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Chiropteran (Chiroptera; Mammalia) taxonomy in light of modern methods and approaches

Sergei V. Kruskop* & Ilya V. Artyushin

ABSTRACT. Bats are the second largest mammalian order with an almost worldwide distribution. Bat taxonomy remained almost unchanged for decades, and the diversity of the order was underestimated. The advent of molecular methods brought change to chiropteran taxonomy. The number of families increased from 17–18 to 21, and the relationships between them were revised, as were the composition of suborders and superfamilies. The number of recognized species and genera went up by almost a third. As a discipline, bat taxonomy has changed much methodologically and conceptually. After its long reign, comparative morphology has faded into the background. It has become clear that characters can diverge and converge in related species, masking true phylogenetic relationships. Not writing morphology off entirely, it does necessitate resorting to finer structures or multivariate data analysis. Karyology is of limited use in bat taxonomy, but methods such as FISH add to the understanding of relationships between suprageneric taxa. Mitochondrial DNA sequences are easy to obtain, and their analysis yields well-supported phylogenetic trees, but reticular processes and other factors may mask taxon boundaries. To resolve the uncertainty, nuclear markers are used, and their number and choice depends on taxon characteristics. Overall, building a consistent chiropteran system calls for an integration of all mentioned approaches.

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Систематика рукокрылых (Chiroptera; Mammalia) в свете современных методов и подходов

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РЕЗЮМЕ. Рукокрылые — второй крупнейший (после грызунов) отряд млекопитающих, имеющий почти всесветное распространение. Взгляды на их систематику десятилетиями оставались почти неизменными, и, как теперь понятно, разнообразие отряда на всех таксономических уровнях было в значительной степени недооценено. Однако с распространением молекулярных методов и постепенным совершенствованием самих этих методов представления о систематике рукокрылых стали значительно меняться. Оказались пересмотрены количество семейств (их число возросло с 17–18 до 21) и родственные связи между ними, состав подотрядов и надсемейств. Число признаваемых видов и родов за два десятилетия выросло почти на треть. За последние три десятилетия сформировались представления об эффективных методах и подходах при изучении систематики рукокрылых. Сравнительная морфология, доминировавшая ранее, отошла на второй план. Стало понятно, что на уровне родственных видов качественные и количественные признаки могут легко как дивергировать, так и конвергировать, маскируя истинные родственные связи. Это, однако, не списывает морфологию со счетов, а лишь требует обращения к более тонким структурам или к многомерному анализу данных. Кариология у рукокрылых — в среднем менее эффективный инструмент, однако такие методы как FISH дополняют представления о родственных связях надродовых таксонов. Получать последовательности митохондриальной ДНК сравнительно легко, а их анализ нередко дает хорошо поддержанные филогенетические деревья. Однако ряд факторов, таких как ретикулярные процессы, маскирует границы таксонов. Соответственно, широкое применение

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находят ядерные маркеры, выбор и количество которых зависит от особенностей анализируемого таксона. В целом же, для построения непротиворечивой системы необходима разумная интеграция перечисленных подходов.

КЛЮЧЕВЫЕ СЛОВА: Chiroptera, рукокрылые, молекулярная генетика, морфология, палеонтология, кариология, филогения.

Introduction

Bats are second largest Mammalian order, accounting for about 1/5 of total taxonomic diversity of the class (Wilson & Reeder, 2005; Wilson & Mittermeier, 2019). There is a belief, as ingrained as it is wrong, that bats are poorly studied and that we know little of their taxonomy and paleontology. In reality, bats are very actively studied, and many discoveries have been made over recent decades, many of them intriguing and conducive to further research.

Chiropteran taxonomy remained remarkably stable for most of the 20th century, changing little from Tate's classic works (Tate, 1941a, b, c, 1942) to Koopman's checklists (Koopman, 1993, 1994). The number of recognized species changed insignificantly over the period, always staying near 900 (Koopman, 1984, 1993, 1994). "A species is what a good taxonomist considers a species" was the motto of the era. It was the same for large taxa, adopted with slight variation from Dobson (1875) and Miller (1907). From thirties to nineties, only one new family, Craseonycteridae, was recognized following the discovery of the enigmatic *Craseonycteris thonglongyai* (Hill, 1974). Little change in chiropteran taxonomy meant few researchers took interest in it, producing, in turn, little change. Those few experts reigned the field uncontestedly, following their heart in their largely arbitrarily judgment.

Karyology fad, for all its impact on the taxonomy of other mammalian groups, in the case of bats had surprisingly little influence. One reason for that was inaccessibility of materials from the tropics, where the main diversity of the order is concentrated. The other reason was low variability of karyotypes in the groups of bats that were accessible to European and North American researchers. For instance, all *Eptesicus* species have the same number of chromosomes and chromosome arms 2n/FN = 50/48 (Volleth & Heller, 1994). In the second largest mammalian genus, *Myotis*, most species have karyotypes with 2n/FN = 44/50-52 (Volleth, 1987; Volleth & Heller, 2012).

Things changed with the advent of molecular genetic techniques. Sampling tissue for DNA analysis is easier and more permissive than chromosomal preparations, facilitating material collection even in the tropics. The progress in methods themselves has allowed to analyze legacy material from old collections (Nachman, 2013; Almeida *et al.*, 2014; Bailey *et al.*, 2016; Castañeda-Rico *et al.*, 2020). Bat capture techniques have improved as well. As a result, more extensive and varied material is now available for analysis than ever before. At the same time, the Genetic Species Concept (GSC) became key to alpha-level mammalian taxonomy (e.g., Bradley & Baker, 2001; Baker & Bradley, 2006). GSC was followed by the General Lineage Concept (GLC), where species are defined as metapopulation lineages identifiable by secondary recognition criteria (De Queiroz, 2007). Building on GSC is the idea of determining the rank of higher taxa by the time of their genetic isolation (see Avise & Liu, 2011).

As a result, chiropteran taxonomy was revised at many levels, from suborders (Teeling, 2005; Hutcheon & Kirsch, 2006) to genera and species complexes (Ruedi & Mayer, 2001; Appleton *et al.*, 2004; Spitzenberger *et al.*, 2006; Ruedi *et al.*, 2013; Foley *et al.*, 2017). The number of recognized species went up by ~55% (Wilson & Mittermeier, 2019). Here we review current bat taxonomy at different taxonomic levels and how it changed over the past two decades.

Molecular genetic methods in bat taxonomy

Since the late nineties, evidence from molecular genetics has changed chiropteran systematic at every level. In the late nineties and the noughties, infraorders were rearranged in the course of the grand molecular revision of high level mammalian taxonomy. At the same time, results from molecular barcoding projects led to changes in many families (discussed below) and genera, revealing a plethora of cryptic species in Emballonuridae (Goodman *et al.*, 2012), Hipposideridae (Thabah *et al.*, 2006; Vallo *et al.*, 2008), Rhinolophidae (Sun *et al.*, 2009), Phyllostomidae (Solari & Baker, 2006; Porter *et al.*, 2007), Miniopteridae (Miller-Butterworth, 2005), Vespertilionidae (Kawai *et al.*, 2003; Jacobs *et al.*, 2006; Spitzenberger *et al.*, 2006; Mayer *et al.*, 2007; Hulva *et al.*, 2010).

Late 2000s saw a major shift in perspective on molecular systematics (Edwards, 2009). The notions of phylogeny and tree diverged in two distinct concepts each. Today, anyone involved in phylogenetic research is aware of the terms "gene tree" and "species tree" and the divide between them. The change in attitude came with the realization that molecular barcoding was not, in fact, the taxonomic silver bullet. Incomplete lineage sorting, speciation with gene flow retention, and hybridization are among the things that make gene trees and species trees incongruent (Elworth *et al.*, 2019).

Barcoding can still be used, with due caution, for specimen identification. Even in convoluted taxa, most species can be reliably identified using mitochondrial cytochrome-*c* oxidase subunit I gene (COI), which is the standard barcoding marker for mammals (Ivanova *et al.*, 2012). If the study area likely has undiscovered taxonomic diversity, complex taxa can be still identified to the genus level (Caraballo *et al.*, 2020).

Mitochondrial markers are also useful for preliminary biodiversity survey and discovery of taxonomical problems in insufficiently studied regions and groups (Giménez *et al.*, 2019). For bats, COI in many cases does not provide sufficient resolution, hence cyt*b*, ND1 or rRNA genes are often additionally used (Çoraman *et al.*, 2020).

The relative ease of sequencing of mitochondrial genes, unfortunately, provokes their use as the main, or even the only, argument for solving taxonomic issues instead of considering them together with other, for example, morphological data.

This approach is justified in some cases, when for example the status of undoubtedly related, but geographically separated taxa is considered (e.g., Benda *et al.*, 2016; Dietz *et al.*, 2016). In other cases, drawing conclusions using a single mitochondrial marker creates more confusion and problems than it solves. An example is the African "pipistrelles", which were divided into several questionable genera in recent works. And the boundaries between these genera vary depending on the number of analyzed taxa (Hutterer *et al.*, 2019; Monadjem *et al.*, 2021) and require further clarification.

The fact that each group has its own set of available markers creates problems for combining datasets, but things are getting better as the number of sequences in public databases grows. Hypervariable fragments of mtDNA, the D-loop/control region, have been successfully used for certain groups (Gager *et al.*, 2016; Centeno-Cuadros *et al.*, 2019). This marker, however, should also be used with caution, as it is prone to heteroplasmy at least in some genera (Petri *et al.*, 1996), besides there are very limited taxonomical coverage of reference sequences.

As high-throughput sequencing technology advances, acquiring whole mitogenomes becomes cheaper and faster. At the time of writing, there are about 400 mitogenomes of bats in the NCBI database. Unfortunately, most of them are useless to resolving taxonomy (compare Hassanin *et al.*, 2020; and Nesi *et al.*, 2021). The main pitfall of mitochondrial phylogenies is not the lack of information to resolve deep short branches, but rather the phylogenetic incongruence at the short branches.

At the species level and beneath population samples of mitochondrial sequences can be used to characterize gene flow barriers (as deviation from isolation by distance model) and to reconstruct historical demography (Tu *et al.*, 2021). These two kinds of data can become a meaningful taxonomic argument in context of certain species concepts, or at least help pinpoint contact zones or range discontinuities. Intraspecific population structure, demographic and behavioral traits, such as population size or sex-dependent dispersion, in mitochondrial trees sometimes produce branching patterns usually associated with species-level divergence (Dávalos & Russell, 2014). The authors propose to approach the species status as a statistical hypothesis and validate it by comparing a series of evolutionary models, some of which assume species divergence and others do not. A recommendation is also given to formally test datasets for sufficiency for drawing conclusions.

Most current works on taxonomic and biodiversity issues use up to three mitochondrial and a few nuclear genes, commonly 2–10 of them (Foley *et al.*, 2017; Demos *et al.*, 2019; Garbino *et al.*, 2020; Tu *et al.*, 2021). This set of markers is generally adequate to identify species and construct correct phylogenies even in the presence of introgressive hybridization. In more complex cases it can show the group needs more study.

Introgressive hybridization frequently followed by a complete replacement of certain haplotype is common in bats. Initially discovered as discordance between morphological and mitochondrial traits it was found in the last decade in many genera of Vespertilionidae (e.g., Sztencel-Jabłonka *et al.*, 2012; Morales *et al.*, 2017; Centeno-Cuadros *et al.*, 2019), Pteropodidae (Nesi *et al.*, 2021), Rhinolophidae (Mao *et al.*, 2019), Mormoopidae (Méndez-Rodríguez *et al.*, 2021) and other families. It therefore makes sense to exercise caution when considering taxonomical revisions which are based solely on mitochondrial markers.

Genotyping population samples of appropriate size using a limited number of sites allows to directly trace hybridization and localize zones where it has occurred previously or is still happening (Méndez-Rodríguez *et al.*, 2021). For bats, the most frequently used nuclear genes are ABHD11, BGN, PRKC1, STAT5A, ROGDI, THY (Igea *et al.*, 2010; Foley *et al.*, 2014), RAG1, RAG2, BRCA1 (Teeling *et al.*, 2000), vWF, DMP1, and ApoB (Meridith *et al.*, 2011). Unfortunately, different authors use different gene sets even for the same taxa. This can in part be overcomed by combining trees with non-matching leaf set (supertree methods; see Akanni *et al.*, 2015), instead of combining character matrices. A concatenated matrix of multiple genes can be used in conjunction with methods which assume or directly implement coalescent and species tree models (*BEAST, ASTRAL, BPP, SVDquartets and others). Multi-locus sequencing projects are costly and time-consuming, but multiplex PCR and high-throughput sequencing alleviate this to some extent, especially when the number of genes that need to be considered reaches a few dozen.

Microsatellites are still worthwhile as a relatively cheap method for assessing genetic pool isolation and finding traces of hybridization (Centeno-Cuadros *et al.*, 2019; Méndez-Rodríguez, 2021). Question remains, how to interpret allopatric forms that are distinguishable by microsatellites, but otherwise very close (Dool, 2020). Even if not considered as species such forms deserve close attention of conservation scientists (Andriollo *et al.*, 2018). Phylogenetic reconstructions using microsatellite markers demand external estimates of evolutionary rates, which contribute substantially to divergence time errors (Ellegren, 2004).

For complex phylogenies even dozens of markers are sometimes not enough. Some of the reasons for that are short branches at deep divergences, reticulated evolution, and recent speciation. In such cases, high-throughput sequencing can be used instead, resulting in datasets that are orders of magnitude larger than a few dozen Sanger-sequenced amplicons could provide, at a comparable price. Low coverage whole genome sequences, however, while being useful in population genetics applications and work with archived samples, are typically too redundant and still too expensive for taxonomic purposes (O'Toole *et al.*, 2021). To address this matter, a broad spectrum of methods is employed. Their main purpose is to limit the sequenced fraction of genome to several percent, while yielding same loci across all samples.

Baits (UCE, exome sequencing, and custom baits panels) are sometimes used to that end, although the method still remains too expensive for mass use. Despite this limitation, it was successfully applied to several groups (Mao & Rossiter, 2020; Nesi *et al.*, 2021). It is suitable for museum specimens, and needs little adaptation or none at all to apply to wide systematic groups, coping fine with up to 15% nucleotide mismatches between bait and target (Bragg *et al.*, 2016), or up to 39% with modified protocol (Li *et al.*, 2013).

Restrictase-aided methods (RAD-seq: Elshire *et al.*, 2011) are cheaper but more labor-intensive and sensitive to DNA quality Using a closely related species reference genome is highly recommended for proper selection of restrictases and read mapping.

RNA-seq is an alternative to exome sequencing. It is cheaper at preparation stage, while the sequencing itself is priced comparably. RNA-seq requires RNA, so it cannot be used on preserved specimens, unless formaldehyde was used as fixative, and even then with limitations. Euthanasia and internal organs tissue sampling or cell culture growing are required, which can be a problem when studying protected species. Only a few phylogenetic studies were thus published that used RNA-seq (Lei & Dong, 2016; Hawkins *et al.*, 2019).

The number of sites required for analysis varies depending on the phylogenetic analysis algorithm. Many algorithms require all specimens or most of them to be characterized by all sites (tags, SNP etc.). In such cases filtration can reduce the data volume by an order of magnitude (e.g., Morales & Carstens, 2018). The resulting ratio varies depending on the number of samples, and gets worse when low-quality specimens are added. The effect of diminished input on algorithm performance should be carefully considered (Molloy & Warnow, 2017). The computational cost of analysis grows together with the dataset size, often forcing the use of less complex evolutionary models and simpler algorithms. This can result in major artifacts in the reconstructions. Care should be taken to ensure the analyzed loci meet the assumptions of the models and algorithms used. It makes sense to group loci by parameters of molecular evolution (evolutionary rate, GC-content, gamma-distribution parameter) and then to assess the contribution of each group in the support for each phylogenetic hypothesis.

Extensive datasets can be misleading by producing high values of traditional "quality of reconstruction" metrics (bootstrap index and Bayesian posterior probability) even in the presence of alternative phylogenetic signal (Huang *et al.*, 2020). A correct model of evolutionary process is of crucial importance when dealing with such data (Philippe *et al.*, 2011). This can be demonstrated on the studies of New World mouse-eared bats. Apparently, several species hybridized more than once in their history. Application of different coalescent methods not taking into account possible hybridization resulted in a number of very different, but well-supported phylogenies. Moreover, even for the nodes that were reconstructed correctly, divergence times will be estimated with significant systematic error if an algorithm is used that cannot handle correctly the gene flow retention after speciation (Leaché *et al.*, 2014; Morales *et al.*, 2017).

Papers, however, still appear where data is not checked for traces of reticulated evolution. For example, in Loureiro *et al.* (2020), the authors, revising the genus *Molossus*, consider monophyletic and very low-divergence groups which correspond to morphologically distinguishable entities sufficient evidence to make taxonomical decisions

It is indeed complicated question how to treat forms, for which the gene flow retention or hybridization was shown, even if there is enough data to quantitatively describe this process. Taxonomical conclusions can be arbitrary and ultimately depend on the choice of species concept. For higher taxonomical levels, monophyly and divergence time are the main considered criteria (Avise & Liu, 2011). Many nodes above the generic level that lack resolution can be easily resolved just by increasing the number of genes in the dataset. However, divergence events occurring in rapid succession can produce patterns close to true polytomy. In that case, the number of loci that corroborate alternative phylogenies can be nearly equal, and uttermost care should be taken to apply correct data filtration, that is excluding paralogs, genes with deviant evolutionary parameters, genes under positive selection etc.

Role of morphology

Since the very inception of zoology, morphological structures have been a precious source of information, which should not be discarded even with the advent of new methods. Until very recently, bat taxonomy studies at all levels based itself primarily on morphological data. First works trying to adapt molecular genetics to the needs of bat taxonomy date back to the late nineties. In the early 2000s, the approach gained traction — and shook the old system. Even after that, however, new studies based on morphological data kept coming out, with some of them pertaining to low-level taxonomy, (e.g., Csorba *et al.*, 2007; Görföl *et al.*, 2013; Reeder *et al.*, 2013). Moreover, an important role in understanding the evolution of vertebrate taxonomy is played by paleontology, inevitably relying on morphological criteria (Wiens *et al.*, 2010). Calibration of divergence times is particularly dependent on paleontological evidence (see, e.g., Wiens, 2009; Ksepka *et al.*, 2015; Warnock *et al.*, 2017).

On the other hand, morphological structures are prone to a large degree of individual, age-dependent, sexual, and geographic variability, as well as to homoplasy (Freeman, 2000; Evin *et al.*, 2008; etc.). In alpha-level taxonomy, unless the sampling across the putative species range is sufficient to assess the variability, it is easy to misinterpret ecomorphs, remote but reproductively non-isolated populations, or just animals from different samples as a species. Conversely, when dealing with geographically distant populations representing ecological vicariates, it is difficult to critically assess their taxonomic relationships solely by morphological similarity. The long-standing notion of extremely wide transcontinental ranges of some bats is an example of this. The species *Myotis daubentonii* and *Plecotus auritus* had forms from eastern parts of their transpalaearctic ranges moved out into distinct species *M. petax* and *P. ognevi* (Matveev *et al.*, 2005; Spitzenberger *et al.*, 2006). The range of *Miniopterus schreibersi,* formerly spanning three continents, is now divided into a number of species, some of them not even related to each other (Appleton *et al.*, 2004; Tian *et al.*, 2004; Bilgin *et al.*, 2012; Šrámek *et al.*, 2013).

The situation is worse, in a sense, in the high-rank taxa. On the one hand, almost every family-rank taxon has its own morphological diagnosis matching its member taxa. Perhaps only the wing-gland bats Cistugidae represent the exception. The morphological distinction between Cistugidae and the related Vespertilionidae is obscure, and it is no more pronounced than the differences between suprageneric groups within Vespertilionidae itself (Lack *et al.*, 2010).

On the other hand, syndromes of morphological traits, no matter how obvious they are, tend to say little about phylogenetic relationships, and even can mislead when they do. Pteropodidae, a family of Old World fruit bats, is a most striking example. Owing to their unique morphology, for more than a century they have been treated as special suborder Megachiroptera (Koopman, 1994; McKenna & Bell, 1997). Molecular genetic and karyological evidence, however, places Pteropodidae close to the superfamily Rhinolophoidea (Teeling *et al.*, 2002, 2005; Eick *et al.*, 2005; Hutcheon & Kirsch, 2006; Ao *et al.*, 2007; Volleth *et al.*, 2011), which today is usually no longer contested. Worthy of note is also the placing of all nectarivorous fruit bats into subfamily Macroglossinae, and of all nectarivorous leaf-nosed bats into subfamilies Phyllonycterinae and Glossophaginae (e.g., Koopman, 1994; McKenna & Bell, 1997). It has been shown recently that adaptations to feeding on pollen and nectar had evolved several times in both families, giving rise to convergent syndromes of traits (Almeida *et al.*, 2011, 2020; Baker *et al.*, 2016; Camacho *et al.*, 2019). "Serotines" and "pipistrelles" used to be formerly recognized as supra-genus groups, based on their formal dental features (e.g., Koopman, 1994), but other approaches showed this completely untenable (Volleth & Heller, 1994; Kearney *et al.*, 2002; Hoofer & Van den Bussche, 2003; Roehrs *et al.*, 2010, 2011).

Given all this, morphological evidence in modern bat taxonomy has come to play a secondary role, especially at the alpha level. Morphological characters are selected to describe the taxa already identified using molecular methods. Still, morphology remains an important source of information on many issues, including the rank of taxa (Springer *et al.*, 2008; Cirranello *et al.*, 2016; Rossini *et al.*, 2019), which is one of the keys to the integrative approach in taxonomy (Padial *et al.*, 2010; also see Davalos *et al.*, 2014).

As with other mammals, in bats the most important, or indeed the most popular sets of discriminating characters are associated with the skull and dental structures. Bats do not have such noticeable differences in the shape of chewing surface as do the rodents. However, the totality of all teeth in a row usually creates a syndrome of traits specific to a particular taxon. This fact is well known to paleontologists and heavily used by them (Horáček *et al.*, 2006; Gunnell *et al.*, 2008; Rosina & Rummel, 2012; Sigé *et al.*, 2014; etc.). Neontologists, with more diverse and complete material at their disposal, usually limit themselves to general characterization of teeth structure, only occasionally showing interest in the particulars of dental morphology.

Morphological features such as teeth shape, however, should be interpreted with certain caution. For example, in the most extensive bat family, Vespertilionidae, there are two prevalent types of talonid structure of the lower molars, myotodontia and nyctalodontia (Menu & Sigé, 1971; Horacek & Hanak, 1986; Menu, 1987; Martie, 2014). Myotodontia is believed to be ancestral in Vespertilionidae, which is supported by the description of a myotodont bat, *Premonycteris* (Hand *et al.*, 2016) from a late early Eocene. Menu (1987) assigned taxonomic significance to the distinction between myotodontia and nyctalodontia, and in most known cases it serves well as a marker for taxon boundaries. It is particularly helpful in paleontology, since the lower molars preserve well. However, a number of cases are known when members of closely related taxa possess different types of molars. For instance, all but few species in the extensive genus *Myotis* have molars of the myotodont type. Certain species in the generally morphologically compact complex "*siligorensis*", however, are an exception (Borisenko *et al.*, 2008; Tiunov *et al.*, 2011; Ruedi *et al.*, 2013).

It is appropriate to say here few words about the paleontology of bats. Fossil evidence of bats is abundant, covering all continents and time periods in which chiropterans have ever lived, though gaps do remain (Gunnell & Simmons, 2005; Eiting & Gunnell, 2009). However, complete bone remnants allowing for comparison of multiple characters are rare. Most chiropteran fossil records are jaw fragments and isolated teeth, which limits the already scarce possibilities to construct phylogeny (see Smith *et al.*, 2007; Rosina & Rummel, 2012; Sigé *et al.*, 2014; etc.). Still, the paleontological history of many modern bat genera and most modern bat families is fairly well described.

From a neontologist's perspective, paleontological approach meets two common problems. With fossils from completely extinct taxa, paleontologists must somehow deal with their classification and phylogenetic placement. But whenever the fossils in question have morphological features that give clues to place them with extant taxa, it would often be done even when contradicted by biogeographic reasons and molecular dating. To mention a few examples, some European long-eared bat fossils were assigned to an endemic American genus *Corynorhinus* (e.g., Ziegler, 2003; but see Arita *et al.*, 2014; Rosina *et al.*, 2019); the description of *Myotis* species from the Early Oligocene of Belgium (Gunnell *et al.*, 2017) and the assignment of the Oligocene genus *Quinetia* to the Plecotini tribe (Czaplewski *et al.*, 2019) followed the same pattern. In two latter cases the fossil records are almost two times older than the molecular dating for basal divergence of their alleged taxa (see Teeling *et al.*, 2005; Lack *et al.*, 2010).

Integrating morphological evidence, including that from fossil records, into molecular phylogenetic reconstructions makes sense at least for taxa with extant species. In a study on American leaf-nosed bats Phyllostomidae, fossil evidence from Miocene genera *Notonycteris* and *Palynephyllum* is integrated into the molecular based reconstruction by isolating conflicting phylogenetic signals in analysis of non-independent morphological structures. As a result, a scenario for morphological evolution of Phyllostomidae is proposed (Davalos *et al*., 2014).

An interesting morphological study used computed microtomography to compare of the structure of the shoulder joint and inner ear of *Tachypteron franzeni* and modern Taphozoinae, showing the same level of adaptation to open-space aerial hawking in the modern and Eocene species. It had no direct relation to taxonomy, but it is important for understanding the time of formation of morphologically "modern" bats (Habersetzer *et al.*, 2012).

Geometric morphometrics allows to formally describe and compare the shape of objects (Marcus *et al.*, 2000; Zelditch *et al.*, 2012). At the level of large taxa geometric morphometrics methods have been successfully applied to the New World leaf-nosed bats Phyllostomidae (Camacho *et al.*, 2019; Rossoni *et al.*, 2019; Hedrick *et al.*, 2020). The latter work also examines how the shape of skull changes in leaf-nosed bats compared to closely related families. An earlier study focuses on the range of disparity within and between the three bat families Phyllostomidae, Molossidae, and Vespertilionidae (Hedrick & Dumont, 2018). These and many other bat-related morphological studies have more to do with mechanisms and directions of evolution than with taxonomic research as such, making use of existing phylogenetic schemes derived earlier from molecular evidence. Methodologically, however, they may clue in new phylogenetic research by demonstrating the possibility of identifying and describing the trajectories of morphological evolution within known taxa.

More specific taxonomic papers use geometric morphometrics as one of the arguments for identifying a new taxon (Jarrín-V & Kunz, 2011; Tu *et al.*, 2015) or for finding boundaries between known species (Evin *et al.*, 2008; Sztencel-Jablonka *et al.*, 2009; Huang *et al.*, 2014). The number of bat-related studies of this kind is small. Noteworthy is the work of Schmieder *et al.* (2015), comparing the reliability of geometric and traditional morphometrics, using European horseshoe bats *Rhinolophus* as an example.

In another study, 2D geometric morphometrics was used to explore the phylogenetic relationships between fossil and modern Rhinolophoidea (Wilson *et al.*, 2016). Similarly to Davalos *et al.* (2014), fossil taxa were integrated into modern phylogenetic schemes (Murray *et al.*, 2012; Foley *et al.*, 2015). For the first time the fossil forms of Rhinonycteridae and Hipposideridae were reliably separated, clearly demonstrating the viability of the approach.

A recent study gives an example of morphology helping resolve doubts that molecular research creates. Since the early days of molecular-based research in bat phylogeny, question remained: in light of the relationship between fruit bats and rhinolophoids, did echolocation in the two bat suborders develop independently, or did they inherit it from a common ancestor, and then Pteropodidae lost it (Springer *et al.*, 2001; Jones & Teeling, 2006; Teeling, 2009)? An embryological study showed that in non-echolocating fruit bats the inner ear morphology is similar to that of non-bat placental mammals not only in adults, but also during embryonic development. In echolocating bats from both suborders, though, the development of the inner ear differs noticeably both from non-echolocating mammals and from each other. The balance thus shifts in favor of the independent origin of echolocation in two suborders (Nojiri *et al*., 2021).

Role of chromosome studies in bat taxonomy

Compared to molecular genetics and morphology, chiropteran taxonomy owes relatively little to karyology. As already mentioned, the "karyological boom" in mammalian taxonomy did not significantly affect bat taxonomy. At that time most studies were conducted on the accessible boreal species, mainly in the family Vespertilionidae, known for conservatism in chromosome morphology and numbers (e.g., Heller & Volleth, 1984; Volleth, 1987). Bats in general, compared to other mammals, are also conservative in that respect (Sotero-Caio *et al.*, 2017). As a result, until late nineties, karyological studies of bats were mostly descriptive and did not result in mass recognition of new taxa, as was the case with rodents and insectivores (e.g., Warner *et al.*, 1974; Zima, 1976; Bickham *et al.*, 1986; Hood *et al.*, 1988; Zima *et al.*, 1992; etc.).

Karyological evidence, however, did provide clues that helped correct the system, as it did for the placement of the genus *Barbastella* within the tribe Plecotini

(Uchida & Ando, 1972; Fedyk & Ruprecht, 1983; Volleth, 1985); the assignment of species status to named taxa such as *Macrotus californicus* (Nelson-Rees *et al.*, 1968) and *Nyctalus furvus* (Volleth, 1992); the removal of forms *societatis* and *circumdatus* from the genus *Pipistrellus* (Heller & Volleth, 1984), etc.

Phyllostomidae have relatively high chromosomal variability among Chiroptera, with the largest number of chromosomal rearrangements and the greatest variety of diploid numbers within the order (Baker, 1973, 1979; Baker & Bickham, 1980). The progress in Phyllostomidae taxonomy that could have been made by exploiting these properties, however, was made using molecular genetic evidence instead.

Fluorescence *in-situ* hybridization (FISH) technique has become a valuable tool, allowing to establish chromosome region homology even between unrelated species — an important insight into the evolution of karyotype (Wienberg, 1995; Graphodatsky *et al.*, 2012). It was apparently first applied to bats by Volleth *et al.* (1999) to study the karyotype of *Glossophaga soricina*. A later study used homologies established by ZOO-FISH to identify synapomorphies, supporting the monophyly of the order Chiroptera, and also consistent with the hypothesis of the close relationship between Pteropodidae and Rhinolophoidea (Volleth *et al.*, 2002, 2011).

Modern methods of chromosome painting and mapping have allowed to describe the karyotypes of diverse chiropteran species from all modern bat families, except Craseonycteridae. A detailed review of current knowledge in bat karyology was given by Sotero-Caio *et al.* (2017). The growing knowledge of bat karyotype evolution highlights many issues important to bat taxonomy, from intraspecific variability (e.g., Volleth *et al.*, 2013; Gorobeiko *et al.*, 2020; etc.) to composition and boundaries of suprageneric taxa. For example, karyological data allowed to question the existence of the tribe Nycticeiini in its traditional understanding (Volleth *et al.*, 2006), in full agreement with the results of molecular genetic studies (e.g., Hoofer & Van Den Busche, 2003; Roehrs *et al.*, 2010). Study of the karyotypes of horseshoe bats (*Rhinolophus*) revealed cryptic taxonomic diversity in the species group "*trifoliatus*". As a result, species status was acknowledged for two taxa and a new species was described, *R. luctoides* (Volleth *et al.*, 2015, 2017). Karyological data supported the clade Nullicauda within the family Phyllostomidae and did not support the merging of genera *Carollia* and *Rhinophylla* into one taxon (Gomes *et al.*, 2018). Another studies, in Phyllostomidae, identified cryptic diversity in the genus *Rhinophylla* (Gomes *et al.*, 2010) and clarified phylogenetic relationships in the subfamilies Micronycterinae (Benathar *et al.*, 2019) and Vampyressinae (Gomes *et al.*, 2016). The latter work revealed translocations between sex chromosomes and autosomes, unique among mammals, explaining the emergence of sex tri- and tetravalents. Although important for understanding the evolution of bat karyotypes, at this stage it does not introduce any novelty into phylogenies.

Many studies use karyological evidence as an element of integrated approach, in which case it becomes an extra argument to support a taxonomic hypothesis. Examples include the confirmation of generic rank of *Neoromicia* (Kearney *et al.*, 2002), the description of cryptic diversity in *Carollia castanea* species complex (Solari *et al.*, 2006), the description of the genus *Hsunycteris* and the tribe Hsunycterini (Parlos *et al.*, 2014), and the study of phylogenetic relationships and cryptic diversity in the genus *Kerivoula* (Khan *et al.*, 2010).

In a series of studies of the Emballonuridae family (Volleth *et al.*, 2019a, b), cytogenetic evidence, in good agreement with the results from previous molecular genetic research, confirmed the relationship between Emballonuridae and Nycteridae, as well as a very ancient, divergence of Taphozoinae, possibly dating back to early Eocene, confirming Taphozoinae as an independent family.

Recent changes in supra-generic taxonomy

Traditional views

So what exactly changed in the taxonomy of bats over the past two decades, besides the rise in known species diversity? As Solari *et al.* (2019) point out, the construction of a stable and consistent bat taxonomy based on reliably reconstructed phylogenetic relationships is still a work in progress. However, as we demonstrate above, a lot has been done since the coming of molecular genetic methods and the integrative approach to makes use of them. Below, we briefly review the problems of supra-generic bat taxonomy seem to be solved or ready to be solved, as well as those that still await research.

As mentioned above, chiropteran system in pre-molecular era was mostly proposed by authors from the late 19th to early 20th century. It changed slightly by the end of the 20th century, acquiring apparent completeness in the works by Koopman (1984, 1994) and Simmons (1995, 1998, 2005). The system comprised unranked taxon Eochiroptera where Eocene fossil families were lumped together; suborder Megachiroptera with the single family Pteropodidae; and suborder Microchiroptera comprising all other extant families grouped in two infraorders. Infraorder Yinochiroptera included families Rhinolophidae, Hipposideridae (sometimes within Rhinolophidae), Megadermatidae, Craseonycteridae, Nycteridae, Rhinopomatidae, and Emballonuridae). Infraorder Yangochiroptera comprised families Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Molossidae, Vespertilionidae, Tyropteridae, Furipteridae, Myzopodidae, and Mystacinidae.

This taxonomic scheme with minor variations was generally agreed upon and reproduced in numerous checklists and zoology texts. So what changed since then?

Recent changes

First of all, the composition of the suborders was revised. It was suggested (Teeling *et al.*, 2000, 2002; Springer *et al.*, 2001), and then convincingly shown (Volleth *et al.*, 2002, 2011; Hutcheon & Kirsch, 2004, 2006; Teeling *et al.*, 2005; Lei & Dong, 2016) that Microchiroptera are paraphyletic; that the superfamilies Pteropodoidea (with a single family) and Rhinolophoidea are in sister positions to each other and together in sister position to all other extant taxa in the order. It was thus proposed to divide the order into suborders Yinpterochiroptera and Yangochiroptera, which Hutcheon & Kirsch (2006) proposed to call Pteropodiformes and Vespertilioniformes. Among other things, this has raised the question of the origin of echolocation in bats. Since fruit bats, with their archaic structure of the inner ear, were no longer the basal branch in this system, is the absence of echolocation secondary in them, or was it acquired independently in both suborders (Eick *et al.*, 2005; Teeling, 2009)? As already mentioned, the brilliant work of Nojiri *et al.* (2021) showed the second scenario was more likely.

This, in turn, raises the question of the relationship between families placed with Eochiroptera (e.g., sensu Sigé, 1991). Some of them (e.g. Tanzanycteridae) had already been suggested as putative archaic Rhinolophoidea (Gunnell *et al.* 2005; Hulva *et al.*, 2007). The cladistic constructions of Simmons and Geisler (1998) suggested that Pteropodidae were in many respects more archaic, and thus more basal than all known fossil families, with possible exception for Icaronycteridae, as well as Onychonycteridae, latter still not known at the time (Simmons *et al.*, 2008). According to current views, it automatically puts each of these extinct families into an extant suborder. The auditory anatomy paper mentioned earlier (Nojiri *et al.*, 2021) undermines the counter-argument about primitivity of the inner ear structure in Onychonycteridae and Icaronycteridae. Current dating of the origin of bat superfamily taxa (Teeling, 2009; Teeling *et al.*, 2016; Amador *et al.*, 2018), partly supported by the recent discoveries of very early yet morphologically advanced bats (Storch *et al.*, 2002; Hand *et al.*, 2016), implies that that the divergence of modern bat suborders dates back to about the same period as the earliest bat fossil findings, or even earlier. This line of reasoning lends extra support to the placement of Eocene bat families with modern suborders.

According to recent evidence, Emballonuridae, some of the most morphologically archaic living bats, do not belong to Yinpterochiroptera, but rather to Yangochiroptera along with Nycteridae, placing the two families as sister groups (Van Den Busche & Hoofer, 2004; Eick *et al.*, 2005; Teeling *et al.*, 2005). This scheme was initially proposed based on molecular findings and later supported by cytogenetic evidence (Volleth *et al.*, 2019b). Conversely, Rhinopomatidae and Craseonycteridae are undoubtedly placed with Rhinolophoidea and are thus in no close relation to Emballonuridae (Hulva & Horáček, 2002; Teeling *et al.*, 2005; Hulva *et al.*, 2007; Foley *et al.*, 2015; Amador *et al.*, 2018).

Natalidae and Molossidae are almost definitely related to Vespertilionidae and belong to the same superfamily (Hoofer *et al.*, 2003). There is also not much doubt that Tyropteridae, Furipteridae, and Mystacinidae are related to other Noctilionoidea (Van Den Busche & Hoofer, 2000, 2001; Hoofer *et al.*, 2003; Agnarsson *et al.*, 2011). In this list, the family Mystacinidae stands out as the only undoubted non-American member of the superfamily Noctilionoidea, indicating pre-Oligocene divergence of the latter (Teeling *et al.*, 2003). Madagascar sucker-footed bats Myzopodidae thus remain the only family o uncertain position. Various studies place Myzopodidae as part of basal radiation of either Vespertilionoidea (Van Den Busche & Hoofer, 2004; Eick *et al.*, 2005), Noctilionoidea (Teeling *et al.*, 2005; Agnarsson *et al.*, 2011), or even Yangochiroptera in general (Hoofer & Van Den Busche, 2003), with invariably low support. Given the undoubted antiquity of Myzopodidae (Gunnell *et al.*, 2014), the solution, for some reason never explicitly proposed before, might be to recognize them as a superfamily of their own.

The traditionally accepted set of families has been supplemented in the two recent decades by an extra three. Bent-wing bats Miniopteridae have long been considered a part of Vespertilionidae (see Koopman, 1994). Their independent status was substantiated by morphological evidence (Mein & Tupinier, 1977) and, decades later, confirmed by molecular genetics. Among other things, it indicates pre-Oligocene divergence of Miniopteridae from other Vespertilionoidea (Miller-Butterworth *et al.*, 2007; Lack *et al.*, 2010). The placement of the genus *Cistugo* as a separate family was also based primarily on its ancient divergence, predating the divergence of modern groups within Vespertilionidae (Lack *et al.*, 2010).

For all the morphological similarities between Rhinolophidae and Hipposideridae, especially striking in their early fossils (Ravel *et al.*, 2016), their undoubted divergence in the Eocene (Ravel *et al.*, 2014) rules out uniting them under one family. Additionally, phylogenetic analysis revealed a third lineage, almost as ancient, subsequently recognized as the family Rhinonycteridae (Foley *et al.*, 2015).

Molecular (Ruedi *et al.*, 2012), cytogenetic (Volleth *et al.*, 2019a), and paleontological evidence (Storch *et al.*, 2002; Habersetzer *et al.*, 2012) indicates that Emballonurinae and Taphozoinae, the two subfamilies recognized within Emballonuridae, diverged no later than beginning of Middle Eocene. By analogy with other taxa in the order, this warrants assigning family rank to both subfamilies, which we reflected in the scheme below.

The structure of large families

At the turn of the 21st century, phylogenetic studies of the family Pteropodidae, including early molecular genetic efforts, revealed multiple contradictions within the existing system. Examples include paraphyly of nectarivorous genera, uncertain position of the genus *Eidolon*, paraphyly of the genus *Rousettus* in its traditional sense etc. (Kirsch *et al.*, 1995; Hollar & Springer, 1997; Alvarez *et al.*, 1999; Juste *et al.*, 1999; Romagnoli & Springer, 2000). Molecular phylogenetic studies with representative taxonomic sampling formed a fairly consistent system of Pteropodidae (Almeida *et al.*, 2011, 2016, 2020). These works confirmed a number of assumptions and made certain adjustments to them. They supported the subfamily status of Cynopterinae; showed the relation of *Boneia*, *Dobsonia*, and *Aproletes* to Harpyonycterinae (and not Rousettinae); the endemic African clade previously identified as subfamily Epomophorinae (Bergmans *et al.*, 1997) was included in Rousettinae, which in turn was split into seven tribes. The genus *Eidolon* and the peculiar genus *Notopteris*, endemic to Fiji, Vanuatu, and New Caledonia, received the status of distinct monotypic subfamilies (Eidoloninae and Notopterinae, respectively).

The modern system of the family Phyllostomidae was developed by a number of authors based on molecular data and integrative approach (Baker *et al.*, 2003, 2016; Davalos *et al.*, 2014; Cirranello *et al.*, 2016; Hedrick *et al.*, 2019; Rossoni *et al.*, 2019). In particular, the paraphyletic nature of Phyllostominae in its traditional understanding was shown (Baker *et al.*, 2003; Hoffman *et al.*, 2008). As a result, the genus *Macrotus* was recognized as a distinct and most basal subfamily (Baker *et al.*, 2003), whereas Micronycterinae, Glyphonycterinae, and Lonchorhininae were designated as separate subfamilies (Cirranello *et al.*, 2016). As mentioned earlier, it was also demonstrated that the transition to nectar diet had independently occurred on multiple occasions; producing nectarivorous leaf-nosed bats in different subfamilies Glossophaginae and Lonchophyllinae, both of which include not nectar-feeders as well (Baker *et al.*, 2016; Rossoni *et al.*, 2019).

The structure of another large family Vespertilionidae went through less revision. Tribe composition in the nominotypical subfamily received more attention, yet remains insufficiently established (Hoofer & Van den Bussche, 2003; Roehrs *et al.*, 2010, 2011). Decisive adoption of nomenclature for the tribes Vespertilionini and Pipistrellini is hindered, by the uncertain placement of the genus *Vespertilio* (close to the rest of Vespertilionini according to, e.g., Koubínová *et al.* (2013) and to Pipistrellini according to Roehrs *et al.* (2010), and also by the lack of formal description of "Hypsugine" group. The unity of the tribe Nycticeiini raises doubts (Hassanin *et al.*, 2017; Amador *et al.*, 2018). The boundaries and composition of the tribe Plecotini are not clear. In its traditional sense, it has weak support in all reconstructions (Hoofer & Van den Bussche, 2001, 2003; Roehrs *et al.*, 2010), with the position of the genera *Otonycteris*, *Idionycteris*, and *Euderma* especially controversial (Amador *et al.*, 2018). High rate of substitutions in the family and the rapid diversification of its main clades in the Miocene (Lack & Van Den Bussche, 2010) obstruct solution of these problems. As regards the composition and rank of subfamilies, molecular genetic evidence supports some of the earlier proposals. The existence of subfamilies Kerivoulinae and Murininae is well-supported. Subfamily Myotinae, earlier proposed by Simmons & Gaisler (1998), was not recognized by other taxonomists until molecular evidence came along (Hoofer & Van den Bussche, 2003; Hoofer *et al.*, 2003). Antrozoidae, proposed by Simmons & Gaisler as a separate family, is now recognized as a tribe within Vespertilioninae *s.str*. (Roehrs *et al.*, 2010; Amador *et al.*, 2018).

Phylogenetic relationships within other families are partially reviewed in the following works: for Hipposideridae — Murray *et al.*, 2012; Wilson *et al.*, 2016; Foley *et al.*, 2017; Patterson *et al.*, 2020; Yusefovich *et al.*, 2020; for Molossidae — Lamb *et al.*, 2011; Ammerman *et al.*, 2012; Reardon *et al.*, 2014; Gregorin & Cirranello, 2016.

A more or less consistent modern chiropteran system, thus, looks as follows. Number of accepted living genera in each taxon is shown in parentheses after symbol #.

Order Chiroptera
Suborder Yinpterochiroptera (=Pteropodiformes)
Superfamily Pteropodoidea
Family Pteropodidae
(subfamilies Pteropodinae: Pteropodini (#4), Melonycterini (#2), Pteralopini (#3); Eidolinae (#1); Rousettinae: Rousettini (#1), Eonycterini (#1), Epomophorini (#4), Myonycterini (#2), Stenonycterini (#1), Scotonycterini (#2), Plerotini (#1); Cynopterinae: Cynopterini (#3), Balionycterini (#11); Macroglossuinae (#2); Harpyonycterinae: Harpyonycterini (#2), Dobsoniini (#2); Nyctimeninae (#2), Notopterisinae (#1))
Superfamily Rhinolophoidea
Family Rhinolophidae (#1)
Family Hipposideridae (#8)
Family Rhinonycteridae (#4)
Family Megadermatidae (#5)
Family Rhinopomatidae (#1)
Family Craseonycteridae (#1)
Suborder Yangochiroptera (=Vespertilioniformes)
Superfamily incertae sedis
Family Myzopodidae (#1)
Superfamily Emballonuroidea
Family Nycteridae (#1)
Family Emballonuridae (two tribes: Emballonurini (#4), Diclidurini (#8); which subsequently could be raised to subfamilies)
Family Taphozoidae (see comments above; #2)
Superfamily Noctilionoidea
Family Tyropteridae (#1)
Family Furipteridae (#2)
Family Mystacinidae (#1)
Family Noctilionidae (#1)
Family Mormoopidae (#)
Family Phyllostomidae (subfamilies Macrotinae (#1); Micronycterinae (#2); Desmodontinae: Desmodontini (#2), Diphyllini (#1); Lonchorhininae (#1); Phyllostominae: Macrophyllini (#2), Phyllostomini (#5), Vampyrini (#3); Glossophaginae: Glossophagini (#3), Brachyphyllini (#3), Choeronycterini (#7); Lonchophylinae: Lonchophyllini (#4), Hsunycterini (#1); Carolliinae (#1); Glyphonycterinae (#3); Rhinophyllinae (#1); Stenoderminae: Sturnirini (#1), Stenodermatini (#19))
Superfamily Vespertilionoidea (sometimes divided into three superfamilies)
Family Natalidae (#3)

Family Molossidae (subfamilies Tomopeatinae (#1), Molossinae (#20–21))

Family Miniopteridae (#1)

Family Cistugidae (#1)

Family Vespertilionidae (subfamilies Kerivoulinae (#2); Murininae (#3): Myotinae (#3); Vespertilioninae: Vespertilionini (#15–18), Pipistrellini (#6), Nycticeiini s.l. (probably paraphyletic; #11), Antrozoini (#2–4), "Perimyotini"* (#2), Scotophilini (#1), Plecotini (#5–6), Lasiurini (#1–3), Vespertilioninae inc. sedis (#2))

* — this name is already in use (Wilson & Mittermeier, 2019), but actually have no formal description.

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