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Molecules, morphometrics and new fossils provide an integrated view of the evolutionary history of Rhinopomatidae (Mammalia: Chiroptera)

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Abstract

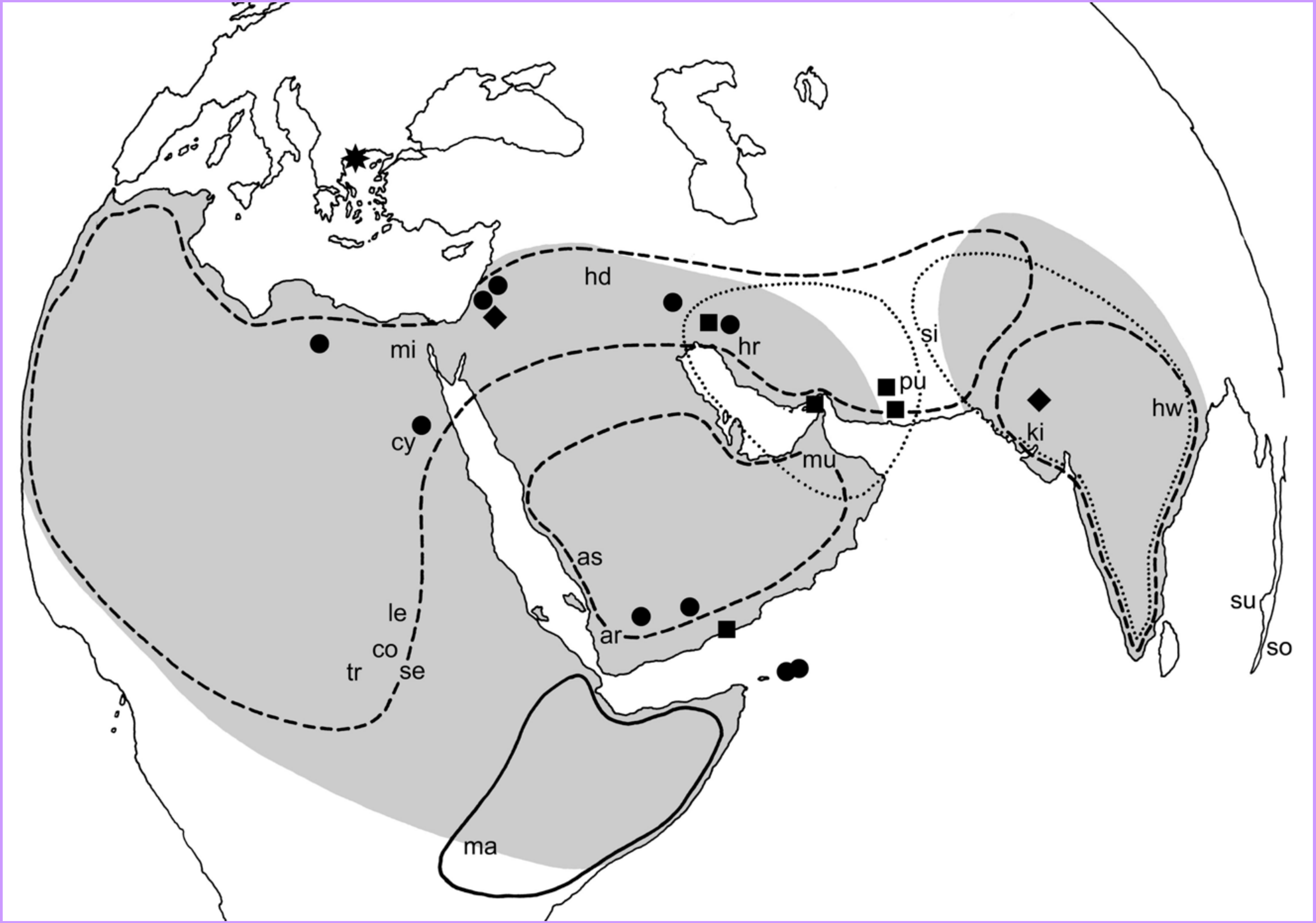
Background: The Rhinopomatidae, traditionally considered to be one of the most ancient chiropteran clades, remains one of the least known groups of Rhinolophoidea. No relevant fossil record is available for this family. Whereas there have been extensive radiations in related families Rhinolophidae and Hipposideridae, there are only a few species in the Rhinopomatidae and their phylogenetic relationship and status are not fully understood.

Results: Here we present (a) a phylogenetic analysis based on a partial cytochrome *b* sequence, (b) new fossils from the Upper Miocene site Elaiochoria 2 (Chalkidiki, Greece), which represents the first appearance datum of the family based on the fossil record, and (c) discussion of the phylogeographic patterns in both molecular and morphological traits. We found deep divergences in the *Rhinopoma hardwickii* lineage, suggesting that the allopatric populations in (i) Iran and (ii) North Africa and the Middle East should have separate species status. The latter species (*R. cystops*) exhibits a shallow pattern of isolation by distance (separating the Middle East and the African populations) that contrasts with the pattern of geographic variation in the morphometrical traits. A deep genetic gap was also found in *Rhinopoma muscatellum* (Iran vs. Yemen). We found only minute genetic distance between *R. microphyllum* from the Levant and India, which fails to support the sub/species distinctness of the Indian form (*R. microphyllum kinneari*).

Conclusion: The mtDNA survey provided phylogenetic tree of the family Rhinopomatidae for the first time and revealed an unexpected diversification of the group both within *R. hardwickii* and *R. muscatellum* morphospecies. The paleobiogeographic scenario compiled in respect to molecular clock data suggests that the family originated in the region south of the Eocene Western Tethyan seaway or in India, and extended its range during the Early Miocene. The fossil record suggests a Miocene spread into the Mediterranean region, followed by a post-Miocene retreat. Morphological analysis compared with genetic data indicates considerable phenotypic plasticity in this group.

Background

The mammalian order Chiroptera serves as an excellent example of how molecular phylogenetics has influenced the taxonomy of a seemingly well resolved group. Genetic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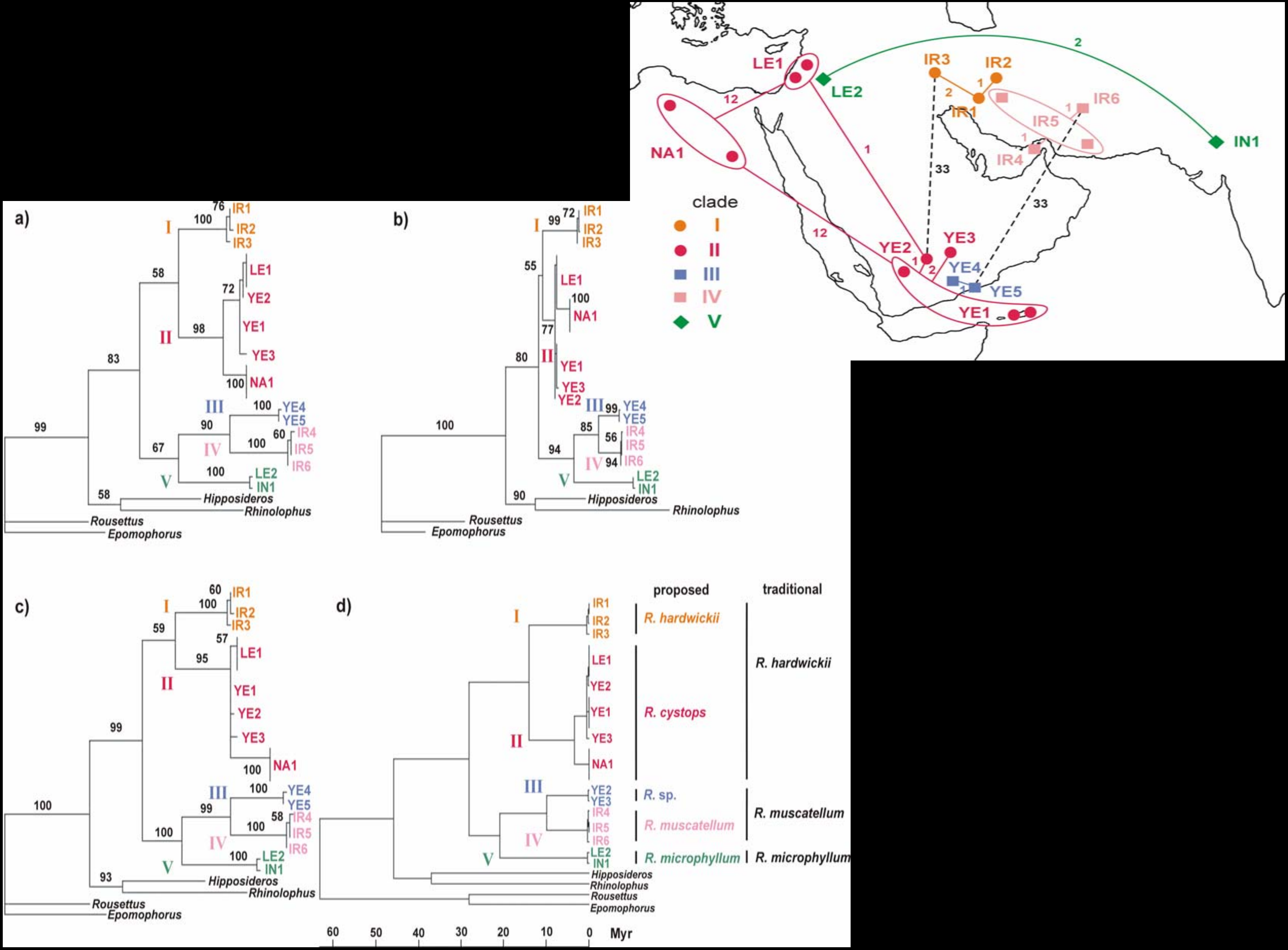
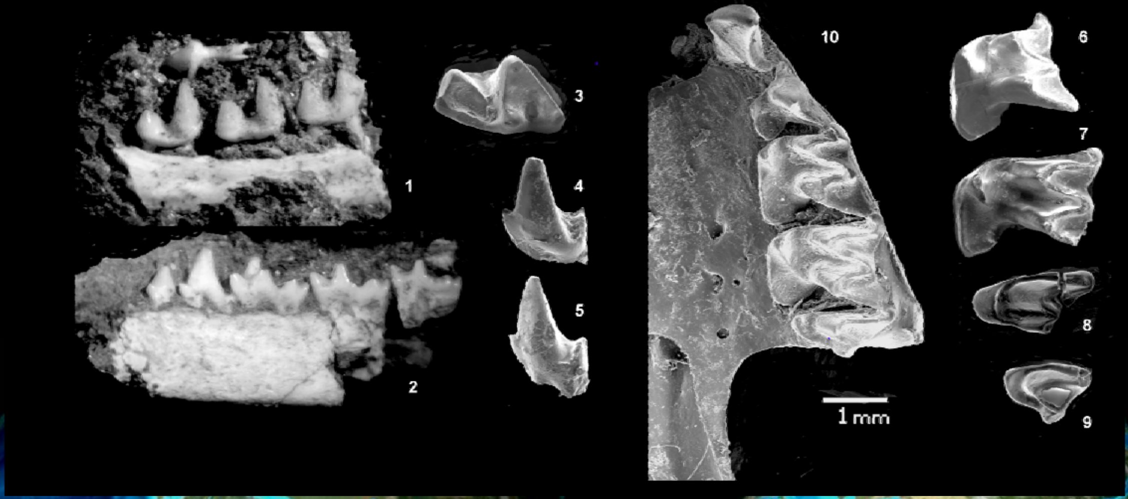
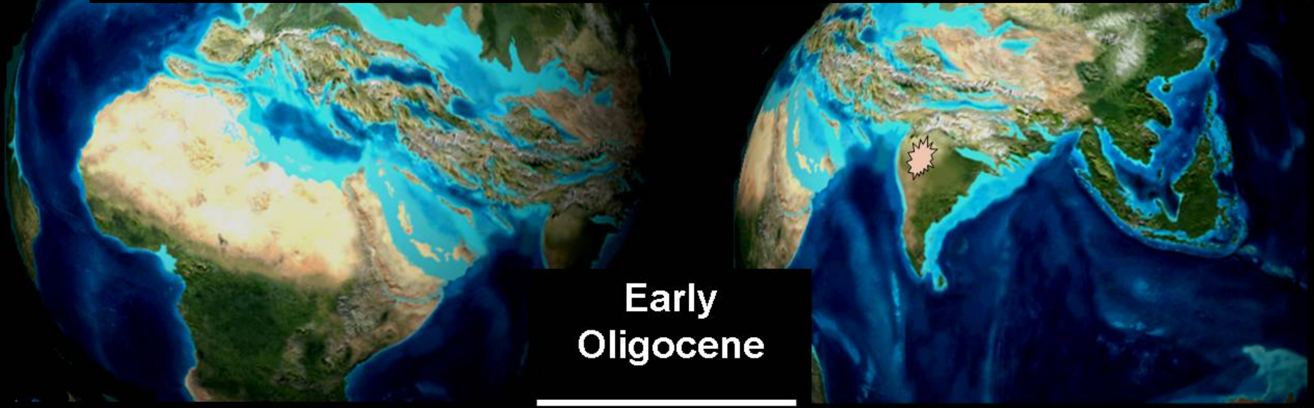


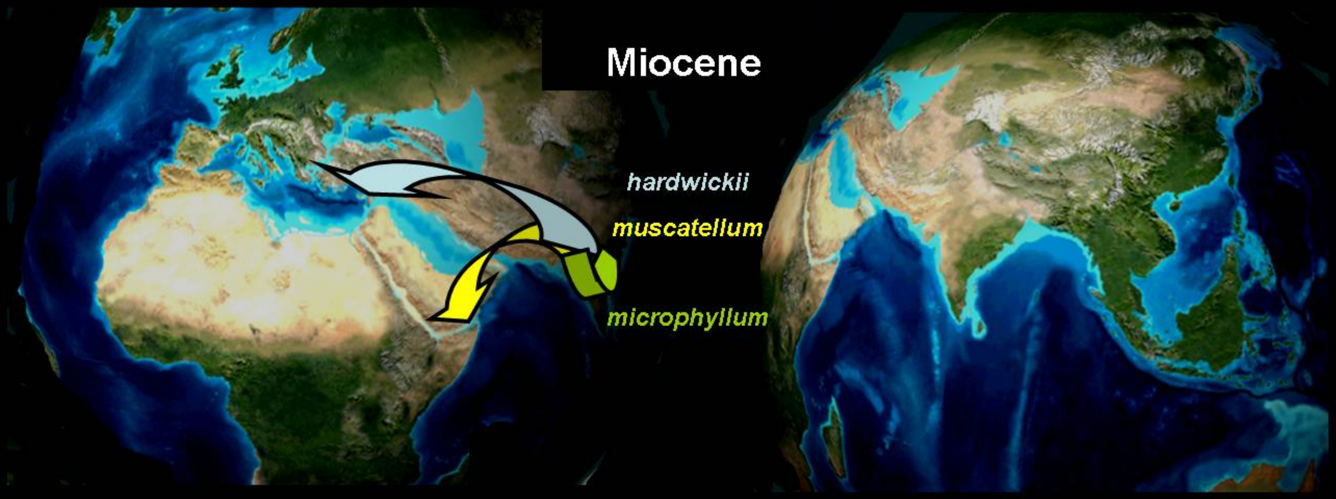
a)
b)
c)
d)
I
II
III
IV
V
IR1
IR2
IR3
IR4
IR5
IR6
LE1
LE2
YE1
YE2
YE3
YE4
YE5
NA1
IN1
Hipposideros
Rhinolophus
Rousettus
Epomophorus
proposed
traditional
R. hardwickii
R. cystops
R. sp.
R. muscatellum
R. microphyllum
60
50
40
30
20
10
0
Myr
clade





Early Oligocene

Miocene



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New mitochondrial lineages within the *Pipistrellus pipistrellus* complex from Mediterranean Europe

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Abstract. In this study we are adding further information to phylogeography of *Pipistrellus pipistrellus* complex by discovery of isolated mitochondrial lineages in Europe, from the island of Crete (Greece) and central Mediterranean (Sicily, Corsica) and by adding new data about geographic distribution of clades within the complex. We performed phylogeographic study with aid of partial sequence of cytochrome *b* and with focus to the radiation centre of this group in the Mediterranean Basin. Within the clade *P. pygmaeus* s.l., we have discovered isolated lineage from Crete, which is sister taxon to *P. hanaki* from Libya. We have detected the occurrence of *P. pygmaeus* s.str. in northern Iran. In the clade *P. pipistrellus* s.l. we have discovered isolated cluster represented by populations from Sicily and Corsica, with phylogenetic relation to Moroccan lineage. This is a first evidence of separated phylogroup within the complex from central Mediterranean. We refer the occurrence of *P. pipistrellus* s.str. from the island of Cyprus. These data represent further arguments for importance of the Mediterranean region in phylogeny of the *P. pipistrellus* species complex. Proposed allopatric speciation scenario considers the role of environmental fragmentation during the Messinian Salinity Crisis, strengthen by preference of mountain habitats in Mediterranean populations. The species status of Cretan and central Mediterraenan forms is also discussed.

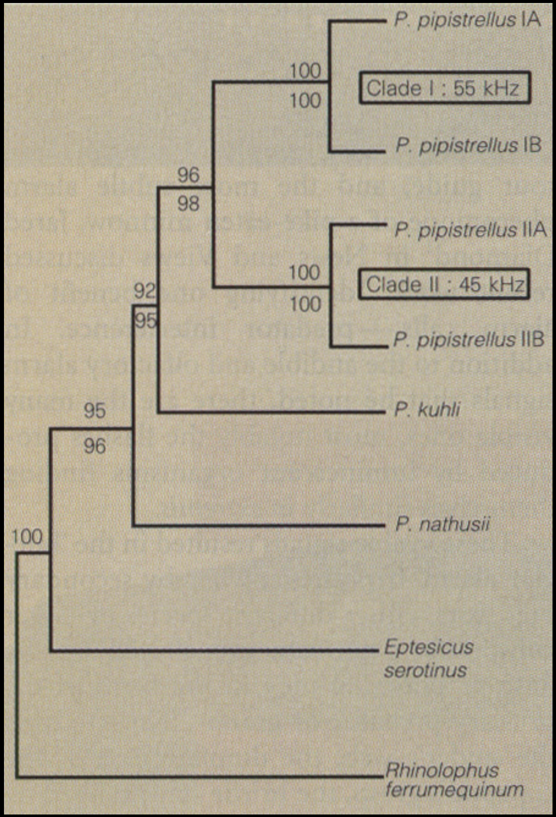
Key words: *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, Crete, Sicily, Corsica, Mediterranean, molecular phylogenetics, cytochrome b, cryptic species

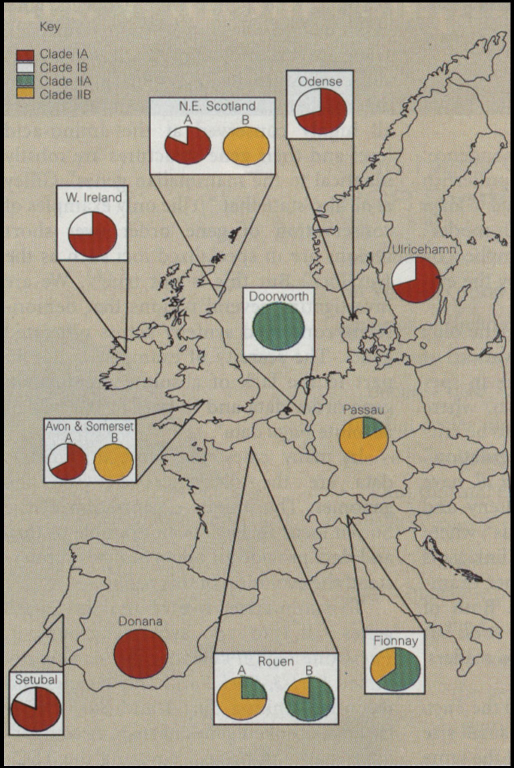
Introduction

Unique characters of molecular markers compared to traditionally studied phenotypes enabled many new insights into biology of many widespread and well known species. In a model bat species, the common pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774), the species status of two phonic types (Ahlén 1981, Miller & Degn 1981, Weid & von Helversen 1987, Zingg 1990) was confirmed by an application of molecular markers (Barrat et al. 1995, 1997, Mayer & von Helversen 2001a,b, Benda et al. 2003, Hulva et al. 2004, Racey et al. 2007, Mayer et al. 2007): *P. pipistrellus* s.str. and *P. pygmaeus* (Leach, 1825). This division was supported by behavioural (Jones & van Parijs 1993, Barlow & Jones 1997, Park et al. 1996) data and despite the fact that pronounced morphological differences were not discovered (Barlow et al. 1997, Sendor et al. 2002), other analyses reported minor or nonmetric discrimination traits (Häussler et al. 2000, von Helversen & Holderied 2003).

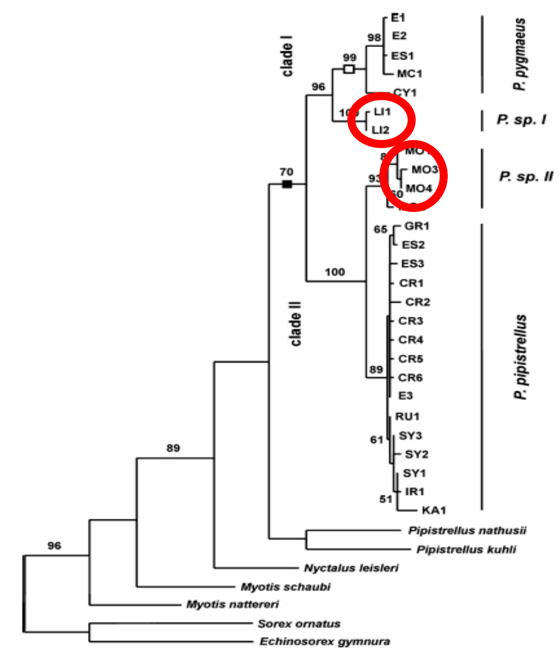
Many recent studies have shown that sampling representing whole range is necessary to reconstruct phylogeography properly (see e.g. Eggert et al. 2002). The data from a large

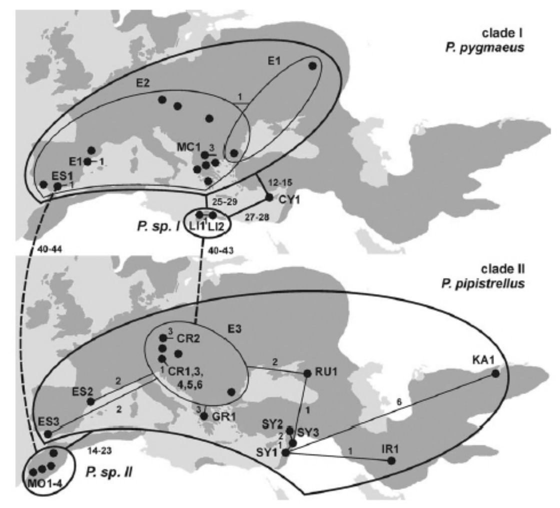
molecular phylogenetics and phylogeography





Barrat et al. 1997, 630 bp cytochrome *b*

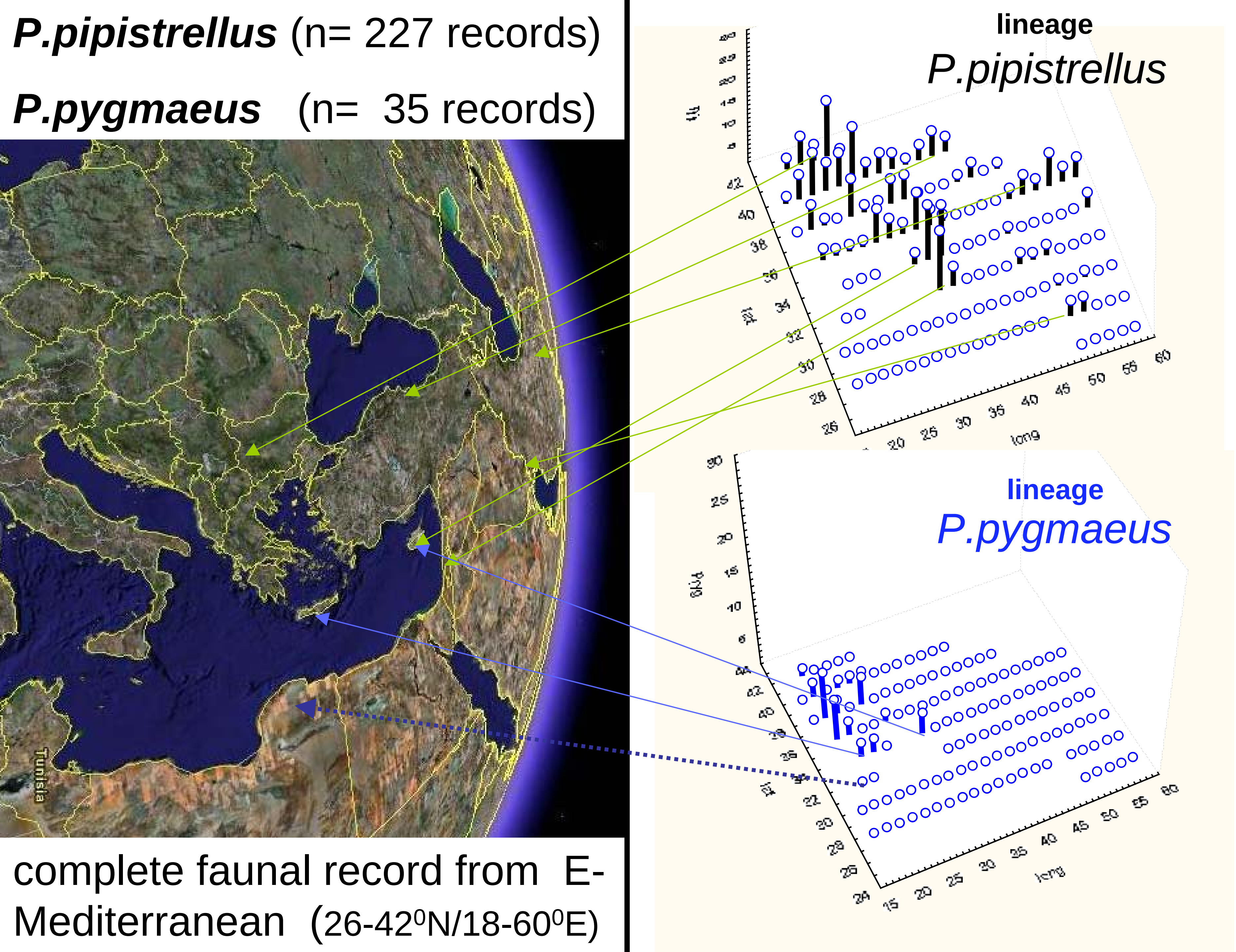




Hulva et al. 2004, 402 bp cytochrome *b*

P.pipistrellus (n= 227 records)

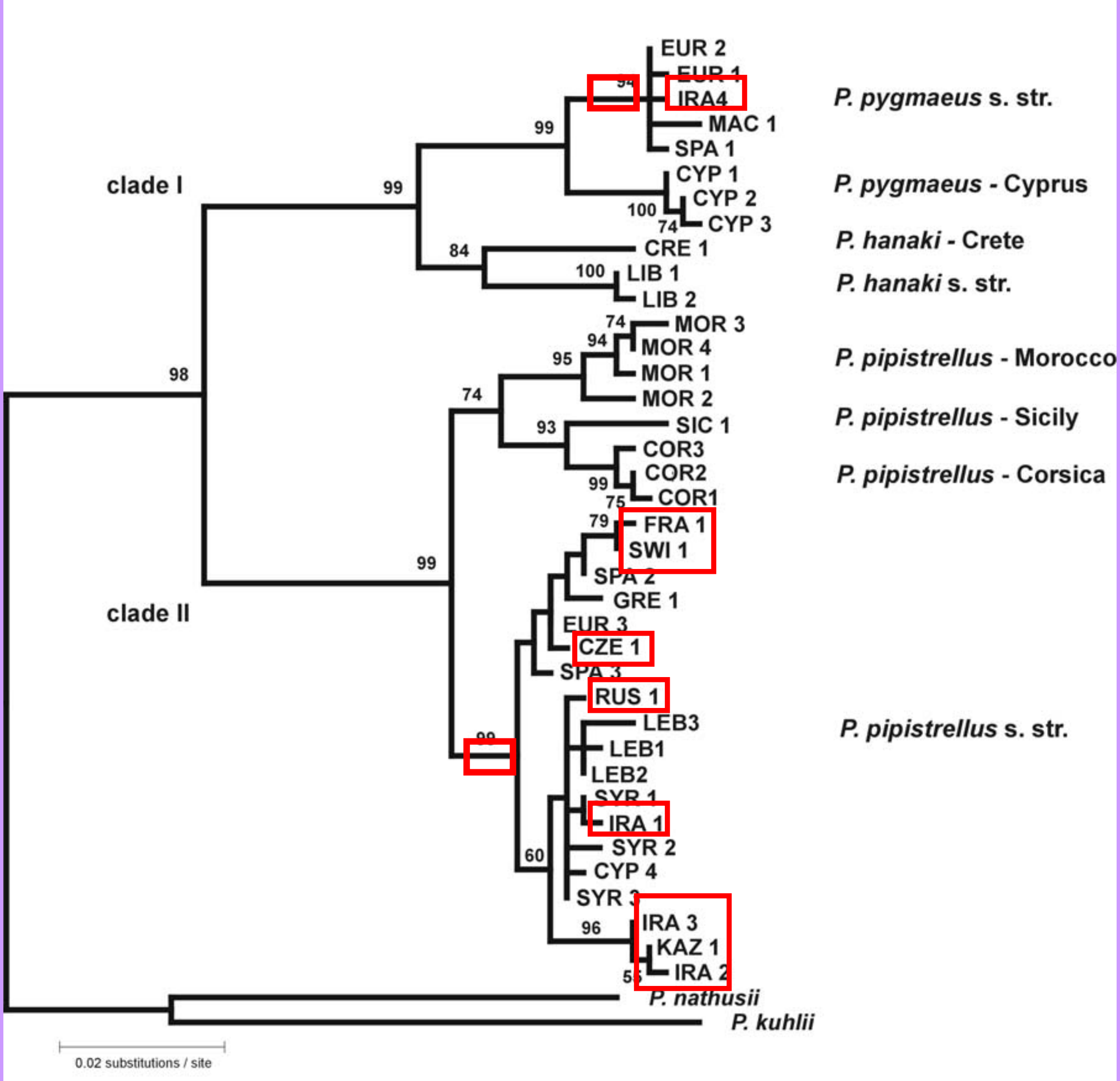
P.pygmaeus (n= 35 records)



complete faunal record from E-Mediterranean (26-42^{0}N/18-60^{0}E)

Hypotheses based on mtDNA

support of mediterranean origin of the complex



conclusions

- three mediterranean subcentres
- western and eastern colonization route