence of body size, habitat structure, and geographic location. Canadian Journal of Zoology 77, 530–534.
11. Barlow, K.E., Briggs, P., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., Walsh, A.L. & Langton, S.D. (2015). Citizen science reveals trends in bat populations: The national bat monitoring programme in Great Britain. Biological Conservation 182, 14–26.
12. Bates, P.J.J. & Harrison, D.L. (eds.) (1997). Bats of the Indian Subcontinent. Harrison Zoological Museum Publication, Sevenoaks, Kent, UK. 258 p.

13. Benda, P. & Gaisler, J. (2015). Bats (Mammalia: Chiroptera) of the Eastern Mediterranean and Middle East. Part 12. Bat fauna of Afghanistan: revision of distribution and taxonomy. Acta Societatis Zoologicae Bohemicae 79: 267–458.
14. Blaxter, M.L. (2004). The promise of a DNA taxonomy. Philosophical Transactions of the Royal Society B: Biological Sciences, 359(1444), 669–679.
15. Blehert, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T., Darling, S.R., Gargas, A., Niver, R., Okoniewski, J.C., Rudd, R.J. & Stone, W.B. (2009). Bat white-nose syndrome: an emerging fungal pathogen? Science 323(5911):227.
16. Borissenko, A. V. & Kruskop, S.V. (eds.) (2003). Bats of Vietnam and Adjacent Territories: An Identification Manual. Russian Vietnamese Science and Technological Tropical Centre, and the Zoological Museum of Moscow. 300 p.
17. Bradley, R.D. & Baker, R.J. (2001). A test of the genetic species concept: Cytochrome-b Sequences and Mammals. Journal of Mammalogy 82(4): 960–973.
18. Brigham, R.M., Kalko, E.K.V., Jones, G., Parsons, S. & Limpens, H.J.G. (eds.) (2004). A Bat Echolocation Research: Tools, Techniques and Analysis. Bat Conservation International, Austin, Texas. 167 p.
19. Cannam, C., Landone, C. & Sandler, M. (2010). Sonic visualiser: An open source application for viewing, analysing, and annotating music audio files. In Proceedings of the 18th ACM international conference on Multimedia 1467–1468 (ACM, Firenze Italy).
20. Castella, V., Ruedi, M. & Excoffier, L. (2008). Contrasted patterns of mitochondrial and nuclear structure among nursery colonies of the bat *Myotis myotis*. Journal of Evolutionary Biology 14: 708–720.
21. Ceballos, G., Ehrlich, P., Barnosky, A., Garcia, A., Pringle, R., Palmer, T. (2015). Accelerated Modern Human-Induced Species Losses: Entering the Sixth Mass Extinction. Science Advances 1, e1400253.
22. Chakravarty, R., Ruedi, M. & Ishtiaq, F. (2020). A recent survey of bats with descriptions of echolocation calls and new records from the western Himalayan region of Uttarakhand India. Acta Chiropterologica 22, 197–224.
23. Clare, E.L., Lim, B.K., Engstrom, M.D., Eger, J.L. & Hebert, P.D.N. (2007). DNA barcoding of Neotropical bats: species identification and discovery within Guyana, Molecular Ecology Notes 7. 184-190.

24. Collen, A. (2012). The evolution of echolocation in bats: a comparative approach. Doctoral thesis. London: University College London.
25. Corbet, G.B. & Hill, J.E. (eds.) (1992). The Mammals of the Indomalayan Region: A Systematic Review. Oxford University Press, Oxford, UK. 496 p.
26. Csorba, G. (2011). A new species of *Glischropus* from the Indochinese subregion (Mammalia: Chiroptera: Vespertilionidae). Zootaxa 2925, 41–48.
27. Csorba, G., Chou, C.-H., Ruedi, M., Görföl, T., Motokawa, M., Wiantoro, S., Thong, V.D., Son, N.T., Lin, L.-K. & Furey, N. (2014). The reds and the yellows: a review of Asian Chrysopteron Jentink, 1910 (Chiroptera: Vespertilionidae: Myotis), Journal of Mammalogy 95. 663-678.
28. Csorba, G., Furey, N., & Görföl, T. (2020). *Murina walstoni*, The IUCN Red List of Threatened Species. e.T84562267A84562270. (Accessed 20 March 2025).
29. Csorba, G., Görföl, T., Wiantoro, S., Kingston, T., Bates, P.J.J. & Huang, J.C.-C. (2015). Thumb-pads up – a new species of thick-thumbed bat from Sumatra (Chiroptera: Vespertilionidae: Glischropus), Zootaxa, 3980. 267-278.
30. Csorba, G., Son, N.T., Ith, S. & Furey, N.M. (2011). Revealing cryptic bat diversity: three new *Murina* and redescription of *M. tubinaris* from Southeast Asia, Journal of Mammalogy 92. 891-904.
31. Csorba, G., Thong, V.D., Bates, P.J.J. & Furey, N.M. (2007). Description of a new species of Murina from Vietnam (Chiroptera: Vespertilionidae: Murininae). Occasional Papers, Museum of Texas Tech University 268, 1–10.
32. Csorba, G. & Topál, G. (1994). First record and taxonomic status of *Megaderma lyra* from Vietnam (Mammalia, Chiroptera). Annales Historico-Naturales Musei Nationalis Hungarici 86: 125–132.
33. Dahal, D.R., Thapa, S., Baral, S., Thapa, T.B., & Singh, N.B. (2022a). First record of East Asian tailless leaf-nosed bat (*Coelops frithii*) from Nepal and extension of its global range. Mammalia 86(5): 521–523.
34. Dahal, D.R., Thapa, S., Ghimire, R., Csorba, G., & Singh, N.B. (2022b). First records of the Hairy-winged bat (*Harpiocephalus harpia*) from Nepal. Journal of Bat Research & Conservation 15(1): 49-52.
35. Dahal, D.R., Thapa, S., & Singh, N.B. (2024a). Responses of insectivorous bats to climate change in Nepalese Journal of Zoology 323(1): 29–44.
36. Dahal, D.R., Thapa, S., & Singh, N.B. (2024b). Species diversity and elevational distribution of bats in Nepal. Acta Chiropterologica 26(1): 101–111.

37. Douangboubpha, B., Bumrungsri, S., Soisook, P., Satasook, C., Thomas, N.M. & Bates, P.J.J. (2010). A taxonomic review of the *Hipposideros bicolor* species complex and *H. pomona* (Chiroptera: Hipposideridae) in Thailand. Acta Chiropterologica 12(2): 415–438.
38. Eick, G.N., Jacobs, D.S. & Matthee, C.A. (2005). A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). Molecular Biology and Evolution 22(9): 1869–1886.
39. Flanders, J., Frick, W., Nziza, J., Nsengimana, O., Kaleme, P., Dusabe, M.C., Ndikubwimana, I., Twizeyimana, I., Kibiwot, S., Ntihemuka, P., Cheng, T., Muvunyi, R. & Webala, P. (2022). Rediscovery of the critically endangered Hill's horseshoe bat (*Rhinolophus hilli*) and other new records of bat species in Rwanda. Arpha Preprints.
40. Francis, C.M. & Eger, J.L. (2012). A review of tube-nosed bats (Murina) from Laos with a description of two new species. Acta Chiropterologica 14, 15–38.
41. Francis, C.M., Borisenko, A.V., Ivanova, N.V., Eger, J.L., Lim, B.K., Guillen-Servent, A., Kruskop, S.V., Mackie, I. & Hebert, P.D. (2010). The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia, PLoS ONE, 5. e12575.
42. Frick, W.F. (2013). Acoustic monitoring of bats, considerations of options for long-term monitoring. Therya 4:6978.
43. Frick, W.F., Baerwald, E.F., Pollock, J.F., Barclay, R.M.R., Szymanski, J.A., Weller, T.J., Russell, A.L., Loeb, S.C., Medellin, R.A. & Mcguire, L.P. (2017). Fatalities at wind turbines may threaten population viability of a migratory bat. Biological Conservation 209, 172–177.
44. Frick, W.F., Kingston, T., Flanders, J. (2020). A review of the major threats and challenges to global bat conservation. Annals of the New York Academy of Sciences 1469, 5–25.
45. Friley, C.E. (1947). Preparation and preservation of the baculum of mammals. Journal of Mammalogy 28(4): 395–397.
46. Fukui, D., Tu, V., Thanh, H., Arai, S., Harada, M., Csorba, G. & Son, N. (2020). First Record of the Genus Plecotus from Southeast Asia with Notes on the Taxonomy, Karyology and Echolocation Call of *P. homochrous* from Vietnam. Acta Chiropterologica 22, 57–74.
47. Fundel, F., Braun, D. & Gottwald, S. (2023). Automatic bat call classification using transformer networks. Ecological Informatics 78, 102288.

48. Funk, D.J. & Omland, K.E. (2003). Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. Annual Review of Ecology, Evolution, and Systematics 34: 397–423.
49. Furey, N.M., Mackie, I.J. & Racey, P. (2009a). A. The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. Current Zoology 55, 327–341.
50. Furey, N.M., Mackie, I.J. & Racey, P.A. (2010). Bat diversity in Vietnamese limestone karst areas and the implications of forest degradation. Biodiversity and Conservation 19, 1821–1838.
51. Furey, N.M., Thong, V.D., Bates, P.J.J. & Csorba, G. (2009b). Description of a new species belonging to the *Murina* '*suilla* -group' (Chiroptera: Vespertilionidae: Murininae) from North Vietnam. Acta Chiropterologica 11, 225–236.
52. Gibb, R., Browning, E., Glover-Kapfer, P. & Jones, K.E. (2019). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods in Ecology and Evolution 10:169185.
53. Goerlitz, H.R. (2018). Weather conditions determine attenuation and speed of sound: environmental limitations for monitoring and analyzing bat echolocation. Ecology and Evolution 8:5090–5100.
54. Görföl, T., Csorba, G., Eger, J.L., Son, N.T. & Francis, C.M. (2014). Canines make the difference: a new species of *Hypsugo* (Chiroptera: Vespertilionidae) from Laos and Vietnam, Zootaxa, 3887. 239-250.
55. Görföl, T., Kruskop, S.V., Tu, V.T., Estók, P., Son, N.T. & Csorba, G. (2020). A new genus of vespertilionid bat: the end of a long journey for Joffre's Pipistrelle (Chiroptera: Vespertilionidae). Journal of Mammalogy 101, 331–348.
56. Görföl, T., Huang, J.C.-C., Csorba, G., Győrössy, D., Estók, P., Kingston, T., Szabadi, K.L., McArthur, E., Senawi, J., Furey, N.M., Tu, V.T., Thong, V.D., Khan, F.A.A., Jinggong, E.R., Donnelly, M., Kumaran, J.V., Liu, J.-N., Chen, S.-F., Tuanmu, M.-N., Ho, Y.-Y., Chang, H.-C., Elias, N.-A., Abdullah, N.-I., Lim, L.-S., Squire, C.D. & Zsebők, S. (2022). ChiroVox: a public library of bat calls. PeerJ 10, e12445.
57. Győrössy, D., Csorba, G., Szabadi, K.L., Estók, P., Tu, V.T., Thong, V.D., Furey, N.M., Huang, J.C.-C., Tuanmu, M.-N., Fukui, D., Zsebők, S., Görföl, T. (2024). The calls of Vietnamese bats: a major step toward the acoustic characterization of Asian bats. *Scientific Reports* 14, 23335.

58. Hackett, T.D., Holderied, M.W. & Korine, C. (2017). Echolocation call description of 15 species of Middle-Eastern desert dwelling insectivorous bats. Bioacoustics 26:217–235.
59. Hassanin, A., Colombo, R., Tungaluna, G.-C., Merle, M., Tu, V., Görföl, T., Akawa, P., Csorba, G., Kearney, T., Monadjem, A., Ing, R. (2017). Multilocus phylogeny and species delimitation within the genus Glauconycteris (Chiroptera, Vespertilionidae), with the description of a new bat species from the Tshopo Province of the Democratic Republic of the Congo. Journal of Zoological Systematics and Evolutionary Research 56, 1–22.
60. Hauser, C.L. (2009). The debate about the biological species concept - a review. Journal of Zoological Systematics and Evolutionary Research, 25 (4), 241-257.
61. Hebert, P.D.N. & Gregory, T.R. (2005). The Promise of DNA Barcoding for Taxonomy. Systematic Biology, 54(5), 852–859.
62. Hollander, J., Verzijden, M., Svensson, E. & Brönmark, C. (2014). Dispersal and phenotypic plasticity. In: Hansson, L.-A. & Åkesson, S. (eds.) Animal Movement Across Scales. Oxford University Press, Oxford, 110–125.
63. Hughes, A.C., Satasook, C., Bates, P.J.J., Soisook, P., Sritongchuay, T., Jones, G. & Bumrungsri, S. (2011). Using echolocation calls to identify Thai bat species: Vespertilionidae, Emballonuridae, Nycteridae and Megadermatidae. Acta Chiropterologica 13:447–455.
64. Ith, S., Bumrungsri, S., Furey, N.M., Bates, P.J., Wonglapsuwan, M., Khan, F.A.A., Thong, V.D., Soisook, P., Satasook, C. & Thomas, N.M. (2015). Taxonomic implications of geographical variation in *Rhinolophus affinis* (Chiroptera: Rhinolophidae) in mainland Southeast Asia. Zoological Studies 54:31.
65. Jones, G. & Holderied, M.W. (2007). Bat echolocation calls: Adaptation and convergent evolution. Proceedings of the Royal Society B: Biological Sciences 274, 905–912.
66. Jones, G., Parsons, S., Zhang, S.Y., Stadelmann, B., Benda, P. & Ruedi, M. (2006). Echolocation calls, wing shape, diet and phylogenetic diagnosis of the endemic Chinese bat *Myotis pequinius*. Acta Chiropterologica 8: 451–463.
67. Jones, G. & Teeling, E.C. (2006). The evolution of echolocation in bats. Trends in Ecology & Evolution 21, 149–156.

68. Jones, G., Vaughan, N. & Parsons, S. (2000). Acoustic identification of bats from directly sampled and time expanded recordings of vocalizations. Acta Chiropterologica 2, 155–170.
69. Kanuch, P., Aghova, T., Meheretu, Y., Šumbera, R. & Bryja, J. (2015). New discoveries on the ecology and echolocation of the heart-nosed bat Cardioderma cor with a contribution to the phylogeny of Megadermatidae. African Zoology 50(1): 1–5.
70. Karine, C. & Kalko, E.K.V. (2001). Toward a global bat-signal database. IEEE Engineering in Medicine and Biology Magazine 20:81–85.
71. Katoh, K. & Standley, D.M. (2013). MAFFT Multiple Sequence Alignment Software Version 7: Improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.
72. Kawai, K., Nikaido, M., Harada, M., Matsumura, S., Lin, L.K., Wu, Y., Hasegawa, M. & Okada, N. (2003). The status of the Japanese and East Asian bats of the genus *Myotis* (Vespertilionidae) based on mitochondrial sequences. Molecular Phylogenetics and Evolution 28: 297–307.
73. Khajuria, H. (1980). Taxonomical and ecological studies on the bats of Jabalpur Dist. Madhya Pradesh, India (families Megadermatidae, Rhinolophidae and Vespertilionidae). Records of the Zoological Survey of India, Occasional Paper 19: 1–69.
74. Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequence. Journal of Molecular Evolution 16: 111–120.
75. Kingston, T. (2010). Research priorities for bat conservation in Southeast Asia: A consensus approach. Biodiversity Conservation 19, 471–484.
76. Kingston, T. (2013). Response of bat diversity to forest disturbance in Southeast Asia: Insights from long-term research in Malaysia. In: Adams, R.A. & Pedersen, S.C. (eds.) Bat Evolution, Ecology, and Conservation. Springer, New York, 169–185.
77. Kingston, T., Jones, G., Akbar, Z. & Kunz, T. H. (1999). Echolocation signal design in Kerivoulinae and Murininae (Chiroptera: Vespertilionidae) from Malaysia. Journal of Zoology 249, 359–374.
78. Kingston, T., Jones, G., Akbar, Z. & Kunz, T.H. (2003). Alternation of echolocation calls in 5 Species of aerial-feeding insectivorous bats from Malaysia. Journal of Mammalogy 84:205215.
79. Kingston, T. & Rossiter, S.J. (2004). Harmonic-hopping in Wallacea's bats. Nature 429:654657.

80. Kolev, M., Acosta-Pankov, I., Toshkova, N. & Deleva, S. (2024). Acoustic study of urban bat diversity in Veliko Tarnovo, Bulgaria. Historia Naturalis Bulgarica 46, 273–284.
81. Kruskop, S.V. (2013). Bats of Vietnam: Checklist and an identification manual. Russian Academy of Sciences, Moscow. 316 p.
82. Kruskop, S., Artyushin, I. (2021). Chiropteran (Chiroptera; Mammalia) taxonomy in light of modern methods and approaches. Russian Journal of Theriology 20, 111–128.
83. Kruskop, S.V., Solovyeva, E.N., Dudorova, A.V. & Artyushin, I.V. (2023). Same but different: Towards taxonomic status of *Myotis ater* (Chiroptera: Vespertilionidae) from the mainland Asia. Mammalia 87: 527–538.
84. Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018). MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549.
85. Kumar, S., Stecher, G. & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874.
86. Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. & Fleming, T. H. (2011). Ecosystem services provided by bats. Annales of the New York Academy of Sciences 1223: 1–38.
87. Kuo, H.-C., Soisook, P., Ho, Y.-Y., Csorba, G., Wang, C.-N. & Rossiter, S.J. (2017). A taxonomic revision of the *Kerivoula hardwickii* complex (Chiroptera: Vespertilionidae) with the description of a new species. Acta Chiropterologica 19: 19–39.
88. Kusuminda, T., Mannakkara, A., Ukuwela, K.D.B., Kruskop, S.V., Amarasinghe, C.J., Saikia, U., Venugopal, P., Karunarathna, M., Gamage, R., Ruedi, M., Csorba, G., Yapa, W.B., Patterson, B.D. (2022). DNA barcoding and morphological analyses reveal a cryptic species of Miniopterus from India and Sri Lanka. Acta Chiropterologica 24, 1–17.
89. Lack, J.B., Roehrs, Z.P., Stanley, C.E., Ruedi, M. & van den Bussche, R.A. (2010). Molecular phylogenetics of *Myotis* indicate familial-level divergence for the genus Cistugo (Chiroptera). Journal of Mammalogy 91: 976–992.
90. Lane, D.J.W., Kingston, T. & Lee, B.P.Y.H. (2006). Dramatic decline in bat species richness in Singapore, with implications for Southeast Asia. Biological Conservation 131, 584–593.
91. Latorre, D.V.D. (2023). Fossil bacula of five species of Borophaginae (Family: Canidae): Implications for their reproductive biology. PLOS ONE 18(1): e0280327.

92. Letunic, I. & Bork, P. (2016). Interactive tree of life (iTOL) v3: An online tool for the display and annotation of phylogenetic and other trees. Nucleic Acids Research 44: 242–245.
93. Li, S., Mou, X., Li, M., Li, F., Li, M., Li, B., Li, M., Luo, X., Csorba, G. & Kuo, H. (2024). New records of *Harpiola isodon* (Chiroptera, Vespertilionidae) from the Chinese mainland. Biodiversity Data Journal 12: 1–13.
94. López-Bosch, D., Huang, J.C.-C., Wang, Y., Palmeirim, A., Gibson, L. & Lopez-Baucells, A., (2021). Bat echolocation in continental China: a systematic review and first acoustic identification key for the country. Mammal Research 66.
95. Mace, G.M. (2004). The role of taxonomy in species conservation. Philosophical Transactions of the Royal Society London. Series B: Biological Sciences 359, 711–719.
96. Mao, X., He, G., Hua, P., Jones, G., Zhang, S., Rossiter, S.J. (2013). Historical introgression and the persistence of ghost alleles in the intermediate horseshoe bat (*Rhinolophus affinis*). Molecular Ecology 22, 1035–1050.
97. Mayer, F., Dietz, C., Kiefer, A. (2007). Molecular species identification boosts bat diversity. Frontiers in zoology 4, 4.
98. McArthur, E. & Khan, F. A. A. (2021). Towards a regional call library: Classifying calls of a species-rich bat assemblage in a Bornean karst rainforest. Barbastella 14, 95–117.
99. Miller, B., Ochoa G., J., García, F. & O’Farrell, M. (2024). Distribution of Ghost Bats of the Genus Diclidurus Wied-Neuwied 1820 (Chiroptera: Emballonuridae) in Venezuela, with a Review of Their Vocal Signatures. Acta Chiropterologica 25.
100. Millon, L., Colin, C., Brescia, F. & Kerbiriou, C. (2018). Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. Ecological Engineering 112, 51–54.
101. Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020). IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. Molecular Biology and Evolution 37, 1530–1534.
102. Monadjem, A., Shapiro, J.T., Mtsetfwa, F., Reside, A.E. & McCleery, R.A. (2017). Acoustic call library and detection distances for bats of Swaziland. Acta Chiropterologica 19:175–187.

103. Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B., Worm, B. (2011). How Many Species Are There on Earth and in the Ocean? PLOS Biology 9, e1001127.

104. Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

105. Novaes, R.L.M., Cláudio, V.C., Díaz, M.M., Wilson, D.E., Weksler, M. & Moratelli, R. (2022). Argentinean Myotis (Chiroptera, Vespertilionidae), including the description of a new species from the Yungas. Vertebrate Zoology 72: 1187–1216.

106. Novaes, R.L.M., Cláudio, V.C., Moratelli, R. (2023). The (integrative) taxonomy driving conservation of cryptic species: an example of Neotropical Myotis. Therya 14, 313–317.

107. Nylander, J.A.A. (2004). MrModeltest v2. Program distributed by the author.

108. O'Farrell, M.J., Corben, C. & Gannon, W. (2000). Geographic variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*). Acta Chiropterologica 2, 185–196.

109. Papadatou, E., Butlin, R.K. & Altringham, J.D. (2008). Identification of bat species in Greece from their echolocation calls. Acta Chiropterologica 10, 127–143.

110. Parsons, S. & Jones, G. (2000). Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. Journal of Experimental Biology 203, 2641–2656.

111. Pfalzer, G. & Kusch, J. (2003). Structure and variability of bat social calls: Implications for specificity and individual recognition. Journal of Zoology 261, 21–33.

112. Pham, L.K., Tran, B.V., Le, Q.T., Nguyen, T.T. & Voigt, C.C. (2021). Description of echolocation call parameters for urban bats in Vietnam as a step towards a more integrated acoustic monitoring of urban wildlife in Southeast Asia. Diversity 13, 18.

113. Phauk, S., Sarith, P. & Furey, N.M. (2013). Cambodian bat echolocation: A first description of assemblage call parameters and assessment of their utility for species identification. Cambodian Journal of Natural History 2013, 16–26.

114. Poma-Urey, J.L., Acosta, S.L.H., Rivero, K., Hidalgo-Cossio, M., Hingst-Zaher, E., Gualda-Barros, J., Natividade, B.D. da, Barboza-Marquez, K., Ramírez-Chaves, H.E., Salazar-Bravo, J., Ochoa, J.G. (2023). Taxonomic

revision and additional comments of some bats (Mammalia, Chiroptera) reported from Bolivia, with an updated checklist based on voucher material with verified identities. Check List 19, 409–427.

115. Rai, V., Thapa, S., Chalise, P. & Shah, K. B. (2021). Record of bats and their echolocation calls from southern Dolakha, central Nepal. Mammalia 85, 557–567.

116. Rakotondramanana, C.F. & Goodman, S.M. (2017). A review of the bacular morphology of Malagasy bats. Acta Chiropterologica 19(1): 51–70.

117. Raman, S. & Hughes, A. C. Echobank for the bats of Western Ghats biodiversity hotspot. Acta Chiropterologica 22, 349–364 (2021).

118. R Core Team (2018) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.Available at: https://www.R-project.org/.

119. R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

120. Rivers, N.M., Butlin, R.K. & Altringham, J.D. (2005). Genetic population structure of Natterer’s bats explained by mating at swarming sites and philopatry. Molecular Ecology 14: 4299–4312.

121. Ronquist, F. & Huelsenbeck, J.P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.

122. Roux, C., Fraïsse, C., Romiguier, J., Anciaux, Y., Galtier, N. & Bierne, N. (2016). Shedding light on the grey zone of speciation along a continuum of genomic divergence. PLoS Biology 14: e2000234.

123. Ruedi, M., Biswas, J. & Csorba, G. (2012). Bats from the wet: Two new species of tube-nosed bats (Chiroptera: Vespertilionidae) from Meghalaya, India. Revue Suisse de Zoologie 119: 111–135.

124. Ruedi, M., Csorba, G., Lin, L.-K. & Chou, C.-H. (2015). Molecular phylogeny and morphological revision of *Myotis* bats (Chiroptera: Vespertilionidae) from Taiwan and adjacent China. Zootaxa 3920, 301–342.

125. Ruedi, M. & Mayer, F. (2001). Molecular systematics of bats of the genus *Myotis* (Vespertilionidae) suggests deterministic ecomorphological convergences. Molecular Phylogenetics and Evolution 21: 436–448.

126. Ruedi, M., Saikia, U., Thabah, A., Görföl, T., Thapa, S. & Csorba, G. (2021). Molecular and morphological revision of small Myotinae from the Himalayas shed new light on the poorly known genus Submyotodon (Chiroptera: Vespertilionidae). Mammalian Biology 101, 465–480.

127. Ruedi, M., Stadelmann, B., Gager, Y., Douzery, E.J.P., Francis, C.M., Lin, L.K., Guillén-Servent, A. & Cibois, A. (2013). Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus *Myotis* (Mammalia, Chiroptera). Molecular Phylogenetics and Evolution 69: 437–449.
128. Russ, J. (2012). British bat calls: a guide to species identification. Exeter: Pelagic Publishing.
129. Russo, D. & Ancillotto, L. (2015). Sensitivity of bats to urbanization: a review. – Mammalian Biology 80: 205–212.
130. Russo, D., Ancillotto, L. & Jones, G. (2018). Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification. Canadian Journal of Zoology 96:63–78.
131. Russo, D. & Jones, G. (2002). Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. Journal of Zoology 258, 91–103.
132. Russo, D., Voigt, C.C. (2016). The use of automated identification of bat echolocation calls in acoustic monitoring: a cautionary note for a sound analysis. Ecological Indicators 66:598–602.
133. Rydell, J., Nyman, S., Eklöf, J., Jones, G. & Russo, D. (2017). Testing the performances of automated identification of bat echolocation calls: A request for prudence. Ecological Indicators 78:416–420.
134. Schnitzler, H.-U., Moss, C.F. & Denzinger, A. (2003). From spatial orientation to food acquisition in echolocating bats. Trends in Ecology & Evolution 18, 386–394.
135. Shahbaz, M., Ullah, H., Khan, W., Javid, A., Attaullah, Rasheed, S.B., Anwar, K., Ullah, A., Zeb, J., Khan, M.I., Ahmad, Q.A., Khan, B.T., Khan, M., Ullah, I., Farooq, Z. & Hussain, A. (2020). Morphometrics of the Indian false vampire bat (Megaderma lyra) from district Jhelum, Pakistan. Brazilian Journal of Biology 81(4): 934–939.
136. Sharma, B., Chakravarty, R. & Acharya, P.R. (2021). The first record of European free tailed bat, *Tadarida teniotis* Rafinesque, 1814, and note on probable elevational movement from Nepal. Journal of Asia-Pacific Biodiversity 14(2): 248–253.
137. Sharma, B., Subedi, A., Subedi, B., Panthee, S. & Acharya, P.R. (2019). First record of the Small Bamboo Bat *Tylonycteris fulvida* (Peters, 1872) (Mammalia: Chiroptera: Vespertilionidae) from Nepal. Journal of Threatened Taxa 11(9): 14216–14219.

138. Siemers, B.M. (2004). Bats in the field and in a flight cage: recording and analysis of their echolocation calls and behavior. In: Bat Echolocation research. Austin, Texas: Bat Conservation International, 107113.

139. Simmons, N.B. & Cirranello, A.L. (2020). Bat Species of the World: A taxonomic and geographic database. Version 1.7. Accessed on 04/27/2022.

140. Simmons, N.B. & Cirranello, A.L. (2024). Bat Species of the world: A taxonomic and geographic database. Version 1.5. Accessed on 03/28/2024.

141. Singh, D. & Sharma, D.K. (2023). New distribution record of the Greater False Vampire Bat (*Megaderma lyra*, Geoffroy 1810) from North-Western Himalaya. Journal of Tropical Life Science 13(2): 377–382.

142. Sinha, Y.P. (1980). The bats of Rajasthan: taxonomy and zoogeography. Records of the Zoological Survey of India 76: 7–63.

143. Slatkin, M. (1985). Rare alleles as indicators of gene flow. Evolution 39:53–65.

144. Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K.L. (2004). Southeast Asian biodiversity: An impending disaster. Trends in Ecology & Evolution 19, 654–660.

145. Soisook, P., Karapan, S., Satasook, C. & Bates, P.J.J. (2013). A new species of *Murina* (Mammalia: Chiroptera: Vespertilionidae) from peninsular Thailand. Zootaxa 3746: 567–579.

146. Soisook, P., Prajakjitr, A., Karapan, S., Francis, C.M. & Bates, P.J.J. (2015). A new genus and species of false vampire (Chiroptera: Megadermatidae) from peninsular Thailand. Zootaxa 3931(4): 528–550.

147. Soisook, P., Thaw, W.N., Kyaw, M., Oo, S.S.L., Pimsai, A., Suarez-Rubio, M. & Renner, S.C. (2017). A new species of *Murina* (Chiroptera: Vespertilionidae) from sub-Himalayan forests of northern Myanmar. Zootaxa 4320: 159–172.

148. Solari, S., Sotero-Caio, C.G., Baker, R.J. (2019). Advances in systematics of bats: towards a consensus on species delimitation and classifications through integrative taxonomy. Journal of Mammalogy 100, 838–851.

149. Son, N.T., Csorba, G., Tu, V.T., Thong, V.D., Wu, Y., Harada, M., Oshida, T., Endo, H. & Motokawa, M. (2015). A new species of the genus *Murina* (Chiroptera: Vespertilionidae) from the Central Highlands of Vietnam with a review of the subfamily Murininae in Vietnam. Acta Chiropterologica 17: 201–232.

150. Son, N.T., Görföl, T., Francis, C.M., Motokawa, M., Estók, P., Endo, H., Thong, V.D., Dang, N.X., Oshida, T. & Csorba, G. (2013). Description

of a new species of *Myotis* (Vespertilionidae) from Vietnam. Acta Chiropterologica 15: 473–483.

151. Son, N., O’Shea, T., Gore, J., Nguyen, K., Thanh, H., Motokawa, M., Dang, H., Le, M., Nguyen, T., Oshida, T., Endo, H., Tran, T., Tuan Hai, B., Tú, L., Duong, V., Chu, H., Tu, V., (2021). Bats (Chiroptera) of Bidoup Nui Ba National Park, Dalat Plateau, Vietnam. Mammal Study 46.

152. Srinivasulu, B., Kaur, H., Shah, T., Gundena, D., Asad, G., Raman, S. & Srinivasulu, C. (2020). A review of the bacular morphology of some Indian bats (Mammalia: Chiroptera). Journal of Threatened Taxa 12(9): 15985–16005.

153. Srinivasulu, B. & Srinivasulu, C. (2019). *Myotis sicarius*. The IUCN RedList of Threatened Species: e.T14202A22063965.

154. Srinivasulu, C., Srinivasulu, A., Srinivasulu, B., Jones, G. (2019). Integrated approaches to identifying cryptic bat species in areas of high endemism: The case of *Rhinolophus andamanensis* in the Andaman Islands. PLOS ONE 14, e0213562.

155. Srinivasulu, C. & Srinivasulu, B. (2012). South Asian Mammals: Their Diversity, Distribution, and Status. Springer, Berlin, Germany.

156. Stadelmann, B., Herrera, L.G., Arroyo-Cabrales, J., Flores-Martínez, J.J., May, B.P. & Ruedi, M. (2004a). Molecular systematics of the fishing bat *Myotis* (Pizonyx) *vivesi*. Journal of Mammalogy 85: 133–139.

157. Stadelmann, B., Jacobs, D.S., Schoeman, C. & Ruedi, M. (2004b). Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences. Acta Chiropterologica 6: 177–192.

158. Stathopoulos, V., Zamora-Gutierrez, V., Jones, K.E. & Girolami, M. (2018). Bat echolocation call identification for biodiversity monitoring: A probabilistic approach. Journal of the Royal Statistical Society: Series C (Applied Statistics) 67, 165–183.

159. Stockley, P. (2012). The baculum. Current Biology 22(24): PR1032–R1033.

160. Sun, K., Luo, L., Kimball, R.T., Wei, X., Jin, L., Jiang, T., Li, G., Feng, J., (2013). Geographic variation in the acoustic traits of greater horseshoe bats: testing the importance of drift and ecological selection in evolutionary processes. PLoS One 8, e70368.

161. Tamura, K., Stecher, G. & Kumar, S. (2021). MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology and Evolution 38: 3022–3027.

162. Tanshi, I., Obitte, B., Monadjem, A., Rossiter, S., Fisher-Phelps, M. & Kingston, T. (2022). Multiple dimensions of biodiversity in paleotropical hotspots reveal comparable bat diversity. Biotropica 54.

163. Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'brien, S.J. & Murphy, W.J. (2005). A molecular phylogeny for bats illuminates biogeography and the fossil record, Science, 307. 580-584.

164. Thapa, S. (2014). A checklist of mammals of Nepal. Journal of Threatened Taxa 6(8): 6061–6072.

165. Thapa, S., Baral, S., Hu, Y., Huang, Z., Yue, Y., Dhakal, M., Jnawali, S.R., Chettri, N., Racey, P.A., Yu, W., Wu, Y. (2021). Will climate change impact distribution of bats in Nepal Himalayas? A case study of five species. Global Ecology and Conservation 26, 1-14. e01483.

166. Thomas, O. (1915). The penis-bone, or baculum, as a guide to the classification of certain squirrels. Annals and Magazine of Natural History 8(15): 383–387.

167. Thong, V. D. (2019). New records of *Hipposideros griffini* from lava caves and the threats to its conservation in Vietnam. Tap Chi Sinh Hoc Journal of Biology 41, 31.

168. Thong, V. D. (2023a). Remarks on the diversity and echolocation calls of hipposiderid bats (Chiroptera: Hipposideridae) in Cuc Phuong National Park, northeastern Vietnam. Academia Journal of Biology 45, 1–9.

169. Thong, V. D. (2023b). New data on distribution, morphology and echolocation of *Hipposideros khaokhouayensis* Guillén-Servent & Francis, 2006 (Chiroptera: Hipposideridae). Acta Zoologica Bulgarica 75, 469–476.

170. Thong, V.D., Denzinger, A., Long, V., Sang, N.V., Huyen, N.T.T., Thien, N.H., Luong, N.K., Tuan, L.Q., Ha, N.M., Luong, N.T., Schnitzler, H.-U. (2022). Importance of Mangroves for Bat Research and Conservation: A Case Study from Vietnam with Notes on Echolocation of *Myotis hasselti*. Diversity 14, 258.

171. Thong, V.D., Dietz, C., Denzinger, A., Bates, P.J.J., Furey, N.M., Csorba, G., Hoye, G., Thuy, L.D., Schnitzler, H.-U. (2011). Further records of *Murina tiensa* from Vietnam with first information on its echolocation calls. Hystrix 22, 129–138.

172. Thong, V.D., Limbert, H. & Limbert, D. (2022). First records of bats (Mammalia: Chiroptera) from the world's largest cave in Vietnam. Diversity 14, 534.

173. Thong, V.D., Loi, D.N., Thanh, H.T., Nha, P.V., Nga, C.T.T., Sengmanichanh, P., Ha, N.M., Toan, V.D., Thai, D.V. & Viet, N.V. (2022).

Echolocation calls of *Myotis alticraniatus* (Chiroptera: Vespertilionidae) in Vietnam. Hnue Journal of Science, Natural Sciences 67, 133–140.

174. Thong, V., Puechmaille, S., Denzinger, A., Csorba, G., Dietz, C., Bates, P., Teeling, E., Schnitzler, H. (2012). A new species of *Hipposideros* (Chiroptera: Hipposideridae) from Vietnam. Journal of Mammalogy 93, 1–11.

175. Topál, G. (1970). On the systematic status of *Pipistrellus annectans* Dobson, 1871 and *Myotis primula* Thomas, 1920 (Mammalia). Annales Historico-Naturales Musei Nationalis Hungarici 62: 373–379.

176. Tu, V.T., Csorba, G., Görföl, T., Arai, S., Son, N.T., Thanh, H.T. & Hassanin, A. (2015). Description of a new species of the genus *Aselliscus* (Chiroptera, Hipposideridae) from Vietnam. Acta Chiropterologica 17:233–254.

177. Tu, V.T., Csorba, G., Ruedi, M., Furey, N.M., Son, N.T., Thong, V.D., Bonillo, C. & Hassanin, A. (2017b). Comparative phylogeography of bamboo bats of the genus *Tylonycteris* (Chiroptera, Vespertilionidae) in Southeast Asia. European Journal of Taxonomy 274: 1–38.

178. Tu, V.T., Görföl, T., Csorba, G., Arai, S., Kikuchi, F., Fukui, D., Koyabu, D., Furey, N.M., Bawm, S., Lin, K.S., Alviola, P., Hang, C.T., Son, N.T., Tuan, T.A. & Hassanin, A. (2021). Integrative taxonomy and biogeography of Asian yellow house bats (Vespertilionidae: Scotophilus) in the Indomalayan Region. Journal of Zoological Systematics and Evolutionary Research 59: 772–795.

179. Tu, V.T., Hassanin, A., Furey, N.M., Son, N.T. & Csorba, G. (2018). Four species in one: multigene analyses reveal phylogenetic patterns within Hardwicke’s woolly bat, *Kerivoula hardwickii*-complex (Chiroptera, Vespertilionidae) in Asia. Hystrix 29, 111–121.

180. Tu, V.T., Hassanin, A., Görföl, T., Arai, S., Fukui, D., Thanh, H.T., Son, N.T., Furey, N.M. & Csorba, G. (2017a). Integrative taxonomy of the *Rhinolophus macrotis* complex (Chiroptera, Rhinolophidae) in Vietnam and nearby regions. Journal of Zoological Systematics and Evolutionary Research 55:177198.

181. Tsang, S.M., Cirranello, A.L., Bates, P.J.J. & Simmons, N.B. (2015). The Roles of Taxonomy and Systematics in Bat Conservation, In: Voigt, C.C. és Kingston, T. (eds.): Bats in the anthropocene: Conservation of Bats in a Changing World, Springer, New York, pp. 503-538.

182. Tuan, L.Q., Thong, V.D., Son, N.T., Tu, V.T., Tuan, T.A., Luong, N.T., Vy, N.T., Thanh, H.T., Huang, J.C.-C., Csorba, G., Görföl, T. &

Tuanmu, M.-N. (2023). Potential individual and interactive effects of climate and land-cover changes on bats and implications for conservation planning: a case study in Vietnam. Biodiversity Conservation 32, 4481–4508.

183. Uhrin, M., Kaňuch, P., Krištofík, J. & Paule, L. (2010). Phenotypic plasticity in the greater mouse-eared bat in extremely different roost conditions. Acta Theriologica 55: 153–164.

184. Vercillo, F. & Ragni, B. (2011). Morphometric discrimination between *Martes martes* and *Martes foina* in Italy: The use of the baculum. Hystrix 22(2): 325–331.

185. Voigt, C.C., Bernard, E., Huang, J.C.-C., Frick, W.F., Kerbiriou, C., MacEwan, K., Mathews, F., Rodríguez-Durán, A., Scholz, C., Webala, P.W., Welbergen, J., Whitby, M., (2024). Toward solving the global green–green dilemma between wind energy production and bat conservation. BioScience 74, 240–252.

186. Voigt, C.C. & Kingston T. (eds.) (2016). Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer, Cham. 606 p.

187. Wang, X., Guo, W., Yu, W., Csorba, G., Motokawa, M., Li, F., Zhang, Q., Zhang, C., Li, Y.& Wu, Y. (2017). First record and phylogenetic position of *Myotis indochinensis* (Chiroptera, Vespertilionidae) from China. Mammalia 81: 605–609.

188. Will, K.W., Mishler, B.D. & Wheeler, Q.D. (2005). The Perils of DNA Barcoding and the Need for Integrative Taxonomy. Systematic Biology, 54(5), 844–851.

189. Wilson, D.E. & Mittermeier, R.A. (eds.) (2019). Handbook of the Mammals of the World (Volume 9): Bats. Lynx Edicions, Barcelona, Spain. 1008 p.

190. Yu, W.H., Csorba, G. & Wu, Y. (2020). Tube-nosed variations – a new species of the genus *Murina* (Chiroptera: Vespertilionidae) from China. Zoological Research. 41: 70–77.

191. Zachos, F.E. (2018). Mammals and meaningful taxonomic units: The debate about species concepts and conservation. Mammal Review 48: 153–159.

192. Zamora-Gutierrez, V., Lopez-Gonzalez, C., Gonzalez, M.C. MacSwiney, Fenton, B., Jones, G., Kalko, E.K.V., Puechmaille, S.J., Stathopoulos, V. & Jones, K.E. (2016). Acoustic identification of Mexican bats based on taxonomic and ecological constraints on call design. Methods in Ecology and Evolution 7:1082–1091.

193. Zamora-Gutierrez, V., MacSwiney G.M.C., Balvanera, S.M. & Esquivelzeta, E.R. (2021). The evolution of acoustic methods for the study of bats. In: Lim, B.K., Fenton, M.B., Brigham, R.M., Mistry, S., Kurta, A., Gillam, E.H., Russell, A. & Ortega, J. (eds.) 50 years of bat research: Foundations and new frontiers. Springer International Publishing, Switzerland, 43-59.

194. Zamora-Gutierrez, V., Ortega, J., Avila-Flores, R., Aguilar-Rodríguez, P.A., Alarcón-Montano, M., Avila-Torresagatón, L.G., Ayala-Berdón, J., Bolívar-Cimé, B., Briones-Salas, M., Chan-Noh, M., Chávez-Cauich, M., Chávez, C., Cortés-Calva, P., Cruzado, J., Cuevas, J.C., Del Real-Monroy, M., Elizalde-Arellano, C., García-Luis, M., García-Morales, R., Guerrero, J.A., Guevara-Carrizales, A.A., Gutiérrez, E.G., Hernández-Mijangos, L.A., Ibarra-López, M.P., Iñiguez-Dávalos, L.I., León-Madrazo, R., López-González, C., López-Téllez, M.C., López-Vidal, J.C., Martínez-Balvanera, S., Montiel-Reyes, F., Murrieta-Galindo, R., Orozco-Lugo, C.L., Pech-Canché, J.M., Pérez-Pérez, L., Ramírez-Martínez, M.M., Rizo-Aguilar, A., Robredo-Esquivelzeta, E., Rodas-Martínez, A.Z., Rojo-Cruz, M.A., Selem-Salas, C.I., Uribe-Bencomo, E., Vargas-Contreras, J.A. & MacSwiney G.M.C. (2020). The Sonozotz project: Assembling an echolocation call library for bats in a megadiverse country. Ecology and Evolution 10, 4928–4943.

7 PUBLICATIONS RELATED TO THE TOPIC OF THE THESIS

7.1 Publications in scientific journals

Görföl, T., Huang, J.C.-C., Csorba, G., **Győrössy, D.**, Estók, P., Kingston, T., Szabadi, K.L., McArthur, E., Senawi, J., Furey, N.M., Tu, V.T., Thong, V.D., Khan, F.A.A., Jinggong, E.R., Donnelly, M., Kumaran, J.V., Liu, J.-N., Chen, S.-F., Tuanmu, M.-N., Ho, Y.-Y., Chang, H.-C., Elias, N.-A., Abdullah, N.-I., Lim, L.-S., Squire, C.D., Zsebők, S., 2022. ChiroVox: a public library of bat calls. *PeerJ* 10, e12445. https://doi.org/10.7717/peerj.12445

Győrössy, D., Csorba, G., Szabadi, K.L., Estók, P., Tu, V.T., Thong, V.D., Furey, N.M., Huang, J.C.-C., Tuanmu, M.-N., Fukui, D., Zsebők, S., Görföl, T., 2024. The calls of Vietnamese bats: a major step toward the acoustic characterization of Asian bats. *Scientific Reports* 14, 23335. https://doi.org/10.1038/s41598-024-72436-6

Feng, L., **Győrössy, D.,** Miguez, R.P., Kokkini, P., Görföl, T., Khan, S.A., Saikia, U., Talmale, S.S., Yu, W., Liu, S., Jiang, T., Csorba, G., 2024. A reassessment of the taxonomic status and distribution of the subspecies of Lyroderma lyra (Chiroptera: Megadermatidae). *Contributions to Zoology* 2024:1-21. https://doi.org/10.1163/18759866-bja10073

Győrössy, D., Tu, V.T., Csorba, G., Thapa, S., Estók, P., Földvári, G., Görföl, T., 2024. The grey zone of taxonomy—The case of the Sikkim Myotis (Chiroptera: Vespertilionidae: Myotis sicarius), first recorded from Southeast Asia. *Vertebrate Zoology* 74, 737–749. https://doi.org/10.3897/vz.74.e127269

Dahal, D., **Győrössy, D.,** Thapa, S., Csorba, G., Görföl, T., Pandey, K., Budha, P. and Singh, N. (2025) First record of *Murina walstoni* (Chiroptera: Vespertilionidae) outside Southeast Asia. *Mammalia* 0117 https://doi.org/10.1515/mammalia-2024-0117

7.2 Conference articles, abstracts and presentations

Győrössy, D., (2019). Csövesorrú denevérek (Murininae) mitokondriális diverzitása. In: XII. Magyar Denevérvédelmi Konferencia, Alsódobsza, Magyarország

Szabadi, K. L., **Győrössy, D.**, Estók, P., Zsebők, S., Csorba, G., Görföl, T. (2019). Délkelet-ázsiai denevérek bioakusztikai vizsgálata. In: XII. Magyar Denevérvédelmi Konferencia, Alsódobsza, Magyarország

Görföl, T., **Győrössy, D.,** Szabadi, K. L., Csorba, G. (2019). Bat Tissues in the HNHM Collection of Genetic Resources. In: XVIII. International Bat Research Conference, Phuket, Thaiföld - Book of Abstracts (p.335).

Görföl, T., Csorba, G., **Győrössy, D.**, Estók, P., Szabadi, K. L., Zsebők, S. (2021). ChiroVox: a denevérhangos weboldal. In: XIII. Magyar Denevérvédelmi Konferencia, Lakitelek, Magyarország

Győrössy, D. (2021). Vietnámi denevérek bioakusztikai vizsgálata. In: Intézményi Új Nemzeti Kiválóság Program (ÚNKP) Konferencia, Gödöllő, Magyarország

Győrössy, D., Szabadi, K. L., Csorba, G., Zsebők, S., Estók, P., Görföl, T. (2022) Vietnámi denevérek bioakusztikai vizsgálata. In: XIII. Magyar Természetvédelmi Biológiai Konferencia, Pécs, Magyarország - Absztrakt kötet (p.59).

Győrössy, D. (2023). Referencia genetikai adatbázis létrehozása délkelet-ázsiai denevérek azonosítására. In: Intézményi Új Nemzeti Kiválóság Program (ÚNKP) Konferencia, Gödöllő, Magyarország

Győrössy, D., Csorba, G., Vuong, T. T., Sanjan, T., Estók, P., Görföl, T. (2024). A Himalájai kapcsolat – a *Myotis sicarius* denevérfaj váratlan előfordulása Délkelet-Ázsiában. In: III. Emlőskutatók Szakmai Napja, Eger, Magyarország

Görföl, T., Huang, J. C. C., Csorba, G., **Győrössy, D.**, Estók, P., Kingston, T., Szabadi, K. L., Bán, M., Zsebők, S. (2024). ChiroVox: a public library of bat calls. In: XVI. European Bat Research Symposium, Tarragona, Spanyolország - Book of Abstracts (p.94).

Görföl, T., Huang, J. C. C., Csorba, G., **Győrössy, D.**, Estók, P., Kingston, T., Szabadi, K. L., Bán, M., Zsebők, S. (2024). An update for ChiroVox: Current status and future plans. In: V. International Southeast Asian Bat Conference, Ho Chi Minh, Vietnám - Book of Abstracts

Győrössy, D., Zsebők, S., Bán, M., Csorba, G., Huang, J. C. C., Szabadi, K. L., Estók, P., Görföl, T. (2025). ChiroVox: the largest global bat call library, now enhanced with new features. In: IX. European Congress of Mammalogy, Patras, Görögország - Book of Abstracts (p.290).

Győrössy, D., Zsebők, S., Csorba, G., Szabadi, K. L., Vuong, T. T., Furey, N. M., Huang, J. C. C., Bán, Miklós, Estók, P., Thong, V. D., Görföl, T. (2025). ChiroVox and the acoustic characterization of Vietnamese bats: expanding global resources for bat research. In: XX. International Bat Research Conference, Cairns, Ausztrália - Book of Abstracts (pp.208-209).