

Higher level classification of phyllostomid bats with a summary of DNA synapomorphies

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The family Phyllostomidae is recognized as representing the most extensive radiation known in any mammalian family. Creating a Linnaean classification for this clade has been difficult and controversial. In two companion papers, we here propose a revised classification drawing on the strengths of genetic and morphological data and reflecting current ideas regarding phylogenetic relationships within this monophyletic clade. We recognize 11 subfamilies (Macrotinae, Micronycterinae, Desmodontinae, Phyllostominae, Glossophaginae, Lonchorhininae, Lonchophyllinae, Glyphonycterinae, Carollinae, Rhinophyllinae, and Stenodermatinae), 12 tribes (Diphyllini, Desmodontini, Macrophyllini, Phyllostomini, Vampyrini, Glossophagnini, Brachyphyllini, Choeronycterini, Lonchophyllini, Hsunycterini, Sturnirini, and Stenodermatini), and nine subtribes (Brachyphyllina, Phyllonycterina, Anourina, Choeronycterina, Vampyressina, Enchisthenina, Ectophyllina, Artibeina, and Stenodermatina). The proposed arrangement avoids non-monophyletic associations, only keeping those detected based on analyses of DNA sequence data. We propose that a classification based on the strengths of the most complete morphological and genetic data sets will provide the most robust classification for multiple uses by science and society.

Key words: Phyllostomidae, higher-level classification, DNA sequence data

Morphological diagnoses of higher-level phyllostomid taxa (Chiroptera: Phyllostomidae)

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Phyllostomidae (New World leaf-nosed bats), the second most speciose chiropteran family, is one of the best-known and well-studied chiropteran groups. Due to the ecological and morphological diversity of this family, comparative studies of phyllostomids abound in the literature, and numerous systematic and phylogenetic analyses have been published. Unfortunately, many of these studies have reached different conclusions concerning phyllostomid relationships, and have proposed different classification schemes. This has led to confusion, and highlighted the need for a well-supported and stable classification of the family, particularly at the level of subfamilies and tribes, areas of the greatest controversy. The goal of this paper is to provide morphological diagnoses of higher-level taxa (subtribes, tribes, and subfamilies). Herein we provide morphological diagnoses for 11 subfamilies (Macrotinae, Micronycterinae, Desmodontinae, Lonchorhininae, Phyllostominae, Glyphonycterinae, Glossophaginae, Lonchophyllinae, Carollinae, Rhinophyllinae, and Stenodermatinae), 12 tribes (Desmodontini, Diphyllini, Macrophyllini, Phyllostomini, Vampyrini, Choeronycterini, Glossophagini, Brachyphyllini, Lonchophyllini, Hsunycterini, Sturnirini, and Stenodermatini), and nine subtribes (Anourina, Choeronycterina, Brachyphyllina, Phyllonycterina, Vampyressina, Enchisthenina, Ectophyllina, Artibeina, and Stenodermatina).

Key words: morphology, taxonomy, Phyllostomidae

The evolutionary history of the African fruit bats (Chiroptera: Pteropodidae)

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Bats of the family Pteropodidae, also known as megabats or Old World fruit bats, are widely distributed in tropical areas of Africa, Asia, and Oceania. Of 45 genera in the family, 12 are endemic to the Afro-tropical region and two others have representative species on the African continent. African megabats inhabit wooded habitats and are nearly ubiquitous on the mainland and nearby islands with the exception of desert areas. Some species have been implicated as possible reservoirs of the Ebola Zaire virus. We studied the phylogenetic relationships of mainland African megabats using both mitochondrial and nuclear loci in separate and combined analyses. The phylogenetic trees obtained showed four main African clades: *Eidolon*, Scotonycterini (including two genera), African *Rousettus* (three species), and the previously identified 'endemic African clade' (nine genera). The latter three lineages form a clade that also includes the Asian species of *Rousettus* and the Asian genus *Eonycteris*; *Eidolon* does not show close relationships to other African genera, instead nesting elsewhere in the megabat tree. Although our results confirm many of the conclusions of previous studies, they challenge the taxonomic status and placement of *Epomops dobsonii* and *Micropteropus*, and provide evidence indicating that a new classification at subfamilial and tribal levels is highly desirable. The principal clades we detected represent four independent colonizations of Africa from most probably Asian ancestors. Estimates of divergence dates suggest that these events occurred in different periods and that although local diversification appears to have started in the late Miocene, the more extensive diversification that produced the modern fauna occurred much later, in the Pleistocene.

Key words: phylogenetic analysis, Africa, Epomophorinae, molecular systematics, molecular clock, pteropodids, *Rousettus*, classification

Evolutionary scenarios associated with the *Pteronotus parnellii* cryptic species-complex (Chiroptera: Mormoopidae)

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One of the major challenges to understanding the evolution of Neotropical bats concerns our capacity to successfully scrutinize phylogenetic patterns associated with cases of cryptic species complexes. In this study *Pteronotus parnellii* is examined as a selected example of a known lineage of mormoopid bat that potentially contains several cryptic species. A samples of 452 individuals from 83 different localities, essentially covering its entire mainland distribution, was evaluated using two genetic markers: COI (mitochondrial) and DBY (nuclear) genes. The findings of this study strongly support the hypothesis of high genetic variability and identify at least six lineages within *P. parnellii*, some of which appear to be cryptic species.

Key words: bats, COI, DBY, Neotropical America, genetic diversity, biogeography, phylogeny, taxonomy

Hill forest dweller: a new cryptic species of *Rhinolophus* in the ‘*pusillus* group’ (Chiroptera: Rhinolophidae) from Thailand and Lao PDR

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A new species of *Rhinolophus* in the *pusillus* group is described from Ratchaburi, Kamphaeng Phet and Loei Provinces where it was found in evergreen forest at elevations ranging from 550 to 1,320 m a.s.l. It is distinguished from *R. shortridgei* and other similar species in the same group by its broad, parallel-sided sella, which is squared-off at the tip, relatively large body size with a forearm length of 42.2–44.1 mm, and bulbous rostral swellings. The echolocation frequency from hand-held individuals is 84.1–93.0 kHz. Bayesian analyses of a 654 bp of cytochrome oxidase subunit I (DNA barcode), and an 878 bp fragment of cytochrome *b* also support differences at the species level. Three specimens from Loang Namtha, Lao PDR are referred to this new species based on DNA barcodes. Based on distinctive DNA barcodes and craniodental morphology, the taxon *refulgens*, is here regarded as a separate species from *R. lepidus*. Morphological comparisons between similar species are discussed and notes on ecology included.

Key words: new species, *Rhinolophus*, horseshoe bats, Thailand, evergreen forest, Southeast Asia

Geographical variation of *Rhinolophus affinis* (Chiroptera: Rhinolophidae) in the Sundaic subregion of Southeast Asia, including the Malay Peninsula, Borneo and Sumatra

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Rhinolophus affinis sensu lato is a widespread bat species in South and Southeast Asia which shows considerable geographical variation in its morphology, echolocation call frequencies and genetics. The taxonomic status of the taxon in the Sundaic subregion remains uncertain however as the limited studies to date have been largely based on morphology. The aim of the present study was to determine the taxonomic status of subspecific forms recognized in the subregion and to evaluate phylogeographic distinctiveness between those occurring in Borneo and the Malay Peninsula using genetic, morphological and acoustic datasets. Two forms were confirmed: *R. a. nesites* from Borneo and *R. a. superans* from the peninsula. The previous recognition of a population from southernmost Sumatra as *R. a. superans* was not supported, however, as this form is likely *R. a. affinis*. Genetic divergence between these three forms is rather deep and is estimated to have occurred during the arid climatic period of the Pleistocene when suitable habitats were reduced to isolated pockets. Our results support the phylogeographic distinctiveness hypothesis as *R. affinis* sensu lato shows discrete affinities between Borneo and the Malay Peninsula. Discovery of new forms of *R. affinis* is likely with greater sampling effort throughout the region. Our study also demonstrates the importance of employing multiple datasets in taxonomic evaluations, as the use of morphological and/or acoustic datasets alone could lead to erroneous conclusions.

Key words: echolocation, genetics, morphology, *Rhinolophus affinis*, subspecies, Sundaic subregion

Cranial shape and diet variation in *Myotis* species (Chiroptera: Vespertilionidae): testing the relationship between form and function

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The relationship between cranial morphology and diet has long been investigated in bats. Bats of the genus *Myotis* include insectivorous, facultatively piscivorous, and piscivorous species. We tested the hypothesis that facultatively piscivorous (five *Myotis* species) and piscivorous species (*M. vivesi*) present cranial morphological and functional changes with respect to insectivorous taxa (16 *Myotis* species). Cranial shapes in skull and mandible modules were described with four geometric landmark configurations in these dietary groups. Gape capacity was measured with the stretch factors for temporal and masseter muscles. Geometric configurations from two skull and two mandible shapes were analyzed to detect differences in cranial morphology in relation to diet. Differences in cranial morphology were found between piscivorous and insectivorous species involving the mandibular process where masticatory muscles are attached. Linear regression analysis of Procrustes distances and gape capacity showed that the shape of the mandibular process region was highly correlated with the stretch factor of the masseter muscle in piscivorous and facultatively piscivorous species. These results suggest differences in cranial morphology and performance among diets but the hypothesis of gradual changes in cranial shape among diets was only accepted for the mandible and not for the skull. *Myotis vivesi* appears to improve mechanical advantage of masticatory muscles at lower gapes, presumably allowing more efficient chewing of slippery prey.

Key words: *Myotis*, geometric morphometrics, piscivory, stretch factor, masticatory muscles

Molecular dietary analysis of the endangered Ozark big-eared bat (*Corynorhinus townsendii ingens*)

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Molecular techniques allow amplification of a mitochondrial barcoding gene, cytochrome *c* oxidase (COI), of prey DNA in bat fecal material that can be used to identify insect species. Most studies designed to use a molecular approach for dietary studies of bats suggest that fecal material should be collected within one week of deposit to prevent environmental degradation or contamination. However, Ozark big-eared bats (*Corynorhinus townsendii ingens*) are highly susceptible to human disturbance. The purpose of this study was to performing a molecular dietary analysis of Ozark big-eared bats. Our study detected 40 species representing two orders (Diptera and Lepidoptera) and 11 families of insects and thus, providing new information regarding dietary habits of Ozark big-eared bats.

Key words: molecular analysis, cytochrome *c* oxidase, diet, Ozark big-eared bat

A novel food preference in the greater short-nosed fruit bat, *Cynopterus sphinx*: mother-pup interaction a strategy for learning

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The greater short-nosed fruit bat *Cynopterus sphinx* relies on the diverse food resources available in its habitat, with individuals identifying and discriminating between food sources using their sense of smell, in relation to volatile compounds released from fruit, flowers and leaves. The work detailed in this article tested whether pups learn about novel food from interactions with their mothers during foraging and develop preferences. Mother-pup pairs or pups alone were trained during postnatal days (PND) 46–50 using *Mangifera indica* as a novel fruit. They were then tested during PND 61–65 for food preferences in relation to a known fruit (*Achras sapota*) and the novel fruit (*M. indica*). When the trained pups and untrained pups were tested for food preferences independently, those trained with the mother were found to exhibit significantly more marked preferences for the novel fruit as compared with either the pups trained without their mothers or the untrained pups. They made a greater number of feeding attempts and bouts in respect of the novel fruit. However, pups trained without their mothers and untrained pups also both showed a response to the novel fruit during the later period of testing. The results suggest that mother-pup interactions during the early foraging period may provide an opportunity for *C. sphinx* pups to learn about novel food sources thanks to their mother. Later they may learn independently on the basis of experience from mother's milk and/or social interaction with conspecifics.

Key words: *Cynopterus sphinx*, mother-pup interaction, olfactory learning, food preference

Daily and seasonal variation in non-acoustic communicative behaviors of male greater short-nosed fruit bats (*Cynopterus sphinx*)

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Monthly observations were made at a natural roosting site of *Cynopterus sphinx*, with a view to the behavior of males being observed over a period of one year. Here, we report seasonal, daily and inter-individual variation in three communicative behaviors engaged in by male bats. The frequency of male behaviors identified as scent-marking, vigorous wing-flapping and the making of an opening gesture were found to vary seasonally, depending on the reproductive status of conspecific females in the study colony. The duration of scent-marking was markedly high during mating seasons, in comparison with wing-flapping and wing-gesturing. In mating seasons, the pattern to the daily variation in behavior correlated strongly with the gender of the responder present in the diurnal roost and/or colony. For instance, scent-marking and vigorous wing-flapping were more frequent during late-evening and early-morning hours, mostly when females were absent from the day roost, while male-male encounters were possible. In contrast, wing-gesturing was more frequent during morning and early-evening hours, when females were present in the day roost. The results from our study suggest that male scent-marking and wing-flapping are directed towards competitor males in the colony, with a view to resource-defense behavior being manifested. Furthermore, male wing-gesturing is predicted to be directed towards co-roosting females, with the aim in this case being for some form of social information to be communicated, particularly during the mating season. However, marginal inter-individual variation in the frequency of occurrence of behaviors between seasons was apparent, suggesting that these communicative behaviors could be tied to male-male competition in this species.

Key words: communicative behavior, mate competition, resource defence, scent marking, sociality, wing gesturing

Opportunistic use of banana flower bracts by *Glossophaga soricina*

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The evolution of cue reception and cue production is well documented. The ability of species to use cues they did not evolve with is important in understanding flexibility in behaviour. We observed Neotropical nectar-feeding bats (*Glossophaga soricina*) feeding at Old World banana flowers (*Musa acuminata*) in a Belize garden. The flowers produce a rich source of nectar that is exposed as a bract lifts before dusk. We tested the hypothesis that the bracts serve as beacons to foraging bats and discuss this approach and the use of acoustic information by bats feeding at flowers. We ensounded a bract with cues like those of echolocating *G. soricina*, which revealed the production of strong echoes from the bract. Additionally, the removal of bracts from the flowers influenced the bats' flower-visiting behaviour. We suggest that the bats use the echoes from the bract opportunistically as a cue to find the nectar source. Our findings provide an example of an interaction between a plant and flower visitor not reflecting a shared evolutionary past.

Key words: acoustic cues, echolocation, nectar-feeding

Foraging strategy of Kuhl's pipistrelle at the northern edge of the species distribution

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Rapid range expansion of Kuhl's pipistrelle (*Pipistrellus kuhlii*) has been observed throughout Europe, and in addition to its natural habitats of temperate grasslands and agricultural areas, the species is common in city centres, where it roosts in human-made structures. It has been suggested that the flexibility of this species in regard to different human-induced changes, such as climate change and urbanization, is responsible for the apparent range shift. Although *P. kuhlii* exhibits one of the highest degrees of synanthropy among bat species in Europe, its ecology has thus far not been thoroughly studied. This study aims to describe its foraging and roosting selection in Central Europe (eastern Slovakia), where the northernmost maternity colony of *P. kuhlii* roosts in human settlements. Radio-tracking was conducted during the pre-parturition and post-lactation periods. We identified six artificial roosts within the study area that were interlinked, with bats switching between them. Ten individuals were used for modelling foraging-habitat utilization, which revealed that bats were highly selective. The only habitat type that bats clearly preferred, regardless of season, was an urban illuminated area close to a river. Only slight avoidance — of open areas — was observed during the pre-parturition period.

Key words: Chiroptera, urban, telemetry, prefabricated houses, foraging habitat

Activity patterns and use of night roosts by lesser horseshoe bats *Rhinolophus hipposideros* (Borkhausen, 1797)

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Close approach radio-tracking was used to investigate time and space use for both sexes of *Rhinolophus hipposideros*. Fifteen bats (nine males and six females, from three roosts) were radio-tracked (\bar{x} = 6.7 nights) within and around the National Trust Sherborne Park Estate, Gloucestershire (UK), between June and October 2003, at least seven of which (six males and one female) relocated to a different day roost after capture. The mean number of activity bouts per night was 3.5, each lasting for an average of 148 minutes. The mean distance travelled between fixes during each bout of activity was 3.8 km, and per night was 14.2 km. An average of 3.3 (SE = 1.8, range = 1–7, n = 12) night roosts were used per bat. Those individuals which continued roosting within the estate (n = 13) occupied a group foraging range covering approximately 1,175 ha with a 6.3 km range span (100% minimum convex polygon). The corresponding areas using the 95% Kernel isopleth and 95% Dirichlet tessellation enclosed approximately 539 ha and 1,553 ha, respectively. The maximum distance a bat was tracked from the roost of capture was 4.6 km, although the mean (n = 15) was much lower (2.2 km). A mean of 42% of the radio-tracking fixes from bats with at least one whole night of data were associated with night roosting, and of those, 56% were from the boiler room of a residential property within Sherborne village (used by 12 of the 15 bats). Therefore a range of suitable night roosts (i.e. sheltered locations adjacent to foraging areas) should be available throughout the foraging range (a minimum of 3 km from the roost) of a *R. hipposideros* colony. Night roosts on the edge of the home range, and warm night roosts are especially important.

Key words: range, time budget, minimum convex polygon, dirichlet tessellation, kernel analysis, night roost

Home range of Noack's round-leaf bat (*Hipposideros aff. ruber*) in an agricultural landscape of central Ghana

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Thirteen individuals of Noack's round-leaf bat, *Hipposideros aff. ruber*, were radio-tracked for 38 nights in an agricultural landscape in Kwamang, Ashanti Region, Ghana. Local convex hulls were used to estimate home range sizes of the bats. Based on 1,192 fixes, the mean (\pm SD) home range size was 36 ha \pm 35 ha. Individual home range size ranged from six to 95 ha and frequently overlapped among individuals. The foraging area covered 50% of the home range while the core area formed 2%. The mean maximum foraging distance was 1.1 km, with individual distances up to 2.6 km, suggesting *Hipposideros aff. ruber* is capable of covering relatively long distances. Male bats returned to the cave more often than females during the night. Although the cave was the main roost, each bat also had individual night roosts on trees.

Key words: core area, foraging area, local convex hull, maximum foraging distance, radio-tracking

First record of Streblidae, *Raymondia alulata* Speiser, 1908 (Diptera: Streblidae), in Swaziland and a review of the genus *Raymondia* and their hosts in Africa

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Species of the genus *Raymondia* (Diptera: Streblidae) are obligate ectoparasites of bats. They have a wide distribution across Africa and are associated with many different bat species. Here we present the first record of this family in Swaziland. The ectoparasites were of the species *Raymondia alulata* and were found parasitizing individuals of the species *Nycteris thebaica*. We review the status of *Raymondia* species known in Africa, including specimen records, hosts, and host distributions and provide an updated identification key for species in this genus.

Key words: distribution, Chiroptera, bat flies, ectoparasite, host-parasite relationships, parasitism

Records of the cave-dwelling bats (Mammalia: Chiroptera) of Hispaniola with an examination of seasonal variation in diversity

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Despite a long history of scientific collection of bats, Hispaniola remains the least studied island of the Greater Antilles. Using standardized trapping methods during the wet and dry season at four major caves — Honda de Julián, La Chepa, Los Patos, and Pomier #4, we sampled a total of 1,472 individuals in four families, 11 genera and 12 species (of 18 recorded for the island). We report significantly fewer captures on the second night of sampling. We document seasonal variation in abundance of *Macrotus waterhousii*, *Monophyllus redmani*, and *Artibeus jamaicensis*, that results in 1–4 more species captured in the wet season. Additionally, singleton captures at all caves except for Honda de Julian produced wide confidence intervals in estimates of richness. Finally, we highlight the role of caves as major ecosystems for maintaining Hispaniolan mammal biodiversity. The high diversity recorded at La Chepa, together with possible declines at the historically very diverse Los Patos, highlight the conservation importance of all surveyed caves.

Key words: Chiroptera, harp trap, Natalidae, Phyllostomidae, wet and dry season

Bat boxes — a review of their use and application, past, present and future

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Loss of tree cavities presents a threat to tree roosting echolocating bat populations. Bat boxes have been used for over a century to provide artificial cavities. The aims of this review were to provide a synthesis of bat box use in temperate parts of the world, to discuss the applications and effectiveness of bat boxes, to provide box deployment recommendations and to identify areas requiring further research. The 109 publications reviewed originated from four regions. The majority were from Europe (70%) followed by North America (16%), Australia (12%) and Asia (3%). Publications reported box use for research ($n = 67$), conservation management ($n = 42$) and public bat awareness ($n = 1$). The most commonly used bat box designs could be divided into five basic types, four originating from Europe and one from North America. Woodcement as a box material was frequently used in Europe and was practically absent elsewhere with timber boxes most commonly used overall. Seventy-one species of bats have been recorded using boxes, although only 18 were identified as using boxes commonly and 31 species were reported to have formed maternity roosts. The lack of maternity and overwintering roost records in boxes is a concern. There is a need to test current box types across geographical regions and to develop designs further. Where boxes are used as a conservation tool, consideration should be given to the long-term maintenance costs of a box program. Unless known to be unsuitable to target species, boxes should be made from durable materials, be unattractive to non-target species and be ‘self-cleaning’. Deploying a variety of box designs in clusters, time since box installation, non-target species box competition and target species-specific box design elements are likely influencing box uptake. The provision of boxes that comprise different microclimates and box aspects are likely best suited to meet the varying needs of a given tree roosting echolocating bat community. No conclusive evidence was found that box installation height is important for box uptake. There is concern that boxes may provide a competitive advantage for bat species commonly using boxes. Bat boxes should not be used as a justification for the removal of trees that comprise potential roost cavities.

Key words: bat box, bat house, artificial roost, tree cavity-roosting bats, conservation