Rates of Species Diversification of Bats (Chiroptera) Compared with Paleobiotic and Paleoevironmental Variables

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Introduction

Current evidence suggests that the transition from stem to crown bats occurred near the Early Eocene Climatic Optimum (EECO) ~53-49 Ma, which saw a dramatic increase in temperatures globally. To test whether this transition to crown bats occurred in either direct relationship to the EECO, or as a result of it, we improved the occurrence dates of the bat fossil record and compared diversification rates through time with global surface temperature and various other biotic and abiotic variables to isolate the factors that influenced this transition.

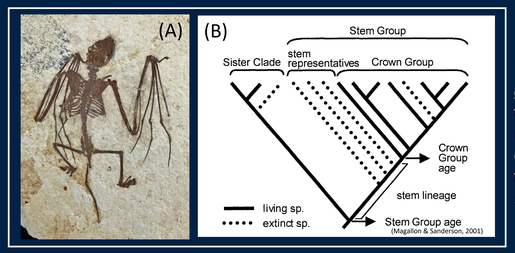

Figure 1. (A) *Icaronycteris gunnelli,* a fossil bat belonging to stem Chiroptera. **(B)** The relationship between stem and crown groups; figure modified from Magallon & Sanderson, 2001.

Methods

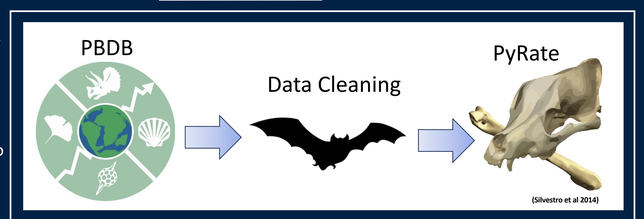

Figure 2. Workflow from fossil occurrence acquisition using the Paleobiology Database (PBDB) to data generation using PyRate.

1) Downloaded 1,565 fossil bat occurrences from PBDB.

2) Age intervals > 5 Ma for fossils of the genus/species taxonomic rank were refined using the most up to date literature about the fossil localities.

3) The diversification dynamics of all modified occurrences were analyzed using PyRate.

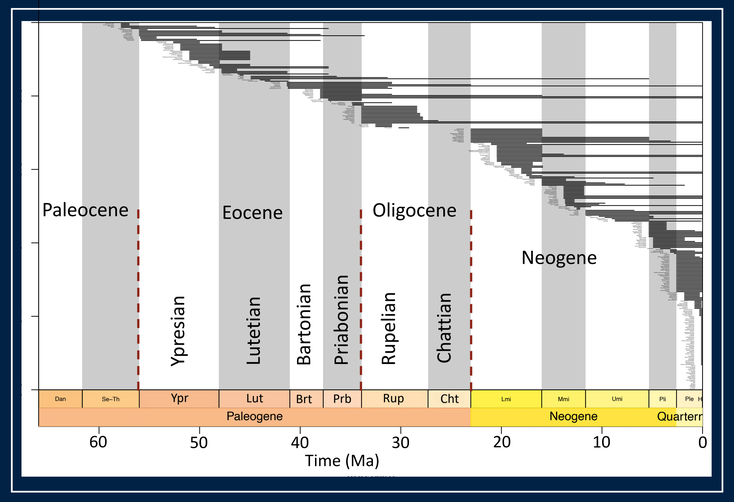

Figure 3. Stratigraphic age intervals for all known bat fossil taxa within the PBDB.

Our modifications resulted in 205 fossil occurrences being constrained by 76.6% on average, with 42% of those updates resulting in < 1 Ma age intervals.

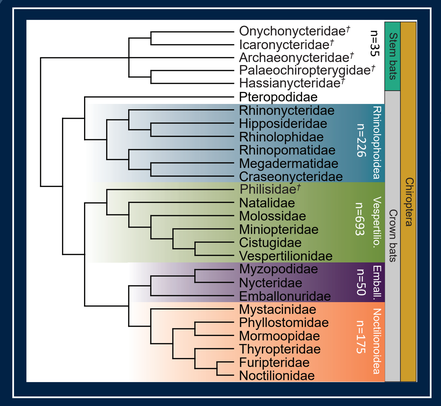

Figure 4. Family-level bat phylogeny after Amador et al. (2018) and Rietbergen et al. (2023). Numbers correspond to the count of PBDB occurrences belonging to the fossil group and used in this study. † symbols represent extinct lineages. Colored boxes represent living bat families, excluding Pteropodidae.

Vespertilio. = Vespertilionoidea; Emball. = Emballonuroidea

Table 1. Paleobiotic and paleoenviromental correlates used in the multivariate birth-death analysis in figure 6. The data extracted from the paleobiology database column is novel. The other correlates were extracted from previous studies and downloaded through PyRate. The variables chosen are informed by modern and known deep-time interactions.

Variable	Type	Source
Bat fossil Occurrences	Biotic	Paleobiology Database
Strigiformes (Owls) diversity	Biotic	Paleobiology Database
Caprimulgiformes (Night Jar) diversity	Biotic	Paleobiology Database
Insecta (Insects) genus diversity	Biotic	Paleobiology Database
Angiosperm (Flowering plants) diversity	Biotic	Lehtonen et. al. 2017
Magmatism	Abiotic	Lehtonen et. al. 2017
Mountain	Abiotic	Lehtonen et. al. 2017
Continental Fragmentation	Abiotic	Lehtonen et. al. 2017
Sea Level	Abiotic	Lehtonen et. al. 2017
Global Mean Temperature	Abiotic	Lehtonen et. al. 2017
Tropical Biome Extent	Abiotic	Lehtonen et. al. 2017
Temperate Biome Extent	Abiotic	Lehtonen et. al. 2017
Arid Biome Extent	Abiotic	Lehtonen et. al. 2017

Results

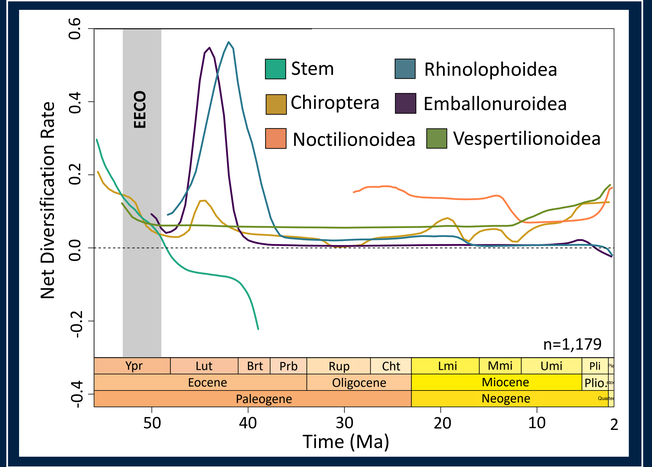

Figure 5. Diversification rates through time for bat fossil taxa on the Order and Superfamily taxonomic levels using Birth-Death MCMC. The time frame of the EECO is denoted by the grey bar.

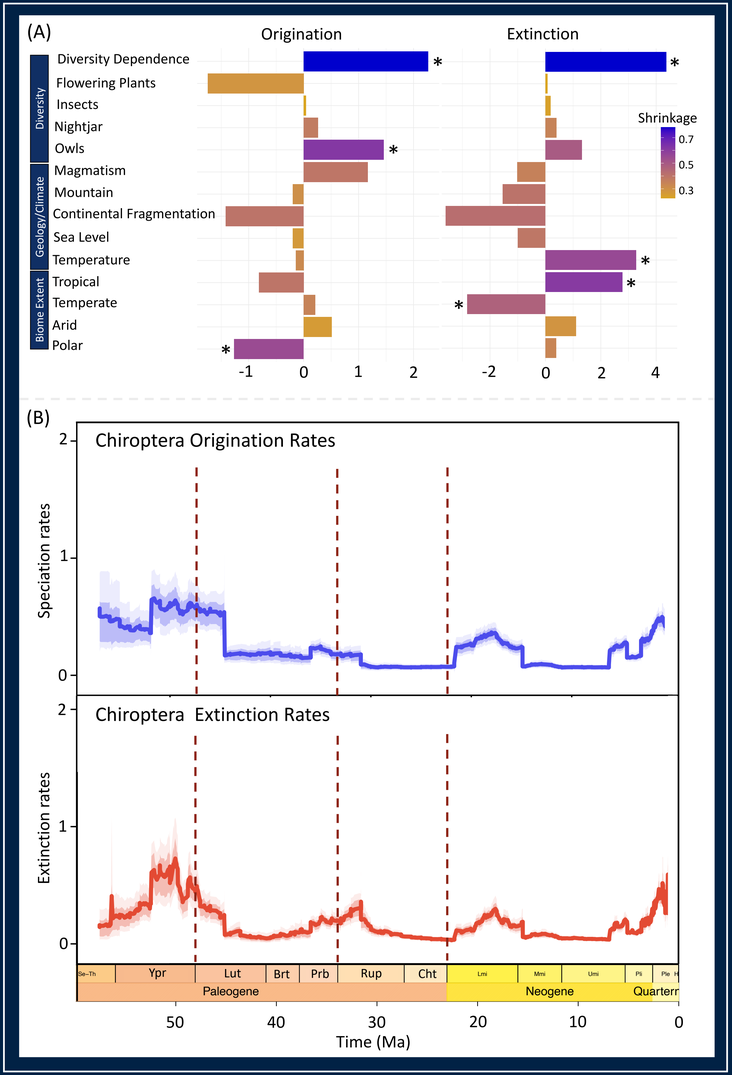

Figure 6. (A) Magnitude of correlation parameter and strength of correlation for Order Chiroptera under the exponential correlation model. Shrinkage weights >0.5 are significant correlations and are denoted with a star. **(B)** Speciation and extinction rates through time of Order Chiroptera under the multivariate birth-death and exponential correlation models.

Discussion/Future Work

- The extinction rates of bats are strongly correlated with global surface temperature, and the extent of the tropical biome. Origination is strongly correlated with owl diversification and the extent of the polar climate.
- Next, Chiroptera will be split into the stem and crown groups, and the analysis will be rerun with the statistically significant correlates to further interrogate the stem to crown bat transition.

Citations

Amador, L. I. et. al. (2018). Bat systematics in the light of unconstrained analyses of a comprehensive molecular supermatrix. *Journal of Mammalian Evolution*, *25*(1), 37-70.
Lehtonen, S. et. al. (2017). Environmentally driven extinction and opportunistic origination explain fern diversification patterns. *Scientific Reports*, *7*(1), 4831.
Rietbergen, T. B. et. al. (2023). The oldest known bat skeletons and their implications for Eocene chiropteran diversification. *Plos one*, *18*(4), e0283505.
Silvestro, D. et. al. Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytol.* **207**, 425–436 (2015).
Silvestro, D. et. al. PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. *Methods Ecol. Evol.* **5**, 1126–1131 (2014).
The data were downloaded from the Paleobiology Database on 03 October, 2022, using the group name 'chiroptera' and the following parameters: time intervals = Eocene and Neogene, region = Global, paleoenvironment = Terestrial, Order = Chiroptera.