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**Phylogeographic trends within the family  
Pteropodidae**

**Bakalářská práce**

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## Abstract

Studies concerning fruit bats (Chiroptera: Pteropodidae), their classification, distribution were employed to draw up current attitude towards evolutionary history of this unique family of flying mammals. Many up-to-date forms of research work and data acquisition has led to marked reevaluation of a traditional approach in solving phylogenetic relations, biogeography and biology of populations.

The most recent studies related to phylogeny of Pteropodidae, were based mainly on various molecular data of combined mitochondrial and nuclear genes, and have substantially changed the traditional opinion to internal division and also to the position of the family among other Chiroptera. The family is now considered to be part of Yinpterochiroptera clade and subdivide into series of successive branches occupied by: *Melonycteris*, *Nyctimene*, *Eidolon* + *Pteralopex*, *Acerdon* + *Pteropus* and a more furcate major clade, which splits into two branches, one comprising all of the African genera but *Eidolon*, the other covering *Notopterus* on a single branch sister to *Dobsonia* + *Aprotes* clade. The origin of the family, its historical diffusion and theories of the colonization events were subject to some deeper studies of particular genera and species. The origin of Pteropodidae was situated to Australasia and three possible migration routes leading to Africa were described. Although there has been made a big effort to resolve complicated context of these problems, contradictory opinions of several authors indicate, that further studies are necessary and lots of questions remain to be answered.

## **Abstrakt**

Studie zabývající se kaloni (Chiroptera: Pteropodidae) jako takovými, jejich klasifikací a rozšířením byly použity pro načrtnutí současného přístupu k rekonstrukci evoluční historie této jedinečné čeledi létajících savců. Mnoho moderních forem výzkumu a získávání dat vedlo k výraznému přehodnocení tradičních přístupů k řešení fylogenetických vztahů a biogeografie. Nejnovější studie věnované fylogenezi čeledi Pteropodidae byly založeny halvně na různých molekulárních datech (zejména analýze sekvencí mitochondriálních a jaderných genů) a výrazně změnily názory na vnitřní dělení i pozici čeledi mezi ostatními z řádu Chiroptera. Čeleď je nyní považována za součást kládu Yinpterochiroptera. Skupina má na bázi pektinální topologii obsazenou rody *Melonycteris*, *Nyctimene*, *Eidolon* + *Pteralopex*, *Acerdon* + *Pteropus* a terminální klastr, který se dělí do dvou větví, jedné zahrnující všechny africké rody kromě rodu *Eidolon*, druhé obsahující rod *Notopteris* a jeho sesterskou skupinu rodů *Dobsonia* a *Aprotes*.

Původ této čeledi, její historické šíření a teorie o průběhu osídlování byly předmětem některých hlubších studií jednotlivých rodů a druhů. Vznik této skupiny byl umístěn do Australasie a byly popsány tři možné cesty, kterými mohli kaloni migrovat. Přestože bylo vynaloženo velké úsilí k rozřešení složitých souvislostí této problematiky, protichůdné názory vyskytující se v mnoha publikovaných pracích naznačují, že některé otázky nelze považovat za uzavřené a k jejich zodpovězení budou třeba další studie.

**Key words:** Pteropodidae, fruit bats, phylogeny, distribution, phylogeography, population structure

## **1. Introduction**

Bats form an extraordinary order among mammals since they evolved series of unequalled traits as are e.g. front limb with elongated fingers transformed into wing, inverted rest position with derived morphology of leg, ability of laryngeal echolocation and unique sensoric apparatus associated with nocturnal activity, ability of hibernation, etc. These salient particularities formed as a set of preadaptations, which were further diversified mainly by selection pressures connected with foraging strategies, enable bats to occupy unique niches. In this respect, bats widely radiated throughout the world and now form a second most diverse group of mammals comprising over one thousand species. Combination of gathered capabilities like powered flight, echolocation and cave-dwelling, conduces to an effective way of dispersion and is reflected in current distribution. The arrival of molecular biology and its expansion in the last decade resulted in transformation of traditional classifications, helped to resolve many phylogeographic patterns, cryptic diversities and other aspects of bats evolutionary history.

My work aims to show integrated view of the impact of new technologies on the theories relevant to phylogeny and phylogeography of the family Pteropodidae. This taxon presents many curious adaptations, connected mostly with their herbivorous diet (like loss of echolocation, excellent vision and olfaction etc.), which has led to their classification separately from other bats and proposal of a suborder consisting of this one and only family. However, molecular reconstructions has shown previous grouping as artificial and included Pteropodidae in a Yinpterochiroptera taxon. These characteristic traits have affected also their distributional patterns.

## **2. Basal characteristics of the family Pteropodidae**

The family Pteropodidae, commonly named fruit bats or flying foxes, is obviously distinct from other bats in many aspects. One of the most well-known characters is its diet, consisting of nectar, pollen or fruit, which is reflected on variety of adaptations including the dentition (longitudinal grooves in molars), oral cavity (transverse ridges in palate), increased length of digestive tubule (appendix is missing) and in some genera tongue morphology (well-developed papillae and ability to protrude). All of the members of this family have well-developed eyes with the surface area of the rods greatly increased by villiform projections, enclosing blood vessels, of the inner coat of the eyeball that penetrate the outer layer of the retina. Their advanced vision refers correspondingly to the loss of laryngeal echolocation in this taxon. The only genus *Rousettus* has evolved the echolocation ability, however the sound is emitted by tongue vibrations, which is much less sophisticated and incomparably energetically demanding.

Fundamental differences between Pteropodidae and other Chiroptera are in the nervous system modifications. Brain and spinal cord of Pteropodidae present rather modern constitution, with an extraordinary development of cerebellum and telencephalon (18% of the total brain size in Pteropodidae against 3-4% in other Chiroptera), which is generally considered as progressive trait in evolution. The latter discrepancy led to the controversial theory of Chiroptera paraphyly.

There are some more morphological characters to specify the flying foxes, e.g. except for four genera they have a claw on the second finger which all the other bats lack, the external ear is rather simple and the tragus is absent; external year of other bats is often complex and a tragus is usually present etc. (Nowak, 1999)

Depending on geographical latitude representatives of this family breed throughout the year (closer to the equator) or in well-defined breeding seasons (further from the equator). The reproduction etology covers multifarious pre-copulation rituals including acoustic, visual and olfactory effects. There is usually only one young in a birth. (Nowak, 1999; Horáček, 1986)

It is worth mentioning that fruit bats are animals of extraordinary ecological and economic importance. Nearly 200 species play an essential role as forest pollinators and seed dispersers, yet they are frequently misunderstood, intensely persecuted, and a lot of them is exceptionally vulnerable due to their limited range size and other factors. Many appear to be in severe decline, and several species are already extinct (Fujita and Tuttle, 1991, p.455).

### **3. Phylogenetics of the family Pteropodidae**

#### **3.1. Phylogenetic position of the family Pteropodidae:**

The position of Chiroptera among Mammals and its monophyly has been investigated many times by many authors using a variety of morphological, neurological, immunological, behavioural or DNA-based characters as the leading ones. Until almost the end of last century the order stayed accepted as closely related to Dermoptera, Scandentia and Primates within the Archonta supraordinal taxon (Pettigrew, 1984; Baker, 1991). The order used to be divided into two suborders – Microchiroptera and Megachiroptera – with the internal relationships of Microchiroptera slightly changing in agreement with different authors (Koopman, Simmons), Megachiroptera consisting of a single family Pteropodidae. Most of the conclusions were based on the assessment of flight apparatus and the dental characteristics.

The concept was entirely rewritten by *the paraphyletic hypothesis of bat origins* proposed in the 1980's, following primarily neuroanatomical traits and leaving microbats widely separated from megabats (Pettigrew, 1984). However, the current view gathered from analysis of vast range of molecular data, do not support such theory. According to latest phylogenetic studies the order Chiroptera is a monophyletic taxon which is divided into two groups, the Yinpterochiroptera including families Pteropodidae, Rhinolophidae, Hipposideridae, Megadermatidae, Craseonycteridae and Rhinopomatidae; and the Yangochiroptera which covers all remaining families clustered in three superfamilies Emballonuroidea, Noctilionoidea and Vespertilionoidea (Teeling et al., 2005).

Molecular studies place the order in the superordinal clade Laurasiatheria, which also includes Eulipotyphla, Carnivora, Pholidota, Cetartiodactyla and Perissodactyla. Laurasiatheria form one of the four major placentalia groups. Certain studies favour a basal split of Placentalia into Boreoplacentalia which encompasses Laurasiatheria and Archontoglires; and Notoplacentalia covering Xenarthra and Afrotheria. This Notoplacentalia/Boreoplacentalia relationship also allows for two primary hypotheses related to the early dispersal of placental mammals (Arnason et al., 2008).

The diversification of extant bats was placed at the Cretaceous-Tertiary boundary approximately 65 MYA (Eick et al., 2005), whereas the branching of Pteropodidae from other bats is estimated to occur about 58 MYA (Nikaido et al., 2000; Teeling et al., 2005). Although using similar approaches, two extensive studies have lately come to differing conclusions regarding the origin of chiropterans. From the paleontological evidence and further phylogenetic studies, the center of origin of bats was located in the Old World tropics in Africa by Eick (Eick et al., 2005). However, a geographic ancestral reconstructions made by Teeling, suggested North America as the cradle of both extinct and extant bats (Teeling et al., 2005).

The oldest found bat fossil from the Early Eocene Green River Formation of Wyoming, USA, *Onychonycteris finneyi* has been recently described, resolving the long-lasting question of echolocation and powered flight evolution pathways. By comparing the morphology of extant bats with fossil findings (*Onychonycteris*, *Icaronycteris*, *Archeopteropus*) it has been proved that the echolocation ability

evolved after flapping flight already used by *Onychonycteris*, yet without echolocation (Simmons et al., 2008).

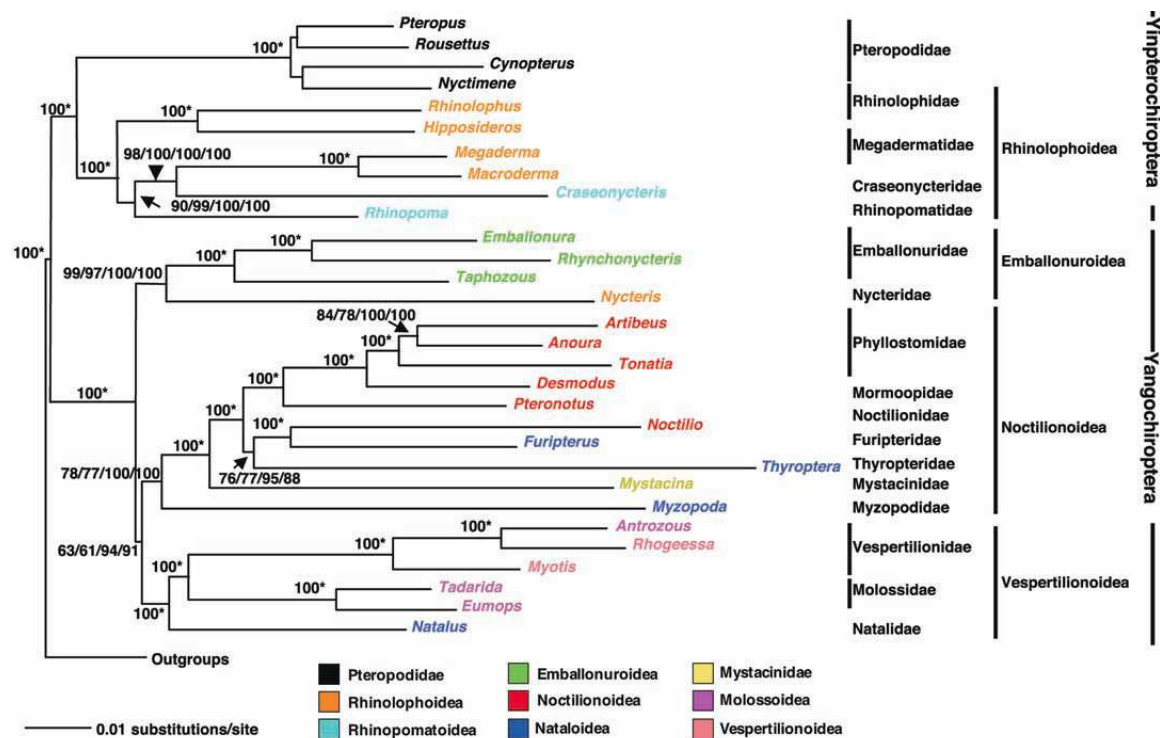


Fig. 1. The maximum likelihood tree made by Teeling (Teeling et al., 2005). Numbers at the nodes are the (ML unconstrained bootstrap values)/(ML constrained bootstrap values)/Bayesian (single model posterior probabilities shown as percentages)/Bayesian (partitioned model posterior probabilities shown as percentages). 100\* signifies clades that received 100% bootstrap support in all analyses and had posterior probabilities of 1.000. The genera are color coded according to Simmons & Geisler's higher-level classification (Simmons & Geisler, 1998).

### 3.2. Relationships among Pteropodidae:

Despite extensive studies of fruit bat phylogenetic relations, the root of its phylogeny cannot be well determined with the present data. However, there is a strong support for certain clades and groups within the taxon.

Most of the interpretations based on morphological data, fundamental to previously presented trees, have turned out to be erroneous compared with genetic analyses. Hence the division of Pteropodidae has changed thoroughly during the last decade.

While the existence of a major African clade, containing Myonictetine and Epomophorine subgroups, has been agreed by many authors, the position of biogeographically neighboring genera such as *Rousettus* and *Eonycteris* remain equivocal (Juste, 1999). Grouping of *Nyctimene* + *Melonycteris*, *Dobsonia* + *Aprotes*, *Macroglossus* + *Syconycteris*, *Acerdon* + *Pteropus*, *Cynopterus*, *Eidolon* and *Pteralopex* as single branches is well supported in many studies (Kirsh et al., 1995; Hollar and Springer, 1997; Romagnoli and Springer, 2000; Colgan and da Costa, 2002; Colgan & Flannery, 1995; Giannini & Simmons, 2003).



Similarly to the reconstruction of mammalian internal relations, the arrival of molecular biology and its expansion resulted in utter transformation of traditional classification of Pteropodidae proposed in 1912 by Andersen. It stands to reason that Andersen's work was based solely on bats morphology which many up-to-date studies discard in favour of genes. However, a comprehensive study, which took in account all previously published works, brought out a resolution, that is despite the application of molecular data partly recalling the original morphological conception.

The family has been studied with few different mitochondrial genes, e.g.: 12S rDNA (Hollar and Springer, 1997; Romagnoli and Springer, 2000; Colgan and da Costa, 2002), 16S rDNA (Juste et al., 1999; Romagnoli and Springer, 2000), tDNA-valine (Hollar and Springer, 1997; Romagnoli and Springer, 2000), cytochrome *b* (Juste et al., 1997) and a nuclear gene *c-mos* (Colgan and da Costa, 2002). All the sequences cited above were used by Giannini and Simmons in the previously mentioned study published in 2003, which is by authors considered as a first step in a larger project, which will ultimately combine gene sequence data with a comprehensive morphological data set now in preparation (Giannini and Simmons, 2003, p.498).

Genetic data support monophyly of the family and all recognized genera (Colgan & da Costa, 2002; Giannini & Simmons, 2003). Due to number of studies (Koopman, 1994; Colgan & Flannery, 1995; Kirsch et al., 1995; Springer et al., 1995; Juste et al., 1999; Teeling et al., 2005) the Pteropodidae is split into two clades, one containing species traditionally classified in the tribe Cynopterinae: cynopterines: *Cynopterus*, *Megaerops* (not including *Myonycteris*), and nyctimenes: (*Nyctimene* and *Paranyctimene*), and a second clade that contains the rest of the family (*Pteropus* branch and *Rousettus* branch). However, according to Giannini and Simmons (2003) the ramification appears to be different. In their combined analysis tree the genus *Melonycteris* was strongly indicated as a genus of the most basal branch with a series of successive branches occupied by: *Nyctimene*, *Eidolon* + *Pteralopex*, *Acerdon* + *Pteropus* and a more furcated major clade (marked A in the tree depicted below). The authors named branches of the major clade with capital letters from B to I enabling easier description.

Clade A splits into two branches, one (C) comprising all of the African genera but *Eidolon*, the other (B) covering *Notopterus* on a single branch sister to *Dobsonia* + *Aprotes* clade, which in agreement with the most recent study (Giannini et al., 2006) includes also the enigmatic genus *Harpyionycteris* (not illustrated), and a clade of cynopterines – group of Indo-Malayan genera of tube-nosed bats with affinities to *Cynopterus* (Colgan and Flannery, 1995).



Fig. 2. Strict consensus of two most parsimonious tree of 43 species in 26 genera made by Giannini & Simmons when using 5 loci: rDNA, 16S rDNA, tDNA-valine, cytochrome b, nuclear c-mos. There are two rootings indicated by arrows. Rooting 1 corresponds to the currently most supported division of Chiroptera into Yinpterochiroptera and Yangochiroptera. Rooting 2 agrees with the older taxonomy, which splits the order into suborders Megachiroptera & Microchiroptera. Bremer support values are depicted by numbers above branches. The branches marked with black cover the groups that were recovered in the semi-strict supertree based on results from individual locus analyses. Capital letters stress major clades. Species endemic to Africa are in boldface (Giannini & Simmons, 2003).

#### **4. Diversity and distribution**

The family Pteropodidae consists of 42 genera comprising approximately 173 species (further cryptic diversity is revealed using molecular markers). The estimates of extant number of species depend upon the author and species concept applied.

Currently, bats are distributed throughout the globe although they are not found in the colder parts of either hemisphere beyond the limit of tree growth. The range of fruit bats is encompassing tropical and sub-tropical Africa, Asia, Indo-Australia and Eastern Pacific as seen on the map below (fig.3). Two relatively isolated diversity hotspots are known for this group; one in rainforests in Congo basin, the second in Malay-Indonesian rainforests. All of the recognized genera with their ranges are listed in appendix A.

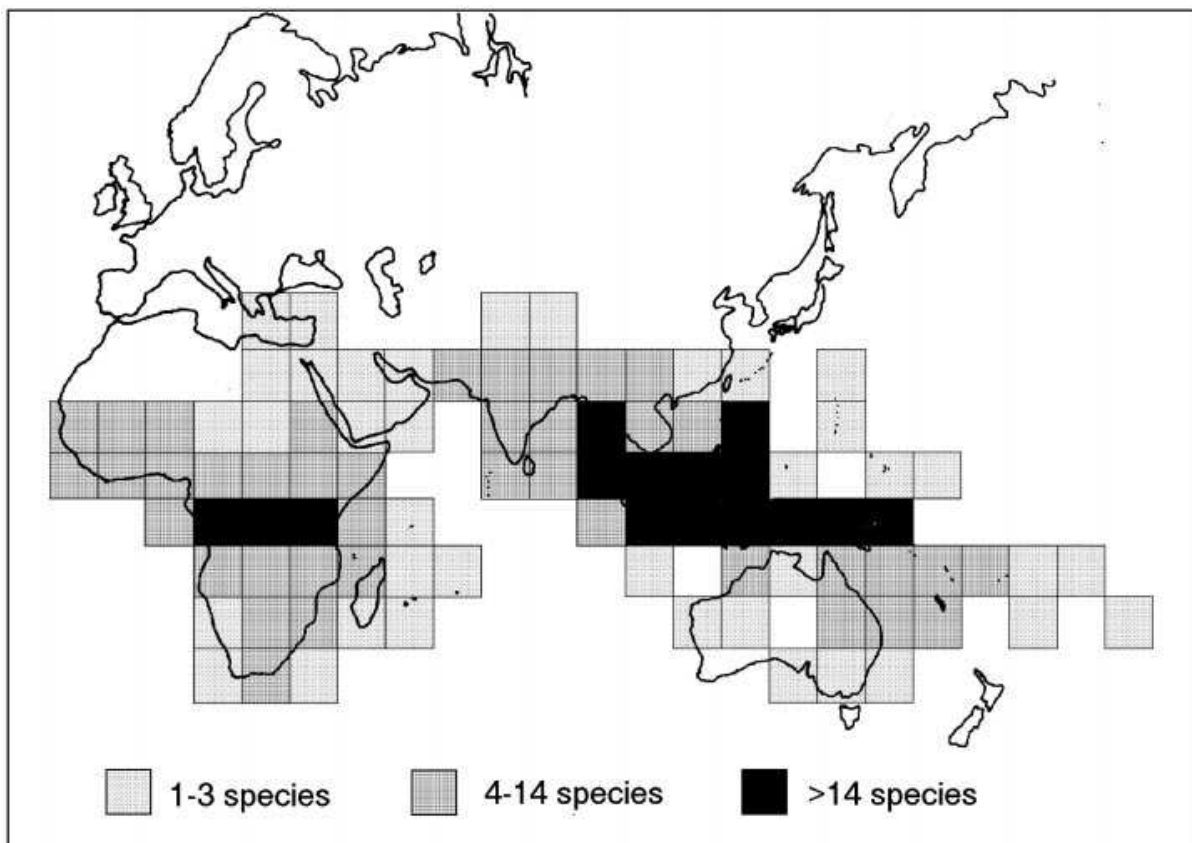


Fig.3. Map of the occurrence of the family Pteropodidae regarding species abundance. Map includes data shared for all genera included in the family Pteropodidae in a 10 x 10-degree frame according to Corbet and Hill (1992), Mickleburgh et al. (1992), Bergmans (1994, 1997), and Bates and Harrison (1997)

Due to their diet, fruit bats are somewhat irregular in their presence in a region, because they often leave areas where fruit, pollen or nectar is not available. They fly long flights between their roosting and feeding areas with the large forms capable of flying as far as 15 km to satisfy their needs (Nowak, 1999).

## **5. Phylogeography of particular lineages**

The current distribution of fruit bats has been influenced by many factors, from which historical geography and vagility of respective genera has played an important role. Studies of genetic differentiation of various species in various parts of the world, has led to some very important conclusions.

Based on a study of mtDNA sequences and scDNA hybridization, grouping of African fruit bats in a monophyletic clade was proposed by Hollar & Springer, suggesting that an ancestor of a clade, comprising genera *Megaloglossus*, *Lissonycteris* and *Epomophorus*, resided in Africa. From a phylogenetic tree, where the African clade is nested rather far from the fruit bat radiation (as also seen on Fig.2), the origin of the whole family Pteropodidae was situated within Indo-Australo-Pacific region. An ancestor of the next closest taxon to the *Epomophorus-Lissonycteris-Megaloglossus* cluster, both Africa and Asia inhabiting *Rousettus*, was considered to initiate the diversification in Africa 15 Myr ago or little bit earlier (Hollar & Springer, 1997)

In 1999 a study based on mitochondrial sequences of a wide representation of fruit bats has brought another interesting view of their origin and dispersion. The earliest fruit bat fossil record from Thailand (Ducrocq et al., 1993), the derived position of African genera and a fact, that diversity in Malay-Indonesian rainforest is higher than in African rainforest, has led the authors to locate the origin of fruit bats in Australasia (Juste et al., 1999). The idea was later supported by Giannini and Teeling, whose ancestral reconstructions showed Asia as the origin of the whole suborder Yinpterochiroptera (Giannini & Simmons, 2003; Teeling et al., 2005). There were described three routes (Fig. 4) possibly enabling the arrival to Africa: one across Europe and stepping-stone islands and/or Gibraltar bridge, one through corridors along the Arabian Peninsula and one across the Indian Ocean via stepping-stone islands. Although the colonization of Africa proceeded in three or more separate episodes, an ancestor of most of the extant African species probably came during the Neogene colliding of Africa and Asia via forest corridors through Europe and/or Arabia as also other tropical-forest dwellers did (Thomas, 1985, cited in Juste et al., 1999).

After the disappearance of forest corridors, the only echolocating (and consequently cave-roosting) genus of the family, *Rousettus*, could have dispersed thanks to his ability to survive in dry or seasonally cold habitats, which are inaccessible by typical tree dwelling species (Kirsh et al., 1995; Juste et al., 1999). The current distribution of this only genus among fruit bats, which is widely spread throughout both continents and reaches the northernmost borders of the family distribution, is accredited to these unique traits. However, the timing of its arrival to Africa has not yet been fully settled, because of the Early and Middle Miocene fossil teeth found in France and – if correctly classified as teeth of *Rousettus* – pointing to an early radiation of the genus (Aguilar et al., 1986).

The genus *Eidolon*, which stays separately from other African fruit bats (clustering rather with *Pteralopex*) in molecular phylogenetics reconstructions (Fig. 2), shows also unique morphological and physiological traits, some of which are associated with its high migratory capacity (narrow wings, delayed implantation, see e.g.

Thomas, 1983). The genus probably reached Africa separately from other fruit bats, and because of its high flight capacity, his ascendant could have used any of the above mentioned routes even earlier than other African colonizers (Juste et al., 1999). Although the colonization of Africa seems to be a well-supported theory, there are more studies concerning phylogeographic relationships necessary, to give priority to either the dispersal or the vicariance model of explanation.

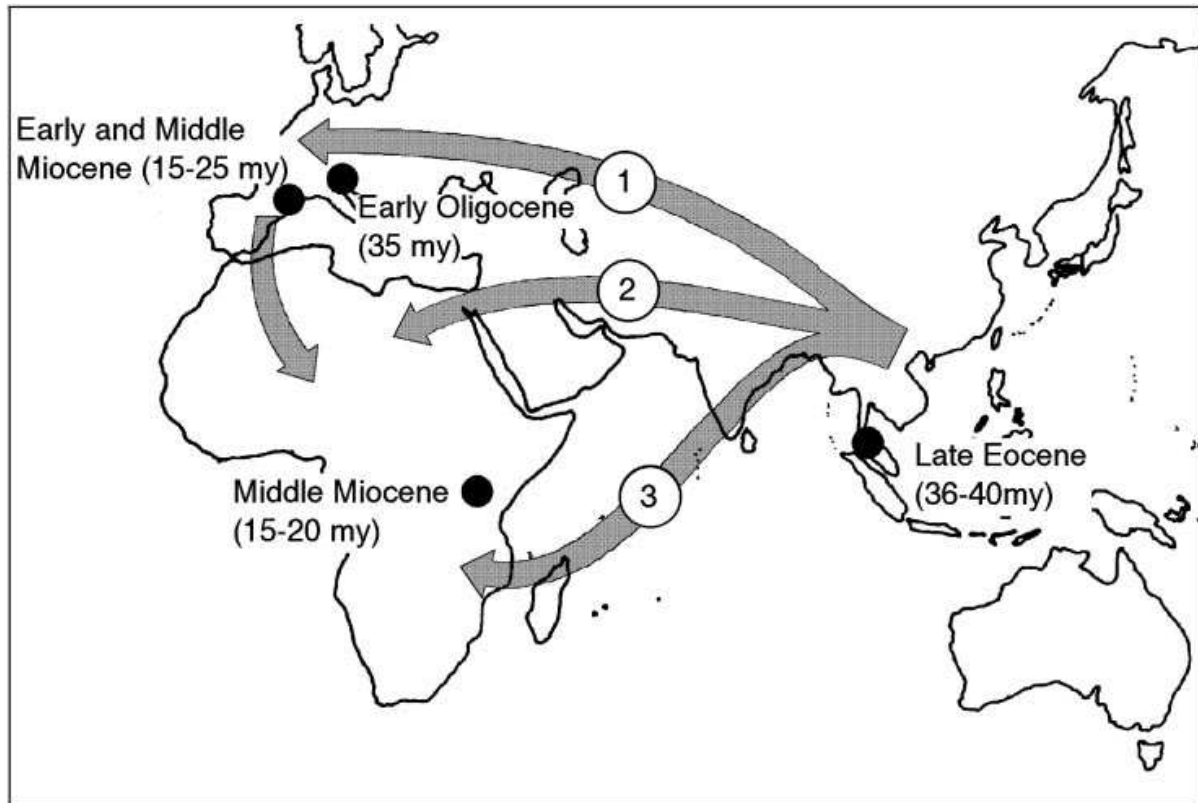


Fig.4. Fruit bat colonization of Africa. Arrows 1-3 illustrate the three alternative routes. Black dots show locations of the fossil records and estimated age of each is noted in parenthesis (Juste et al., 1999).

It has been discovered in Philippine bats of the genera *Cynopterus* and *Haplonycteris* that, aspects such as island or population size do not affect the area of their expansion much. Levels of genetic differentiation between populations of either *Cynopterus brachyotis* or *Haplonycteris fischeri* prove to be significantly correlated with degree of geographic isolation during Pleistocene periods of low sea level, vagility and consequent levels of gene flow among populations (Peterson and Heaney, 1993, p.203). Species of genus *Cynopterus* as effective dispersers are widespread in south-east Asia, ranging from Sri Lanka to Sulawesi, whereas *Haplonycteris fischeri*, the only species of the genus *Haplonycteris* is restricted to Philippines as one of four endemic genera (Peterson and Heaney, 1993). In 2004 an extensive research focused on the phylogenetic relationships within the genus *Cynopterus* has led to identification of three times more species than previously believed. Used genetic analysis has shown *Cynopterus brachyotis* as a complex of geographically localized lineages instead of a single species. Clades of the other two phenotypically distinct species, *Cynopterus horsfieldi* and *Cynopterus sphinx*, already known by that time, nested within these new subclades of *Cynopterus*

*brachyotis* complex (Fig. 6) (Campbell et al., 2004). Further phylogenetic study from the island of Sulawesi has reported a single lineage of *Cynopterus brachyotis* (Fig.5) in the area, condemning multiple colonization theory. The Sunda shelf was suggested a center of origin of given lineage of *Cynopterus*, however, the dispersal routes remain unresolved. Campbell has proposed the Borneo-Sulawesi route, which is assumed to be possible occasionally during a long period of time (ca. 5.2 MYA – ca. 18000 years ago) due to glacial cycles leading to the rising and dropping of sea level (Campbell, 2007a).

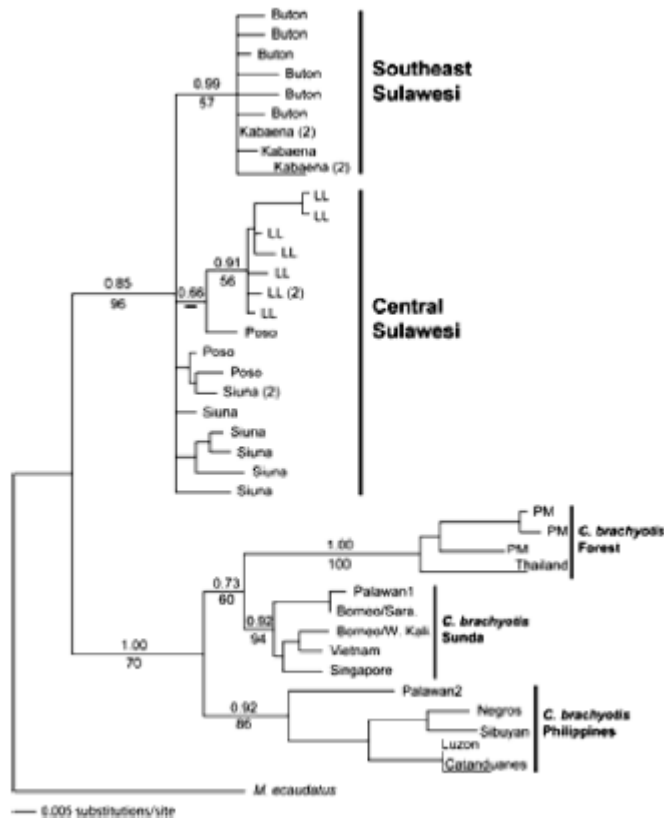


Fig. 5. "Phylogram representing the consensus trees found using 2,000,000 generations of MCMC sampling in MRBAYES (Huelsenbeck and Ronquist, 2001, cited in Campbell et al., 2007, p.478) for *Cynopterus brachyotis* under a GTR + C + I model of nucleotide substitution with parameters estimated during the course of the run. Numbers above branches supporting main clades are posterior probabilities; numbers below branches are parsimony bootstrap values based on 100 bootstrap replicates, each with five replicates of random taxon addition, a full heuristic search and TBR branch-swapping. Tip labels correspond to sampling localities, LL, Lore Lindu; TT, Tana Toraja; PM, peninsular Malaysia; Sara, Sarawak; W. Kali, West Kalimantan; numbers in parentheses denote number of haplotypes. The tree is rooted with *Megaerops ecaudatus* (AY629151). Genbank Accession Nos. for Philippine, Sunda and Forest *C. brachyotis* lineages are: AY629024, AY6290047, AY629049, AY629051, AY629066, AY629090, AY629093, AY629099, AY629100, AY629104, AY629105 (Campbell et al., 2004), and AY974394, AY974429, AY974450 (Campbell et al., 2006)." (Campbell et al., 2007a, p.478)



colonization simultaneously illustrating the directions of distribution throughout an Indonesian archipelago (Fig. 7). A contrary relationship occurs between genetic differentiation and colonization history shown on the islands. The expansion of *Eonycteris spepaea* is clearly eastward (Fig. 7, 8) as many other studied bats, e.g. *Cynophs nusatenggara* (Schmitt, Kitchener & How, 1995), *Rhinolophus afiis* (Maharadatunkamsi, 1991, cited by Hisheh et al., 1998, p.341) and *Macroglossus minimus* (Suyanto, 1994, cited by Hisheh et al., 1998, p.341), which demonstrates a decline in heterozygosity towards the east (Hisheh et al., 1998).

Both studies mentioned above (Peterson and Heaney, 1993; Hisheh et al., 1998) prove that genetic distance between populations reflects geographic relationships, especially historical connectedness, as measured by Pleistocene sea-crossing distances. Genetic data from the islands connected in the past were much more continuous than data from islands historically isolated although presently close to each other. The more differentiated and less variable genetic information is present, the more recent colonization took place.



Fig. 7. Map of the Indonesian archipelago surveyed by Hisheh et al. in 1998

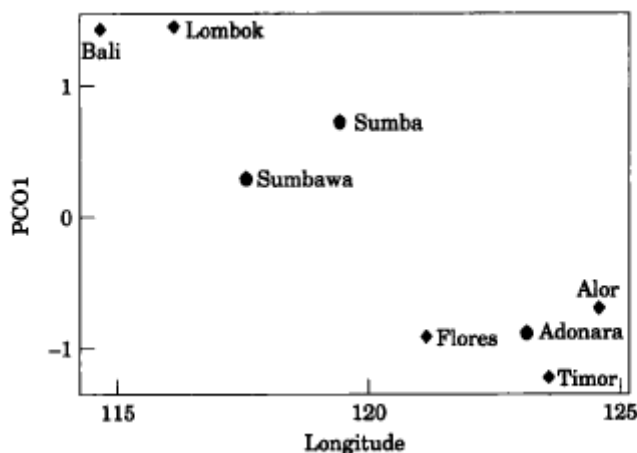


Fig.8. "First principal coordinate (PCO1) versus longitude of eight island populations of *E. spelaea*." (Hisheh et al., 1998, pp.339)



In Australia, genetic variation of three species of the genus *Pteropus* (*Pteropus alecto*, *Pteropus poliocephalus*, *Pteropus scapulatus*) was examined by Webb and Tidemann (1996) mainly to find out more details about their movements and subsequently design sophisticated conservation methods. The values of among population genetic variation turned out to be much closer to those of birds, rather than other mammals, reflecting effective panmixia. Although high degree of gene flow and mobility of the taxon has been recorded, the presented data reflect the conditions of the past, not a current situation, which might be worse concerning fruit bats.

## **6. Social organization**

Since the recent phylogeographic patterns reflect particular historical demographies connected with rules of Mendelian inheritance, the analysis of reproductive systems of recent species may help to uncover factors that have led to recent distributions.

Several different ways of population organising among bats of the family were described. In the tropics, where roosting sites reach nearly unlimited quantity, a harem social organization often prevails. Such harem is usually formed by one adult male and a group of adult females with their dependent young. The members of a harem are well scent marked by their male who uses olfactory cues to defend his resource (Hodgkison et al., 2003; Horáček, 1986). Each male guards its territory by strong vocal signalization. Not all of the males possess their own harem and those roost separately. This type of arrangement has been found in many African genera, e.g. *Casinycteris*, *Micropteropus*, *Nanonycteris*, *Epomophorus*, *Epomops*, *Hyposignathus*, *Scotonycteris* or *Pteropus*. Some of them show derived physical adaptations for better vocal intensity (*Hyposignathus*) or stronger scent production with marked tufts of hair on the shoulders (*Epomophorus*) allowing them to occupy higher positions in population hierarchy.

Few genera have evolved an ability to build their own shelters out of foliage and other parts of a forest (*Cynopterus*, *Dobsonia*) (Bonaccorso et al., 2002; Nowak, 1999; Storz et al., 2000).

Also cave-dwelling genera, which occupy a common roost, keep certain position in a cluster of individuals (Horáček, 1986).

Genetic tools, namely those which enable individual identification and surveys of parentage (microsatellite genotyping), have provided a lot of new information in uncovering of social organizations in animals. However, since the development of respective technologies is quite recent, the covering of the subject in fruit bats could not be rated as comprehensive. This situation is not suitable for performing formalized comparative study of genetic aspects of different social systems in fruit bats, but rather a survey of case studies.

Although a sets of suitable microsatellite loci were developed for several species in last decade (Andrianaivoarivelo (2008); Fox (2007), Hua (2006); Shao (2008); Storz (2001)), not all of them were used in population genetics studies published to date.

A detailed study using microsatellite genotypes of a natural population of *Cynopterus sphinx* tested a hypothesis, that polygyny inferred from harem-forming behaviour results in a reduced effective population size ( $N_e$ ) in an age-structured population.

By directly and indirectly analysed paternity during two consecutive breeding periods variance in reproductive success, by which  $N_e$  is primarily determined, was assessed. Demographic and genetic data were then used in a mathematical model to resolve the dependence of  $N_e/N$  (where  $N$  is an adult census number) on mating success (Storz et al., 2001). Markedly high within-season variance in reproductive success of males had been predicted according to polygynous society (Storz et al., 2000) and corresponding results were obtained. However, although relatively low, the  $N_e/N$  ratio stayed less influenced due to extensive overlap of generations of the genus caused by short sexual maturation period in proportion to adult lifetime. Such conclusion might be applied to most of the Pteropodidae as they meet the above mentioned conditions (Storz et al., 2001).

Relations among harem size, male roost fidelity, distribution of potential roosts and male-female association were described in two lineages (Campbell et al., 2004) of *Cynopterus brachyotis* in Malaysia by Campbell (2006). The two lineages (*Cynopterus brachyotis* Sunda, *Cynopterus brachyotis* Forest), which differ in habitat type has shown even more disparities in their social lives. *Cynopterus brachyotis* Forest females grouped in smaller numbers, their association with males was stronger than between each other and their conspecific males displayed lower roost fidelity. In comparison, *Cynopterus brachyotis* Sunda females grouped in bigger numbers, their association between each other exceeded male-female ones and their conspecific males displayed higher roost fidelity.

Presented results demonstrated a positive relation between accumulation of females and high roost fidelity of males in areas with clustered resources whereas in areas rich in roosts, the ability of males to form a harem seemed to be dependent on wheather females accompany them when they move or not (Campbell et al., 2006).

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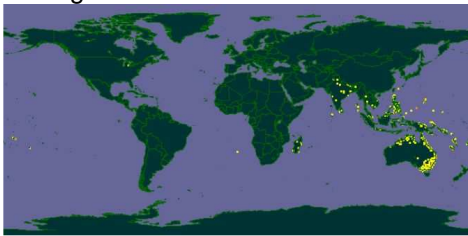

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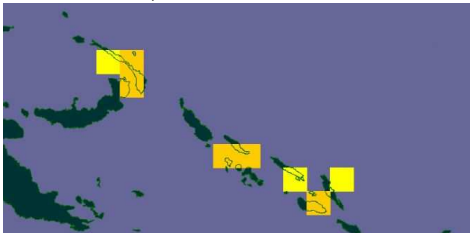
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## Apendix A






A table of all recognized genera with their ranges. The higher-level classification is taken from Bermans (1997), the most recent formal classification of Pteropodidae. However, lacking application of cladistic principles and no relationships among suprageneric groups shown here led to visible dicrepancy between the view of Bergmans and the results of molecular genetics.

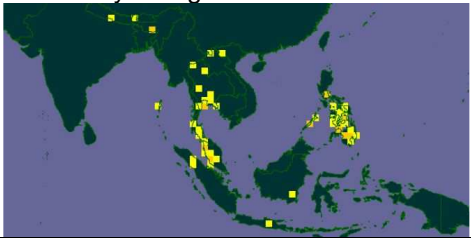

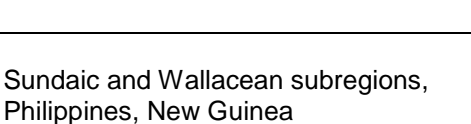



The maps of occurance of each genus are taken from the Encyclopedia of life (EOL) available online. A probability distribution using the Envelope Score Algorithm is generated by openModeller. Biodiversity occurrence data provided by: Louisiana State University Museum of Natural Science, Museum of Comparative Zoology, Harvard University, Michigan State University Museum, Museum of Texas Tech University (TTU), San Diego Natural History Museum, Royal Ontario Museum, NLBIF, Sternberg Museum of Natural History, University of Tennessee - Chattanooga (UTC), UNIBIO, IBUNAM, University of Nebraska State Museum, SysTax, University of Minnesota Bell Museum of Natural History, University of Colorado Museum of Natural History, University of Alberta, GBIF-Sweden, Arctos, Humboldt-Universität Berlin, Senckenberg, Bernice Pauahi Bishop Museum, BeBIF Provider, University of Washington Burke Museum, Cornell University Museum of Vertebrates, California Academy of Sciences, Field Museum, GBIF-Spain, Los Angeles County Museum of Natural History, Yale University Peabody Museum, Finnish Museum of Natural History (Accessed through GBIF Data Portal, www.gbif.net, 2009-04-21).


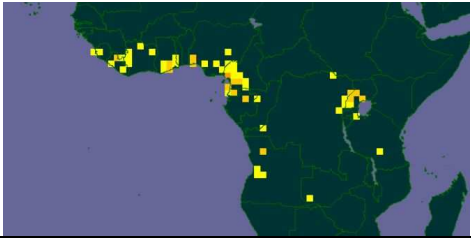




Subfamily	Tribe	Genus	Area
Pteropodinae	Pteropodini	<i>Pteropus</i>	Middle E Asia to E Pacific, Australia, Madagascar 
		<i>Acerdon</i>	Sundaic and Wallacean subregions, Philippines 



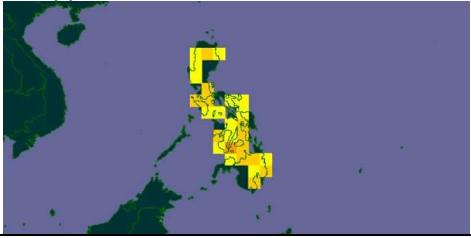


		<i>Pteralopex</i>	New Guinea, E Pacific 
		<i>Styloctenium</i>	Sulawesi 
		<i>Neopteryx</i>	Sulawesi 
	Macroglossini	<i>Macroglossus</i>	Indian and Indochinese subregions, New Guinea, Australia 
		<i>Syconycteris</i>	Sundaic and Wallacean subregions, New Guinea, Australia 
	Notopterini	<i>Notopteryx</i>	E Pacific 
		<i>Melonycteris</i>	New Guinea, E Pacific 












		<i>Nesonycteris</i>	E Pacific 
Nyctimeninae		<i>Nyctimene</i>	Wallacean subregion, Philippines, New Guinea, Australia 
		<i>Paranyctimene</i>	New Guinea 
Harpyionycterinae		<i>Harpyionycteris</i>	Sundaic and Wallacean subregions, Philippines 
Rousettinae	Rousettini	<i>Rousettus</i>	Africa, Madagascar, Middle E Asia, Indomalayan region, E Pacific 

		<i>Eonycteris</i>	Indomalayan region 
		<i>Eidolon</i>	S Arabia, Africa, Madagascar 
	Dobsoniini	<i>Aproteles</i>	New Guinea 
		<i>Dobsonia</i>	Sundaic and Wallacean subregions, Philippines, New Guinea 
Epomophorinae	Epomophorini	<i>Epomophorus</i>	Africa 
		<i>Micropteropus</i>	Africa 

		<i>Hypsignathus</i>	Africa 
		<i>Epomops</i>	Africa 
		<i>Nanonycteris</i>	Africa 
	Myonycterini	<i>Myonycteris</i>	Africa 
		<i>Lissonycteris</i>	Africa 
		<i>Megaloglossus</i>	Africa 

	Scotonycterini	<i>Scotonycteris</i>	Africa 
		<i>Casinycteris</i>	Africa
	Plerotini	<i>Plerotes</i>	Africa
Cynopterinae		<i>Cynopterus</i>	Indomalayan region 
		<i>Ptenochirus</i>	Philippines 
		<i>Megaerops</i>	Indian and Indochinese subregions, Sundaic subregion, Philippines 
		<i>Dyacopterus</i>	Indochinese and Sundaic subregions, Philippines 

		<i>Balionycteris</i>	Indochinese subregion 
		<i>Chironax</i>	Indochinese, Sundaic, and Wallacean subregions 
		<i>Thoopterus</i>	Sulawesi 
		<i>Sphaerias</i>	Indian and Indochinese subregions 
		<i>Aethalops</i>	Sundaic subregion 

		<i>Penthetor</i>	Sundaic subregion 
		<i>Latidens</i>	India 
		<i>Alionycteris</i>	Philippines 
		<i>Otopteropus</i>	Philippines 
		<i>Haplonycteris</i>	Philippines 