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Author for correspondence:
Jeffrey L. Weinell
e-mails: jweine2@gmail.com; jweinell@amnh.org

†Present address: Department of Herpetology, American Museum of Natural History, 200 Central Park West, New York, NY, USA.

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Novel phylogenomic inference and 'Out of Asia' biogeography of cobras, coral snakes and their allies

Jeffrey L. Weinell[1,2,†], Frank T. Burbrink[2], Sunandan Das[3] and Rafe M. Brown[1]

[1]Department of Ecology and Evolutionary Biology and Biodiversity Institute, University of Kansas, 1345 Jayhawk Blvd, Lawrence, KS 66045, USA
[2]Department of Herpetology, American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA
[3]Ecological Genetics Research Unit, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki 00014, Finland

JLW, 0000-0002-9568-0672; FTB, 0000-0001-6687-8332; SD, 0000-0002-1597-1147; RMB, 0000-0001-5338-0658

Estimation of evolutionary relati
rapidly diversified can be challe
inaccurate or unresolved phyloge
to erroneous conclusions regardi
ranges of lineages. One example
has been the historical challeng
biogeographic origin of elapoid
numerous dangerously venomous spe
not known to be dangerous to hu
distribution of this lineage ma
testing hypotheses related to h
among the many continents and ot
by contemporary elapoid species.
of genomic resources, included v
inferred a robust estimate of evo
we leveraged to quantitatively e
evolution through the deep-time
radiation. Our phylogenetic and b
historical ranges definitively r
of Africa' hypothesis and suppor
involving multiple faunal exchan
Australasia, the Americas and Eur

1. Introduction

How, why and when geographic distributions of linea questions motivating the conceptual unification of p history in the multi-disciplinary field of modern b species interactions and historical contingency hav geographic ranges [1]. Tests of specific biogeographic hypotheses exchanges require well-documented information about of Earth history and historical environmental chang evolutionary relationships and historical geographi field-based exploration and [2–6], biogeographical ranges hav characterized, at least at a continental resolution [7,8] and evolutionary relationships have been inferred fo phylogenetic studies over [9–15]. However, for groups w known about species diversity, evolutionary relatio monly known as Linnean, Darwinian and Wallacean [16–19] biogeographic sh often unknown and can be hard to accurately estimate

One such group is the snake superfamily Elapoidea families and is geographically distributed in trop major continents and in marine habitats (figure 1; [20–22]). The group biogeographic origin, however, has remained uncerta origin for this lineage—implying its ancestral expa diversification in Africa [21–29]. An African origin has also been su vertebrate groups presently or historically [30–37]. Only distrib barrier that has precluded robust quantitative biog strongly supported, time-calibrated estimate of evo (family-rank level) lineages and sublineages, has re

Here, we used a targeted sequence capture approac major elapoid lineages and outgroups. We used this fossil record of snakes to estimate a strongly sup for implementation of modern biogeographical infere biogeographical inference performed to date with re the use of powerful, statistically coherent methods we assess previous hypotheses related to historical supported by previous phylogenetic, biogeographic studies [21,25,38] supporting ancestral range expansions into or out o tion between this continent and Eurasia would neces stemmed from historical oceanic dispersal events.

2. Material and methods

2.1. Sequence capture dataset

We sampled 66 individuals from 65 species in 52 gene from ethanol-preserved tissue samples or from previo tary material, table S1). Tissues were collected by material) during field expeditions (1990–2018) and deposited in the tissue of Kansas Biodiversity Institute, University of Texa

We targeted 3128 loci and 1 517 011 nucleotides (probe kit (Arbor BioSciences) containing 20 020 120 1652 rapidly evolving exons (REEs), 907 UCEs [38], histo-compatibility, 119 vision-associated and 95 s material; Open Science Framework project [7501x3]. Targ or more entire exons and partial upstream, downstre regions. Sequence capture libraries were dual-indexe Illumina HiSeq X sequencer (NovoGene).

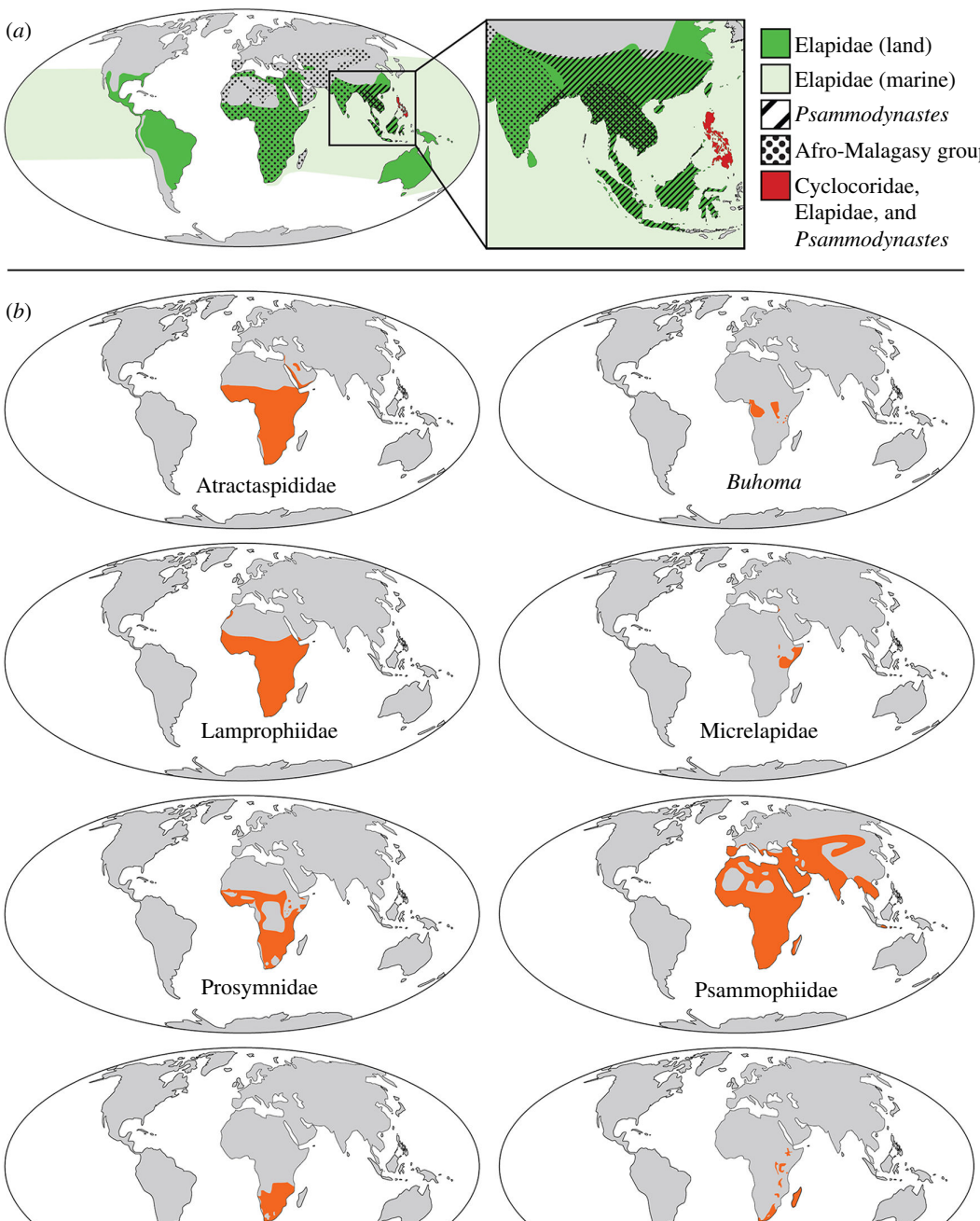

Figure 1. Geographic extents of major lineages of Elapoidea; (*a*) geographic distributions for Cyclocoridae (red), Elapidae (green or red), *Psammodynastes* (diagonal black stripes or red) and the group comprising non-elapid Afro-Malagasy lineages (black circle pattern); (*b*) geographic extent (orange) for each major lineage (family-rank or similar) of the Afro-Malagasy group.

We demultiplexed fastq files [39], trimmed by adapters [40], filtered contaminant reads by comparison with a [41,42] removed duplicate reads with 'dedupe' tool in [43]. To de novo assemble reads and dipSPAdes [45] for SPAdes [46]. To mask remaining contigs, we used BLAS contigs against probe target reference sequences, contigs into disjoint clusters [47–49] with R package 'igrap

To obtain orthologous sequences from previously as material, table S1) for each locus in our novel seq

using MAFFT 7.310 [50] generated a consensus sequence of t
'Biostrings' [51]; searched for matches to the consensus s
assembly scaffolds [52]; using BLAST+ [53] aligned sequences with
50); trimmed contiguous sites at ends of each pairw
sequence; retained the genome-derived sequence from
gaps. We excluded loci, when multiple homologous r
assembly, and we considered sequences of included l
locus alignment used for phylogenetic estimation of
genome-derived orthologs using MAFFT 7.310, and tr
contiguous region containing 90% complete data. To g
ated single locus alignments using Seqkit 2.3.0 [54] and R pa

2.2. Sanger dataset

To estimate a chronogram with dense taxonomic sampli
genetic data for 450 individuals from 434 species
non-nominate subfamilies. We combined 4D2N8A enrichment
generated novel genetic data from ethanol-preserved
genera (electronic supplementary material, table S
protein-coding genes cytochrome b (CYTB), and five
phic factor (BDNF), oocyte maturation factor mos (
activating 1 (RAG1) and recombination activating 2
digested tissues using Proteinase K enzyme and use
Instrument with Maxwell® 16 Tissue DNA Purification
of polymerase chain reaction (PCR) with annealing
designed PCR and sequencing primers (electronic sup
base pairs (bp) of CYTB and 580 bp of C-MOS. Amplif
phoresis on 1.5% agarose gels. Purification of PCR p
ups and nucleotide sequence determination were cond
de novo assembled and edited in Staden Package [55] and
aligned sequences separately with MAFFT 7.310 [50] and
Seqkit 2.4.0 [54] to trim alignment ends, identify reading fr
codons in protein coding regions and concatenate ali

2.3. Phylogenetic inference

To estimate maximum likelihood (ML) gene trees using loci
from concatenated nucleotide alignments with IQ-TREE 2.2.5
ultrafast bootstrap (UFBoot) [56]. To estimate ML gene trees
partitioned by codon position for protein-coding genes
protein-coding genes from genomes were aligned using
supplementary material; Open Science Framework, proj
ModelFinder in IQ-TREE 2.2.5 [57] to find the best-fit
substitution model for each partition. To provide
sites alignment, sites were unpartitioned in ModelFinder
to identify the best substitution model. We considere
for monophyly [

To infer the species tree with local posterior pr
ASTRAL-III 5.7.8 [58] and 1 quartet trees sampled from our estima
(UFBoot) collapsed into polytomies; we considered P
[59]. We used R package 'ape' 5.7 [60] to calculate metrics
and dissimilarity among gene, species and concatena
Distance (RFD), Strict Joint Assertions and Quartet

We inferred phylogenetic relationships using IQ-TREE 2.2.3 [57]
and optimal site-partitioning schemes in ModelFinder implemented in IQ-TREE
option '-m TESTMERGEONLYNEW'. During phylogenetic
topological constraint tree congruent at the family

additional topological constraints correspondi[ng] to previous phylogenetic studies (electronic supplemen[tary] krhx3). To initiate tree optimization, we used a st[...] resolving multichotomies in our constraint tree usi[ng] [58]. For unconstrained nodes, we assessed node suppo[rt] Shimodaira–Hasegawa-like approximate likelihood rati[o] [59,60].

2.4. Divergence time estimation

We estimated divergence times for our inferred seq[...] using RelTime-ML in MEGA [61–63]; 11 an [alignment with 10 000 sites [...] replacement from our sequence capture dataset for [...] Sanger sequence alignment (for analysis with infer[...] constraints with lognormally distributed probabilit[...] fossil record (electronic supplementary material, ta[...] (CIs) of calibrated node age probability densities: [...] 51.2 Ma); Elapidae stem node (CI: 26.8–54.0 Ma); Colubroidea [...] 41.6 Ma); [...] node (CI: 33.7–64.1 Ma); and the stem node of the clade tha[t] [...] common ancestor of Hydrophiinae (CI: 11.9–39.1 Ma).

2.5. Historical hybridization and incomplete lineage sorting

To test for historical hybridizations, we estimate[d] [...] factors (gCFs) [64] using SNaQ implemented in Julia package 'PhyloNetworks' [65,66]. [...] compared quartet trees sampled from our gene trees [...] decomposition of the species tree to estimate gCFs, [...] maximum number of reticulations (which we varied from 0 to [...] network for each number [64,67]. To estimate the optimal numb[er] [...] the set of maximum pseudolikelihood networks, we us[ed] [...] age 'capushe' [68], which calculate slope heuristics consi[...] v1.1.1 in pseudolikelihood with each increase in number [69]. We considered the [...] phylogenetic network to be the maximum pseudolikeli[hood] [...] correctly inferred as the outgroup, and number of [...] number of reticulations. We also considered histori[...] phylogenetic network contained a hybrid edge.

To assess if our phylogenetic results deviated fro[m] [...] ance factors (gDF1 and gDF2) and site discordance [...] our species tree and the phylogeny estimated from o[...] IQ-TREE 2.1.3, our single-locus alignments and quartets samp[led] [...] χ^2-tests of the hypothesis of no difference between [...] and gDF2, with significance [70,71]. Following the recommen[dation of] [...] $p < 0.05$ Lanfear [70], we binned putatively unlinked sites from o[...] bootstrap sampled one site per locus (100 bootstrap[s] [...] and sDFs from each bootstrap 'unlinked sites align[ment'] [...] repeated χ^2-tests on each bootstrapped sample to determine [...] χ^2-test results considered evidence against ILS [70], and we considered [...] whether combined with the gCF, as evidence suggesting ancestral hybridization.

2.6. Biogeographic inference

We inferred historical biogeography using BioGeoBEARS v1.1.2 [72,73] on our Sanger chro[nogram] pruned to one tip per genus of superfamilies Colub[roidea] [...] bution data compiled [74] from relevant literature [7,20,75–82]. We [...] pruned all but one species lineage per genus and tr[eated] [...] lineage as equal to the total range of the correspon[ding] [...]

We coded geographic distributions as either ...esen
mentary material, figure S1), including five physio
Australasia and Europe) and one marine region enco
Indian and Pacific oceans). Within the 'Africa' regi
most of the Arabian Plate in the Middle East. We con
islands of the Caribbean, western Atlantic and east
region. The division between 'Asia' and 'Europe' wa
Turgai Strait probably separated them ~29 Ma [83,84]. We concluded ... su
the Sunda Shelf and the Philippines within our conc
continental Australia and Sahul Shelf and southwest
biogeographic analyses because they are thought to
physiogeographical areas for most of the time hypoth
than or equal to approx. 30 Ma).

During biogeographical analyses, we used six geogr
Extinction-Cladogenesis (DEC), (ii) DEC+J, (iii) D
and (vi) BAYAREALIKE+J models, which differ in the
occur during cladogenesis [72,73]. The BAYAREALIKE model does not a
occur during cladogenesis; the DEC model allows vic
daughter lineage occupies a single region. The DIVA
if both daughter lineages have ranges spanning mul
ancestor occupies a single area. The models DEC+J, D
speciation, whereby one daughter lineage acquires a
and range evolution processes allowed by DEC, DIVAL
[72,73]. Ree and Sanmartín [85] warned against using statistical mod
DEC+J models against other biogeographic models [86], ... compared ..., wh
model selection as valid. We considered the optimal
information criterion (AIC) ... during statistical model selection.
a single biogeographic estimate and implied evolutio
ranges estimated under each suboptimal biogeographi
optimal model.

3. Results

3.1. Sequence data

Using targeted sequence capture, we obtained new ge
(electronic supplementary material, table S1), and o
included 3066 single-locus alignments and a concate
560 sites, and 77% total missing or ambiguous data (
of loci sampled per individual ... (range ... 2017 ... 2041 ...) (i p
Single-locus alignments included ... 6 ... sequences (m
5288 675 sites (median ...) ... informative sites ... 7 ... total ... 3 ...s s
ambiguous data (median 65.12%); alignment length an
correlated with number of ... (R^2 = 0.021 ... 0.062, p < 0.0...
Our Sanger genetic dataset included ... n = ... 4 ... CYTB ... 1069 ... sampled ...
nuclear loci were sampled for ... (n = 24 ... 673 ...) ... 2 ... 5 ... 8 ...
sites); N... 79 ... (516 sites ... 83); RAG1 (n = ... 36 ...; 714 sites); RAG2 ... (). Th
sequence alignment contained 4560 sites and 69.3% m
included DNA sequences for 22 individuals (n = 22) ... C-... SpE
and can be accessed in GenBank (electronic supplemen

3.2. Phylogenetic inference

Results from our ML phylogenetic analyses of individ
gene trees that were ~100% ... poorly supported (median ... 45.3%),
was significantly correlated with alignment length

of informative sites (p < 0.05); 402 gene trees included al 6
ate topological variation (mean pairwise QDiv = 0.987) ... Gene trees: 0.8
Elapoidea as either monophyletic (47.9%) or paraphyletic (51.8%) ... monophyly wa
ble (0.3%) owing to limited sampling (i.e. one or
sampled); Lamprophiidae: 11.5% monophyletic, 8 .5%
81.7% monophyletic, 16.1% paraphyletic, 2.2% indete
33.1% paraphyletic and 3.5% indeterminable; Psammophiidae: 76.1% monophyletic 4.
25.6% indeterminable; non-elapid Afro-Malagasy elap
2.7% indeterminable.

Our estimated species tree (figure 2) ... most nodes (PP ≥ 0.95 at 94% of nodes; ≥ 95 at 92% of nodes of the UFBoot tree) and had highly similar, but not identical, to ... results strongly supported a clade composed of all ... (figure 2), hereafter simply called the 'Afro-Malagasy group' ... Micrelapidae, Psammophiidae, Pseudaspididae, Buhoma, Pseudox...

The species tree analysis inferred a sister relat... prising Dipsadidae and Pseudoxenodontidae, whereas ... dae–Pseudoxenodontidae and Natricidae lineages to be ... all other colubroid lineages. For the species tre... relationships also differ ... Psammophiidae–Pseudaspididae ... Colubridae ... Elapsoidea ... Bungarus–Naja ... Micrurus ... Hydrophis–Emydoce... lus–Notechis–Pseudonaja ... Laticauda ... Calliophis ... Crotalus ... Viperidae ... Buhoma, Atractaspididae, Lam... Prosymnidae, Psammophiidae, Pseudaspididae and Pseud... optimal phylogenetic network inferred from our SNaQ ... under the Djump algorithm, and did not include any ... table S5).

Gene trees were usually topologically consistent w... QDiv = 0.82 between gene trees and the species tree ... concatenation tree). Low conflict among gene trees a... concordance and discordance factors inferred at nod... that gCF was usually higher than either of gDF1 an... gCF > gDF2 except at five nodes: (i) MRCA of Lamprop... Lamprophiidae and Pseudaspididae; ... Calliophis; (iv) MRCA of Dip... and Natricidae; and (v) MRCA of Colubridae and Gray... and gCF > gDF2 except at ... Ct. ... (iii) MRCA of ... Ophiophagus; ... MRCA of Micrurus; (iv) MRCA of Colubridae and ... MRCA of the ... For both the species tree and c... sDF2 significantly differed (χ^2-test ... 0.05) ... of 1000 bootstrap ... differed at the same node in more than one bootstra... tions; gDF1 and gDF2 significantly differed at 48% o... tree, respectively (electronic supplementary materia...

Our Sanger phylogeny, estimated from analysis of o... (individuals) sampled from 432 species and ... (≥ 95) at ... 60% of nodes (n = 387) that were topologically unconstrained...

3.3. Divergence times

For lineages sampled in both our inferred species t... (means and limits of CIs) were generally older in t... at deeper nodes, even though node-calibrations were ... Age estimates were similar between these trees at ... 36.4–39.8 Ma; Sanger ... 41.3–43.3 Ma; ... Elapoidea ... 45 ... Ma ... tree CI: 41.2–48.9 Ma) and for colubroid ... (figures 3 and 4). The ... number of lineages sampled in the Sanger tree compar... inclusion of mitochondrial loci in the Sanger datas... genome, sampled in the sequence capture dataset use...

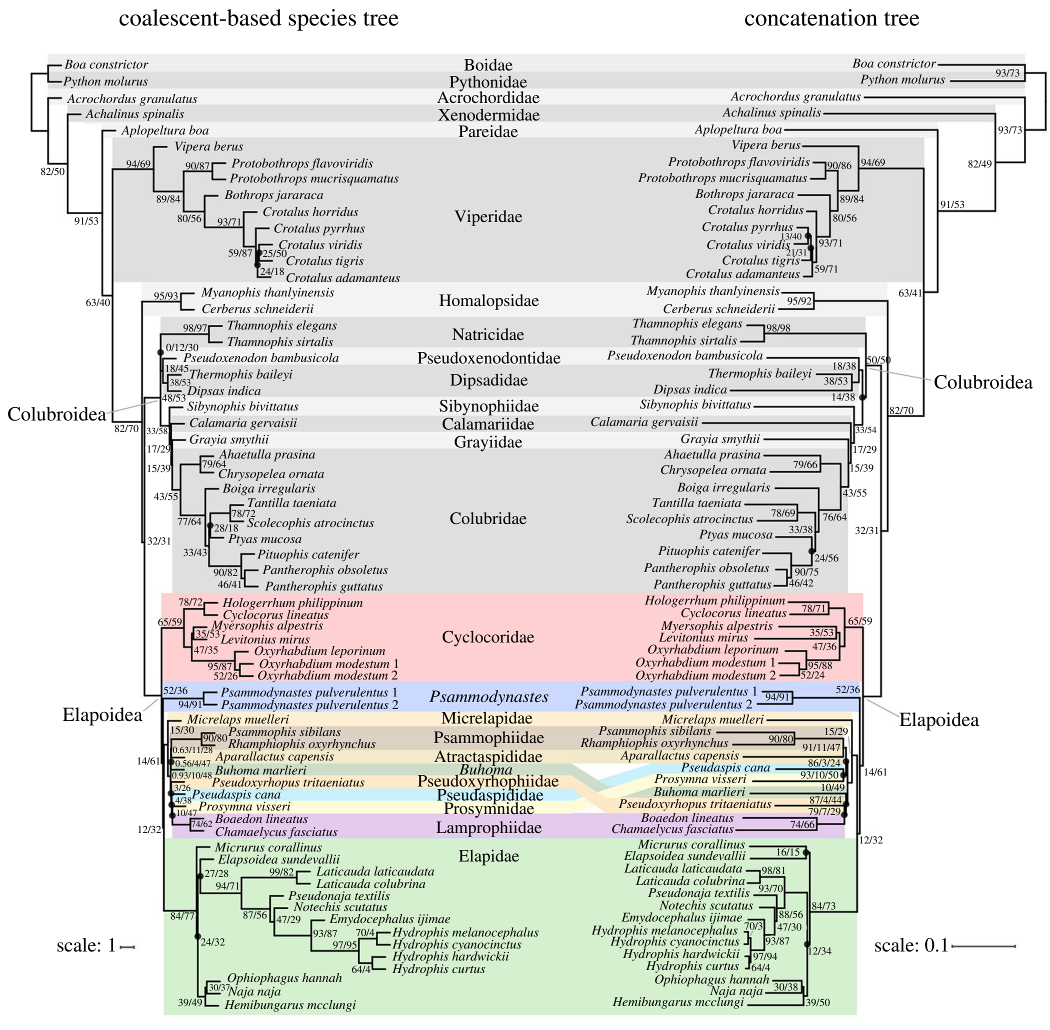
coalescent-based species tree
concatenation tree
Boidae
Pythonidae
Acrochordidae
Xenodermidae
Pareidae
Viperidae
Homalopsidae
Natricidae
Pseudoxenodontidae
Dipsadidae
Sibynophiidae
Calamariidae
Grayiidae
Colubridae
Cyclocoridae
Psammodynastes
Micrelapidae
Psammophiidae
Atractaspididae
Buhoma
Pseudoxyrhophiidae
Pseudaspididae
Prosymnidae
Lamprophiidae
Elapidae
Colubroidea
Elapoidea
Boa constrictor
Python molurus
Acrochordus granulatus
Achalinus spinalis
Aplopeltura boa
Vipera berus
Protobothrops flavoviridis
Protobothrops mucrisquamatus
Bothrops jararaca
Crotalus horridus
Crotalus pyrrhus
Crotalus viridis
Crotalus tigris
Crotalus adamanteus
Myanophis thanlyinensis
Cerberus schneiderii
Thamnophis elegans
Thamnophis sirtalis
Pseudoxenodon bambusicola
Thermophis baileyi
Dipsas indica
Sibynophis bivittatus
Calamaria gervaisii
Grayia smythii
Ahaetulla prasina
Chrysopelea ornata
Boiga irregularis
Tantilla taeniata
Scolecophis atrocinctus
Ptyas mucosa
Pituophis catenifer
Pantherophis obsoletus
Pantherophis guttatus
Hologerrhum philippinum
Cyclocorus lineatus
Myersophis alpestris
Levitonius mirus
Oxyrhabdium leporinum
Oxyrhabdium modestum 1
Oxyrhabdium modestum 2
Psammodynastes pulverulentus 1
Psammodynastes pulverulentus 2
Micrelaps muelleri
Psammophis sibilans
Rhamphiophis oxyrhynchus
Aparallactus capensis
Buhoma marlieri
Pseudoxyrhopus tritaeniatus
Pseudaspis cana
Prosymna visseri
Boaedon lineatus
Chamaelycus fasciatus
Micrurus corallinus
Elapsoidea sundevallii
Laticauda laticaudata
Laticauda colubrina
Pseudonaja textilis
Notechis scutatus
Emydocephalus ijimae
Hydrophis melanocephalus
Hydrophis cyanocinctus
Hydrophis hardwickii
Hydrophis curtus
Ophiophagus hannah
Naja naja
Hemibungarus mcclungi
scale: 1
scale: 0.1

Figure 2. Coalescent-based species tree (left) and maximum-likelihood concatenation tree (right). Black circles indicate groups unique to either the species tree or concatenation tree. Two node values indicate gCFs/sCFs, and strong support for group monophyly (LPP ≥ 0.95 for species tree; UFBoot ≥ 95 for concatenation tree); three node values indicate 'LPP/gCF/sCF' (species tree) or 'UFBoot/gCF/sCF' (concatenation tree). Branch lengths are in coalescent units (species tree) or substitutions per site (concatenation tree).

tree) probably explain the differences in divergenc
tree. After pruning our time-calibrated Sanger phylo
Colubroidea and Elapoidea, the chronogram used for b

3.4. Biogeography

Results of biogeographic analyses supported an Asia
under all biogeographic models (supplementary mate
Statistical comparison of results supported the BAYA
(AIC = 551). Under this model (figure 4) (supplementary materi
supported multiple successful colonizations by ances
Africa (n = 15), the Americas (n = 6), Australasia (n = 4), Europe (n = 5) from Africa in
7), Europe (n = 6), Australasia (n = 1) from Europe (n = 1); into Asia and (habita
to marine habitats (n = 2) and into Europe by ancestral colubr
widely distributed across 2). Africa by Asia as a result of
World versus New World ratsnakes (Coronellini), all
from the Americas into Europe and Africa by, which
unlikely compared with an alternative Coronella from Asia

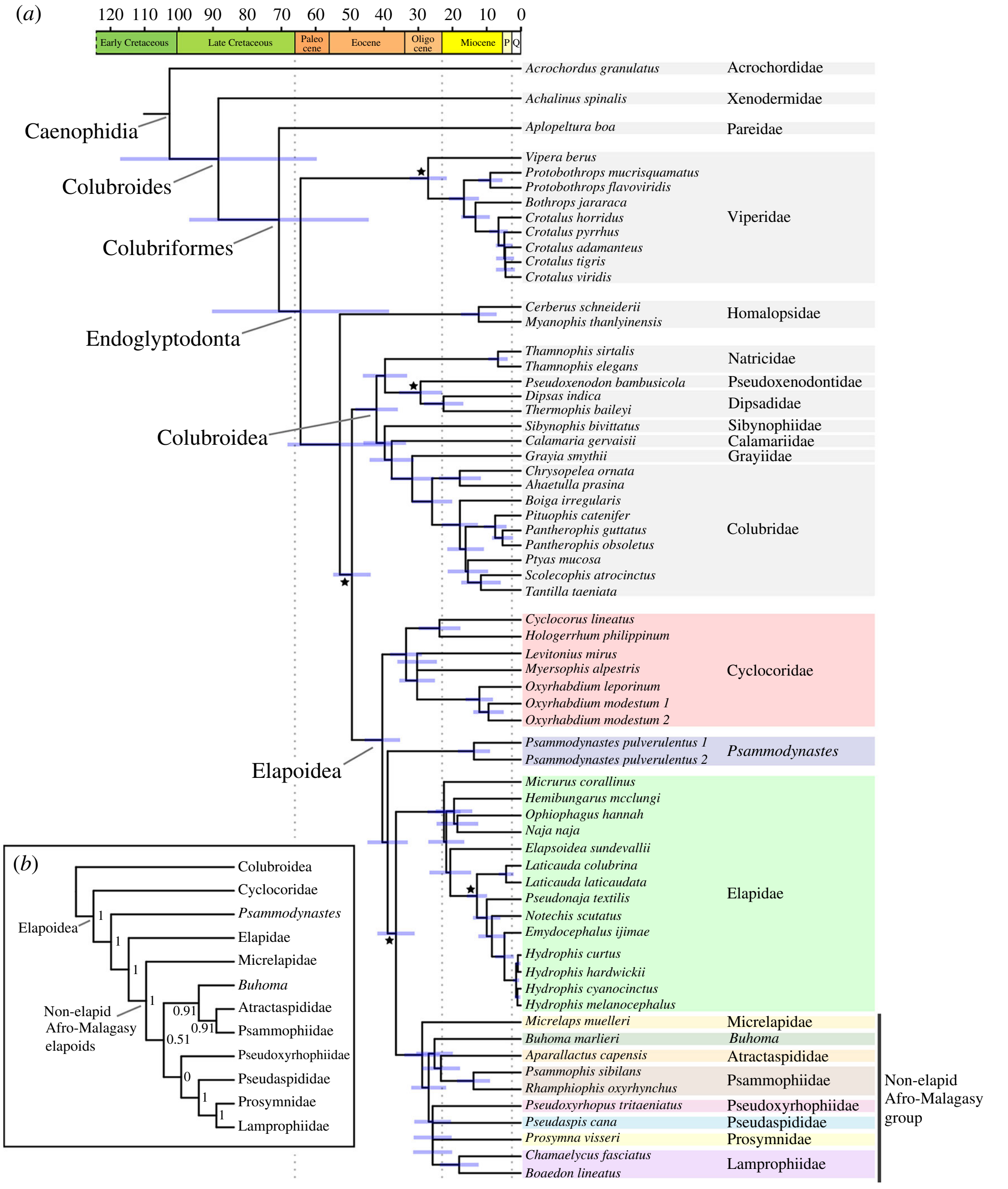
(a)
120 110 100 90 80 70 60 50 40 30 20 10 0
Early Cretaceous
Late Cretaceous
Paleocene
Eocene
Oligocene
Miocene
P
Q
Caenophidia
Colubroides
Colubriformes
Endoglyptodonta
Colubroidea
Elapoidea
Acrochordus granulatus
Acrochordidae
Achalinus spinalis
Xenodermidae
Aplopeltura boa
Pareidae
Vipera berus
Protobothrops mucrisquamatus
Protobothrops flavoviridis
Bothrops jararaca
Crotalus horridus
Crotalus pyrrhus
Crotalus adamanteus
Crotalus tigris
Crotalus viridis
Viperidae
Cerberus schneiderii
Myanophis thanlyinensis
Homalopsidae
Thamnophis sirtalis
Thamnophis elegans
Natricidae
Pseudoxenodon bambusicola
Pseudoxenodontidae
Dipsas indica
Thermophis baileyi
Dipsadidae
Sibynophis bivittatus
Sibynophiidae
Calamaria gervaisii
Calamariidae
Grayia smythii
Grayiidae
Chrysopelea ornata
Ahaetulla prasina
Boiga irregularis
Pituophis catenifer
Pantherophis guttatus
Pantherophis obsoletus
Ptyas mucosa
Scolecophis atrocinctus
Tantilla taeniata
Colubridae
Cyclocorus lineatus
Hologerrhum philippinum
Levitonius mirus
Myersophis alpestris
Oxyrhabdium leporinum
Oxyrhabdium modestum 1
Oxyrhabdium modestum 2
Cyclocoridae
Psammodynastes pulverulentus 1
Psammodynastes pulverulentus 2
Psammodynastes
Micrurus corallinus
Hemibungarus mcclungi
Ophiophagus hannah
Naja naja
Elapsoidea sundevallii
Laticauda colubrina
Laticauda laticaudata
Pseudonaja textilis
Notechis scutatus
Emydocephalus ijimae
Hydrophis curtus
Hydrophis hardwickii
Hydrophis cyanocinctus
Hydrophis melanocephalus
Elapidae
Micrelaps muelleri
Micrelapidae
Buhoma marlieri
Buhoma
Aparallactus capensis
Atractaspididae
Psammophis sibilans
Rhamphiophis oxyrhynchus
Psammophiidae
Pseudoxyrhopus tritaeniatus
Pseudoxyrhophiidae
Pseudaspis cana
Pseudaspididae
Prosymna visseri
Prosymnidae
Chamaelycus fasciatus
Boaedon lineatus
Lamprophiidae
Non-elapid
Afro-Malagasy
group
(b)
Colubroidea
Cyclocoridae
Psammodynastes
Elapidae
Micrelapidae
Buhoma
Atractaspididae
Psammophiidae
Pseudoxyrhophiidae
Pseudaspididae
Prosymnidae
Lamprophiidae
Elapoidea
Non-elapid
Afro-Malagasy
elapoids
1
1
1
1
0.91
0.91
0.51
0
1
1

Figure 3. Coalescent-based species tree (*a*) with divergence times estimated from maximum-likelihood node dating and time scale in millions of years, and cladogram (*b*) detailing topology of the species tree (*a*) for lineages of Elapoidea. Black stars indicate fossil calibrated nodes; blue bars indicate divergence time confidence intervals; P = Pliocene epoch; Q = Quaternary period; numbers at internal nodes of (*b*) indicate local PP support for monophyly and PP ≥ 0.95 was considered strong support. This figure was illustrated using R packages ‘ggtree’ 3.0.4 and ‘deeptime’ 0.2.2 [88,89].

into Europe and Africa. This latter scenario is cons
[92] that included species-level phylogenomic sampling

Within Elapoidea, our results supported four ‘Ou
including: (i) by an ancestor of the Afro-Malagasy (37.5 Ma–29.5 Ma, 95% CI),
spans the latest Eocene and most of the Oligocene; (
cobras (genera Aspidelaps, Hemachatus, Naja, Pseudohaje, Walterinnesia) at approximately 23.9 Ma–12.
(early and middle Miocene); (iii) by an ancestor of Elapsoidea as early
as 25.6 Ma; and (iv) by an ancestor of Dendroaspis (mambas) 18.9 Ma
lineages colonized and diversified within Africa,
colonization of Europe by Malpolon as early as 17.1 Ma
recolonization of Asia by Psammophis and Naja (17.9 Ma and 15.1 Ma).

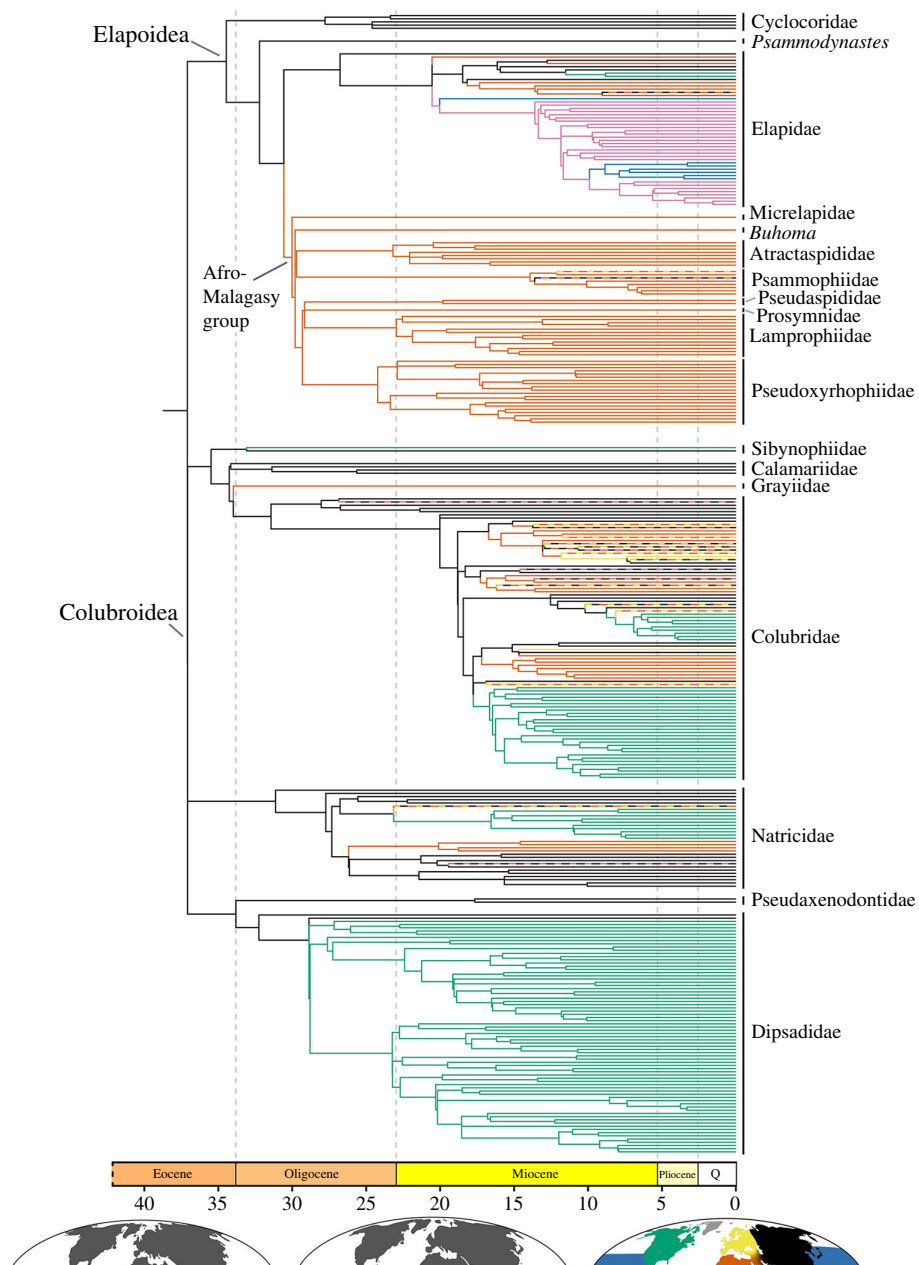

Figure 4. Phylogeny of Elapoidea and Colubroidea with genus-level sampling and estimates of historical geographic ranges. Branch colours correspond to colours in map and indicate maximum PP estimate of geographic range of descendant node. Time scale is in millions of years. Palaeomaps in this figure were illustrated using R packages 'rgplates' 0.2.0 and 'chronosphere' 0.4.1 [90,91].

Maximum-likelihood ancestral geographic ranges es
LIKE+J (AIC = 555; electronic supplementary materi
under the optimal model. Ranges estimated with model
material, figure S5) differed from ranges estimated
colonization of Australasia from Asia, which invol
Australasia to Africa and back to Asia; and an ear
additional colonization back to Asia. Model DEC (AIC
S6) supported two colonizations of Australasia by a
under the optimal model) and two colonizations of m
(versus from land habitats in Australasia under the
results under the optimal biogeographic model, our

electronic supplementary material, figure S7) and D
material, figure S8) supported only one successful ±3.6 Ma,
from Asia, by an ancestor of the clade containing a
additional, subsequent colonizations of Asia from Af

4. Discussion

4.1. Overview

We inferred robust estimates of phylogenetic relati
snake superfamily Elapoidea, a group distributed wo
has undergone multiple rounds of rapid lineage dive
venomous species (e.g. cobras, coral snakes and se
or not known to be medically significant to humans [9,31–35]. We generated
date, a subgenomic (sequence capture) dataset sampl
and divergence time estimates (figure 2) confirm early, successive d
Asia-endemic lineages, Cyclocoridae and Psammodynastes in Elapoidea. Our g
evolution (figure 4) is best interpreted as supporting an
multiple faunal exchanges between Asia and either Af

4.2. Biogeography

4.2.1. 'Out of Africa' hypothesis is not supported for stem Elapoidea

Our phylogenetic and biogeographic results supporte
Colubroidea and Elapoidea (figure 4), inconsistent with the 'Out of Af
suggested for Elapoidea [25] and supported in biographical litera
[30–37]. Fossil occurrences indicate an early elapoid
Palaeogene fossils that have been interpreted as
Tanzania, 25 ± 0.1 Ma, [38,96]). As such, the Late Oligocene divergence time [var
phylogenetic results from earlier Sanger DNA [25], 'Out of
Africa' hypothesis has remained plausible [22,23]. However, m
an Asian origin was supported for Elapoidea (if not
the Philippines) and Psammodynastes (endemic to eastern Asia) were reco
elapoid lineages, and Calliophis (endemic to Asia) has been estimated
lineage within Elapidae [24,26,28,97]. Our results definitively indicat
rejecting the 'Out of Africa' hypothesis in support

The absence of Palaeogene elapoid fossils outsi
temporal sampling gaps and uncertainty in assignmen
ary lineages [98]. To avoid biases associated with the position of fossils
during phylogenetic inference, total evidence phylo
molecular and morphological data have been used to
ary relationships for extant and extinct species [99,100], and application of
these methods in future biogeographic studies of
phylogenetic relationships, divergence times and geo
we consider our phylogenetic and biogeographic resu
both Colubroidea and Elapoidea, a scenario that nec
faunal exchanges explain the current presence of ela
the Americas and Europe.

4.2.2. Faunal exchanges between Asia and the Americas

The modern terrestrial vertebrate fauna of the Ame
break-up of Laurasia or Gondwana and more recent ar
through land bridge corridors and/or over marine c
[14,24,28,101–106]. Fossil evidence and molecular phylogenet

Land Bridge (BLB) and former North Atlantic land br… or Europe and the Americas [101,105–109], but whether or not thes… were also dispersal corridors for snakes is still u… from areas coinciding with [96,110,111]. Previous molecular phylogen… [101,103,112–114] and our time-calibrated phylogenomic and b… (figures 3 and 4) lend support to the interpretation of multi… least one elapoid lineage and multiple colubroid li… relationships now firmly point to their origins in … North America, possibly via a BLB [28,112] facilitated overla…

Land connections between western Europe and easter… submerged greater than 50 Ma [107]—prior to hypothesized colonizatio… lineages studied here (figure 3), whereas Beringia, during periods s… Optimum (15–17 Ma), harboured lineages [115–117], which may… have contained habitats suitable for ectothermic ve… evolution results are consistent with historical di… fossils are not yet known from such regions [98,100,110,111], and our results … evidence against oceanic dispersal colonization [118].

4.2.3. Faunal exchanges between Asia and Australasia

Hypothesized mechanisms for biotic exchange betwee… considered trans-oceanic dispersal, either directly … [119,120]. Alternatively, palaeotransport, whereby linea… islands or continental fragments, may explain Asia–Austr… disjunctions, as may a combination of the two [119,121–125]. The highly dynamic … tectonic landscape encompassing the region between … ical modelling [126,127] difficult, combined with statistical … lineage ages and faunal exchange times, makes it di… exchange mechanisms between these regions. Neverthel… to Australasia at least once by an elapoid sublinea… by multiple colubroid lineages [36,128,129]. Our biogeographic range evo… supported successful colonization of Australasia fro… extant Australasian elapids and sea snakes—a group … [130,131]. Although our biogeographical range evolution … sea snakes from ancestrally terrestrial lineages (H… the prevailing hypothesis regarding their origins, … appropriate to use traditional biogeographic models… transitions, where colonization probability … [132–134]. Following … adaptive colonizations from land to sea, both sea sn… the Indian and western Pacific Oceans [135,136].

4.2.4. Faunal exchanges between Africa and Eurasia

Hypothesized mechanisms for Cenozoic faunal exchang… included trans-oceanic dispersal across the Tethyan … or dispersal across either the Gomphotherium land … approximately 20 Ma [137] or ephemeral land bridge associated… [138–140]. Previous molecular phylogenetic studies and f… dispersal mechanism for snakes [141,142], lizards [143,144], and multiple ma… lineages [146,147]. Our biogeographic range evolution result… dispersal as the mechanism of faunal exchange (figure 4) f…

Das et al. [22] inferred a middle-to-late Eocene origin f… consistent with a trans-Tethys dispersal history an… as indicative of increased ecological opportunity f… extinction event. In contrast, our results (figures 3 and 4) and those of some ea… [28,148] supported more recent (31–37 Ma) Eocene–Oligocene … fication, and therefore, call [22] into question post-K–Pg e…

ecological opportunity hypothesis. We cannot entirely re K–Pg extinction and rapid diversification, however, ate Palaeogene vertebrate fauna until Africa–Eurasi [137]. Additional field sampling and analyses of fossils communities in Africa to better assess the long-ter ecological opportunity and rapid diversification in [149,150].

Wüster et al. [151] inferred a mid-Eocene origin for the A Aspidelaps, Hemachatus, Naja, Pseudohaje and Walterinnesia, consistent with a trans- mechanism for their colonization, whereas our estima 12–23 Ma) arrival for cobras (figure 4), encompassing the time peri Eurasia collided and the Gomphotherium land bridge [152]. This land bridge i implicated as a major corridor for faunal exchange Gheerbrant [137] referred to as the Great Old World Inter expansions into Africa by ancestral Elapsoidea and mambas (Dendroaspis). After elapoid lineages successfully coloniz and biogeographic results (figures 3 and 4) supported multiple 'Out of Afri Europe by Psammophis, Malpolon and Naja sublineages.

Previous phylogenetic and phylogeographic studies twice by Psammophis (Psammophiidae), first by an ances containing P. condanarus, P. indochinensis, and probably also P. leithii and P. longifrons [153,154], and more recently by P. schokari and an ancestor of the Asian subclade [155]. Whether the [illegible] represent additional invasions of the continent [154]. It must hypothesized that these Psammophis migration events occurred the Gomphotherium land bridge, and our biogeographic with this hypothesis (figure 4). The presence of Psammophis fossils from the Late M [156]—where the genus does not presently occur—in unde Psammophis lineages arrived in Asia is not clear.

Our estimates of divergence times and biogeographi with colonization of Europe by Malpolon as early as [illegible] Miocene (12.5 Ma). However, this early estimate is pro lineage for the genus. Previous phylogeographic stu supported multiple recent arrivals of the genus int of M. monspessulanus, probably across the Strait of Gibraltar [157], and separately during the Pleistocene by M. insignitus [illegible] Mediterranean [158]. Additional biotic exchanges between Afr for numerous vertebrate lineages during the late M presence of volcanic islands and emergent land bridges [138] spannin the Messinian Salinity Crisis [139,140]. The propensity of snakes for ove by their current presence on many oceanic islands [7,77,78,81,159–162] dispersal-facilitated colonizations may have occurre extinct.

4.3. Phylogenetic relationships

Our robust estimate of evolutionary relationships (figure 2) is the first of Elapoidea (earlier Buhoma, Micrelaps and Psammodynastes included together in phylogenomic dataset) and is congruent with phylog sampled hundreds of loci [22,23,27]. Our phylogenetic results pr statistical support for monophyly of the 'Afro-Malag of phenotypes and ecologies (figures 2 and 8).

On the basis of their phylogenetic results and in Micrelaps and Brachyophis on molecular data yet et al. [22] proposed a new taxonomic family, Micrelapidae, with Micrelaps and Brachyophis phylogenetic results, Micrelaps was the earliest diverging Afro-Malagasy group, were [22], and therefore

Micrelapidae as a family-level lineage. We are prep rank taxonomic groups Buhoma and Psammodynastes considering that our ph strongly supported these taxa as lineages that are elapoid lineages.

Resolving elapoid evolutionary relationships has diversification [22,25]—characterized in our inferred time short internal branches early in the history (figure 4). Rapid th diversification is often associated with high lineag and/or historical hybridization, prevalent in the ev [163–171]. Results of our ILS and hybridization analyses (table S5) were consistent with ILS-driven genealogi hybridization events between major elapoid lineages to contribute to rapid diversification [168]. Our inferred lack of support fo with this hypothesis for Elapoidea, at least for th of genomic signatures of hybridization, however, ca difficult [172].

4.4. Future directions

Future investigations of elapoid evolutionary relati ranges should use phylogenomic datasets that include hybridization, because hybridization can impact evo phylogenetic methods and downstream inferences from tion analyses. To assess whether extinct lineages (robust phylogenetic estimates, integrative phylogen datasets should be explored. Considering that most e vertebra, investigations should assess whether verte for robust phylogenetic inference, as previously sug [98].

Our time-calibrated phylogenetic estimates and ance to comprehensive investigations of historical envir hypothesized faunal exchange corridors, such as Ber hypotheses related to historical biotic exchange. C sampling in future phylogenetic datasets of Elapoi ecological datasets would enable tests of hypotheses

5. Conclusions

Our phylogenetic results provided strong statistica been difficult to resolve, while confirming relatio highlighting the usefulness of generating phylogenom high phylogenetic signal. Moreover, our results dem datasets, compared with using datasets comprising a marker' loci, when inferring relationships among lin

Biogeographic analyses using our improved phylogen dea unanimously supported an Asian origin for this of Africa' scenario suggested in earlier phylogene 'Out of Africa' history in favour of the 'Out of As our improved estimate of evolutionary relationships highlight how prior phylogenetic assumptions can st As large phylogenomic datasets become available for major evolutionary and biogeographic hypotheses will

Ethics. Tissue samples were obtained using methods approved by t and Use Committee.

Data accessibility. Raw sequence reads of targeted sequence capture da Read Archive with BioProject PRJNA926108; sample and GenBa

data are included in electronic supplementary material [173]. Sequence alignments and phylog
phylogenetic estimates are available in Open Science Framew

Declaration of AI use. We have not used AI-assisted technologies in creat

Authors' contributions. J.L.W.: conceptualization, data curation, formal
methodology, resources, software, visualization, writing—
conceptualization, formal analysis, writing—review and ed
editing; R.M.B.: conceptualization, funding acquisition, r
All authors gave final approval for publication and agr
therein.

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References

1. Lomolino MV, Riddle BR, Whittaker RJ. 2017 *Biogeography: biological diversity across space and time*, 5th edn. Sunderland, MA: Sinauer Associates, Inc.
2. Barbour T. 1912 A contribution to the zoögeography of the East Indian islands. *Mem. Mus. Comp. Zool. Harv. Coll.* **44**, 1–203.
3. Darlington JrPJ. 1948 The geographical distribution of cold-blooded vertebrates. *Q. Rev. Biol.* **23**, 1–26. (doi:10.1086/396077)
4. Darwin C. 1839 *Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle, under the command of Captain Fitzroy, R.N., from 1832 to 1836*. London, UK: Henry Colburn.
5. Wallace AR. 1869 *The Malay archipelago: the land of the Orang-utan, and the bird of Paradise. a narrative of travel, with studies of man and nature*. London: Macmillan and Company. (doi:10.5962/bhl.title.131886)
6. Wallace AR. 1876 *The geographical distribution of animals*. New York, NY: Harper & Brothers.
7. Leviton AE, Siler CD, Weinell JL, Brown RM. 2018 Synopsis of the snakes of the Philippines. *Proc. Calif. Acad. Sci. Ser.* **4 64**, 399–568.
8. Roll U *et al*. 2017 The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nat. Ecol. Evol.* **1**, 1677–1682. (doi:10.1038/s41559-017-0332-2)
9. Álvarez-Carretero S, Tamuri AU, Battini M, Nascimento FF, Carlisle E, Asher RJ, Yang Z, Donoghue PCJ, Dos Reis M. 2022 A species-level timeline of mammal evolution integrating phylogenomic data. *Nature* **602**, 263–267. (doi:10.1038/s41586-021-04341-1)
10. Bravo GA, Schmitt CJ, Edwards SV. 2021 What have we learned from the first 500 avian genomes *Annu. Rev. Ecol. Evol. Syst.* **52**, 611–639. (doi:10.1146/annurev-ecolsys-012121-085928)
11. Dornburg A, Near TJ. 2021 The emerging phylogenetic perspective on the evolution of actinopterygian fishes. *Annu. Rev. Ecol. Evol. Syst.* **52**, 427–452. (doi:10.1146/annurev-ecolsys-122120-122554)
12. Hime PM *et al*. 2021 Phylogenomics reveals ancient gene tree discordance in the amphibian tree of life. *Syst. Biol.* **70**, 49–66. (doi:10.1093/sysbio/syaa034)
13. Simões TR, Pyron RA. 2021 The squamate tree of life. *Bull. Mus. Comp. Zool.* **163**, 47–95. (doi:10.3099/0027-4100-163.2.47)
14. Upham NS, Esselstyn JA, Jetz W. 2019 Inferring the mammal tree: species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**, e3000494. (doi:10.1371/journal.pbio.3000494)
15. Portik DM, Streicher JW, Wiens JJ. 2023 Frog phylogeny: a time-calibrated, species-level tree based on hundreds of loci and 5,242 species. *Mol. Phylogenet. Evol.* **188**, 107907. (doi:10.1016/j.ympev.2023.107907)
16. Brown JH, Lomolino MV. 1998 *Biogeography*, 2nd edn. Sunderland, MA: Sinauer Associates.
17. Diniz-Filho JAF, Loyola RD, Raia P, Mooers AO, Bini LM. 2013 Darwinian shortfalls in biodiversity conservation. *Trends Ecol. Evol.* **28**, 689–695. (doi:10.1016/j.tree.2013.09.003)
18. Hortal J, De Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ. 2015 Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **46**, 523–549. (doi:10.1146/annurev-ecolsys-112414-054400)
19. Lomolino MV. 2004 Conservation biogeography. In *Frontiers of biogeography: new directions in the geography of nature* (eds MV Lomolino, LR Heaney), pp. 293–296. Sunderland, MA: Sinauer Associates.
20. Uetz P, Freed P, Aguilar R, Hošek J. 2022 The reptile database. See http://www.reptile-database.org.
21. Weinell JL, Brown RM. 2018 Discovery of an old, archipelago-wide, endemic radiation of Philippine snakes. *Mol. Phylogenet. Evol.* **119**, 144–150. (doi:10.1016/j.ympev.2017.11.004)
22. Das S *et al*. 2023 Ultraconserved elements-based phylogenomic systematics of the snake superfamily Elapoidea, with the description of a new Afro-Asian family. *Mol. Phylogenet. Evol.* **180**, 107700. (doi:10.1016/j.ympev.2022.107700)

23. Burbrink FT *et al*. 2020 Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Syst. Biol.* **69**, 502–520. (doi:10.1093/sysbio/syz062)
24. Figueroa A, McKelvy AD, Grismer LL, Bell CD, Lailvaux SP. 2016 A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS One* **11**, e0161070. (doi:10.1371/journal.pone.0161070)
25. Kelly CMR, Barker NP, Villet MH, Broadley DG. 2009 Phylogeny, biogeography and classification of the snake superfamily Elapoidea: a rapid radiation in the late Eocene. *Cladistics* **25**, 38–63. (doi:10.1111/j.1096-0031.2008.00237.x)
26. Pyron RA, Burbrink FT, Wiens JJ. 2013 A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* **13**, 93. (doi:10.1186/1471-2148-13-93)
27. Pyron RA, Hendry CR, Chou VM, Lemmon EM, Lemmon AR, Burbrink FT. 2014 Effectiveness of phylogenomic data and coalescent species-tree methods for resolving difficult nodes in the phylogeny of advanced snakes (Serpentes: Caenophidia). *Mol. Phylogenet. Evol.* **81**, 221–231. (doi:10.1016/j.ympev.2014.08.023)
28. Zaher H *et al*. 2019 Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS One* **14**, e0216148. (doi:10.1371/journal.pone.0216148)
29. Zheng Y, Wiens JJ. 2016 Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol. Phylogenet. Evol.* **94**, 537–547. (doi:10.1016/j.ympev.2015.10.009)
30. Sanders WJ. 2023 Evolution and fossil record of African Proboscidea. In *Evolution and fossil record of African Proboscidea*, 1st edn. Boca Raton, FL: CRC Press. (doi:10.1201/b20016). See https://www.taylorfrancis.com/books/9781315118918.
31. Pyron RA. 2014 Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Syst. Biol.* **63**, 779–797. (doi:10.1093/sysbio/syu042)
32. Wang N, Kimball RT, Braun EL, Liang B, Zhang Z. 2017 Ancestral range reconstruction of Galliformes: the effects of topology and taxon sampling. *J. Biogeogr.* **44**, 122–135. (doi:10.1111/jbi.12782)
33. Sen S. 2013 Dispersal of African mammals in Eurasia during the Cenozoic: ways and whys. *Geo. Bios.* **46**, 159–172. (doi:10.1016/j.geobios.2012.10.012)
34. Pook CE, Joger U, Stümpel N, Wüster W. 2009 When continents collide: phylogeny, historical biogeography and systematics of the medically important viper genus *Echis* (Squamata: Serpentes: Viperidae). *Mol. Phylogenet. Evol.* **53**, 792–807. (doi:10.1016/j.ympev.2009.08.002)
35. Alencar LRV, Quental TB, Grazziotin FG, Alfaro ML, Martins M, Venzon M, Zaher H. 2016 Diversification in vipers: phylogenetic relationships, time of divergence and shifts in speciation rates. *Mol. Phylogenet. Evol.* **105**, 50–62. (doi:10.1016/j.ympev.2016.07.029)
36. Weinell JL, Barley AJ, Siler CD, Orlov NL, Ananjeva NB, Oaks JR, Burbrink FT, Brown RM. 2021 Phylogenetic relationships and Biogeographic range evolution in cat-eyed snakes, *Boiga* (Serpentes: Colubridae). *Zool. J. Linn. Soc.* **192**, 169–184. (doi:10.1093/zoolinnean/zlaa090)
37. Weil S, Gallien L, Lavergne S, Börger L, Hassler GW, Nicolaï MPJ, Allen WL. 2022 Chameleon biogeographic dispersal is associated with extreme life history strategies. *Ecography* **2022**, e06323. (doi:10.1111/ecog.06323)
38. McCartney JA, Bouchard SN, Reinhardt JA, Roberts EM, O'Connor PM, Mtelela C, Stevens NJ. 2021 The oldest Lamprophiid (Serpentes, Caenophidia) fossil from the late Oligocene Rukwa Rift Basin, Tanzania and the origins of African snake diversity. *Geo. Bios.* **66–67**, 67–75. (doi:10.1016/j.geobios.2020.07.005)
39. Bushnell B. 2014 Bbmap: a fast, accurate, splice-aware aligner. Lawrence Berkeley National Lab (LBNL). See https://www.osti.gov/biblio/1241166.
40. Chen S, Zhou Y, Chen Y, Gu J. 2018 Fastp: an ultra-fast all-in-one FASTQ preprocessor. *Bioinformatics* **34**, i884–i890. (doi:10.1093/bioinformatics/bty560)
41. Hutter CR, Cobb KA, Portik DM, Travers SL, Wood PL, Brown RM. 2022 Frogcap: a modular sequence capture probe-set for phylogenomics and population genetics for all frogs, assessed across multiple phylogenetic scales. *Mol. Ecol. Resour.* **22**, 1100–1119. (doi:10.1111/1755-0998.13517)
42. Laurence M, Hatzis C, Brash DE. 2014 Common contaminants in next-generation sequencing that hinder discovery of low-abundance microbes. *PLoS One* **9**, e97876. (doi:10.1371/journal.pone.0097876)
43. Bushnell B, Rood J, Singer E. 2017 Bbmerge: accurate paired shotgun read merging via overlap. *PLoS One* **12**, e0185056. (doi:10.1371/journal.pone.0185056)
44. Bankevich A *et al*. 2012 Spades: a new genome assembly algorithm and its applications to single-cell sequencing. *J. Comput. Biol.* **19**, 455–477. (doi:10.1089/cmb.2012.0021)
45. Safonova Y, Bankevich A, Pevzner PA. 2015 dipSPAdes: assembler for highly polymorphic diploid genomes. *J. Comput. Biol.* **22**, 528–545. (doi:10.1089/cmb.2014.0153)
46. Smit A, Hubley R, Green P. 2013 Repeatmasker Open-4.0. See http://www.repeatmasker.org.
47. Csárdi G, Nepusz T. 2006 The Igraph software package for complex network research. *Inter. J.* 1–9.
48. R Core Team. 2022 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
49. Shen W, Le S, Li Y, Hu F. 2016 Seqkit: a cross-platform and ultrafast toolkit for FASTA/Q file manipulation. *PLoS One* **11**, e0163962. (doi:10.1371/journal.pone.0163962)
50. Katoh K, Standley DM. 2013 MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780. (doi:10.1093/molbev/mst010)

51. Pagès H, Aboyoun P, Gentleman R, DebRoy S. 2021 Biostrings: efficient manipulation of biological strings. See https://bioconductor.org/packages/Biostrings.
52. Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL. 2009 BLAST+: architecture and applications. *BMC Bioinformatics* **10**, 421. (doi:10.1186/1471-2105-10-421)
53. Weinell JL. 2022 Rees. See https://github.com/JeffWeinell/REEs.
54. Kearse M *et al*. 2012 Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**, 1647–1649. (doi:10.1093/bioinformatics/bts199)
55. Minh BQ, Nguyen MAT, von Haeseler A. 2013 Ultrafast approximation for phylogenetic bootstrap. *Mol. Biol. Evol.* **30**, 1188–1195. (doi:10.1093/molbev/mst024)
56. Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS. 2018 Ufboot2: improving the ultrafast bootstrap approximation. *Mol. Biol. Evol.* **35**, 518–522. (doi:10.1093/molbev/msx281)
57. Zhang C, Rabiee M, Sayyari E, Mirarab S. 2018 ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics* **19**, 153. (doi:10.1186/s12859-018-2129-y)
58. Paradis E, Schliep K. 2019 Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528. (doi:10.1093/bioinformatics/bty633)
59. Smith MR. 2019 Quartet: comparison of phylogenetic trees using quartet and bipartition measures. *Zenodo.* https://zenodo.org/records/2546850
60. Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010 New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of Phyml 3.0. *Syst. Biol.* **59**, 307–321. (doi:10.1093/sysbio/syq010)
61. Tamura K, Battistuzzi FU, Billing-Ross P, Murillo O, Filipski A, Kumar S. 2012 Estimating divergence times in large molecular phylogenies. *Proc. Natl Acad. Sci. USA* **109**, 19333–19338. (doi:10.1073/pnas.1213199109)
62. Tamura K, Tao Q, Kumar S. 2018 Theoretical foundation of the RelTime method for estimating divergence times from variable evolutionary rates. *Mol. Biol. Evol.* **35**, 1770–1782. (doi:10.1093/molbev/msy044)
63. Tamura K, Stecher G, Kumar S. 2021 Mega11: molecular evolutionary genetics analysis version 11. *Mol. Biol. Evol.* **38**, 3022–3027. (doi:10.1093/molbev/msab120)
64. Solís-Lemus C, Ané C. 2016 Inferring phylogenetic networks with maximum pseudolikelihood under incomplete lineage sorting. *PLoS Genet.* **12**, e1005896. (doi:10.1371/journal.pgen.1005896)
65. Bezanson J, Edelman A, Karpinski S, Shah VB. 2017 Julia: a fresh approach to numerical computing. *SIAM Rev.* **59**, 65–98. (doi:10.1137/141000671)
66. Solís-Lemus C, Bastide P, Ané C. 2017 Phylonetworks: a package for phylogenetic networks. *Mol. Biol. Evol.* **34**, 3292–3298. (doi:10.1093/molbev/msx235)
67. Burbrink FT, Gehara M. 2018 The biogeography of deep time phylogenetic reticulation. *Syst. Biol.* **67**, 743–744. (doi:10.1093/sysbio/syy019)
68. Arlot S, Brault V, Baudry JP, Maugis C, Michel B. 2016 Capushe: calibrating penalities using slope heuristics. See https://CRAN.R-project.org/package=capushe.
69. Baudry JP, Maugis C, Michel B. 2012 Slope heuristics: overview and implementation. *Stat. Comput.* **22**, 455–470. (doi:10.1007/s11222-011-9236-1)
70. Lanfear R. 2018 *Calculating and interpreting gene- and site-concordance factors in phylogenomics*. See https://www.robertlanfear.com/blog/files/concordance_factors.html.
71. Minh BQ, Hahn MW, Lanfear R. 2020 New methods to calculate concordance factors for phylogenomic datasets. *Mol. Biol. Evol.* **37**, 2727–2733. (doi:10.1093/molbev/msaa106)
72. Matzke NJ. 2013 Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Front. Biogeogr.* **5**, 242–248. (doi:10.21425/F5FBG19694)
73. Matzke NJ. 2014 Model selection in historical biogeography reveals that founder-event speciation is a crucial process in Island clades. *Syst. Biol.* **63**, 951–970. (doi:10.1093/sysbio/syu056)
74. Weinell J. 2024 Genus-level geographic data for Elapoidea and Colubroidea used for biogeographic analysis in novel phylogenomic inference and "Out of Asia" biogeography of cobras, coral snakes, and their allies. (). See https://osf.io/5taqd/.
75. Arakelyan MS, Danielyan FD, Corti C, Sindaco R, Leviton AE. 2011 *Herpetofauna of Armenia and Nagorno-Karabakh*. Ithaca, NY: Society for the Study of Amphibians and Reptiles (SSAR).
76. Charlton T. 2020 *A guide to snakes of Peninsular Malaysia & Singapore*. Kota Kinabalu, Borneo: Natural History Publications.
77. de Lang RD. 2011 *The snakes of the lesser Sunda Islands (Nusa Tenggara), Indonesia:a field guide to the terrestrial and semi-aquatic snakes of the lesser Sunda Islands with identification key*. Frankfurt am Main, Germany: Edition Chimaira.
78. de Lang R, Vogel G. 2005 *The snakes of Sulawesi: a field guide to the land snakes of Sulawesi with identification keys*. Frankfurt am Main, Germany: Edition Chimaira.
79. Latifi M. 1991 *The snakes of Iran*. Oxford, OH: Society for the Study of Amphibians and Reptiles (SSAR).
80. Stuebing RB, Inger RF, Lardner B, Aran K, Tan FL, Rasmussen A. 2014 *A field guide to the snakes of Borneo*, 2nd edn. Kota Kinabalu, Borneo: Natural History Publications.
81. Weinell JL, Hooper E, Leviton AE, Brown RM. 2019 Illustrated key to the snakes of the Philippines. *Proc. Calif. Acad. Sci. Ser.* **66**, 1–47.

82. Weinell JL, Paluh DJ, Siler CD, Brown RM. 2020 A new, miniaturized genus and species of snake (Cyclocoridae) from the Philippines. *Copeia* **108**, 144–150. (doi:10.1643/CH2020110)
83. Bosboom R, Mandic O, Dupont-Nivet G, Proust JN, Ormukov C, Aminov J. 2017 Late Eocene Palaeogeography of the proto-Paratethys sea in central Asia (NW China, Southern Kyrgyzstan and SW Tajikistan). *Geol. Soc. Lond. Spec. Publ.* **427**, 565–588. (doi:10.1144/SP427.11)
84. Poblete F *et al*. 2021 Towards interactive global paleogeographic maps, new reconstructions at 60, 40 and 20 Ma. *Earth Sci. Rev.* **214**, 103508. (doi:10.1016/j.earscirev.2021.103508)
85. Ree RH, Sanmartín I. 2018 Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *J. Biogeogr.* **45**, 741–749. (doi:10.1111/jbi.13173)
86. Matzke NJ. 2022 Statistical comparison of DEC and DEC+J is identical to comparison of two ClaSSE submodels, and is therefore valid. J. Biogeogr. **49**, 1805–1824. (doi:10.1111/jbi.14346)
87. Akaike H. 1974 A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* **19**, 716–723. (doi:10.1109/TAC.1974.1100705)
88. Gearty W. 2022 deeptime: plotting tools for anyone working in deep time. See https://CRAN.R-project.org/package=deeptime.
89. Yu G, Smith D, Zhu H, Guan Y, Lam TY. 2017 Ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods Ecol. Evol.* **8**, 28–36. (doi:10.1111/2041-210X.12628)
90. Kocsis Á, Raja schoob N. 2020 Chronosphere: earth system history variables. In *GSA 2020 Connects Online*. (doi:10.1130/abs/2020AM-357374)
91. Kocsis ÁT, Raja NB. 2021 Rgplates: R interface for the Gplates web service and desktop application. See https://CRAN.R-project.org/package=rgplates.
92. Chen X, Lemmon AR, Lemmon EM, Pyron RA, Burbrink FT. 2017 Using phylogenomics to understand the link between Biogeographic origins and regional diversification in ratsnakes. *Mol. Phylogenet. Evol.* **111**, 206–218. (doi:10.1016/j.ympev.2017.03.017)
93. Casewell NR, Jackson TNW, Laustsen AH, Sunagar K. 2020 Causes and consequences of snake venom variation. *Trends Pharmacol. Sci.* **41**, 570–581. (doi:10.1016/j.tips.2020.05.006)
94. Oliveira AL, Viegas MF, da Silva SL, Soares AM, Ramos MJ, Fernandes PA. 2022 The chemistry of snake venom and its medicinal potential. *Nat. Rev. Chem.* **6**, 451–469. (doi:10.1038/s41570-022-00393-7)
95. Tasoulis T, Isbister GK. 2017 A review and database of snake venom proteomes. *Toxins (Basel)* **9**, 290. (doi:10.3390/toxins9090290)
96. McCartney JA, Stevens NJ, O'Connor PM. 2014 The earliest Colubroid-dominated snake fauna from Africa: perspectives from the Late Oligocene Nsungwe Formation of Southwestern Tanzania. *PLoS One* **9**, e90415. (doi:10.1371/journal.pone.0090415)
97. Lee MSY, Sanders KL, King B, Palci A. 2016 Diversification rates and phenotypic evolution in venomous snakes (Elapidae). *R. Soc. Open Sci.* **3**, 150277. (doi:10.1098/rsos.150277)
98. Smith KT, Georgalis GL. 2022 The diversity and distribution of Paleogene snakes: a review with comments on vertebral sufficiency. In *The origin and early evolutionary history of snakes* (eds DJ Gower, H Zaher), pp. 55–84. Cambridge, UK: Cambridge University Press. (doi:10.1017/9781108938891)
99. Ronquist F, Klopfstein S, Vilhelmsen L, Schulmeister S, Murray DL, Rasnitsyn AP. 2012 A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Syst. Biol.* **61**, 973–999. (doi:10.1093/sysbio/sys058)
100. Simões TR, Vernygora O, Caldwell MW, Pierce SE. 2020 Megaevolutionary dynamics and the timing of evolutionary innovation in reptiles. *Nat. Commun.* **11**, 3322. (doi:10.1038/s41467-020-17190-9)
101. Burbrink FT, Lawson R. 2007 How and when did Old World ratsnakes disperse into the New World *Mol. Phylogenet. Evol.* **43**, 173–189. (doi:10.1016/j.ympev.2006.09.009)
102. Chen X, Huang S, Guo P, Colli GR, Nieto Montes de Oca A, Vitt LJ, Pyron RA, Burbrink FT. 2013 Understanding the formation of ancient intertropical disjunct distributions using Asian and Neotropical hinged-teeth snakes (*Sibynophis* and *Scaphiodontophis*: Serpentes: Colubridae). *Mol. Phylogenet. Evol.* **66**, 254–261. (doi:10.1016/j.ympev.2012.09.032)
103. Guo P, Liu Q, Xu Y, Jiang K, Hou M, Ding L, Pyron RA, Burbrink FT. 2012 Out of Asia: natricine snakes support the Cenozoic Beringian dispersal hypothesis. *Mol. Phylogenet. Evol.* **63**, 825–833. (doi:10.1016/j.ympev.2012.02.021)
104. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature New Biol.* **491**, 444–448. (doi:10.1038/nature11631)
105. Jetz W, Pyron RA. 2018 The interplay of past diversification and evolutionary isolation with present imperilment across the amphibian tree of life. *Nat. Ecol. Evol.* **2**, 850–858. (doi:10.1038/s41559-018-0515-5)
106. Nuñez LP, Gray LN, Weisrock DW, Burbrink FT. 2023 The phylogenomic and biogeographic history of the gartersnakes, watersnakes, and allies (Natricidae: Thamnophiini). *Mol. Phylogenet. Evol.* **186**, 107844. (doi:10.1016/j.ympev.2023.107844)
107. Brikiatis L. 2014 The De Geer, Thulean and Beringia routes: key concepts for understanding early Cenozoic biogeography. *J. Biogeogr.* **41**, 1036–1054. (doi:10.1111/jbi.12310)
108. Farmer JR *et al*. 2023 The Bering Strait was flooded 10,000 years before the Last Glacial Maximum. *Proc. Natl Acad. Sci. USA* **120**, e2206742119. (doi:10.1073/pnas.2206742119)
109. Raff J. 2022 *Origin: a genetic history of the Americas*, 1st edn. New York, NY: Twelve, Hachette Book Group.
110. Holman JA. 2000 *Fossil snakes of North America: origin, evolution, distribution, paleoecology*. Bloomington, IN: Indiana University Press.
111. Ivanov M. 2022 Miocene snakes of Eurasia: a review of the evolution of snake communities. In *The origin and early evolutionary history of snakes* (eds DJ Gower, H Zaher), pp. 85–110. Cambridge, UK: Cambridge University Press. (doi:10.1017/9781108938891)
112. Jiang D, Klaus S, Zhang YP, Hillis DM, Li JT. 2019 Asymmetric biotic interchange across the Bering land bridge between Eurasia and North America. *Natl. Sci. Rev.* **6**, 739–745. (doi:10.1093/nsr/nwz035)

113. Li JT, Wang JS, Nian HH, Litvinchuk SN, Wang J, Li Y, Rao DQ, Klaus S. 2015 Amphibians crossing the Bering Land Bridge: evidence from holarctic treefrogs (*Hyla*, Hylidae, Anura). *Mol. Phylogenet. Evol.* **87**, 80–90. (doi:10.1016/j.ympev.2015.02.018)
114. Vila R *et al*. 2011 Phylogeny and palaeoecology of polyommatus blue butterflies show Beringia was a climate-regulated gateway to the New World. Proc. R. Soc. B **278**, 2737–2744. (doi:10.1098/rspb.2010.2213)
115. Reinink-Smith LM, Leopold EB. 2005 Warm climate in the late Miocene of the south coast of Alaska and the occurrence of Podocarpaceae pollen. *Palynol.* **29**, 205–262. (doi:10.1080/01916122.2005.9989607)
116. Wolfe JA. 1994 An analysis of Neogene climates in Beringia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **108**, 207–216. (doi:10.1016/0031-0182(94)90234-8)
117. Herold N, Huber M, Müller RD. 2011 Modeling the Miocene climatic optimum. Part I: land and atmosphere. *J. Clim.* **24**, 6353–6372. (doi:10.1175/2011JCLI4035.1)
118. de Queiroz A. 2014 *The monkey's voyage: how improbable journeys shaped the history of life*. New York, NY: Basic Books.
119. Oliver PM, Brown RM, Kraus F, Rittmeyer E, Travers SL, Siler CD. 2018 Lizards of the lost arcs: mid-Cenozoic diversification, persistence and ecological marginalization in the West Pacific. Proc. R. Soc. B **285**, 20171760. (doi:10.1098/rspb.2017.1760)
120. Skeels A *et al*. 2023 Paleoenvironments shaped the exchange of terrestrial vertebrates across Wallace's line. *Science* **381**, 86–92. (doi:10.1126/science.adf7122)
121. Siler CD, Oaks JR, Welton LJ, Linkem CW, Swab JC, Diesmos AC, Brown RM. 2012 Did geckos ride the Palawan raft to the Philippines *J. Biogeogr.* **39**, 1217–1234. (doi:10.1111/j.1365-2699.2011.02680.x)
122. Chan KO, Brown RM. 2017 Did true frogs "dispersify"? *Biol. Lett.* **13**, 20170299. (doi:10.1098/rsbl.2017.0299)
123. de Boer AJ, Duffels JP. 1996 Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: a geotectonic explanation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **124**, 153–177. (doi:10.1016/0031-0182(96)00007-7)
124. Jønsson KA, Blom MPK, Päckert M, Ericson PGP, Irestedt M. 2018 Relicts of the lost arc: high-throughput sequencing of the *Eutrichomyias rowleyi* (Aves: Passeriformes) holotype uncovers an ancient biogeographic link between the Philippines and Fiji. *Mol. Phylogenet. Evol.* **120**, 28–32. (doi:10.1016/j.ympev.2017.11.021)
125. Oliver PM, Heiniger H, Hugall AF, Joseph L, Mitchell KJ. 2020 Oligocene divergence of frogmouth birds (Podargidae) across Wallace's line. *Biol. Lett.* **16**, 20200040. (doi:10.1098/rsbl.2020.0040)
126. Hall R. 2013 The palaeogeography of Sundaland and Wallacea since the late Jurassic. *J. Limnol.* **72**, 1–17. (doi:10.4081/jlimnol.2013.s2.e1)
127. Hall R. 2017 Southeast Asia: new views of the geology of the Malay archipelago. *Annu. Rev. Earth Planet. Sci.* **45**, 331–358. (doi:10.1146/annurev-earth-063016-020633)
128. Deepak V *et al*. 2022 Multilocus phylogeny, natural history traits and classification of natricine snakes (Serpentes: Natricinae). *Zool. J. Linn. Soc.* **195**, 279–298. (doi:10.1093/zoolinnean/zlab099)
129. Ruane S, Richards SJ, McVay JD, Tjaturadi B, Krey K, Austin CC. 2018 Cryptic and non-cryptic diversity in New Guinea ground snakes of the genus *Stegonotus* Duméril, Bibron and Duméril, 1854: a description of four new species (Squamata: Colubridae). *J. Nat. Hist.* **52**, 917–944. (doi:10.1080/00222933.2017.1391959)
130. Grundler MC, Rabosky DL. 2014 Trophic divergence despite morphological convergence in a continental radiation of snakes. *Proc. R. Soc. B* **281**, 20140413. (doi:10.1098/rspb.2014.0413)
131. Sanders KL, Lee MSY, Leys R, Foster R, Keogh JS. 2008 Molecular phylogeny and divergence dates for Australasian elapids and sea snakes (Hydrophiinae): evidence from seven genes for rapid evolutionary radiations. *J. Evol. Biol.* **21**, 682–695. (doi:10.1111/j.1420-9101.2008.01525.x)
132. Gutarra S, Rahman IA. 2022 The locomotion of extinct secondarily aquatic tetrapods. *Biol. Rev. Camb. Philos. Soc.* **97**, 67–98. (doi:10.1111/brv.12790)
133. Motani R, Vermeij GJ. 2021 Ecophysiological steps of marine adaptation in extant and extinct non-avian tetrapods. *Biol. Rev. Camb. Philos. Soc.* **96**, 1769–1798. (doi:10.1111/brv.12724)
134. Peng C *et al*. 2020 The genome of Shaw's sea snake (*Hydrophis curtus*) reveals secondary adaptation to its marine environment. *Mol. Biol. Evol.* **37**, 1744–1760. (doi:10.1093/molbev/msaa043)
135. Jackson TNW *et al*. 2016 Rapid radiations and the race to redundancy: an investigation of the evolution of Australian elapid snake venoms. *Toxins (Basel)* **8**, 309. (doi:10.3390/toxins8110309)
136. Sanders KL, Lee MSY, Bertozzi T, Rasmussen AR. 2013 Multilocus phylogeny and recent rapid radiation of the viviparous sea snakes (Elapidae: Hydrophiinae). *Mol. Phylogenet. Evol.* **66**, 575–591. (doi:10.1016/j.ympev.2012.09.021)
137. Rage JC, Gheerbrant E. 2020 Island Africa and vertebrate evolution: a review of data and working hypotheses. In *Biological consequences of plate tectonics* (eds GVR Prasad, R Patnaik), pp. 251–264. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-030-49753-8)
138. Booth-Rea G, Ranero CR, Grevemeyer I. 2018 The Alboran volcanic-arc modulated the Messinian faunal exchange and salinity crisis. *Sci. Rep.* **8**, 13015. (doi:10.1038/s41598-018-31307-7)
139. Hewitt GM. 2011 Mediterranean peninsulas: the evolution of hotspots. In *Biodiversity hotspots: distribution and protection of conservation priority areas*, pp. 123–148. New York, NY: Springer. (doi:10.1007/978-3-642-20992-5)
140. Zhao Z, Hou ZE, Li SQ. 2022 Cenozoic tethyan changes dominated Eurasian animal evolution and diversity patterns. *Zool. Res.* **43**, 3–13. (doi:10.24272/j.issn.2095-8137.2021.322)
141. Karin BR, Metallinou M, Weinell JL, Jackman TR, Bauer AM. 2016 Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): an out-of-Asia diversification. *Mol. Phylogenet. Evol.* **102**, 220–232. (doi:10.1016/j.ympev.2016.05.033)

142. Zaher H, Folie A, Quadros AB, Rana RS, Kumar K, Rose KD, Fahmy M, Smith T. 2021 Additional vertebral material of *Thaumastophis* (Serpentes: Caenophidia) from the early Eocene of India provides new insights on the early diversification of colubroidean snakes. *Geo. Bios.* **66–67**, 35–43. (doi:10.1016/j.geobios.2020.06.009)
143. El-Hares MA, Zaher H, El-Mekkawy D, El-Sayed S, Seiffert ER, Sallam HM. 2021 New records of legless squamates from the lowest upper Eocene deposits of the Fayum Depression, Egypt. *J. Vertebr. Paleontol.* **41**, e1992770. (doi:10.1080/02724634.2021.1992770)
144. Kehlmaier C *et al*. 2023 Ancient DNA Elucidates the lost world of western Indian Ocean giant tortoises and reveals a new extinct species from Madagascar. *Sci. Adv.* **9**, eabq2574. (doi:10.1126/sciadv.abq2574)
145. Hofmeyr MD, Vamberger M, Branch W, Schleicher A, Daniels SR. 2017 Tortoise (Reptilia, Testudinidae) radiations in Southern Africa from the Eocene to the present. *Zool. Scr.* **46**, 389–400. (doi:10.1111/zsc.12223)
146. Beard KC. 2016 Out of Asia: anthropoid origins and the colonization of Africa. *Annu. Rev. Anthropol.* **45**, 199–213. (doi:10.1146/annurev-anthro-102215-100019)
147. Mattingly S. 2022 *New Eurasian immigrants in the Late Paleogene of Africa, and the great Old World biotic interchange: a quantitative analysis of mammalian dispersal*. Lawrence, KS: University of Kansas.
148. Klein CG, Pisani D, Field DJ, Lakin R, Wills MA, Longrich NR. 2021 Evolution and dispersal of snakes across the Cretaceous-Paleogene Mass Extinction. *Nat. Commun.* **12**, 5335. (doi:10.1038/s41467-021-25136-y)
149. Feng YJ, Blackburn DC, Liang D, Hillis DM, Wake DB, Cannatella DC, Zhang P. 2017 Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. *Proc. Natl Acad. Sci. USA* **114**, E5864–E5870. (doi:10.1073/pnas.1704632114)
150. Couvreur TLP *et al*. 2021 Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. *Biol. Rev.* **96**, 16–51. (doi:10.1111/brv.12644)
151. Wüster W, Crookes S, Ineich I, Mané Y, Pook CE, Trape JF, Broadley DG. 2007 The phylogeny of cobras inferred from mitochondrial DNA sequences: evolution of venom spitting and the phylogeography of the African spitting cobras (Serpentes: Elapidae: *Naja nigricollis* complex). *Mol. Phylogenet. Evol.* **45**, 437–453. (doi:10.1016/j.ympev.2007.07.021)
152. Darin MH, Umhoefer PJ. 2022 Diachronous initiation of Arabia–Eurasia collision from eastern Anatolia to the southeastern Zagros mountains since middle Eocene time. *Int. Geol. Rev.* **64**, 2653–2681. (doi:10.1080/00206814.2022.2048272)
153. Chen M, Liu J, Cai B, Li J, Wu N, Guo X. 2021 A new species of *Psammophis* (Serpentes: Psammophiidae) from the Turpan Basin in northwest China. *Zootaxa* **4974**. (doi:10.11646/zootaxa.4974.1.4)
154. Kurniawan N, Septiadi L, Fathoni M, Wibawa GS, Thammachoti P. 2021 Out of Indochina: confirmed specimen record and first molecular identification of *Psammophis indochinensis* Smith, 1943 (Squamata, Psammophiidae) from Bali, Indonesia. *ChkLst.* **17**, 1521–1531. (doi:10.15560/17.6.1521)
155. Gonçalves DV, Martínez-Freiría F, Crochet PA, Geniez P, Carranza S, Brito JC. 2018 The role of climatic cycles and trans-Saharan migration corridors in species diversification: biogeography of *Psammophis schokari* group in North Africa. *Mol. Phylogenet. Evol.* **118**, 64–74. (doi:10.1016/j.ympev.2017.09.009)
156. Georgalis GL, Szyndlar Z. 2022 First occurrence of *Psammophis* (Serpentes) from Europe witnesses another Messinian herpetofaunal dispersal from Africa – biogeographic implications and a discussion of the vertebral morphology of psammophiid snakes. *Anat. Rec.* **305**, 3263–3282. (doi:10.1002/ar.24892)
157. Machado L, Harris DJ, Salvi D. 2021 Biogeographic and demographic history of the Mediterranean snakes *Malpolon monspessulanus* and *Hemorrhois hippocrepis* across the Strait of Gibraltar. *BMC Ecol. Evol.* **21**, 210. (doi:10.1186/s12862-021-01941-3)
158. Carranza S, Arnold EN, Pleguezuelos JM. 2006 Phylogeny, biogeography, and evolution of two mediterranean snakes, *Malpolon monspessulanus* and *Hemorrhois hippocrepis* (Squamata, Colubridae), using mtDNA sequences. *Mol. Phylogenet. Evol.* **40**, 532–546. (doi:10.1016/j.ympev.2006.03.028)
159. Ali JR, Hedges SB. 2021 Colonizing the Caribbean: new geological data and an updated land-vertebrate colonization record challenge the GAARlandia land-bridge hypothesis. *J. Biogeogr.* **48**, 2699–2707. (doi:10.1111/jbi.14234)
160. de Lang R. 2013 *The snakes of the Moluccas (Maluku), Indonesia: a field guide to the land and non-marine aquatic snakes of the Moluccas with identification key*. Frankfurt am Main, Germany: Edition Chimaira.
161. McCoy M. 2006 *Reptiles of the Solomon Islands*. Sofia, Bulgaria: Pensoft.
162. Zug GR. 2013 *Reptiles and amphibians of the Pacific Islands: a comprehensive guide*. Berkeley, CA: University of California Press.
163. Alda F, Tagliacollo VA, Bernt MJ, Waltz BT, Ludt WB, Faircloth BC, Alfaro ME, Albert JS, Chakrabarty P. 2019 Resolving deep nodes in an ancient radiation of neotropical fishes in the presence of conflicting signals from incomplete lineage sorting. *Syst. Biol.* **68**, 573–593. (doi:10.1093/sysbio/syy085)
164. Chan KO, Hutter CR, Wood PL, Su YC, Brown RM. 2021 Gene flow increases phylogenetic structure and inflates cryptic species estimations: a case study on widespread Philippine puddle frogs (*Occidozyga laevis*). *Syst. Biol.* **71**, 40–57. (doi:10.1093/sysbio/syab034)
165. DeBaun D, Rabibisoa N, Raselimanana AP, Raxworthy CJ, Burbrink FT. 2023 Widespread reticulate evolution in an adaptive radiation. *Evolution* **77**, 931–945. (doi:10.1093/evolut/qpad011)
166. Karin BR, Gamble T, Jackman TR. 2020 Optimizing phylogenomics with rapidly evolving long exons: comparison with anchored hybrid enrichment and ultraconserved elements. *Mol. Biol. Evol.* **37**, 904–922. (doi:10.1093/molbev/msz263)
167. Liu L, Edwards SV. 2009 Phylogenetic analysis in the anomaly zone. *Syst. Biol.* **58**, 452–460. (doi:10.1093/sysbio/syp034)

168. Patton AH, Margres MJ, Epstein B, Eastman J, Harmon LJ, Storfer A. 2020 Hybridizing salamanders experience accelerated diversification. *Sci. Rep.* **10**, 6566. (doi:10.1038/s41598-020-63378-w)
169. Pyron RA, O'Connell KA, Lemmon EM, Lemmon AR, Beamer DA. 2022 Candidate-species delimitation in *Desmognathus* salamanders reveals gene flow across lineage boundaries, confounding phylogenetic estimation and clarifying hybrid zones. *Ecol. Evol.* **12**, e8574. (doi:10.1002/ece3.8574)
170. Whitfield JB, Kjer KM. 2008 Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annu. Rev. Entomol.* **53**, 449–472. (doi:10.1146/annurev.ento.53.103106.093304)
171. Whitfield JB, Lockhart PJ. 2007 Deciphering ancient rapid radiations. *Trends Ecol. Evol. (Amst.)* **22**, 258–265. (doi:10.1016/j.tree.2007.01.012)
172. Folk RA, Soltis PS, Soltis DE, Guralnick R. 2018 New prospects in the detection and comparative analysis of hybridization in the tree of life. *Am. J. Bot.* **105**, 364–375. (doi:10.1002/ajb2.1018)
173. Weinell JL, Burbrink FT, Das S, Brown R. 2024. Data from: Novel phylogenomic inference and 'Out of Asia' biogeography of cobras, coral snakes, and their allies. Figshare. (doi:10.6084/m9.figshare.c.7385057)