

The Evolutionary History and Ancestral Biogeographic Range Estimation of Old-world Rhinolophidae and Hipposideridae (Chiroptera)

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Research Article

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Abstract

Background:

Family Rhinolophidae (horseshoe bats), Hipposideridae (leaf-nosed bats) and Rhinonycteridae (trident bats) are exclusively distributed in the Old-World, and their biogeography reflects the complex historic geological events throughout the Cenozoic. Here we investigated the origin of these families and unravel the conflicting family origin theories using a high resolution tree covering taxa from each zoogeographic realms from Africa to Australia. Ancestral range estimations were performed using a probabilistic approach implemented in BioGeoBEARS with subset analysis per biogeographic range (Old-World as whole, Oriental-Oceania-Australia(OOA) and Afrotropical-Madagascar-Palearctic(AMP)).

Result:

Our result supports an Oriental origin for Rhinolophidae, whereas Hipposideridae originated from the Oriental and African regions in concordance with fossil evidence of both families. The fossil evidence indicates that Hipposideridae has diversified across Eurasia and the Afro-Arabian region since the Middle Eocene. Meanwhile, Rhinonycteridae (the sister family of Hipposideridae) appears to have originated from the Sudanian-Somalia-Ethiopia region splitting from the common ancestor with Hipposideridae in Africa. Indomalaya is the center of origin of Rhinolophidae OOA lineages, and Indomalayan + Philippine appears to be center of origin of Hipposideridae OOA lineage indicating allopatric speciation and may have involved jump-dispersal (founder-event) speciation within OOA lineage. Wallacea and the the Philippines may have been used as stepping stones for dispersal towards Oceania and Australia from the Oriental region. Multiple colonization events via different routes may have occurred in the Philippines (i.e., Palawan and Wallacea) since the Late Miocene. The colonization of Rhinolophidae towards Africa from Asia coincided with the estimated time of Tethys ocean closure around the Oligoceneto Miocene (around 27 Ma), allowing species to disperse via the Arabian Peninsula. Additionally, the number of potential cryptic species in Rhinolophidae in Southeast Asia may have increased since Plio-Pleistocene and late Miocene.

Conclusion:

Overall, we highlight that complex historical events, in addition to species specific ecomorphology and specialization of ecological niches may shape current distributions.

Background

Bats constitute the second most diverse group of mammals after rodents, with over 1400 species recognized to date [1]. The rapid diversification of this taxa may be achieved through the capacity of powered flight and echolocation, which has allowed them to colonize a wide range of ecological niches

[2, 3], and is responsible for bats frequently being the only native mammals on oceanic islands. In this study, we focus on exclusively Old-World insectivorous bats, the superfamily Rhinolophoidea.

Rhinolophidae (horseshoe bats) consist of a single genus *Rhinolophus* Lacépède, 1799. They are insectivorous bats distributed throughout the Old-World, primarily in tropical regions, from Africa through Eurasia, Oceania and Australia [4]. Around 106 species have been described to date [1], although this number is likely to be an underestimate given that many species are cryptic [5]. The common name of Rhinolophidae is derived from specialized horseshoe-shaped noseleaf which is used to emit acoustic calls beam emission [6–12]. The distinctive noseleaf structure such as sella, lancet, furrows of lancet, internarial cup and ears shape of each rhinolophids species plays important role in determining calls emission, and may provide useful cues in the identification of cryptic species [5].

Hipposideridae is the sister taxa of Rhinolophidae, commonly known as leaf-nosed bats, they are distributed in the same range as Rhinolophidae across the Old-World [13]. They consist of seven genera of 90 described species, including *Hipposideros*, *Anthops*, *Asellia*, *Aselliscus*, *Coelops*, *Doryrhina*, *Macronycteris* [1], and recently *Cloeotis*, *Paratriaenops*, *Rhinonycteris*, and *Triaenops* were elevated to separated family, Rhinonycteridae (the Trident bats) [14] and is sister family to Hipposideridae [13]. *Hipposideros* is the most diverse genus within Hipposideridae, containing almost 80% of the total species in the family, and many species are cryptic, and thus true diversity may be considerably higher [1].

However, the systematics of these groups have not been well resolved. Although recent years have seen significant progress towards resolving the systematics of bats using an abundance of the phylogenetic datasets [15], these analysis generally had low systematic coverage [13, 16]. As a result, the understanding of systematics and evolution in these predominantly tropical groups are limited by the number of genes in the study, and systematic biases from limited taxon sampling and low geographical coverage [17–19]. Consequently several mutually exclusive hypotheses on the biogeography of these taxa exist [13, 16, 18, 20–23]. As the consequence of contradictory dating estimations, the interfamilial time divergence estimation within Rhinolophidae and Hipposideridae still cannot be reliably estimated, thus assessing the evolutionary history and the biogeographic origin is still challenging (i.e., [13, 16, 24–27]).

Inferring biogeographic history of a taxa is heavily dependant on estimated ages and relationship between taxa, but often lacks rigour when it is presented as a narrative addition to phylogenetic studies without explicit analysis [28–30]. The geographic origin of ancestral Rhinolophidae remains unresolved due to the limited fossil record, lack of representative taxonomic sampling across their distribution [13], and an unresolved basal phylogeny [18].

Several alternative hypotheses of the family origin have been proposed based on different data types and methods, for instance European origin [31], Asian origin [16, 24, 32], African origin [13, 25], and Middle-Eastern origin [18]. The biogeographic history of the Rhinolophidae and Hipposideridae are of particular interest due to their capability of true flight and ability to disperse over a wide geographic area. However, flight ability relates to wing design for each species [2, 33–35]. The broad-short wing design with rounded

tips in Rhinolophidae may limit dispersal of species across large water bodies [36], thus may have enabled vicariance events in the past and shape the current distribution of taxa. Furthermore, different methods have different historical biogeographic event assumptions, which has a significant influence on the inferences. Thus, to distinguish between these competing hypothesis, testing and comparison between statistical approaches is needed to optimize model selection and develop meaningful and well supported biogeographic analysis [37].

In this study, we use probabilistic modeling of geographic range evolution which allows to statistically choose numbers of biogeographic models based on Maximum Likelihood and Bayesian methods implemented in the R package “BioGeoBEARS” [37–40], however, to date, no study has performed this analysis in Rhinolophidae and Hipposideridae. This approach unified multiple models and provides a flexible framework for comparing alternative models in a mathematically explicit context. Here we use representative species distributed in each biogeographic realm ranging from the Afrotropical, Palearctic (Europe and Mediterranean), Oriental, to Oceanic and Australian realms, to the best of our knowledge, this study is the first to infer the ancestral ranges of Rhinolophidae and Hipposideridae using explicit biogeographic analysis. In addition, here we attempt to infer the evolutionary history and biogeographic ranges of potentially cryptic species of Asian Rhinolophidae in particular Southeast Asian region. We aim to understand historical biogeography of Rhinolophoidea (Rhinolophidae, Hipposideridae and Rhinonycteridae) of Old-World and the evolutionary history of potential cryptic species Rhinolophidae.

Methods

Sampling, Systematic coverage and Biogeography

Sampling

In total we included 104 species of Rhinolophidae ($n = 47$; 43% from 110 total described species), Hipposideridae ($n = 50$; 56% of 90 species) and Rhinonycteridae ($n = 7$; 78% of 9 species) were included in this study. Taxonomic sampling coverages were based on number of species used in the tree published in Álvarez-Carretero et al. 2021. The total species coverage per biogeographic area was; OAA = 31; AMP = 16 for Rhinolophidae and OAA = 38; AMP = 12 for Hipposideridae. In addition, total of 26 Rhinolophidae *sensu lato* mainly distributed in Southeast Asia and their potential cryptic species (44 potential cryptic [5]) was used to assess their evolutionary history and ancestral biogeography range.

Mapping the palaeomap and fossil occurrences

To assess species routes based on fossil data and assess the correspondence between fossil data (where present) and ancient coastlines we downloaded recent files showing coastlines for periods between the present (0 Ma) and 45 Ma, including 37 Ma, 30 Ma, 22 Ma, 13 Ma based on [41]. Fossil data from Rhinolophids was then downloaded from the Fossilworks (http://www.fossilworks.org/cgi-bin/bridge.pl?a=taxonInfo&taxon_no=40644) and Global Biodiversity Information Facility (GBIF), using a criteria of fossil species and the search term Rhinolophidae (<https://doi.org/10.15468/dl.uy9gx5>). This

was repeated for Hipposideridae (<https://doi.org/10.15468/dl.2826pj>). Data was cleaned to give putative species name at the highest available level, and age of fossil in millions of years, dates were also checked from associated publications when not available in the spreadsheets. This data was rounded up to the nearest million years, and where not available for any given fossil the dates for the same species in other parts of the region was used where present.

Biogeographic Analysis of Old-World Rhinolophidae and Hipposideridae

We inferred probabilistic modelling of Rhinolophidae ancestral geographic ranges in the R package “BioGeoBEARS version 1.1.2” [40]. We statistically compared the likelihood-based model of geographic range evolution of DEC model (Dispersal-Extinction-Cladogenesis) of LAGRANGE [42], a likelihood implementation of the processes assumed by parsimony aspect of DIVA [43] (therefore named DIVALIKE), a likelihood version of the range evolution model of BAYAREA implied the method in BayArea [38] (therefore named BAYAREALIKE) and a modification of DEC model by prohibiting the transition into null-range (DEC*) [39]. Each model is fully parameterized in BioGeoBEARS supermodels with different assumptions about anagenetic and cladogenetic change processes. A free parameter of “*j*” (jump dispersal or founder-event speciation) was added in DEC + J, DEC*+J, DIVALIKE + J, BAYAREALIKE + J models and nested with another two free parameters (*d* and *e*) within DEC + J, DEC* is nested within DEC*+J, DIVALIKE is nested within DIVALIKE + J and BAYAREALIKE is nested within BAYAREALIKE + J [40].

To infer the ancestral biogeographic ranges of Rhinolophidae and Hipposideridae, we use dated-tree generated from [44] which used a supermatrix of 33.2×10^6 alignment length from 72 genomes (15,268 genes). The date estimation in this published study produce smaller uncertainties in dates estimates, thus are recommended for macro-evolutionary studies, including ancestral biogeography (Supplementary Figure S1). We attempt to analyze the ancestral ranges in 4 subset analyses, including: 1) global Rhinolophoidea superfamily (Rhinolophidae, Hipposideridae and Rhynonycteridae), then subdivided the analysis into sub-regions for each family into: 2) Rhinolophidae Asia-Australia lineages and Rhinolophidae Afrotropical-Palearctic lineages, 3) Hipposideridae Asia-Australia lineages and Hipposideridae-Rhynonycteridae Afrotropical lineages, 4) Potential cryptic species of Rhinolophidae in Asia lineages. This analysis strategy was to optimize the computational efficiency by considering the possible numbers of states for each sub-analysis. We pruned the species tree published from Álvarez-Carretero et al. 2021 to Yinpterochiroptera lineages and trimmed the branches to Hipposideridae, Rhynonycteridae, Rhinolophidae using the function `drop.tip` in R package ‘phytools’ v1.0-1 [45], and removed the outgroups. We merged the subspecies in the tree tip into species level (OTUs) with taxonomy following Simmons and Cirranello 2021, using R package BioGeoBEARS v1.1.2 [40] in the function `prune_specimens_to_species`. The geography files are PHYLIP-formatted files which is the same format used for C++ LAGRANGE editor file, which generated in R using function `save_tipranges_to_lagrangePHYLIP`. To decide the biogeographic region, we use the current distribution of extant taxa from the data provided in previous literature and Global Biodiversity Information Facility GBIF

(<https://www.gbif.org/>) (<https://doi.org/10.15468/39omei>), as IUCN ranges of bats may be unrepresentative and risk being inaccurate [46]. The division of zoogeographic zones defined based on geologic history and area of endemism which define based on previous studies [28, 47–57] (Fig. 1, modified from Holt et al. 2013).

Ancestral Biogeography ranges estimation of Rhinolophoidea Superfamily

For biogeographic regions of Rhinolophoidea superfamily, we divided the current known species distribution into nine zoogeographic areas using updated version of Wallace's zoogeographic regions of the world constructed on the distribution and phylogenetic relationship on 21,037 species of amphibians, birds and mammals [56]. The regions are: Afrotropical + Madagascar (A); Oceanian (B); Philippine (C); Sino-Japanese (D); Oriental (including India + Indo-Malaya (Southeast Asia + Greater Sunda Islands (Sumatra, Java, Borneo)) (E); Palearctic (Europe, Mediterranean) (F); Sahara-Arabian (G); Australia (H); and Wallacea (Sulawesi, Lesser Sunda Islands and area in vicinity) (I). The broad geographic coverage is to achieved the main goals to assess the biogeographic on Rhinolophoidea as whole with 104 species in the tips (outgroup removed). We set the maximum area range into five (according to number of maximum areas occupied by extant taxa) resulting 382 and 381 number of possible ranges with and without null-range, respectively.

Ancestral Biogeography ranges estimation of Rhinolophidae Family

Second, we pruned the *Rhinolophus* species from the tree of Asia lineages, consisting of 27 species. The pruned tree did not include three species of *R. hipposideros*, *R. formosae*, *R. luctus* which are basal in the Oriental and Afrotropical lineages in our initial trees (Fig. 2). We attempted to prune Rhinolophidae as a family including Afrotropical, Oriental and Australian lineages, however causing a computational issue with total of 47 species (OTUs) distributed in 13 biogeographic areas and 5 areas maximum occupied with extant taxa resulting in 2,380 of possible geographic ranges. Therefore, we subset the analysis into Rhinolophus of Oriental-Oceania-Australia and the Afrotropical-Palearctic subdivision. For the Oriental-Oceania-Australia clade, we divided the biogeographic region into a smaller divisions, consisting of: Sino-Japanese (A); India (B); Indomalayan (C); Greater Sunda (Sumatra + Java + Borneo) (D); Philippine (E); Wallacea (Sulawesi + the Lesser Sunda Islands + Halmahera (from Wallace line to Lydekker line)); Oceania (G); and Australia (H) [47, 48, 54, 56, 58, 59]. The total maximum area range was set to five, based on the number of areas occupied by extant species, (i.e *R. affinis* with current distribution in India, Indomalaya, Greater Sunda, Philippines, and Wallacea), resulting in a total of 219 areas occupied.

In addition, we pruned Rhinolophidae in the Afrotropical-Palearctic region consisting of 16 species, with geographic ranges of six areas and number of maximum areas occupied by one species were set to 4, resulting 57 possible geographic ranges. The geographic areas included: Sahara-Arabian (A); Sudanian + Somalia + Ethiopia (B); Guinean + Congolian (C); Zambezian + Kalahari + Southern Africa (D); Europe

and Mediterranean (E); and Sino-Japanese (F) following biogeographic division of Africa, Palearctic and Sino-Japanese [56, 60].

Ancestral Biogeography ranges estimation of Hipposideridae and Rhinonycteridae Family

We firstly ran Hipposideridae and Rhinonycteridae analysis as whole across old-world biogeographic region from 13 total biogeographic regions, of 57 species (OTUs) and maximum total of seven areas can be occupied by a single species. This calculates the total number of possible geographic ranges of 5,812 states and created a large matrix that will cause computational issues. Thus, we analyzed the Oriental-Oceania-Australia lineages separately from Afrotropical-Palearctic region. In total 39 Hipposideridae species were analysed for the Oriental-Oceania-Australia lineages, including nine biogeographic regions and current species occupied a maximum of 7 biogeographic areas, resulting in 502 possible geographic ranges. The biogeographic areas include: Sudania + Somalia + Ethiopia (A); Sino-Japanese (B); India (C); Indomalayan (D); Greater Sunda islands (Sumatra + Java + Borneo) (E); Philippine (F), Wallacean (G); Oceanian (H); and Australia (I). The biogeographic region of Sudanian + Somalia + Ethiopia (A) was being included in the Asian-Australian clades as *H. jonesi* appears to be sisters in Asian clades, and it was suggested that as the result of earlier African-Asian colonization event [61].

Furthermore, we pruned the Afrotropical-Palearctic branches of Hipposideridae and including sister family Rhinonycteridae [13, 14]. The total species number for this subset analysis is 18 distributed in six biogeographic regions, and total area occupied by single extant species (numbers of possible ranges = 63). The biogeographic areas including: Sahara-Arabian (A); Sudanian + Somalia + Ethiopia (B); Guinean + Congolian (C); Zambezian + Kalahari + Southern Africa (D), Madagascar (E); and Australia (F).

Ancestral Biogeography ranges estimation of Cryptic Rhinolophidae in Asia

Additionally, we use the maximum clade credibility tree from Bayesian Evolutionary Analysis by Sampling Trees (BEAST) analysis (see below) for ancestral range estimation analysis in BioGeoBEARS of potential cryptic species in Asia. Here we use eight “areas of endemism” to refer to biogeographic units of Southeast Asia and the West Pacific [48, 55, 62] including India (I), Himalaya (H); Southeast Asia (S); China (C); Isthmus of Kra region to Kangar-Pattani (K); and Kangar-Pattani line to the tip of Malay Peninsula (P); Borneo (B); and Sumatra (S). Maximum range size in analysis were set to eight (to match the number of regions) based on the assumption that OTUs (species) could occur in all areas. These areas represent the biogeographic zones used in former biogeographic analyses [48, 55, 62]. Area assignments for each OTU were based on current species distribution known from sequenced specimens which were intersected with each biogeographic region in ArcMap 10.3 to determine the range each OTU occurred in. The OTUs as tip nodes represent the species and cryptic species assigned from phylogenetic tree based on Maximum Likelihood and Bayesian Inferences.

For all above analyses, we use R package GenSA [63] (Generalized Simulated Annealing) to optimize the maximum likelihood calculation for all models. All BioGeoBEARS supermodels run under non-time-stratified analysis. We use statistical model comparison to compare the best-fit model given the data, a likelihood ratio test (LRT) for nested models and Akaike Information Criterion corrected (AICc) and weighted (AICw) were used for the non-nested models to observe the best model among all biogeographic scenarios.

Evolutionary history of potential cryptic Rhinolophidae species in Asia

To assess the evolutionary relationship and to estimate the time divergences between potential cryptic species, we ran Bayesian Evolutionary analysis by Sampling Trees (BEAST v2.6.3) [64]. Potentially cryptic species in the region delineated using integrative taxonomic approaches [5]. The tree was constructed based on 26 Rhinolophidae species *sensu lato* distributed in Southeast Asia and India, using mtDNA COI 680 bp. Inferring evolutionary history using a single genes can be problematic for a variety of reasons, nonetheless, this is the available data in this region with high systematic coverage [5]. Therefore, a careful justification in inferring the result and broad comparison with previous studies is crucial and we discuss it below. The Nexus file was generated using Mesquite v3.6 [65], prior setting in .xml file was generated in BEAUti v2.6.3 [64] and ESS package was loaded in BEAUti prior the analysis. Relaxed clock log normal [66] was used to allow the clock rate to vary across the tree branches. We used a Birth-Death prior in the tree model which provided better accuracy and provides more precise result in all speciation scenarios based on previous studies [67]. The secondary calibration dates were taken from published papers due to the scarcity of bat fossils. Therefore, we, 1) estimated the time divergence between Rhinolophidae and Hipposideridae was between 39–45 Ma, following 41 Ma (95% highest posterior density (HPD) = 37–47 Ma) [25]; 39 Ma (95% HPD = 37–43 Ma) (Teeling et al. 2005); 42 Ma (95% HPD = 39–45 Ma) [13]. 2) To estimate time divergence between closely related species, we use Foley et al., (2015) for node calibration between *R. shameli* and *R. creaghi* (4 Ma (95% HPD = 3–5 Ma); *R. trifoliatus*-*R. luctus* (3 Ma (95% HPD = 2–4 Ma) and in addition, we calibrated node between *H. armiger* and *A. stoliczkanus* (31 Ma (26.5–31.5 Ma)). Thus, we set the priors to calibrate the nodes in BEAUti with parameterization as follows: 1) For Rhinolophidae and Hipposideridae, we selected *H. armiger* and *R. sedulus* as priors with means (M) = 42 and standard deviations (S) = 0.045 which specifies that the distribution of priors is centred at 42 Ma and 95% probability range covering at 39–45 Ma; 2) *R. shameli* and *R. creaghi* prior, M = 4, S = 0.15 (median = 3.92 Ma, 95% probability range = 3.09–5.06 Ma); 3) *R. trifoliatus* and *R. luctus* prior, M = 3, S = 0.23 (median = 2.92 Ma, 95% probability range = 2–4.27 Ma); 4) *H. armiger* and *A. stoliczkanus* prior, M = 30, S = 0.6 (median = 29.9 Ma, 95% probability range = 27.1–33.1 Ma). All calibration priors are set to log-normal, each configuration of 2.5% quantile and 97.5% quantile set in 'mean in real space' and none of the prior settings enforce to be monophyletic as each species consists of several clades. MCMC algorithms are set to run for 50,000,000 cycles, trees stored every 1,000 cycles. The trace files generated from BEAST were analyzed in TRACER1.7 [68]. 10% of initial tree were discarded in TreeAnnotator v2.6.3 [64]. The final tree was visualized in FigTree and Adobe Illustrator.

Results

Historical biogeography of Rhinolophoidea superfamily

The time-tree pruned from Álvarez-Carretero et al. (2021) is provided in Supplementary Figure S1, further, the time divergence estimations mentioned in this result were cited based on Álvarez-Carretero et al. 2021 study. The probabilistic modeling of historical biogeography of Rhinolophoidea superfamily reveals that models with founder-event speciation parameters (+ J) (i.e., DEC + J, DIVALIKE + J, BAYAREALIKE + J) constantly showed higher likelihood compared to the models without + J, indicated that founder-event speciation is common in these models. Likelihood Ratio Test (LRT) using chi-squared one-tailed test conferred higher LnL (natural log) + j models corresponding to higher data probability and the better model + j fit to the data (Table 1). + j parameter specifies founder-event speciation model, (Matzke 2013; Matzke 2014) which were important events to explain the island biogeography. However, the likelihood ratio test (LRT) shows there was no significant difference between DEC*+J and its nested models, DEC* (LnL = -302.6891; LnL = -302.6879, respectively, $p = 1$). This result may be due to low j (founder-event speciation, the cladogenesis parameter), and to ensure it was not due to the maximum likelihood optimization problems and computational sources issue, we ran the analysis three times and similar result was acquired. The best fit model given the data is DEC* (AIC = 609.38, AICwt = 0.73) and followed with DEC*+J (AIC = 611.38, AICwt = 0.27) (Table 1). In DEC* model, extinction e value is higher than dispersal d ($d < e$; $d = 0.0078$; $e = 0.0685$) indicating the range contraction rate is higher than range expansion event in this superfamily.

Table 1

Best-fit models based on BioGeoBEARS analysis (all models statistical results are provided for Superfamily Rhinolophoidea but only best-fit models provided for the rest of analysis). Abbreviation: LnL: Log-likelihood, np: number of parameters, d: dispersal, e: extinction, j: jump dispersal, AICc: Akaike Information Criterion (corrected); AICc_wt: AICc weighted.

	LnL	np	<i>d</i>	<i>e</i>	<i>j</i>	AICc	AICc_wt
Superfamily Rhinolophoidea							
DEC	-320.09	2	0.00457	0.00024	0	644.346	2.07E-08
DEC + J	-315.26	3	0.00408	0	0.01096	636.871	8.71E-07
DIVALIKE	-339.08	2	0.00576	0.00335	0	682.321	1.18E-16
DIVALIKE + J	-331.65	3	0.00465	0	0.01275	669.634	6.70E-14
BAYAREALIKE	-390.63	2	0.01	0.01	0	785.426	4.81E-39
BAYAREALIKE + J	-331.12	3	0.00328	0	0.02453	668.577	1.14E-13
DEC*	-302.69	2	0.00782	0.06852	0	609.545	0.74802
DEC*+J	-302.69	3	0.00782	0.06846	0	611.721	0.25198
Rhinolophidae: Oriental-Australia lineages							
DEC*	-90.569	2	0.0156	0.04445	0	185.308	0.71898
Rhinolophidae: Afrotropical-Palearctic lineages							
BAYAREALIKE	-56.893	2	0.01371	0.04275	0	117.955	0.71729
Hipposideridae: Oriental-Australia lineages							
DEC + J	-150.61	3	0.00611	0	0.02877	307.558	0.47514
DEC*	-151.9	2	0.01	0.01	0	307.965	0.38752
DEC*+J	-151.88	3	0.01	0.01	0	310.111	0.13252
Hipposideridae and Rhinonycteridae: Afrotropical-Palearctic lineages							
DEC*	-58.64	2	0.54138	2.43769	0	121.448	0.78792
Cryptic Rhinolophidae							
DEC*+J	-194.7	3	0.021	0.298	0.023	395.708	0.81136

Our result suggests that the common ancestor of Rhinolophoidea as a whole (Rhinolophidae, (Hipposideridae, Rhinonycteridae)) were from the Oriental region (Fig. 2), split around middle Eocene at 43.25 Ma (95% highest posterior density/HPD = 39.74–46.76 Ma) with the percentage of relative probability higher from Oriental region than originated from Afrotropical region (Fig. 2). Similarly, more than 50% relative probability showed that the ancestor of Rhinolophidae also from Oriental region, and

then later expanded to colonized Afrotropical region. The common ancestor of Hipposideridae and Rhinonycteridae were suggested to be from Oriental and Afrotropical regions (with almost the same relative probability for each region but slightly higher from Oriental), where Rhinonycteridae split earlier around middle Eocene at 40.55 Ma (95% HPD = 36.03 Ma – 44.14 Ma) from the rest of Hipposideridae of Afrotropical lineages (Fig. 2). The other models that are less fitted to the data showed different origins, i.e., DEC model suggested that ancestral Rhinolophoidea superfamily was widespread, DEC + J, DIVALIKE, DIVALIKE + J and BAYAREALIKE + J concluded the superfamily originated in the Afrotropical region (Supplementary Figure S2-S9), however, these models are less favourable for the dataset with low support AICc_wt value near zero (Table 1.), hence inferring historical biogeography using single method without statistical comparison can be deceptive. Our result supports the importance of statistical model testing as each model have strong assumption and impact on inference, as highlight in Matzke 2014. We focus on reporting the result under the best-fit model given the data.

Historical biogeography of family Rhinolophidae (Horseshoe bats).

Rhinolophidae family split into two major lineages in early Oligocene at 27.68 Ma (95% HPD = 23.96–31.54 Ma): *Rhinolophus* Afrotropical-Palearctic lineages and Oriental lineages (with Australian and Oceanic species). The basal of the two lineages are *R. trifolius*, *R. luctus*, *R. formosae* and *R. hipposideros* split with the above two lineages earlier in early Oligocene at 31.24 Ma (95% HPD = 27.36–35.16 Ma). The main analysis suggests the origin of ancestral Rhinolophidae was from Oriental region (see above result). Here we subset the analysis and increase the geographic resolution of biogeographic regions and divided Oriental region into smaller zoogeographic regions including India, Indomalayan, Sino-Japanese, Greater Sunda islands (Sumatra, Borneo, Java), Wallacea (Lesser Sunda islands to Maluku and Sulawesi separated with Wallace's line and Lydekker's line), Oceania and Australia (Fig. 3). The best fit model given the data was DEC* model (AICc = 185.3075, AICc_wt = 0.718978) followed with DEC*+J (AICc = 187.4642, AICc_wt = 0.244564). Range expansion is lower than extinction ($d < e$, $d = 0.0156$, $e = 0.0444$) suggests that range constriction is higher compared to dispersal rate in historical colonization Rhinolophidae.

The result from DEC* suggests that ancestor of Rhinolophidae species the Oriental-Oceania-Australia lineage originated in Indomalayan region and species diversification started in Early Miocene around 22.77 Ma (95% HPD = 19.25–26.51 Ma) (Fig. 3a). The ancestral range expanded from the Indomalayan region to the north to Sino-Japanese and west to India (within Asia continent) then later colonized towards the Philippine archipelago around end of Middle Miocene at 12.64 Ma (95% HPD = 9.37–16.19 Ma) (Fig. 3a). The result shows ancestral Japanese rhinolophids originated from the Indomalayan region then range expanded to northern before arriving in Japan, the species thus diversified around Middle Pliocene at 3.43 Ma (95% = 1.75–5.67 Ma) with high endemism of extant species such as *R. cornutus*, *R. pumilus*, and *R. perditus* (Fig. 3a). The diversification in the Philippine archipelagoes is estimated around Late Miocene – Early Pleistocene at 6.09 Ma (95% HPD = 3.31–4.53 Ma). The Philippine rhinolophids appears to be the result from multiple colonization events originating from the Indomalayan and Wallacean regions. Colonization in Wallacea region, also occurred in multiple colonization event from the

Indomalayan region through greater Sunda islands and Philippine archipelago, around Late Miocene at 7.12 Ma (95% HPD = 4.46–10.2 Ma). Australian and Oceanian rhinolophids appears to colonized from the Indomalayan region through two pathways, from the Indomalayan region-Sundaland-Wallacea and Indomalayan-Philippine-Wallacea which occurred in Late Miocene to Early Pliocene (Fig. 3a).

Moreover, the Afrotropical-Palearctic Rhinolophidae diversified around the Early Miocene at 21.38 Ma (95% HPD = 17.74–25.36 Ma) showed BAYAREALIKE (AICc = 117.9551; AICc_wt = 0.717294) (Table 1) as the best fit model to elucidate the historical biogeography given the data, and the result exhibit the range contraction rate is higher than dispersal or range expansion ($d < e$, $d = 0.0137$; $e = 0.042755$). The best fit model (BAYAREALIKE) indicated that the ancestral range process in this clade is predominantly explained by sympatry (subset and widespread) events (in cladogenetic) and assumes no vicariance events. The ancestral species were widely distributed in most of Afro-Palearctic region including Europe-Mediterranean, Sahara-Arabian, Sudanian-Somalia-Ethiopia, Zambezan-Kalahari-Southern Africa region (ABDE, Fig. 3b). Interestingly, our result showed that *Rhinolophus* Afrotropical lineages colonized Guinean-Congolian region more recently in the Late Miocene around 8.1 Ma through range expansion (Fig. 3b). The ancestral ranges of Rhinolophidae predominantly occupied Sudanian + Somalia + Ethiopia region and Zambezan + Kalahari + Southern Africa around Middle Miocene to Pliocene (15–3.62 Ma). Re-colonization to Sahara-Arabian and Europe-Mediterranean occur around Late Miocene at 7.63 Ma (95% HPD = 3.9–12.14 Ma) (Fig. 3b). The result showed that a widespread distribution of ancestral Rhinolophidae Afro-Palearctic lineage followed with higher range contraction events (extinction) for descendant distribution.

Historical biogeography of family Hipposideridae (**Leaf-nosed bats**) and Rhinonycteridae (**the Trident bats**).

The ancestors of the Hipposideridae family appears to have wide distribution from Oriental and African region (see above results). Our results showed that DEC + J (AICc = 307.5575, AICc_wt = 0.475144) with 47% probability of being the best fit model in the Oriental-Oceania-Australian lineages, alternatively, the other two models of DEC* (AICc = 307.9653, AICc_wt = 0.387517) and DEC*+J (AICc = 310.1114, AICc_wt = 0.132516) can also identify the best fit model given the data with AIC weighted value as 39% and 13%, respectively. The result of three models exhibit similar patterns in inferring the origin of the Hipposideridae ancestor which proposed the ancestral origin from the Indomalayan region and the Philippines, suggesting the range expansion is primarily allopatry (Fig. 4a). The dispersal rate is higher than range contraction ($d > e$, $d = 0.00611$, $e = 0$, $j = 0.0288$), which is in contrast with Rhinolophidae family, where dispersal rate is smaller than extinction rate. The ancestral range from the Indomalayan region and Philippine then expanded to India, Greater Sunda Islands, Wallacea and Oceania in the early Oligocene (30.52 Ma (95% HPD = 25.26–34.92 Ma). Colonization towards the Greater Sunda islands was directly from the Indomalayan region region which occurred since the early Miocene. Oceanian hipposiderids appear to have colonized the region since early Oligocene and may use the Philippines as a stepping stone. The Wallacea and Australia region, may have colonized from Oceanian and Indomalaya regions through greater Sunda Island coincided with active tectonic plate movement since Oligocene to

Pliocene (Fig. 4a). Jump-dispersal events ($j = 0.0288$) may explained the colonization of lineages to Australia from Oriental and Oceania region (CDEFGH to I, Fig. 4a), as well as colonization of Japanese Hipposideridae (D to B) which originated from the Indomalayan region (around the late Miocene, 10.4 Ma (6.17–14.99 Ma). Paraphyly within Hipposideridae is shown in African species *H. jonesi* (A = Sudanian + Somalia + Ethiopia) which recovered within the rest of Oriental-Oceania-Australian taxa, diverged around early Oligocene at 28.12 Ma (95% HPD = 24.45–31.82 Ma), which may indicated earlier Asian-African colonization event.

Our result showed that DEC* (AICc = 121.4481, AICc_wt = 0.787916) has 79% probability of being the best fit model for Hipposideridae and Rhinonycteridae Afrotropical lineages, followed with DEC*+J (AICc = 124.1533, AICc_wt = 0.20373) with range contraction is higher than range expansion ($d < e$, $d = 0.54$, $e = 2.43$) (Table 1). The result suggested that the ancestral of Hipposideridae Afrotropical lineage were from Sahara-Arabian region (Fig. 4b). The diversification of Hipposideridae Afrotropical lineages began around middle Eocene with splitting of *Asellia tridens* with the rest of *Hipposideros* genera (38.18 Ma (95% HPD = 36.93–41.79 Ma), originated from Sahara-Arabian region (however with little percentage of relative probability, Fig. 4b). Multiple colonization occurred to Guinean-Congolian region by range expansion from Sahara-Arabian through Sudanian + Somalia + Ethiopia and from Southern part (Zambeian + Kalahari + Southern Africa). Madagascar Hipposideridae ancestral originated from Sudanian + Somalia + Ethiopia (B) (Fig. 4b). Additionally, the ancestral Rhinonycteridae originated from Sudanian-Somalia-Ethiopia then colonized Madagascar which began at early Miocene at 21.88 Ma (95% HPD = 16.54–28.48 Ma). Our result showed most of ancestral species of Rhinonycteridae originated from Madagascar, the over-land dispersal event could explain the process of ancestral range from the continents to Madagascar.

The evolutionary history and historical biogeography range of potential cryptic species of Rhinolophidae Asia lineages

The result showed estimation split from relaxed-clock log normal with birth-death prior of tree model between Rhinolophidae and its sister family Hipposideridae suggests that the radiation began in late Eocene, with posterior age 40.26 Ma (95% HPD = 37–43.5 Ma), slightly younger but in general fall within the dating range estimation in previous studies as 42 Ma in Foley et al (2015), 45.47 Ma in Amador et al (2018) and 43 Ma (95% HPD = 39–46 Ma) in [44]. Our analysis showed the diversification of Rhinolophidae in the region started in the late Oligocene till early Miocene, *R. JLEsp*, *R. sedulus*, *R. trifoliatus* and *R. luctus* represent the oldest lineages, separated from other *Rhinolophus* species 24.52 Ma (HPD = 16.5–27 Ma), in concordance with Álvarez-Carretero et al. 2021 positioned *R. luctus*, *R. trifoliatus* and *R. hipposideros* (not included in this analysis) as the basal of Rhinolophidae species but their estimation is higher when Rhinolophidae Afrotropical lineages is included as of 31.24 Ma (95% HPD = 27.36–35.16 Ma)). Rapid speciation and species diversification in Indochina region happened approximately since late Miocene (23 Ma) (Fig. 5), coincided with date estimated from with Álvarez-Carretero et al. (2021) (95% 22.77 Ma (95% HPD = 19.25–26.51 Ma)). The result showed that some species diverged recently in Pliocene and Pleistocene epoch from their closest relatives (2–5 Ma), i.e., *R.*

creaghi, *R. stheno*, *R. coelophyllus*, *R. shameli*, *R. borneensis*, *R. philippinensis*, *R. macrotis* group, *R. marshalli*, *R. rex*. The youngest species lineages represented by *R. coelophyllus* and *R. shameli* diverged around 1.5 Ma (95% HPD = 1–3 Ma) in Pleistocene. The majority of potential cryptic species or incipient species within species complexes diverged in mid-Pliocene within the last 2 Ma indicates rapid radiation in Plio-Pleistocene, with the exception of the *R. pearsonii* complex that diverged during mid-Miocene 7.38 Ma (HPD = 5.2–9 Ma) indicated a support to split *R. pearsonii* into multiple different species. The time divergence construction using secondary calibration at multiple nodes in BEAST supported the evolutionary distinction between the clades within species complexes and the incipient species might further be considered as distinct species.

The result of historical geographic ranges estimation for cryptic Rhinolophidae suggests model with $+j$ parameter performed better than other models without it, as expected when two model with three free parameters (d , e , and j) compared with nested models with only two free parameters (d , and e) (Table 1). The best fit model given the data according to AIC and AICc were DEC*+J (AICc = 395.4, AIC_wt = 0.82) (Table 1). DEC*+J has 82% probability of being the best fit model given the data and DEC* (Dispersal-Extinction-Cladogenetic) has 18% probability of best fit model, and other model shown < 1% of probabilities as fit model given the dataset. DEC*+J showed the estimate extinction rate (range contraction) events was higher compared to dispersal (range expansion) and jump-dispersal events ($d < e$; $d = 0.0205$, $e = 0.298$, $j = 0.0228$).

Moreover, the DEC*+J model shown the transition of geographic change in cladogenetic events (range transformation in splitting the clades) through some series of scenarios (i.e., sympatry-narrow, sympatry-subset, vicariance-narrow and founder-event). Here we only present the best fit model for relative probability of ancestral state DEC*+J. The relative probability of ancestral state inferred the cryptic Rhinolophidae of Asian lineages originated from the Indomalayan region, here in particular Indochina (Fig. 5), in concordance with our result in ancestral biogeographic of Rhinolophidae Oriental-Oceanian-Australian lineages, then expanded to current geographic ranges subsequently. The differences in the results we present here with other section (Rhinolophidae Oriental-Oceanian-Australian lineage) was the biogeographic areas we used in the analysis (see Materials and Methods).

The origin of *R. luctus*, *R. sedulus* and *R. trifolius* ancestors were in the Indomalayan region then occupied Borneo island via vicariance events since middle Miocene (13 Ma). The result suggests the colonization from Indochina then jumped to island supported with high extinction e values and explained by the jump-dispersal events from the best-fit models (DEC*+J). Similarly, colonization to Borneo Islands from Indochina also presented in *R. philippinensis* and *R. borneensis* in began in Pliocene (2–5 Ma). Our result suggests a rapid diversification began in the late Miocene around 7 Ma within *R. pearsonii* ancestor group where the ancestral ranges subset-sympatry into two largely ranges; some remained in Indochina and then subset-sympatry in northern areas (Himalaya region and China), indicated the dispersal and vicariance event with physical barrier for gene flow between southern and northern populations. The co-existence of multiple sympatric sister taxa in the ancestral and current populations are shown in several

groups such as *R. stheno*, *R. coelophyllus*, *R. shameli*, including distant relatives *R. malayanus*, *R. macrotis* group, and *R. rex*.

Our analysis indicated a high probability of recent diversification through subset-sympatry in *R. affinis* and *R. pusillus* group around Isthmus of Kra, Kangar-Pattani line to the tip of Malay Peninsula from the rest of northern population. Genetic drift may explain the emergence of separate geographical ranges of *R. affinis* in Sumatra Island after separation from mainland which shows a closer relationship to Isthmus of Kra, Kangar Pattani and Malay Peninsula lineages dated around Pleistocene (2 Ma) (Fig. 5).

Discussion

The ancestral range estimation for superfamily Rhinolophoidea (Rhinolophidae, (Hipposideridae, Rhinonycteridae)) suggests that the ancestors of family were in the Oriental origin, then diversified to other biogeographic regions, colonized Africa through Sahara-Arabian regions to Madagascar and to other archipelagoes in Asia including the Philippines and Indonesia, then colonized Australian through Philippine, Greater Sunda Island, Wallacea and Oceania. Our study is congruent with the previous hypothesis that Rhinolophidae bats originated in the old world tropics in Asia [16, 24, 32, 70] then the range contracted and expanded to East Asia region including India, Africa and islands in the vicinity, but, in contrast with [13, 25] which hypothesized that the ancestral of *Rhinolophus* species were of African origin based on LAGRANGE biogeographic analysis. Rhinolophidae of Oriental-Oceanian-Australian lineages originated from the Indomalayan region, and the ancestral range of Afrotropical lineages were widespread in the Afro-Palearctic. Allozyme variability also suggests colonization from Eurasia toward North Africa and that subsequent diversification took place in Africa [71], and morphological studies suggest that plesiomorph Oriental rhinolopids were basal and Afro-Palearctic species were more derived [32]. The widespread ancestral and current distribution of taxa in best-fit model BAYAREALIKE indicated the ancestral ranges were similar to those occupied by their descendants, and suggests over-land range expansion in the past around Late Oligocene coincided with diversification of Afrotropical lineages at 27.68–24.38 Ma. The dispersal rate was constantly lower than extinction rate in Rhinolophidae ($d < e$). Similarly with Hipposideridae-Rhinonycteridae Afro-Palearctic lineages ($d < e$), but in contrast with Hipposideridae Oriental lineages where dispersal or range expansion is higher ($d > e$). The estimated rate of dispersal is low suggesting that species have mostly retained the same geographic ranges as their ancestors [37, 39].

The common ancestor of Hipposideridae originated from Oriental or Afrotropical regions (similar posterior probability, Fig. 2), suggesting a possible widespread ancestral ranges of this family. The ancestor of Hipposideridae Oriental-Oceania-Australian lineages originated from the Indomalayan region and the Philippines, which suggests multiple colonization may occurred during range expansion. The common ancestor of Hipposideridae Afro-Palearctic lineages originated from Sahara-Arabian and Sudanian-Somalia-Ethiopia suggested the early colonization from northern part of Africa and Arabian Peninsula (Fig. 4b). Our results are in agreement with previous studies based on fossils which suggest that major the dispersal axis of Hipposideridae was from North Africa toward South Europe during the

Middle Eocene [72]. The result also suggests that Rhinonycteridae in Madagascar split from their common ancestor (Hipposideridae Afro-tropical lineages) around Middle Eocene (~ 40.55 Ma) and ancestral range originated from the Sudanian-Somalia-Ethiopia regions.

Even though our result indicates an Oriental (Indomalayan) origin for the Rhinolophidae, there is a lack of Paleogene fossil finds from the Indomalayan region, though variable taphonomy means that the majority of the fossil record is missing across taxa. The only known possible record of Eocene bats in this region is Megachiroptera from Krabi Mine in Thailand. However, fossil evidence of bats is relatively rare due to delicate skeletons and are therefore rarely preserved, thus, leaving only teeth and postcranial fragments for identification [73]. The latest finding of ancestral Rhinolophidae (*Protorhinolophus shanghuangensis*) was from Shanghuang fissure, Jiangsu (northern part of Asia; Discussed below) [70], although further research in the future may improve the knowledge in the fossil evidence of this group. The oldest bat fossils are from the early Eocene, and are known from North America, Europe, Africa and Australia [73, 74]. There are competing hypotheses of bats originating in Laurasia or Gondwana [75]. The initial explosive radiation of bats occurred in Eocene, the extinct families such as “Eochiroptera” *sensu* Van Valen (1977) found in most of continents except Antarctica [74, 76]. Modern radiation of extant taxa appears to have begun at least by Middle Eocene or earlier, a period characterized by a significant global rise in temperature after K-Pg (Cretaceous-Paleogene) mass extinction event [17, 73, 77], which coincided with 43.25 Ma divergence between Hipposideridae and Rhinolophidae.

The oldest *Rhinolophus* fossils were *Protorhinolophus shanghuangensis* fossil found recently in Shanghuang fissures, China aged Middle Eocene [70], making it older than the *Vaylatsia prisca* (*Rhinolophus priscus*) fossil found in Europe (early Late Eocene to Early Oligocene). The oldest known fossil of *Rhinolophus priscus* is dated to the Late Eocene to Oligocene in the Quercy of France (Europe), but *Protorhinolophus* shows more primitive dental patterns, which indicates the genus is older than *Rhinolophus* [70] (Fig. 2). The oldest fossil known in Africa, *R. mellali* of Bani Mellal in Morocco, North Africa were dated in Late Miocene to Early Pliocene, which is probably closely related with *R. ferrumequinum* [32]. The estimated split between Rhinolophidae and its sister lineages, Hipposideridae in the middle Eocene were supported with *Hipposideros* fossils in North Africa *Pseudorhinolophus africanum* indicated the major dispersal axis of the family from North Africa to South Europe [72] (Fig. 6, Fig. 7). In contrast with Rhinolophidae, the Hipposideridae have diversified in Europe, Africa and Arabia since the middle Eocene [70], this agrees with our ancestral range estimation result, and the widespread ancestral range of Hipposideridae (Fig. 2, Fig. 6).

Another published study hypothesized that European origin of Rhinolophidae [21] but had weaker support for species in basal clades. Bogdanowicz and Owen (1992) also hypothesized that rhinolophids dispersed from Asia to Australia through Indonesia and New Guinea based on morphological data, which indicates the ancestor of *Rhinolophus* were from Asia, which is consistent with our result, and the high Rhinolophid diversity in the Asian region [5]. The colonization of *Rhinolophus* is also limited by over-water barriers, therefore limited the dispersal events from Eurasia by the presence of Tethys oceans in Early Miocene (Fig. 7) In the late Oligocene and Early Miocene, the Tethys was connected the Proto-

Mediterranean Sea to the Indian Ocean [78] (Fig. 7), thus inhibited the ancestral range expansion from Eurasia continent to Africa continent. The Afro-Arabian and Eurasian plates collided during Middle Miocene, caused the presence of land-bridges *Gomphoterium* landbridge due to Tethys Ocean shrinkage around Late Miocene [78–81] (Fig. 7), this event may allow species to disperse from Eurasia to the Afro-Arabian continent. In general, our result suggests the ancestral Rhinolophidae originated from the Oriental region then subsequently the range expanded towards Africa through Europe, and the ancestral Hipposideridae were widespread from Afro-Arabian region to Eurasia, consistent with *Pseudorhinolophus africanum* fossils in Middle Eocene in North Africa [72].

Ancestral Biogeography range of Horseshoe bats (Rhinolophidae)

Four subset analysis (Rhinolophoidea, Rhinolophidae Oriental-Oceanian-Australia lineages and Rhinolophidae-Afro-Palearctic lineage, and cryptic Rhinolophidae) suggests estimation of dispersal rate was lower than range constriction ($d < e$). The high e in best fit model demonstrated all range-changes effectively occurred anagenetically along the branches [39][82]. Thus, we assume the distribution of Rhinolophidae driven primarily by dispersal (i.e., over-land range expansion, land-bridge colonization, and stepping-stone events) mixture with vicariance events. Additionally, jump-dispersal or founder-events was not well supported for Rhinolophidae ancestral ranges especially when we used bigger biogeographic ranges. However, jump-dispersal events were chosen as the best fit model for explaining oceanic-dispersal pattern when we separate each islands as different biogeography units (i.e., Greater Sunda Island: Sumatra, Borneo and Java). This may indicate that founder-even speciation is not a dominant force for long-distance oceanic dispersal in major lineages. Hence, the ability of an organism to disperse and diversify seems to be related to specialization of ecological niches and phenotypic adaptation (where certain ecomorphologies are more or less suited to dispersal and colonization) [83]. Range expansion by dispersal, extinction, sympatry (subset and narrow) and vicariance events appears to be relevant in explaining the historical biogeography of Rhinolophidae in Oriental-Oceania-Australia lineages, however, ancestral range of Rhinolophidae Afro-Palearctic is a better fit with dispersal, extinction, sympatry (narrow and widespread) events (without vicariance). The understanding of how organisms came to be distributed as they are also related to historical events involving complex geological history, such as glacial-inter glaciation, continental drift, biotic turnover and long-distance colonization [30]. The main event in Cenozoic era that shapes the continent including collision between the Indias plate and the Eurasian plate, created mountain ranges in Himalaya regions and acted as physical barrier for species dispersal between Indochina and India in late Eocene (around 50 Ma till present). The continuation of India attachment to Eurasia hugely affects the movement of other plates and influenced the shape of continents, archipelago and affects climatic condition in the region (Fig. 7) [47, 51, 58, 59, 84, 85].

The rapid diversification during Miocene coincided with the Mid-Miocene Climatic Optimum (around 15–18 Ma) which may provide a favourable climate in support for the evolution [86] of the *Rhinolophus* lineages. The high diversification in Miocene not only occurred in bats, but also in the diversification of

modern bird genera in Southeast Asia [62]. The basal position of two lineages in Rhinolophidae are the three species belong to *trifolius* group (*R. trifolius*, *R. luctus*, *R. formosae*) and *R. hipposideros*. The three *trifolius* species are Oriental species distributed from Indian sub-continent, Southeast Asia and Eastern Asia [4], and *R. hipposideros* is distributed throughout the Europe from Ireland in the northwest to Pakistan in the east, and south into northern regions of Africa and Saudi Arabia [20]. Phylogeographic studies suggests early colonization event of *R. hipposideros* and *R. ferrumequinum* from the east (west Asian refugium) and both of species used multiple glacial refugia across Mediterranean during the ice age [20, 87]. Last Glacial Maximum in late Pleistocene have impact on current distribution of *R. ferrumequinum*, with secondary contact was identified between Central/East China and East China/Japan [87].

Our results also show colonization of Rhinolophidae species toward Japanese archipelago may have occurred since the Middle Pliocene, which coincided with fossil from caves and fissure deposits of Middle Pleistocene, Late Pleistocene and Early Holocene in Honshu and Kyushu Island (see [88]). The colonization from continental population toward Japanese archipelago may occurred via a continuous Korean Peninsula-Japanese land bridge due to lower sea levels than at present [87], as similarly used as route for Asian black bear (*Ursus thibetanus*) [89].

Our result showed the colonization towards the Philippines appears to be multiple colonization events via different route originating from the Indomalayan region (which may via Palawan) and Wallacea region in late Miocene (Fig. 7). Similarly with Wallacean and Oceanian region, the ancestral range and colonization events in these region are complex. The thousands of island in these region have different continental, oceanic and volcanic origin, with many of them undergone rapid tectonic movement since Cenozoic [90, 91]. The archipelagoes (including Philippine and Indonesia) with the combination of tectonic movement, climatological oscillation and Pleistocene sea level fluctuations causing the changes of island size, connectivity and boundaries [92–94]. These important geological events may have contributed to current species distributions [95, 96], and as the effect of presence or absence of Pleistocene land-bridge connection [93]. In addition, current distribution of species in the archipelago may be a direct result of when bats reaching the older islands longer ago and younger island more recently which leading to allopatric and vicariance speciation [97].

Two hypothesis of species biogeography in Philippine including Pleistocene aggregate island complexes (PAICs) suggesting land exposure in the Pleistocene due to glaciation allowed species to expand their range inter five major islands [98]. Palawan Ark Hypothesis suggested species “rafted” with North Palawan block since the separation from mainland Asia by Early Oligocene 30 Ma [51], in contact with Borneo around 15 Ma [94] and then move northward toward present position [99, 100]. The multi-route colonization of Rhinolophidae species toward the Philippines is similar to other taxa, for instance *Begonia* [101], *Cynopterus* and *Macroglossus* [102, 103]. This coincided with theory of biotic colonization of Philippines, postulated as submerged land bridges, with many taxa known to have colonized Philippine through northern Philippines (from mainland Asia and Palawan) and through south route (via

Sulu archipelago and Sulawesi) [104]. Previous study also suggested that colonization of the Philippines may have taken place from the Sunda Shelf (Sumatra, Java and Borneo) and Wallacea [93].

Wallacea, including Sulawesi Island, and many small islands surrounding (i.e., Outer Banda Arc (Sumba, Timor, Babar, Yamdena, Kai, Seram), Inner Banda Arc (Bali, Lombok, Sumbawa, Flores, Alor and Wetar), Halmahera etc) result from complex tectonic plate movement from Australian and Asian plate. Some of the islands were never connected in the past (e.g. Inner and Outer Banda Arc), and Inner Banda Arc exposed the land above sea-level and therefore permitted the colonization in Lesser Sunda Islands around 3 Ma [105]. The current arrangement of the islands provides a series of stepping stones facilitating movement of terrestrial mammals, which may include volant mammals, to colonize the Australian region [48].

Furthermore, glacial and sea-level fluctuation repeatedly formed land bridges in Pleistocene [106] and the landmass between Asia, Sumatra, Borneo and Java islands (Sundaland) [51] allowed colonialization and range expansion of Rhinolophidae from Indochina towards Sumatra and Borneo, which is in line with our results here. The diversification of *Rhinolophus* species in Borneo Island may coincide with separation of Sundaic and Indochinese rainforests [54]. The rainforest refugia in some parts of Borneo and Sumatra may have allowed populations of forest-species to diverge and adapt with local climatic conditions and environment [54, 107, 108]. The glaciation and interglacial events during Plio-Pleistocene caused dramatic changes in climate, forest cover and the connection between land areas allowed species to colonize different geographic ranges. Recent diversification within species groups in Pleistocene may coincide with climatic fluctuations which affect the vegetation transition in the region, and the possible savanna corridor in part of the region [107, 109], thus indirectly influencing diversification of forest-dwelling mammals [110] and insects [111]. The divergences of *R. affinis* and *R. pusillus* lineages in Malay Peninsula during Plio-Pleistocene may coincide with the major event in the peninsula. The possible flooding of Isthmus of Kra during Pliocene, the adaptation to specific climatic conditions and long term ecological differences, combined with the peninsula effect may cause the faunal transition between Indochinese taxa and Sundaic taxa, with major transitions at the Isthmus of Kra, and the Kangar Pattani line [108, 110, 112, 113] (Fig. 7). Furthermore, the sea-level rises during Pliocene isolated Sumatra, Borneo and Java Islands in Indonesia created physical barriers between Indochina and species from the islands [51, 62]. Borneo is the largest landmass of former Sundaland and has served as stable land for at least 20 million years and was less affected by sea-level changes compared with Sumatra (which has come together as a stable from 5–10 Ma) and Java (2–5 Ma) [54, 62].

High rhinolophids diversity in Asia compared to the other biogeographic regions may be expected as many species are restricted to islands or group of islands, for instance four endemic species in Japan (i.e., *R. cornutus*, *R. pumilus*, *R. perditus*, *R. imaizumii*) (Ohdachi et al. 2015) and four endemic in the Philippines (i.e., *R. inops*, *R. rufus*, *R. subrufus*, *R. virgo*) and various species endemic in Indonesia islands (i.e., *R. nereis*, *R. madurensis*, *R. keyensis*, *R. montanus*, *R. euryotis*, *R. celebensis*, *R. canuti*) [114], which represents physical barriers for bat dispersal such as water and mountain range. In contrast, Palearctic regions were influenced with repeated glaciation and in Africa, much of the relatively flat landscape that may

cause high species turn-over and high rates of gene flow which decelerating speciation compared to complex biogeographic areas in Asia [71]. The dispersal of Rhinolophidae species to Africa may be via forest corridors that appeared during middle Eocene because of the warm climate [115], and disperse the ancient species throughout southern Palearctic and Mediterranean, through Sahara Arabian and eventually into Africa [16]. The basal lineages within African radiation are *R. landeri* and *R. alcyone*, which occur in in rainforest and may indicate early colonization around late Oligocene (~ 20 Ma) through forest affinities as predicted in [18]. The closure of Tethys Ocean estimated around the Oligocene (around 27) Ma to Miocene [78, 116, 117] formed a land bridge in Arabian Peninsula which connecting Asia and Africa, and may facilitate dispersal of many animals lineages in the Miocene such as lizards [118], frogs [119], chameleons [120], and butterflies [121, 122]. As the consequences of shrinkage of Tethys sea, desert and arid conditions expanded across North Africa in the Late Miocene (around 7 Ma), marking the origin of Sahara Desert and the Middle East Desert and the Arabian Peninsula [79]. Arid adapted species colonized Africa and currently successfully inhabited most of savanna region in Sudanian, Somalia, Ethiopia and deciduous woodland in Southern Africa [19, 32].

Unlike Hipposideridae, currently there are no records of Rhinolophidae species in Madagascar. Madagascar + India + Africa are ancient fragments of Gondwana and has been separated from Gondwana since 120 Ma and, and Madagascar separated from India by 90 Ma [83]. Madagascar started to break away from Africa around 165 Ma [123] and to become isolated in Cretaceous [124], and the invasion from Africa continent toward the island may not occurred due to broad watergaps as physical barriers for dispersal as Rhinolophidae are weak fliers [32]. Additionally, higher diversity richness and endemism in Madagascar appears as a result of dispersal from Africa and followed with diversification [125, 126], and typically reflects more recent events around Plio-Pleistocene [127].

Compared with previous study implementing BioGeoBEARS for bats, the d parameter (for dispersal rate in anagenetic) shown higher than e parameter (for extinction or range contraction rate) in Pteropodidae family across the oceanic island systems, and may explained peripatric speciation within Pteropodidae species [128]. Therefore, we assumed the historical biogeography in bats varied between families which strongly relates to flight performance between species and differences in dispersal ability For instance bat colonization to Madagascar (Pteropodidae, Emballonuridae, Hipposideridae, Vespertilionidae, Nycteridae, Molossidae and Myzopodidae), with a notable of absence Rhinolophidae species (Racey et al., 2009). Wing-loading, wing-span, aspect ratio and wing shape are the main aerodynamic variables in determining the flight performance and flight efficiency of species. Rhinolophid bats generally possess broad and short, low wing loading and aspect ratio adapted for good maneuverability in foraging as slow aerial hawkers, perch hunters and gleaners (Norberg and Rayner 1987; Amador et al. 2020). However, flight would be expensive for a long distance flight and therefore limiting the ability for dispersal. Contrary to Rhinolophidae, most Pteropodidae possess high wing loading and large wing spans, with low aspect ratios that support for long distance travel but are less maneuverable [3], as a consequence many Pteropodids are restricted to various oceanic islands where they are often the only native mammal species.

True-flight abilities together with echolocation has been long considered as remarkable evolutionary features which have driven the success of bat species and enables them to occupy wide range of ecological niches, but the morphological features have evolved into current form from a common ancestor [2]. Other factors such as dispersal filters (isolation, geologic history), environmental filters (present and past climate, and environmental heterogeneity) which influence the diversity of vascular plants [129] may also have contributed in shaping the current biogeographic ranges of Rhinolophidae.

The Systematic and Ancestral Biogeography range of Hipposideridae and Rhinonycteridae.

Hipposideridae and Rhinonycteridae are the sister families within Rhinolophoidea superfamily.. Amador et al (2018), suggested the phylogenetic tree for superfamily as (Rhinonycteridae, (Hipposideridae, Rhinolophidae)) but Foley et al (2015) resolved the relationship as (Rhinolophidae, (Hipposideridae, Rhinonycteridae)), similar with species tree in this study [44]. Foley et al (2015) suggested the African species of *H. abae*, *H. caffer* and *H. jonesi* were within Asian *Hipposideros*, and *Coelops frithii*, *Aselliscus stoliczkanus* were sister to *Hipposideros* African species (*H. commersoni* and *H. vittatus*). Nevertheless, this arrangement has low branch support, and low taxonomic coverage which only includes total of 13 species of Hipposideridae Asian lineages and Afrotropical lineages. In the species tree use in this study, [44] resolved the relationship and *H. jonesi* (Afrotropical species) species fall within Oriental-Australian lineages, similar with tree topology of Amador et al (2018), paraphyly with *Aselliscus* sp, *Coelops frithii* and *Anthops ornatus* in the same lineage, which is in agreement with [130]. *H. abae* and *H. caffer* as Afrotropical species are within Afrotropical lineages (in contrast with Foley et al, 2015, but in concordance with [61]) with *Asellia tridens* in the basal of Afrotropical and Oriental-Australian tree.

For Rhinonycteridae, here we provide seven species out of nine species within family, belonging to four genera, *Triaenops*, *Paratriaenops*, *Cloeotis*, distributed in Madagascar and Afrotropical, and *Rhinonycteris* endemic to Australia with tree topology as ((*Cloeotis*, *Paratriaenops*), (*Rhinonycteris*, *Triaenops*)). This arrangement also in contrasts with Foley et al (2015) with tree topology as ((*Paratriaenops*, ((*Triaenops*, *Cloeotis*), *Rhinonycteris*)) while using six species, and Amador et al (2018) (*Paratriaenops*, (*Triaenops*, *Cloeotis*)) with absence of genus *Rhinonycteris*. Certainly, missing taxa and gene choice compromise these result, thus the tree generated in Álvarez-Carretero et al. 2021 using supermatrix genome-scale of 182 genes may assume as the latest update tree with smaller uncertainties which facilitates precise testing of historical biogeographic analysis.

The historical biogeography of family Hipposideridae is also related to complex historical geology of the Old-World regions (see discussion above) (Fig. 7). The ancestral ranges of Hipposideridae suggests an Oriental and African origin, the Oriental-Oceania-Australia lineages supports the jump-dispersal for species colonization. This explains how new lineages colonized between regions (such as island), and allowed inter-continental disjunction or oceanic-dispersal pattern (dispersal without range expansion) (Matzke 2014).

In contrast with Rhinolophidae, their dispersal rate is higher than range constriction in Hipposideridae. This indicates that ancestor Hipposideridae are able to disperse across water bodies or using land-

bridges and stepping stones. The colonization of Hipposideridae toward Greater Sunda Island may have occurred when the land was connected with Peninsula since early Miocene, followed with multiple fluctuation of sea level until the Sunda Island formed separately at 5 Ma [51, 58, 59, 85], similarly with Rhinolophidae. The Wallacea region might have played an important role as a stepping stone to colonize Oceania and Australia regions, but migration, population exchanges and secondary contact may have occurred in the past between Oceanian-Wallacean region. In concordance with Rhinolophidae ancestral ranges, the range expansion of Hipposideridae to Africa may also occurs via Arabian Peninsula and Sahara-Arabian around Oligocene periods (27–30 Ma). Even though the *Gomphoterium* landbridge and Tethys Ocean closed around the Late Miocene, the marine barriers did not totally prevent mammalia exchanges between Eurasia and Afro-Arabian, for example for proboscideans [131]. Ancestral Hipposideridae were widespread in Eurasia and Africa since the end of Early Eocene with the evidence of fossils records in Africa and Arabia [72].

The colonization of Hipposideridae toward the Philippines, Wallacea, Oceania and Australia coincided with acceleration of the orogeny of Philippine archipelago, Wallacea with the orogeny of Sulawesi and the main stages of the New Guinean orogeny in Oligocene [51, 85, 121]. Our result suggests Oceanian colonization since early Miocene (~ 20 Ma), similarly with passerine birds by [132]. However, central range of present day of Papua New-Guinea likely did not begin to appear as land until the early-middle Miocene (14–16 Ma) [133] and the present form is predicted since 4–5 Ma. Therefore, founder-events may have involved in island-hopping across the final fragments of a proto-Papuan archipelago in Hipposideridae [134].

Rhinonycteridae split earlier from the common ancestor Hipposideridae Afrotropical lineage around Middle Miocene 40.55 Ma (95% HPD = 36.98–44.14 Ma), but species diversification occurred since 21.88 Ma (95% HPD = 16.54–28.48 Ma) with most of extant species distributed in Madagascar, except *Rhinonycteris aurantia* which is distributed in Australia. Our result suggests the origin of Rhinonycteridae in Madagascar was Sudanian + Somalia + Ethiopia with *Paratriaenops* and *Triaenops* was recently emerged in Plio-Pleistocene epoch (1–3 Ma). This coincided with previous study, stated that most the present-day organism in Madagascar is predominantly of African origin [125]. Dispersal over-water may explained the colonization of ancient Rhinonycteridae in Madagascar, followed with diversification and *in-situ* radiation, which coincided with Plio-Pleistocene climate cycles [127]. The ancestral *Cloetis percivali* may have high dispersal ability allowed the ancestor to exchange from Madagascar to Southern Africa. This associated with our result that suggests the higher extinction rate in this lineages, indicates that the extinction on species in ancestral range followed with colonization of descendants to the new area. The endemic species in Australia belong to Rhinonycteridae, *Rhinonycteris aurantia* is the only species that currently distributed outside Africa continent [14]. The colonization event of this species toward Australia is challenging to explain, our result shows the African origin but it is almost impossible to explain range extension from Africa to Australia with diversification around Miocene. Some possible hypothesis maybe long distance dispersal over water barrier from Africa to Australia, however the dispersal mechanisms are unknown considering the species is weak fliers. Some of hypothesis suggests that bats colonized Australia by storm-blown to continental shore, for example red flying foxes (*Pteropus*

scapulatus) [135], though landbridges between North Australia and Papua existed for extended periods of time. Ancestral *Rhinonycteris* may have entered Australia before the Miocene, with fossil evidence of *Rhinonycteris tedfordi* dating around Miocene from Riversleigh, Northwestern Queensland [136]. Alternative hypothesis suggest waif dispersal and stepping stone through Asia, Sundaland, Wallacea and Oceania [135], therefore, how this species colonized the region still debatable, but low diversity means that species in intermediate regions may have become extinct.

The evolutionary history of species divergence in potential cryptic Rhinolophidae and the comparisons with previous study

Indomalaya is the region with particularly high species diversity of Rhinolophidae and Hipposideridae. However, many species are cryptic suggest the number of species currently underestimate [137]. Chornelia et al. (2022) identify around 40% of potential cryptic species within complex species based on integrative taxonomic approaches, with estimated around 44 potential cryptic species from total of 10 *Rhinolophus* species *sensu lato*. In order to estimate the time of divergence between Rhinolophidae *sensu-lato* species and between potential cryptic species, we ran Bayesian Evolutionary Analysis using Sampling Trees (BEAST) as described in Materials and Methods section.

Our posterior ages estimated Rhinolophidae and Hipposideridae split about 40.26 Ma (95% HPD = 37–43.5 Ma, Middle Eocene) falling within the range of time divergence from previous publications 39–45 Ma [13, 24, 25, 44, 112], similarly, *R. shameli* and *R. creaghi* were predicted to split around 3.99 Ma and Foley et al (2015) predicted the time split between two species around 4 Ma (95% HPD = 3–5 Ma), and Álvarez-Carretero et al. (2021) estimated the time divergences as 4.15 Ma (95% HPD = 1.94–7.08 Ma). Our analysis shows the diversification of bats in Southeast Asia was rapid at 24 Ma (95% HPD = 18–31 Ma), in concordance with Álvarez-Carretero et al. (2021) at 22.77 Ma (95% HPD = 19.25–26.51), while Foley et al 2015 predicted the diversification within Rhinolophidae was slightly lower at 17 Ma generated from nuclear exons and introns. The robustness of nodes time estimates in BEAST were related to the choice of clock model and tree priors. A poor choice of tree prior may reduce accuracy of node time estimation [67]. Relaxed clock log normal was the best fit to our data considering the database where it represents a wider geographic region [66, 138]. The birth-death tree prior was selected for our dataset as it consistently provides precise result and were a better choice for mixed dataset. Thus, we expected this analysis to provide a better estimation of dating divergence for cryptic *Rhinolophus* in the region, to complement the analysis from previous studies when some species are missing.

However, comparison of time divergence estimation across the genes is challenging because of the limited number of species used in previous studies, and the paucity of the bat fossil records. We acknowledge the discordance of time tree in this study with other study, which also due to differences in systematic taxa coverage and gene being used (as described in the “Introduction” section). Although we found some discordance between tree topologies we generated in this study and previous studies, we attained similar result across subset analysis related to ancestral range estimation. In terms of species coverage from South China and the Southeast Asia region, we covered most of the described species

representing geographical regions. Our results suggest current species *sensu lato* started to diverge in the late Oligocene and Miocene, meanwhile the potential cryptic species in the region diverged in the Plio-Pleistocene epoch. This analysis indicates that geological events during the epoch contributed in shaping current cryptic diversity patterns seen today. Future directions should aim to include all Rhinolophoid species distributed in the Old-World tropics, as we currently cover around 108 (52%) species of total species identified to date (210 species; Rhinolophidae = 110, Hipposideridae = 90, Rhinonycteridae = 9 species) (Simmons and Cirranello, 2021).

Conclusion

The results presented here provide an overview of biogeographic history of extant Rhinolophoidea superfamily (Rhinolophidae, Hipposideridae and Rhinonycteridae). The result suggests that the Oriental origin, and that the Indomalayan is the ancestral origin of Rhinolophidae and Hipposideridae, but Rhinonycteridae ancestor originated from Africa. The result showed lower dispersal rate (range expansion) than extinction rate (range constriction) in Rhinolophidae, but in contrast with Hipposideridae Oriental-Oceania-Australia lineage. Jump dispersal events were selected to explained the ancestral range in Hipposideridae Oriental lineages. Current distribution of extant taxa appears to be a result of combination dispersal, extinction, sympatry and vicariance events, followed with complex geological history of the Old-World regions. Further study combining complete species coverage of Rhinolophidae, Hipposideridae and Rhinonycteridae may increase the resolution of the historical biogeography of these taxa.

Abbreviations

OOA : Oriental-Oceanian-Australia

AMP : Afrotropical-Madagascar-Palearctic

BioGeoBEARS : Biogeography with Bayesian (and likelihood) Evolutionary Analysis in R Script

Ma : Million of years ago

GBIF : Global Biodiversity Information Facility

DEC : Dispersal-Extinction Cladogenetic

d : dispersal

e : extinction

j : jump-dispersal or founder-event

BEAST : Bayesian Evolutionary Analysis by Sampling Trees

GenSA : Generalized Simulated Annealing

LRT : Likelihood Ratio Test

AICc, AICc_wt : Akaike Information Criterion corrected and weighted

HPD : Highest Posterior Density

Declarations

Ethics approval and consent to participate

This article does not involve any studies with human participants, and the animal study was reviewed and approved by Xishuangbanna Tropical Botanical Garden Ethics Committee.

Consent for publication

Not applicable

Availability of data and materials

All data used in this study are provided in this document.

Competing interests

The authors declare no competing interests and the research conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

Author's contribution

AC and ACH conceived the study, edited and revised the manuscript. AC compiled the data, conducted the analyses and drafted the initial draft of the manuscript, ACH compiled and processed the fossil data. Both of authors read and approved the final manuscript.

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References

1. Simmons NB, Cirranello AL. Bat Species of the World: A taxonomic and geographic database. <https://batnames.org/>. 2021. <https://batnames.org/>. Accessed 1 Jun 2021.
2. Anderson SC, Ruxton GD. The evolution of flight in bats: a novel hypothesis. *Mamm Rev*. 2020;50:426–39.
3. Amador LI, Almeida FC, Giannini NP. Evolution of Traditional Aerodynamic Variables in Bats (Mammalia: Chiroptera) within a Comprehensive Phylogenetic Framework. *J Mamm Evol*. 2020;27:549–61.
4. Csorba G, Ujhelyi P, Thomas N. Horseshoe Bats of the world (Chiroptera: Rhinolophidae). Shropshire: Alana Books; 2003.
5. Chornelia A, Lu J, Hughes AC. How to Accurately Delineate Morphologically Conserved Taxa and Diagnose Their Phenotypic Disparities: Species Delimitation in Cryptic Rhinolophidae. (Chiroptera). 2022;10:1–18.
6. Vanderelst D, Reijniers J, Firzlaff U, Peremans H. Dominant glint based prey localization in horseshoe bats: A possible strategy for noise rejection. *PLoS Comput Biol*. 2011;7.
7. Vanderelst D, Reijniers J, Steckel J, Peremans H. Information generated by the moving pinnae of *rhinolophus rouxi*: Tuning of the morphology at different harmonics. *PLoS One*. 2011;6.
8. Reijniers J, Vanderelst D, Peremans H. Morphology-induced information transfer in bat sonar. *Phys Rev Lett*. 2010;105:1–4.
9. Zhang Z, Truong SN, Müller R. Acoustic effects accurately predict an extreme case of biological morphology. *Phys Rev Lett*. 2009;103:1–4.
10. Zhuang Q, Müller R. Noseleaf furrows in a horseshoe bat act as resonance cavities shaping the biosonar beam. *Phys Rev Lett*. 2006;97.
11. Vanderelst D, Lee YF, Geipel I, Kalko EKV, Kuo YM, Peremans H. The noseleaf of *Rhinolophus formosae* focuses the frequency modulated (FM) component of the calls. *Front Physiol*. 2013;4:1–9.
12. Kingston T, Lara MC, Jones G, Akbar Z, Kunz TH, Schneider CJ. Acoustic divergence in two cryptic *Hipposideros* species: a role for social selection ? *Proceeding R Soc London*. 2001;268:1381–6.
13. Foley NM, Thong VD, Soisook P, Goodman SM, Armstrong KN, Jacobs DS, et al. How and why overcome the impediments to resolution: Lessons from rhinolophid and hipposiderid bats. *Mol Biol Evol*. 2015;32:313–33.
14. Armstrong KN, Goodman SM, Benda P, Hand SJ. A common name for the bat family Rhinonycteridae—the Trident Bats. *Zootaxa*. 2016;4179:115–7.
15. Amador LI, Moyers Arévalo RL, Almeida FC, Catalano SA, Giannini NP. Bat Systematics in the Light of Unconstrained Analyses of a Comprehensive Molecular Supermatrix. *J Mamm Evol*. 2018;25:37–70.
16. Stoffberg S, Jacobs DS, Mackie IJ, Matthee CA. Molecular phylogenetics and historical biogeography of *Rhinolophus* bats. *Mol Phylogenet Evol*. 2010;54:1–9.
17. Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Sci (80-)*. 2005;307:580–4.

18. Dool SE, Puechmaille SJ, Foley NM, Allegrini B, Bastian A, Mutumi GL, et al. Nuclear introns outperform mitochondrial DNA in inter-specific phylogenetic reconstruction: Lessons from horseshoe bats (Rhinolophidae: Chiroptera). *Mol Phylogenet Evol.* 2016;97 January:196–212.
19. Demos TC, Webala PW, Goodman SM, Kerbis Peterhans JC, Bartonjo M, Patterson BD. Molecular phylogenetics of the African horseshoe bats (Chiroptera: Rhinolophidae): expanded geographic and taxonomic sampling of the Afrotropics. *BMC Evol Biol.* 2019;19:1–14.
20. Dool SE, Puechmaille SJ, Dietz C, Juste J, Ibáñez C, Hulva P, et al. Phylogeography and postglacial recolonization of Europe by *Rhinolophus hipposideros*: Evidence from multiple genetic markers. *Mol Ecol.* 2013;22:4055–70.
21. Servent AG, Francis CM, Ricklefs RE. Phylogeny and Biogeography of the Horseshoe Bats. In: *Horseshoe bats of the World (Chiroptera: Rhinolophidae)*. 2003. p. xii–xxiv.
22. Patrick LE, Mcculloch ES, Ruedas LA. Systematics and biogeography of the arcuate horseshoe bat species complex (Chiroptera, Rhinolophidae). *Zool Scr.* 2013;42:553–90.
23. Shi JJ, Rabosky DL. Speciation dynamics during the global radiation of extant bats. *Evol (N Y)*. 2015;69:1528–45.
24. Teeling EC. A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record. *Sci (80-)*. 2005;307:580–4.
25. Eick GN, Jacobs DS, Matthee CA. A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). *Mol Biol Evol.* 2005;22:1869–86.
26. Simmons NB. Evolution. An Eocene big bang for bats. *Science.* 2005;307:527–8.
27. Jones KE, Bininda-Emonds ORP, Gittleman JL. Bats, Clocks, and Rocks: Diversification Patterns in Chiroptera. *Evol (N Y)*. 2005;59:2243.
28. Sanmartín I. Historical Biogeography: Evolution in Time and Space. *Evol Educ Outreach.* 2012;5:555–68.
29. Crisci JV, Katinas L. Darwin, historical biogeography, and the importance of overcoming binary opposites. *J Biogeogr.* 2009;36:1027–32.
30. Crisp MD, Trewick SA, Cook LG. Hypothesis testing in biogeography. *Trends Ecol Evol.* 2011;26:66–72.
31. Guillen-Servent A, Francis CM, Ricklefs RE. Phylogeography and bioeogeography of the horseshoe bats (Chiroptera: Rhinolophidae). In: Csorba G, Ujhelyi P, Thomas N, editors. *Horseshoe bats of the World (Chiroptera: Rhinolophidae)*. Shropshire: Alana Books; 2003. pp. xii–xxii.
32. Bogdanowicz W, Owen RD. Phylogenetic analyses of the bat family Rhinolophidae. *J Zool Syst Evol Res.* 1992;30:142–60.
33. Norberg UM, Rayner JMV. Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philos Trans R Soc Lond B*

- Biol Sci. 1987;316:335–427.
34. Luo B, Santana SE, Pang Y, Wang M, Xiao Y, Feng J. Wing morphology predicts geographic range size in vespertilionid bats. *Sci Rep.* 2019;9:1–6.
 35. Moyers Arévalo RL, Amador LI, Almeida FC, Giannini NP. Evolution of Body Mass in Bats: Insights from a Large Supermatrix Phylogeny. *J Mamm Evol.* 2020;27:123–38.
 36. Burland TM, Wilmer JW, Burland TM, Wilmer JW. Seeing in the dark: molecular approaches to the study of bat populations. *Biol Rev.* 2007;76:389–409.
 37. Matzke NJ. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst Biol.* 2014;63:951–70.
 38. Landis MJ, Matzke NJ, Moore BR, Huelsenbeck JP. Bayesian analysis of biogeography when the number of areas is large. *Syst Biol.* 2013;62:789–804.
 39. Massana KA, Beaulieu JM, Matzke NJ, O’Meara BC. Non-null Effects of the Null Range in Biogeographic Models: Exploring Parameter Estimation in the DEC Model. *bioRxiv.* 2015.
 40. Matzke NJ. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Front Biogeogr.* 2013;5.
 41. Heine C, Yeo LG, Müller RD. Evaluating global paleoshoreline models for the Cretaceous and Cenozoic. *Aust J Earth Sci.* 2015;62:275–87.
 42. Ree RH, Smith SA. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst Biol.* 2008;57:4–14.
 43. Ronquist F. Dispersal-Vicariance Analysis: A New Approach to the Quantification of Historical Biogeography. 1997;46:195–203.
 44. Álvarez-Carretero S, Tamuri AU, Battini M, Nascimento FF, Carlisle E, Asher RJ, et al. A Species-Level Timeline of Mammal Evolution Integrating Phylogenomic Data. *Nature.* 2021. <https://doi.org/10.1038/s41586-021-04341-1>.
 45. Revell LJ. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol.* 2012;3:217–23.
 46. Hughes AC, Orr MC, Ma K, Costello MJ, Waller J, Provoost P, et al. Sampling biases shape our view of the natural world. *Ecography (Cop).* 2021;44:1259–69.
 47. Holloway JD, Hall R. SE Asian geology and biogeography: an introduction. Leiden: Backhuys Publishers; 1996.
 48. Turner H, Hovenkamp P, Van Welzen PC. Biogeography of Southeast Asia and the West Pacific. *J Biogeogr.* 2001;28:217–30.
 49. Huggett R. Biogeographical Regions. In: eLS. Chichester; 2011. p. 1–9.
 50. Parnell J. The biogeography of the Isthmus of Kra region: A review. *Nord J Bot.* 2013;31:001–15.
 51. Hall R. Reconstructing Cenozoic SE, Asia. *Geol Soc Spec Publ.* 1996;106:153–84.
 52. Sieh K, Natawidjaja D. Neotectonics of the Sumatran fault, Indonesia. *J Geophys Res.* 2000;105:28295.

53. Stauffer PH. Malaya and Southeast Asia in the pattern of continental drift. *Bull Geol Soc Malaysia*. 1974;7 June:89–138.
54. De Bruyn M, Stelbrink B, Morley RJ, Hall R, Carvalho GR, Cannon CH, et al. Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Syst Biol*. 2014;63:879–901.
55. Ung V, Zaragueta-Bagils R, Williams DM. Comparative biogeography of Southeast Asia and the West Pacific region. *Biol J Linn Soc*. 2016;117:372–85.
56. Holt BG, Lessard J-P, Borregaard MK, Fritz SA, Araujo MB, Dimitrov D, et al. An update of Wallace's zoogeographic regions of the world. *Sci (80-)*. 2013;339:74–9.
57. Woodruff DS, Turner LM. The Indochinese-Sundaic zoogeographic transition: A description and analysis of terrestrial mammal species distributions. *J Biogeogr*. 2009;36:803–21.
58. Lohman DJ, de Bruyn M, Page T, von Rintelen K, Hall R, Ng PKL, et al. Biogeography of the Indo-Australian Archipelago. *Annu Rev Ecol Evol Syst*. 2011;42:205–26.
59. Hall R. Southeast Asia's changing palaeogeography. *Blumea J Plant Taxon Plant Geogr*. 2009;54:148–61.
60. Linder HP, de Klerk HM, Born J, Burgess ND, Fjeldså J, Rahbek C. The partitioning of Africa: Statistically defined biogeographical regions in sub-Saharan Africa. *J Biogeogr*. 2012;39:1189–205.
61. Patterson BD, Webala PW, Lavery TH, Agwanda BR, Goodman SM, Peterhans JCK, et al. Evolutionary relationships and population genetics of the afro-tropical leaf-nosed bats (Chiroptera, Hipposideridae). *Zookeys*. 2020;2020:117–61.
62. Sheldon FH, Lim HC, Moyle RG. Return to the Malay Archipelago: the biogeography of Sundaic rainforest birds. *J Ornithol*. 2015;156 DECEMBER:90–113.
63. Xiang Y, Gubian S, Suomela B, Hoeng J. Generalized Simulated Annealing for Efficient Global Optimization: the GenSA Package for R. *R J*. 2013;5:2013.
64. Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, et al. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Comput Biol*. 2019;15:1–28.
65. Maddison W, Maddison DR. Mesquite: a modular system for evolutionary analysis. Version 3.70. 2021. <http://www.mesquiteproject.org>.
66. Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. Relaxed Phylogenetics and Dating with Confidence. *PLoS Biol*. 2006;4:699–710.
67. Ritchie AM, Lo N, Ho SYW. The impact of the tree prior on molecular dating of data sets containing a mixture of inter- and intraspecies sampling. *Syst Biol*. 2017;66:413–25.
68. Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst Biol*. 2018;67:901–4.
69. Matzke NJ. Model Selection in Historical Biogeography Reveals that Founder-Event Speciation Is a Crucial Process in Island Clades. 2014;63:951–70.

70. Ravel A, Marivaux L, Qi T, Wang YQ, Beard KC. New chiropterans from the middle Eocene of Shanghuang (Jiangsu Province, Coastal China): New insight into the dawn horseshoe bats (Rhinolophidae) in Asia. *Zool Scr.* 2014;43:1–23.
71. Maree S, Grant WS. Origins of Horseshoe Bats (Rhinolophus, Rhinolophidae) in Southern Africa : Evidence from Allozyme Variability. *J Mamm Evol.* 1997;4:195–215.
72. Ravel A, Adaci M, Bensalah M, Charruault A-L, Essid EM, AMmar HK, et al. Origine et radiation initiale des chauves-souris modernes: nouvelles découvertes dans l'Éocène d'Afrique du Nord. *Geodiversitas.* 2016;38:355–434.
73. Gunnell GF, Simmons NB. Fossil evidence and the origin of bats. *J Mamm Evol.* 2005;12:209–46.
74. Simmons NB, Seymour KL, Habersetzer J, Gunnell GF. Primitive Early Eocene bat from Wyoming and the evolution of flight and echolocation. *Nature.* 2008;451 February:818–21.
75. Springer MS, Meredith RW, Janecka JE, Murphy WJ. The historical biogeography of mammalia. *Philos Trans R Soc B Biol Sci.* 2011;366:2478–502.
76. Jones KE, Bininda-Emonds ORP, Gittleman JL. Bats, clocks, and rocks: Diversification patterns in Chiroptera. *Evol (N Y).* 2005;59:2243–55.
77. Ravel A, Marivaux L, Tabuce R, Adaci M, Mahboubi M, Mebrouk F, et al. The oldest African bat from the early Eocene of El Kohol (Algeria). *Naturwissenschaften.* 2011;98:397–405.
78. Rögl F. Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Ann des Naturhistorischen Museums Wien.* 1998;99A April:279–310.
79. Zhang Z, Ramstein G, Schuster M, Li C, Contoux C, Yan Q. Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. *Nature.* 2014;513:401–4.
80. Ricou LE, Mercier De Lepinay B, Marcoux J. Evolution of the tethyan seaways and implications for the oceanic circulation around the eocene-oligocene boundary. *Dev Palaeontol Stratigr.* 1986;9 C:387–94.
81. Rögl F. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene Paleogeography (Short Overview). *Geol Carpath.* 1999;August:339–49.
82. Massana KA, Beaulieu JM, Matzke NJ, O'Meara BC. Non-null effects of the null range in biogeographic models: exploring parameter estimation in the DEC model. *bioRxiv.* 2015.
83. Pyron RA. Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Syst Biol.* 2014;63:779–97.
84. Fleming TH, Racey P, Woodruff DS, Turner LM, Wilting A, Sollmann R, Meijaard E, et al. The Indochinese-Sundaic zoogeographic transition: A description and analysis of terrestrial mammal species distributions. *J Biogeogr.* 2009;42:803–21.
85. Hall R. Late Jurassic-Cenozoic reconstructions of the Indonesian region and the Indian Ocean. *Tectonophysics.* 2012;570–571:1–41.
86. Zhang L, Sun K, Feng J. Complete mitochondrial genome of the big-eared horseshoe bat *Rhinolophus macrotis* (Chiroptera, Rhinolophidae). *Mitochondrial DNA Part A DNA Mapping. Seq*

- Anal. 2016;27:4078–9.
87. Flanders J, Wei L, Rossiter SJ, Zhang S. Identifying the effects of the Pleistocene on the greater horseshoe bat, *Rhinolophus ferrumequinum*, in East Asia using ecological niche modelling and phylogenetic analyses. *J Biogeogr.* 2011;38:439–52.
 88. Ohdachi S, Ishibashi Y, Iwasa M, Fukui D, Saitoh T. Ohdachi SD, Ishibashi Y, Iwasa MA, Fukui D, Saitoh T. 2015. *The Wild Mammals of Japan*. 2nd Edition. Shoukadoh Book Sellers and the Mammal Society of Japan. Kyoto, Japan. 2nd editio. Kyoto, Japan: Shoukadoh Book Sellers and The Mammals Society of Japan; 2015.
 89. Ohnishi N, Uno R, Ishibashi Y, Tamate HB, Oi T. The influence of climatic oscillations during the Quaternary Era on the genetic structure of Asian black bears in Japan. *Heredity (Edinb).* 2009;102:579–89.
 90. Hall M, Scotia N, Zealand N. Reconstructing recent divergence: evaluating nonequilibrium population structure in New Zealand chinook salmon. 2002;:739–54.
 91. Mitchell AHG, Hernandez F, dela Cruz AP. Cenozoic evolution of the Philippine archipelago. *J Southeast Asian Earth Sci.* 1986;1:3–22.
 92. Voris HK. Maps of Pleistocene sea levels in SoutheastAsia: Shorelines, River Systems and Time Durations. *J Biogeogr.* 2000;27:1153–67.
 93. Heaney LR. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biol J Linn Soc.* 1986;28:127–65.
 94. Hall R. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: Computer-based reconstructions, model and animations. *J Asian Earth Sci.* 2002;20:353–431.
 95. Woodruff DS. Biogeography and conservation in Southeast Asia: How 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodivers Conserv.* 2010;19:919–41.
 96. Esselstyn JA, Brown RM. The role of repeated sea-level fluctuations in the generation of shrew (*Soricidae: Crocidura*) diversity in the Philippine Archipelago. *Mol Phylogenet Evol.* 2009;53:171–81.
 97. Heaney LR, Robert T. New perspectives on the long-term biogeographic dynamics and conservation of Philippine fruit bats. In: Fleming TH, Racey PA, editors. *Island bats: Evolution, Ecology and Conservation*. Chichago: The University of Chicago Press; 2009.
 98. Heaney LR. Zoogeographic evidence for Middle and Late Pleistocene land bridges to the Philippine Islands. *Mod Quarternary Res South East Asia.* 1985;9:127–43.
 99. Blackburn DC, Bickford DP, Diesmos AC, Iskandar DT, Brown RM. An ancient origin for the enigmatic flat-headed frogs (*Bombinatoridae: Barbourula*) from the Islands of Southeast Asia. *PLoS One.* 2010;5.
 100. Siler CD, Oaks JR, Welton LJ, Linkem CW, Swab JC, Diesmos AC, et al. Did geckos ride the Palawan raft to the Philippines? *J Biogeogr.* 2012;39:1217–34.

101. Hughes M, Rubite RR, Blanc P, Chung K-F, Peng C-I. The Miocene to Pleistocene colonization of the Philippine archipelago by *Begonia* sect. *Baryandra* (Begoniaceae). *Am J Bot.* 2015;102:695–706.
102. Roberts TE, Museum F, Shore SL. Multiple levels of allopatric divergence in the endemic Philippine fruit bat *Haplonycteris fischeri* (Pteropodidae). 2006;:329–49.
103. Schmitt L, Kitchener D, How R. A genetic perspective of mammalian variation and evolution in the Indonesian archipelago: biogeographic correlates in the fruit bats genus *Cynopterus*. *Evol (N Y).* 1995;49:399–412.
104. Jones AW, Kennedy RS. Evolution in a tropical archipelago: Comparative phylogeography of Philippine fauna and flora reveals complex patterns of colonization and diversification. *Biol J Linn Soc.* 2008;95:620–39.
105. Schmitt L, Hisheh S, Suyanto A, Maharadatunkamsi, Newbound C, Kitchener D, et al. Crossing the line: the impact of Contemporary and historical sea barriers on the population structure of bats in Southern Wallacea. In: Fleming TH, Racey PA, editors. *Island bats: Evolution, Ecology and Conservation*. Fleming. Chichago: The University of Chicago Press; 2009.
106. Mao XG, Zhu GJ, Zhang S, Rossiter SJ. Pleistocene climatic cycling drives intra-specific diversification in the intermediate horseshoe bat (*Rhinolophus affinis*) in Southern China. *Mol Ecol.* 2010;19:2754–69.
107. Wurster CM, Bird MI, Bull ID, Creed F, Bryant C, Dungait JAJ, et al. Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. *Proc Natl Acad Sci U S A.* 2010;107:15508–11.
108. Hughes AC, Satasook C, Bates PJJ, Bumrungsri S, Jones G. Explaining the causes of the zoogeographic transition around the Isthmus of Kra: using bats as a case study. 2011;:2362–72.
109. Hope G, Kershaw AP, van der Kaars S, Xiangjun S, Liew PM, Heusser LE, et al. History of vegetation and habitat change in the Austral-Asian region. *Quat Int.* 2004;118–119:103–26.
110. Patou ML, Wilting A, Gaubert P, Esselstyn JA, Cruaud C, Jennings AP, et al. Evolutionary history of the *Paradoxurus* palm civets - a new model for Asian biogeography. *J Biogeogr.* 2010;37:2077–97.
111. Morgan K, O'Loughlin SM, Chen B, Linton YM, Thongwat D, Somboon P, et al. Comparative phylogeography reveals a shared impact of pleistocene environmental change in shaping genetic diversity within nine *Anopheles* mosquito species across the Indo-Burma biodiversity hotspot. *Mol Ecol.* 2011;20:4533–49.
112. Woodruff DS, Turner LM. The Indochinese-Sundaic zoogeographic transition: A description and analysis of terrestrial mammal species distributions. *J Biogeogr.* 2009;36:803–21.
113. Meijaard E. Solving mammalian riddles along the Indochinese-Sundaic zoogeographic transition: New insights from mammalian biogeography. *J Biogeogr.* 2009;36:801–2.
114. Wiles GJ, Brooke AP. Wiles GJ, Brooke AP. 2009. Conservation threats to bats in the tropical Pacific Islands and insular Southeast Asia. In *Island Bats: Evolution, Ecology and Conservation*. Eds. Fleming TH and Racey PA. The University of Chicago Press. Chichago and London. In: Fleming TH,

- Racey PA, editors. *Island Bats: Evolution, Ecology and Conservation*. Chichago and London: THE University of Chicago Press; 2009. p. 2009.
115. Janis CM. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu Rev Ecol Syst*. 1993;24:467–500.
 116. Bosworth W, Huchon P, McClay K. The Red Sea and Gulf of Aden Basins. *J Afr Earth Sci*. 2005;43:334–78.
 117. Pirouz M, Avouac JP, Hassanzadeh J, Kirschvink JL, Bahroudi A. Early Neogene foreland of the Zagros, implications for the initial closure of the Neo-Tethys and kinematics of crustal shortening. *Earth Planet Sci Lett*. 2017;477:168–82.
 118. Tamar K, Metallinou M, Wilms T, Schmitz A, Crochet PA, Geniez P, et al. Evolutionary history of spiny-tailed lizards (Agamidae: Uromastyx) from the Saharo-Arabian region. *Zool Scr*. 2018;47:159–73.
 119. Yuan Z-Y, Zhang B-L, Raxworthy CJ, Weisrock DW, Hime PM, Jin J-Q, et al. Natatanuran frogs used the Indian plate to step-stone disperse and radiate across the Indian Ocean. *Natol Sci Rev*. 2018;0:1–5.
 120. Georgalis GL, Villa A, Delfino M. First description of a fossil chamaeleonid from greece and its relevance for the european biogeographic history of the group. *Sci Nat*. 2016;103.
 121. Toussaint EFA, Chiba H, Yago M, Dexter KM, Warren AD, Storer C, et al. Afrotropics on the wing: phylogenomics and historical biogeography of awl and policeman skippers. *Syst Entomol*. 2021;46:172–85.
 122. Sahoo RK, Warren AD, Collins SC, Kodandaramaiah U. Hostplant change and paleoclimatic events explain diversification shifts in skipper butterflies (Family: HesperIIDae). *BMC Evol Biol*. 2017;17:1–9.
 123. Rabinowitz PD, Coffin MF, Falvey D. The separation of Madagascar and Africa. *Sci (80-)*. 1983;220:67–9.
 124. Ali JR, Krause DW. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: Refutation of the Gunnerus Ridge causeway hypothesis. *J Biogeogr*. 2011;38:1855–72.
 125. Yoder AD, Nowak MD. Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annu Rev Ecol Evol Syst*. 2006;37:405–31.
 126. Crottini A, Madsen O, Poux C, Strauß A, Vieites DR, Vences M. Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K-T boundary in Madagascar. *Proc Natl Acad Sci U S A*. 2012;109:5358–63.
 127. Wood HM, Gillespie RG, Griswold CE, Wainwright PC. Why is Madagascar special? the extraordinarily slow evolution of pelican spiders (Aranaeae, Archaeidae). *Evolution (N Y)*. 2015;69:462–81.
 128. Tsang SM, Wiantoro S, Veluz MJ, Sugita N, Nguyen YL, Simmons NB, et al. Dispersal out of Wallacea spurs diversification of Pteropus flying foxes, the world's largest bats (Mammalia: Chiroptera). *J Biogeogr*. 2020;47:527–37.
 129. Weigelt P, Daniel Kissling W, Kisel Y, Fritz SA, Karger DN, Kessler M, et al. Global patterns and drivers of phylogenetic structure in island floras. *Sci Rep*. 2015;5:1–13.

130. Lavery TH, Leung LKP, Seddon JM. Molecular phylogeny of hipposiderid bats (Chiroptera: Hipposideridae) from Solomon Islands and Cape York Peninsula, Australia. *Zool Scr.* 2014;43:429–42.
131. Sen S. Dispersal of African mammals in Eurasia during the Cenozoic: Ways and whys. *Geobios.* 2013;46:159–72.
132. Jønsson KA, Fabre PH, Ricklefs RE, Fjeldså J. Major global radiation of corvid birds originated in the proto-Papuan archipelago. *Proc Natl Acad Sci U S A.* 2011;108:2328–33.
133. van Ufford AQ, Cloos M. Cenozoic tectonics of New Guinea. *Am Assoc Pet Geol Bull.* 2005;89:119–40.
134. Schweizer M, Wright TF, Peñalba JV, Schirtzinger EE, Joseph L. Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lorries and lorikeets (Aves: Psittaciformes). *Mol Phylogenet Evol.* 2015;90:34–48.
135. Hand SJ. On the winds of fortune. *Aust Nat Hist.* 1989;23:131–8.
136. Hand SJ. New Miocene leaf-nosed bats (Microchiroptera: Hipposideridae) from Riversleigh, Northwestern Queensland. In: *Memoirs of the Queensland Museum.* 2nd edition. Brisbane: Queensland Museum; 1997. p. 335–49.
137. Francis CM, Borisenko AV, Ivanova NV, Eger JL, Lim BK, Guillén-Servent A, et al. The role of DNA barcodes in understanding and conservation of mammal diversity in Southeast Asia. *PLoS ONE.* 2010;5:1–12.
138. Ho S. The Molecular Clock and Estimating Species Divergence | Learn Science at Scitable. 2008. <https://www.nature.com/scitable/topicpage/the-molecular-clock-and-estimating-species-divergence-41971/>. Accessed 25 May 2021.
139. Barbolini N, Woutersen A, Dupont-Nivet G, Silvestro D, Tardif D, Coster PMC, et al. Cenozoic evolution of the steppe-desert biome in Central Asia. *Sci Adv.* 2020;6:1–17.
140. De Bruyn M, Rüber L, Nylinder S, Stelbrink B, Lovejoy NR, Lavoué S, et al. Paleo-drainage basin connectivity predicts evolutionary relationships across three southeast asian biodiversity hotspots. *Syst Biol.* 2013;62:398–410.

Figures



Figure 1

The map of terrestrial zoogeographic and regions of the Old-World tropic, modified from Holt et al. (2013). Dashed lines indicate figurative borders between zoogeographic regions which we used for Rhinolophoidea superfamily analysis (Rhinolophidae, Hipposideridae and Rhinonycteridae). Bold lines indicate Wallace's Line, Huxley's Line and Lydekker's Line.

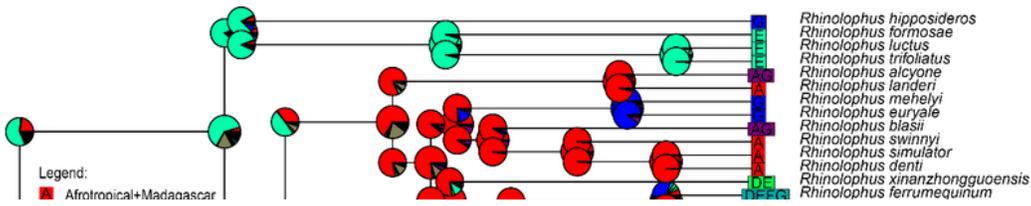


Figure 2

Ancestral range estimation for superfamily Rhinonophoidea (Rhinolophidae, Hipposideridae and Rhinonycteridae (n = 104 extant species)). Tree topology were pruned from Álvarez-Carretero et al. (2021). Pie chart indicates the relative probability of each state in the nodes and corners. The corners represent the states of the descendant lineage instantaneously after speciation and each geographic range represent in encoded colors (See inserted maps and legends). Inserted figure in the low part represent the

fossils of ancestor *Rhinolophus* and *Hipposideros*, the barline below species name indicated the timescale scored after Branch and Bound analysis, adopted from Ravel et al. (2016).

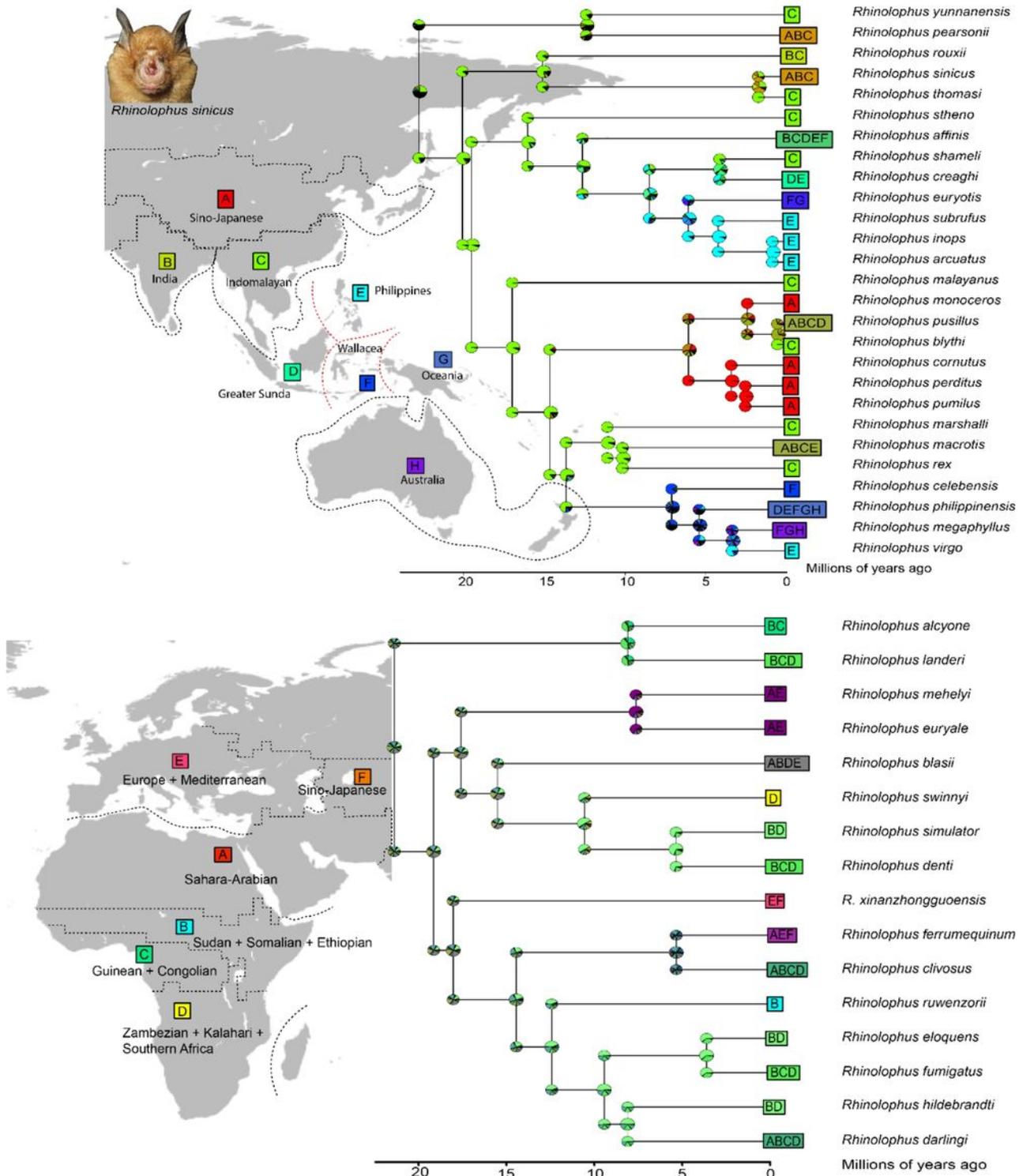


Figure 3

Ancestral range estimation for Rhinolophidae a). Oriental-Oceanian-Australia region; b) Afrotropical-Palearctic (Europe + Mediterranean) region. Inserted maps redrawing from Holt et al. 2013

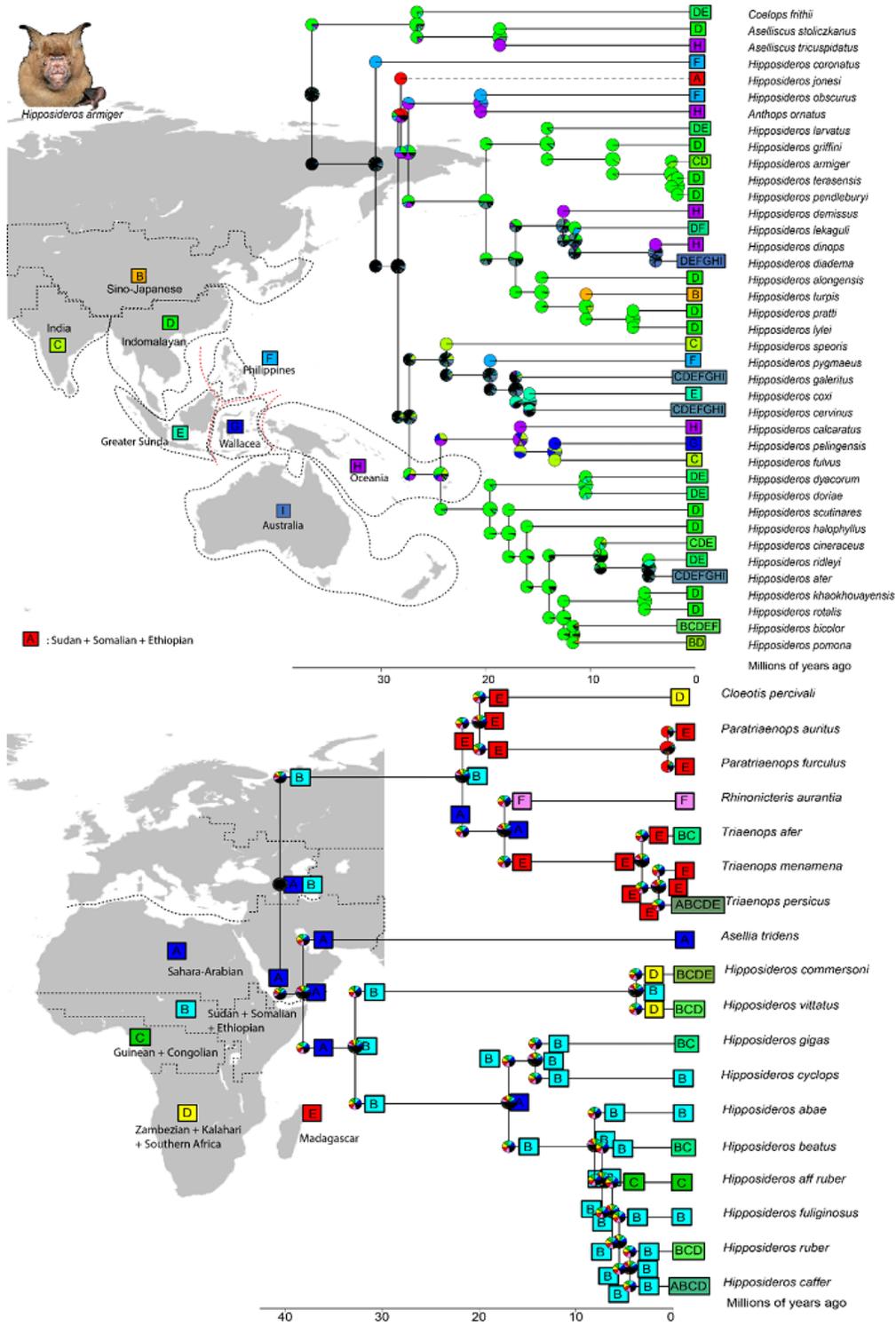


Figure 4

Ancestral range estimation for a). Hippiosideridae of Oriental-Oceanian-Australia region; b) Hippiosideridae and Rhinonycteridae of Afrotropical-Palearctic (Europe + Mediterranean) and Madagascar region. Inserted maps redrawing from Holt et al. 2013

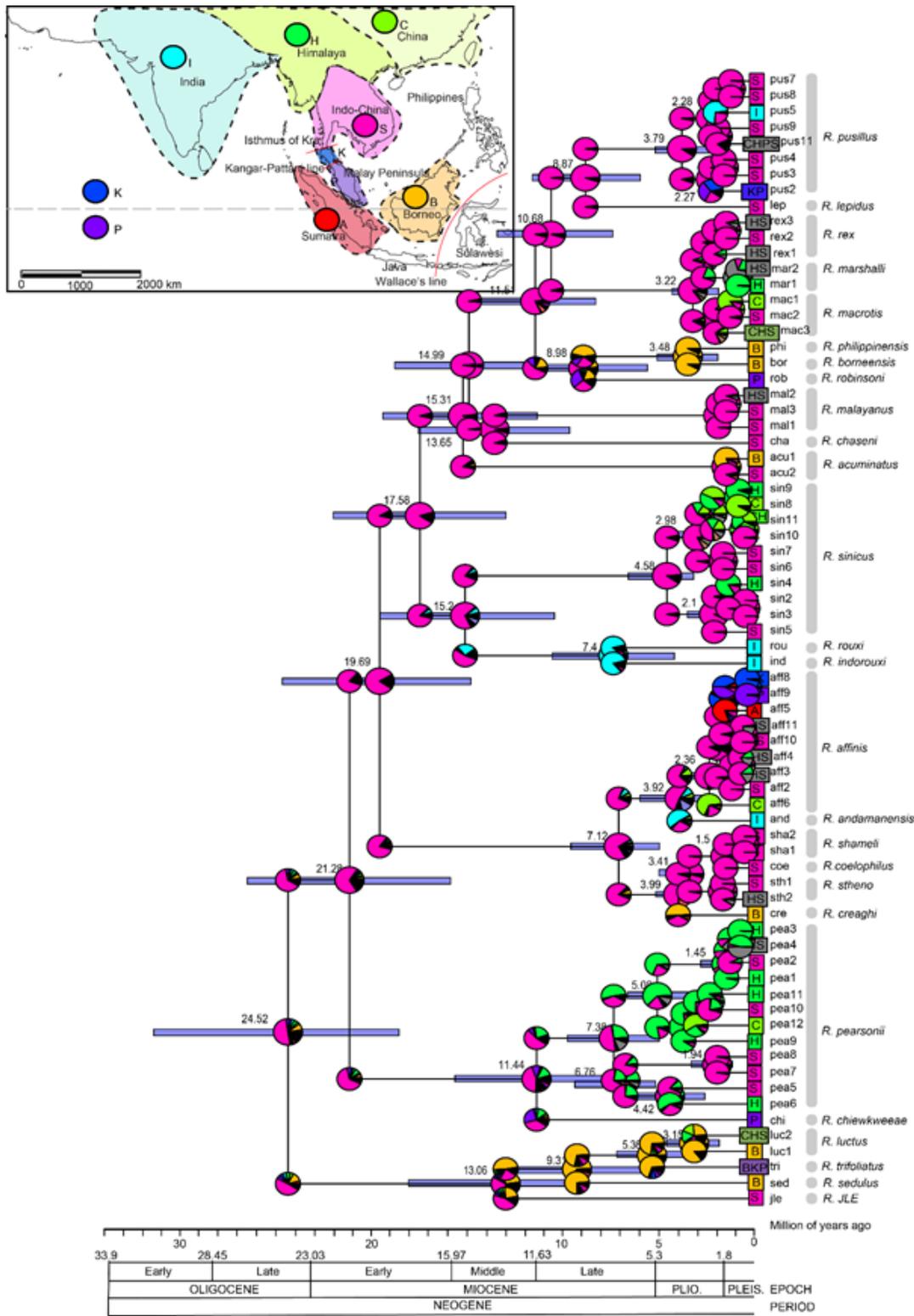


Figure 5

Historical biogeography of Rhinolophidae in Southeast Asia with representation of potential cryptic species. Date estimation with 95% Highest Posterior Density (HPD) are provided in the nodes generated from BEAST. Current distribution of extant taxa based on the distribution of potential cryptic species and sampling included in the study. Each potential cryptic species is given unique identifiers (based on Chornelia et al. 2022).

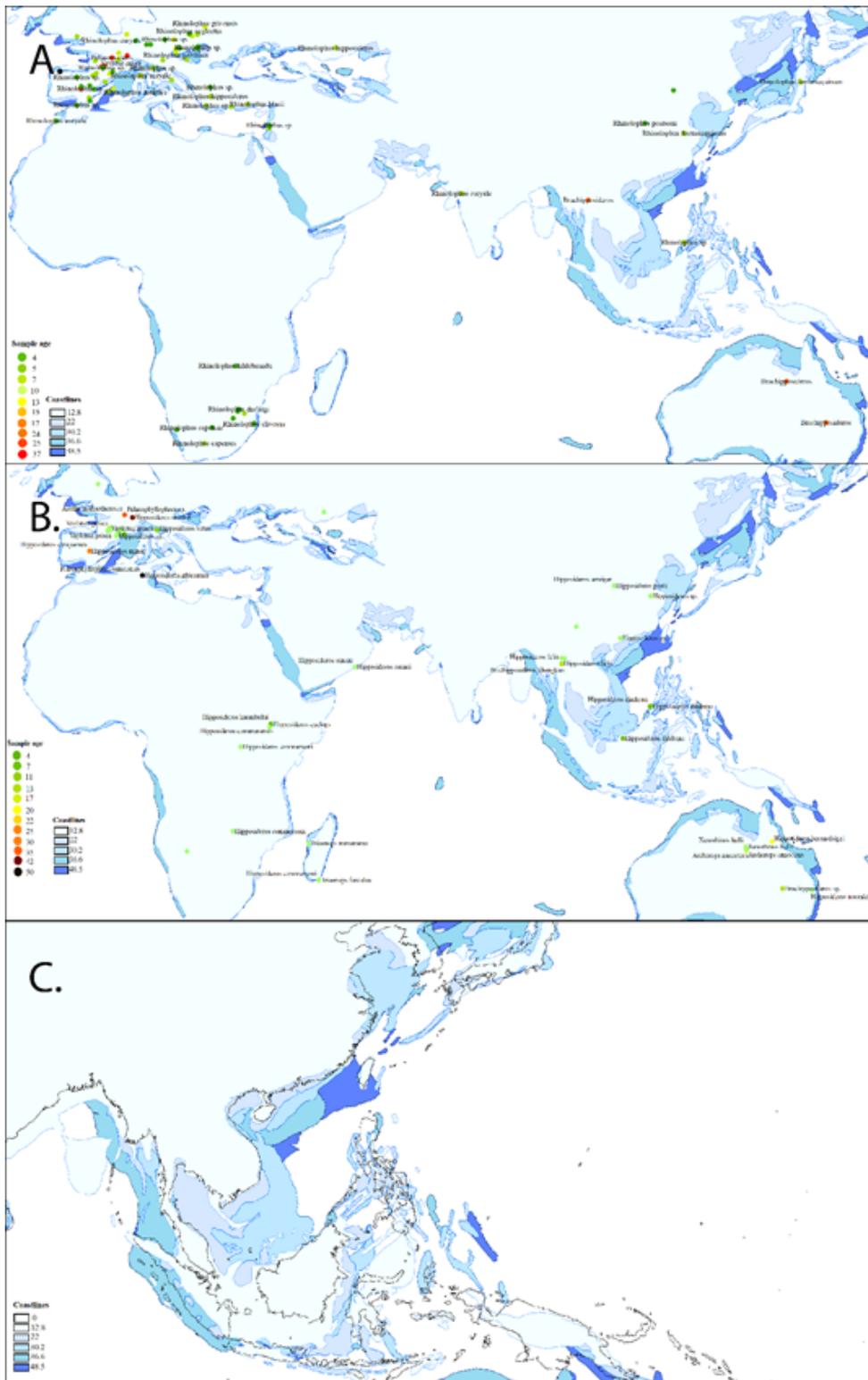


Figure 6

Palaeo map and fossil occurrences of Rhinolophidae a) Distribution of fossils findings of Rhinolophidae in Afro-Palaearctic, Oriental and Australia. Sample age and coastline in unit million of years ago, coastlines were shown per 48.5 Ma-12.8 Ma; b) Distribution of Hipposideridae fossils finding from 48.5 Ma-12.8 Ma; c) Changes in the coastline from the past and present forms of the Asian landmass.

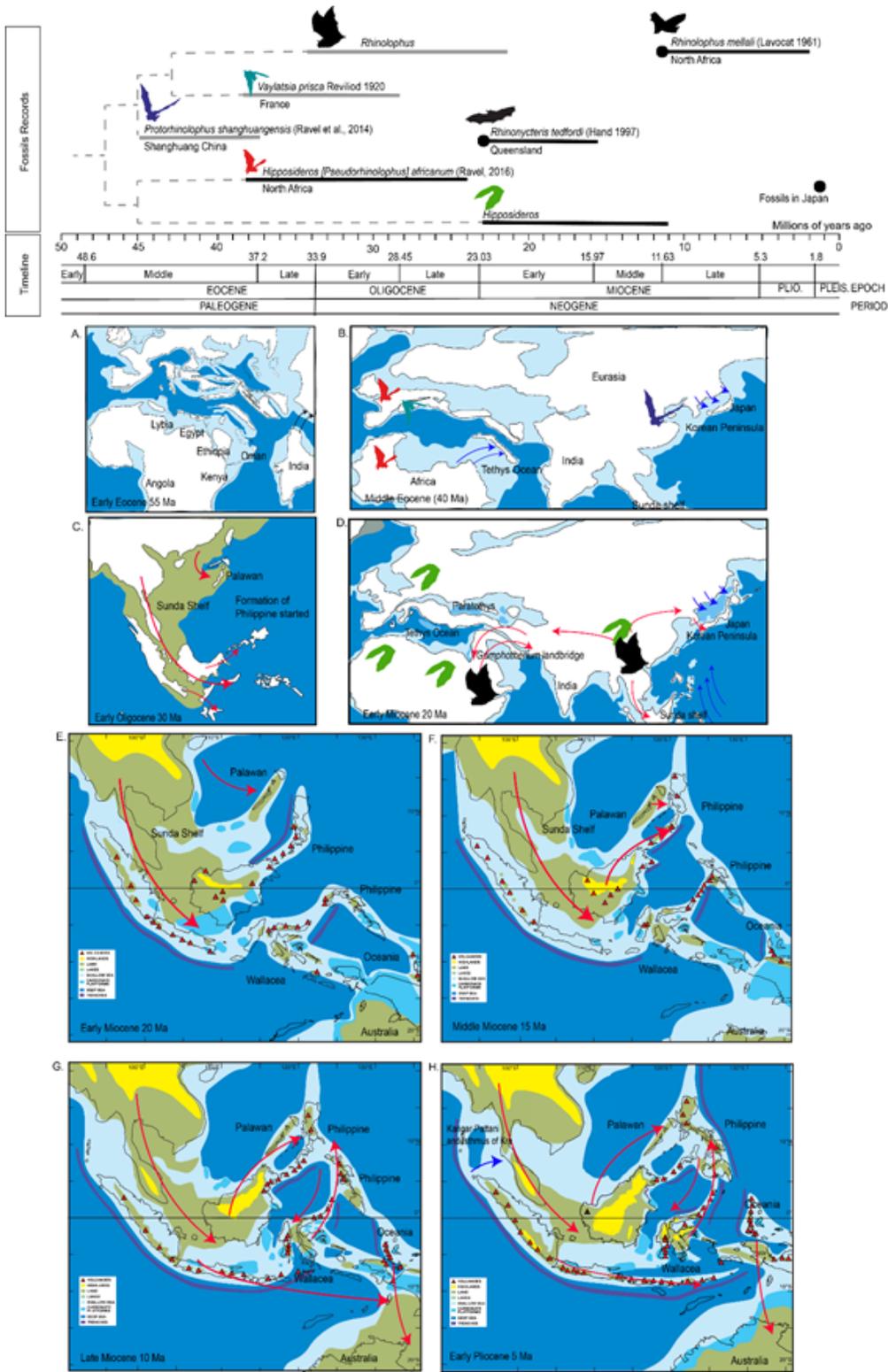


Figure 7

Summarization of historical events in the past and main records of fossils from the common ancestor *Pseudorhinolophus*, *Protorhinolophus* and *Vaylatsia* in Asia and Africa (modified from Ravel et al, 2016), including of records of Rhinolophidae fossils in Australia, Japan and North Africa. Maps A-H showed paleogeographic maps redrawing from previous publications; a) Early Eocene maps showed a sea barrier between Africa and Eurasia, with India moving upward toward Asia (modified from [131]); b) Middle

Eocene map indicated appearance of ancestral Rhinolophidae and Hipposideridae (modified from [139]; c) Early Oligocene by the start formation of Philippine Islands and Palawan still connected with Asia (modified from [100]); d) early Miocene, the closure of Tethys Ocean and formation of *Gomphoterium* landbridge (modified from [139]); e-h) the Cenozoic model per five million years in Southeast Asia with formation of Indonesia, Wallacea, Papua and the Philippines (modified from [85, 140]. The red arrows indicated possible colonization direction and blue arrowe indicated the movement direction of landmass

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