Phylogenetic relationships and biogeographic range evolution in cat-eyed snakes, *Boiga* (Serpentes: Colubridae)

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The genus *Boiga* includes 35, primarily arboreal snake species distributed from the Middle East to Australia and many islands in the western Pacific, with particularly high species diversity in South-East Asia. Despite including the iconic mangrove snakes (*Boiga dendrophila* complex) and the brown tree snake (*Boiga irregularis*; infamous for avian extinctions on small islands of the Pacific), species-level phylogenetic relationships and the biogeographic history of this ecologically and morphologically distinct clade are poorly understood. In this study, we sequenced mitochondrial and nuclear DNA for 24 *Boiga* species and used these data to estimate a robust phylogenetic inference, in order to (1) test the hypothesis that *Boiga* is monophyletic, (2) evaluate the validity of current species-level taxonomy and (3) examine whether geographic range evolution in *Boiga* is consistent with expectations concerning dispersal and colonization of vertebrates between continents and islands. Our results support the prevailing view that most dispersal events are downstream – from continents to oceanic islands – but we also identify a role for upstream dispersal from oceanic islands to continents. Additionally, the novel phylogeny of *Boiga* presented here is informative for updating species-level taxonomy within the genus.

ADDITIONAL KEYWORDS: *Boiga flavescens – Boiga multomaculata – Boiga dendrophila* – dispersal – Philippines – South-East Asia – Sundaland – systematics – Wallace's Line – Weber's Line.

INTRODUCTION

Classic studies of evolutionary radiations have illustrated how continental regions can serve as sources of biodiversity, providing the source stock (i.e. ancestral lineages) for subsequent diversification within island archipelagos (Baldwin & Sanderson, 1998; Gillespie, 2002; Verheyen *et al.*, 2003; Losos, 2009; Magnacca & Price, 2015). In contrast, few studies have shown that oceanic islands can provide source lineages for diversification on continents (Nicholson *et al.*, 2005; Heinicke *et al.*, 2007; Mezzasalma *et al.*, 2017; Tavaras *et al.*, 2018). Some authors have suggested that the greater colonization of archipelagos by continental fauna (i.e. downstream colonization), compared to colonization of continents by archipelago fauna (i.e. upstream or reverse-colonization), can in part be explained by relatively low intraspecific variation, high extinction rates and low interspecific competition on islands compared to continents

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(Elton, 1958; Bellemain & Ricklefs, 2008). However, the ability of island archipelagos to serve as sources of biodiversity for continental regions has more recently become better appreciated (Filardi & Moyle, 2005; Grismer *et al.*, 2013, 2016; Welton *et al.*, 2014; Barley *et al.*, 2015; Poe *et al.*, 2017, Liang *et al.*, 2018). Biogeographic studies of taxonomic groups that span continental and island archipelago systems provide an opportunity to understand the dynamics of how these distinct geographic systems jointly influence the diversification process.

Cat-eyed snakes of the genus *Boiga* Fitzinger, 1826 (Colubridae: Colubrinae) are distributed from Pakistan in western Asia to the Solomon Island Archipelago in the south-west Pacific Ocean. The genus includes 35 species of mostly large-bodied, nocturnal, arboreal snakes (David & Vogel, 1996; de Lang & Vogel, 2005; Grismer, 2011; de Lang, 2011, 2013, 2017; Stuebing *et al.*, 2014; Leviton *et al.*, 2018). The best-studied species, the brown tree snake [*Boiga irregularis* (Bechstein, 1802)], naturally occurs in northern Australasia and islands of Melanesia and Wallacea, and is invasive on the island of Guam where it has devastated native bird and mammal populations to the point of extinction (Rodda & Savidge, 2007). Other species of *Boiga* are also distributed across oceanic and continental landmasses [e.g. *Boiga cynodon* (Boie, 1827) and *B. dendrophila* (Boie, 1827); Stuebing *et al.*, 2014; Leviton *et al.*, 2018], and the widespread distribution of this group renders it an ideal system for examining biogeographic processes related to colonization history, subsequent diversification and resulting patterns of biodiversity (Andersen *et al.*, 2018; Oliver *et al.*, 2018; Pepke *et al.*, 2019). However, the monophyly of *Boiga* is controversial (Pyron *et al.*, 2013; Zheng & Wiens, 2016; Figueroa *et al.*, 2016), and species-level relationships in this genus are unclear, in part because earlier studies included less than one-half of the known species, limiting our ability to study their biogeographic range evolution and broad-scale patterns of biodiversity.

In this study, we used novel DNA sequences from five mitochondrial and four nuclear genes sampled from 24 of the 35 *Boiga* species to infer a species-level phylogeny of the genus. We use our estimated phylogeny to assess whether *Boiga* is monophyletic and to evaluate the validity of current species-level taxa. Furthermore, we perform biogeographic analyses to examine the history of geographic range evolution, transitions between continental and archipelago systems, and patterns of 'upstream' versus 'downstream' dispersal in this charismatic snake radiation.

MATERIAL AND METHODS

TISSUE SAMPLING, DNA EXTRACTION AND SEQUENCING

We sampled DNA sequences from 24 species of *Boiga* (Supporting Information, Table S1) from ethanol-preserved tissue samples (22 species) and from GenBank (nine species). Tissue samples were obtained during field expeditions or from museum or private tissue collections. Additionally, we sampled DNA sequences from GenBank for one or more species from each of the following colubrid genera, which earlier authors placed as close or distant relatives of *Boiga*: *Coelognathus* Fitzinger, 1843, *Coluber* Linnaeus, 1758, *Crotaphopeltis* Fitzinger, 1843, *Dasypeltis* Wagler, 1830, *Dipsadoboa* Günther, 1858, *Farancia* Gray, 1842, *Gonyosoma* Wagler, 1828, *Heterodon* Latreille, 1801, *Lycodon* Fitzinger, 1826, *Pantherophis* Fitzinger, 1843, *Pituophis* Holbrook, 1842, *Telescopus* Fleischmann, 1831 and *Toxicodryas* Hallowell, 1857. We also sampled DNA sequences from GenBank for *Ophiophagus hannah* (Cantor, 1836) (Elapidae) and from the homalopsid genera *Homalopsis* Kuhl & Hasselt, 1822 and *Enhydris* Sonnini & Latreille, 1802, which were used as outgroups for phylogenetic analyses (Pyron *et al.*, 2013; Figueroa *et al.*, 2016; Zaher *et al.*, 2019).

We extracted genomic DNA from tissues stored in 95% ethanol and we performed polymerase chain reaction (PCR) for five mitochondrial and four nuclear loci using previously published primers (Supporting Information, Table S2) (Burbrink *et al.*, 2000; Lawson *et al.*, 2005; Pyron & Burbrink, 2009; Pyron *et al.*, 2011; Ruane *et al.*, 2014). Amplified DNA products were visualized using gel electrophoresis and purified using 1 µL of a 20% dilution of ExoSAP-IT (Amersham Biosciences). Cycle sequencing reactions were performed with ABI Prism Big Dye Terminator v.3.1 chemistry (Applied Biosystems) and cleaned using Sephadex(Amersham Biosciences) in Centri-SepTM 96-well plates (Princeton Separations). Purified cycle sequence products were analysed with an ABI Prism 3130*xl* Genetic Analyzer (Applied Biosystems).

Mitochondrial genes included cytochrome c oxidase I (*COI*), cytochrome oxidase subunit b (*Cytb*), NADH dehydrogenase subunit 1 (*ND1*), NADH dehydrogenase subunit 2 (*ND2*) and NADH dehydrogenase subunit 4 (*ND4*). Nuclear genes sampled included spectrin beta non-erythrocytic 1 (*SPTBN1*), oocyte maturation factor mos (*CMOS*), G protein-coupled receptor 37 (*GPR37*) and prostaglandin E receptor 4 (*PTGER4*). We used SEQUENCER v.4.8 (Gene Codes Corp.) for *de novo* sequence assembly editing and MUSCLE (Edgar, 2004) implemented in GENEIOUS v.6.1 (Biomatters Ltd.) to perform multiple sequence alignment and concatenation.

PHYLOGENETIC INFERENCE

To produce a robust phylogeny of *Boiga* and its putative close relatives (Šmíd *et al.*, 2019; Zaher *et al.*, 2019), we performed Bayesian inference (BI) and maximum likelihood (ML) phylogenetic analyses on our multilocus dataset. For BI analysis, we used the program BEAST v.2.2.0 (Bouckaert *et al.*, 2014) under a yule tree process. For each gene partition of the concatenated BEAST analysis, we assigned a relaxed lognormal clock and we used the reversible-jump model implemented in the RBS v.1.1.1 package (Bouckaert *et al.*, 2014) to explore multiple substitution models simultaneously during phylogenetic inference. We sampled from the posterior distribution every 25 000 generations for 250 million generations and omitted the first 10% of samples as burn-in. To specify Homalopsidae as the outgroup, we constrained the group containing all other taxa (i.e. Elapidae + Colubridae) to be monophyletic (Zaher *et al.*, 2019). We used a lognormal distribution prior to calibrate the divergence time between Elapidae and Colubridae (mean = 30.9 Mya; SD = 0.25), because the oldest known fossil from this clade is *Coluber cadurci* Rage, 1974 (Colubridae), with an estimated age of 30.9–32.6 Mya (Head *et al.*, 2016). To assess posterior convergence (i.e. estimated sample sizes > 200) we used TRACER v.1.7 (Rambaut *et al.*, 2018). We used TreeAnnotator v.2.2.0 (Bouckaert *et al.*, 2014) to generate a maximum clade-credibility tree with median divergence times, and we used FigTree v.1.4.0 (Rambaut, 2012) to visualize trees. We considered posterior probabilities (PP) ≥ 0.95 to be strong support for monophyly (Huelsenbeck & Rannala, 2004).

To infer a ML tree for *Boiga*, we used the program IQ-TREE v.1.6.4 (Nguyen *et al.*, 2014) implemented on the web-server W-IQ-TREE (Trifinopoulos *et al.*, 2016). Taxon and gene sampling were identical in the ML and BI analyses. We treated each locus as a separate partition, and we used the automatic model-selection feature (Chernomor *et al.*, 2016) to identify the optimal substitution model for each partition. We performed 1000 ultrafast bootstraps to assess heuristic support for inferred clades, and we considered support values (UFboot) ≥ 95 to be strong support for monophyly (Minh *et al.*, 2013).

BIOGEOGRAPHY

We used BioGeoBEARS v.0.2.1 (Matzke, 2013) to perform ancestral range reconstruction analysis under 36 alternative model schemes, each of which included one of six alternatives for the dispersal multipliers matrix (hereafter, called the dispersal regime) and one of six possible biogeographic range evolution models. Specifically, we considered the following dispersal regimes: (1) dispersal direction unconstrained and dispersal rates equal for all pairwise combinations of regions, (2) dispersal direction constrained (no upstream dispersal; i.e. dispersal rate = 0 for island to continent dispersal) and non-zero dispersal rates are all equal, (3) dispersal direction unconstrained and dispersal rates random (i.e. randomly sampled from a uniform distribution between zero and one), (4) dispersal direction constrained and non-zero dispersal rates random, (5) dispersal direction unconstrained and dispersal rates equal to a measure of faunal similarity and (6) dispersal direction constrained and non-zero dispersal rates equal faunal similarity. Faunal similarity was measured as the Jaccard similarity (Jaccard, 1912) of the presence or absence of snake families and subfamilies between each pair of regions. Furthermore, each model scheme included one of six possible biogeographic range evolution models: the (1) Dispersal-Extinction-Cladogenesis (DEC), (2) DEC+J, (3) DIVALIKE, (4) DIVALIKE+J, (5) BAYAREALIKE and (6) BAYAREALIKE+J models, which differ in the types of range evolution processes that can occur during cladogenesis (Matzke 2013, 2014). The DEC model allows either vicariance or subset (partial sympatry) speciation if one of the daughter lineages has a narrow (i.e. a single area) range. The DIVALIKE model allows vicariant speciation even if both daughter lineages have widespread ranges, but sympatric speciation is prevented unless the ancestor occupies a single area. The BAYAREALIKE model does not allow range evolution to occur during cladogenesis. The models DEC+J, DIVALIKE+J and BAYAREALIKE+J allow founder speciation, whereby one daughter lineage acquires a narrow range not occupied by the ancestor, and range evolution processes allowed by DEC, DIVALIKE and BAYAREALIKE models, respectively (Matzke, 2013, 2014).

Ree & Sanmartín (2018) showed statistical problems with the DEC and DEC+J models and warned against using statistical model selection to compare these two models with other biogeographic models. As such, we used Akaike Information Criterion (AIC) to assess the relative fit of model schemes having different dispersal regimes and the same biogeographic model, and we considered model schemes with the lowest AIC score to be the best fit (Akaike, 1974). To test whether dispersal regimes are a significantly better fit than expected by chance, we conducted a permutation test for each model scheme, except for the six model schemes that have dispersal rates all equal and dispersal direction unconstrained. Specifically, for each model scheme, we generated a null distribution of AIC scores by rerunning BioGeoBEARS under 100 permutation dispersal regimes; each permutation regime was generated by permuting the values in the dispersal

multipliers matrix. A model scheme was considered significantly better than expected by chance if its AIC score was < 95% of null distribution AIC scores.

All biogeographic models were conducted on a pruned version of the Bayesian phylogeny that includes descendants of the most recent common ancestor of *Boiga* and *Lycodon*. Additionally, we pruned the phylogenetic tree to include only one representative per species, except for species that were recovered as paraphyletic, in which case we included a single tip from each highly supported lineage. To prune the phylogeny, we used the drop.tip function in the R package ape v.5.3 (Paradis & Schliep, 2018). Geographic regions used for biogeographic analyses included Africa, the Indian subcontinent, Indochina, Sundaland, the Philippines, Wallacea and Oceania (Fig. 1). We considered Sundaland to include all of the Sunda Shelf islands that were connected to continental Asia during Pleistocene glacial maxima and the Thai–Malay Peninsula. In particular, we treated the boundary between Indochina and Sundaland as a zone of species turnover (rather than a hard boundary) on the Thai–Malay Peninsula (5º–13º N), where Indochinese species reach their southern limit and Sundaic species reach their northern limit (Hughes *et al.*, 2003; Woodruff & Turner, 2009). We chose these biogeographic units because most *Boiga* species or subspecies are endemic to a single one of these areas. Exceptions in which taxa occur in multiple biogeographic units include *Boiga cynodon* from the Philippines, Sundaland and Indochina (non-peninsular Thailand; Lee Grismer, personal communication), *B. irregularis* from Oceania

and Wallacea and *B. multomaculata* (Boie, 1827) from Indochina and Sundaland (de Lang & Vogel, 2005; de Lang, 2011, 2013, 2017; Chan-ard *et al.*, 2015; Leviton *et al.*, 2018; Weinell *et al.*, 2019). For *B. cynodon* and *B. irregularis*, we included representatives from each of the biogeographic regions where they occur. For *B. multomaculata*, we were only able to include samples from Indochina, but we coded this species as occurring in both Indochina and Sundaland.

RESULTS

DNA SEQUENCES

The DNA alignment includes 153 individuals [535–8436 base pairs (bp) per individual; total missing data = 48.6%], from 31 species or subspecies of *Boiga* and 34 other species. Mitochondrial DNA sequences include the genes *COI* (588 bp), *Cytb* (1117 bp), *ND1* (964 bp), *ND2* (1032 bp) and *ND4* (832 bp) for 58 (89%), 47 (72%), 33 (51%), 28 (43%) and 39 (60%) of the sampled taxa, respectively. Nuclear DNA sequences include the genes *SPTBN1* (2222 bp), *CMOS* (547 bp), *GPR37* (664 bp) and *PTGER4* (472 bp) for 40 (62%), 64 (98%), 36 (55%) and 36 (55%) of the sampled taxa, respectively. GenBank accession numbers for all DNA sequences used in this study are listed in the Supporting Information, Table S1. Aligned DNA sequences and all data and script files used for phylogenetic and biogeographic analyses are available from Open Science Framework (doi: 10.17605/OSF.IO/A5BGZ).
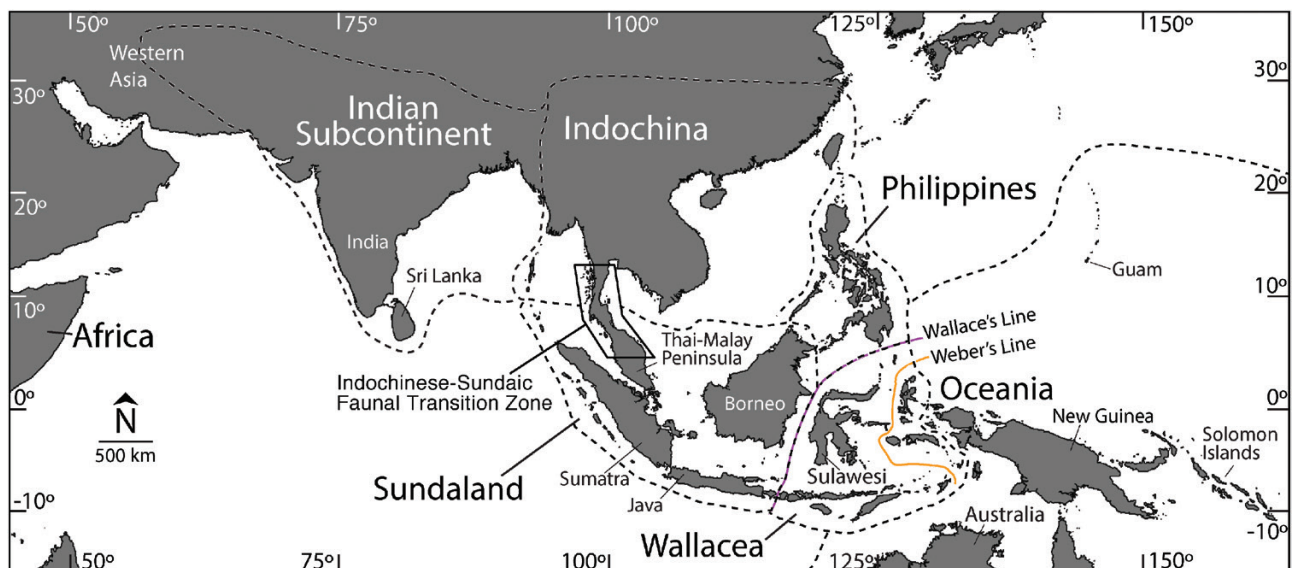
Figure 1. Geographic regions considered for biogeographic analysis (separated by dashed lines: Africa, Indochina, Indian Subcontinent, Oceania, Philippines, Sundaland and Wallacea) and other places mentioned in this article.

PHYLOGENETIC INFERENCE

Optimal substitution models estimated by IQTREE are shown in parentheses following each locus; +G indicates that a model included a discrete Gamma model with four rate categories (Yang, 1994) and +I indicates that a model allowed a proportion of invariable sites: *CMOS* (TN93+G4; Tamura & Nei, 1993); *GPR37* (K81+G4; Kimura, 1981), PTGER (K81+I), *ND1* (GTR+I+G4; Tavaré, 1986), *ND2* (TIM2+I+G4; Posada, 2003), *ND4* (TIM2+I+G4), *Cytb* (TIM2+I+G4), *COI* (TIM2+I+G4) and *SPTBN1* (HKY+G4; Hasegawa *et al.*, 1985).

Both ML and BI analyses support the monophyly of *Boiga* (UFboot = 99; PP = 1) and a sister-group relationship between *Boiga* and the clade containing *Toxicodryas* and *Dasypeltis* (UFboot = 94; PP = 1). The *Boiga* + *Dasypeltis* + *Toxicodryas* clade is strongly supported as the sister-group to the *Crotaphopeltis* + *Dipsadoboa* + *Telescopus* clade (UFboot = 99; PP = 1). Within *Boiga*, analyses strongly support (UFboot = 100; PP = 1) three main clades: clades A, B and C, with clade A being the sister-group to clades B + C (Fig. 2). Clade A includes *Boiga kraepelini* Stejneger, 1902; clade B includes *B. barnesii* (Günther, 1869), *B. beddomei* (Wall, 1909), *B. ceylonensis* (Günther, 1858), *B. jaspidea* (Duméril *et al.*, 1854), *B. multomaculata*, *B. ochracea* (Theobald, 1868), *B. quincunciata* (Wall, 1908) and *B. trigonata* (Schneider, 1802); and clade C includes *B. bourreti* Tillack *et al.*, 2004, *B. nigriceps* (Günther, 1863), *B. philippina* (Peters, 1867) and four species groups that we refer to as the *cynodon*, *dendrophila*, *drapiezii* and *irregularis* species groups (Fig. 2).

Within clade B, our phylogenetic analyses recover paraphyly for both *Boiga multomaculata* and *B. ochracea*, although these species together form a strongly supported clade (UFboot = 100; PP = 1) with shallow substructure. We could not assess if either *B. barnesii* or *B. beddomei* are monophyletic, because we sampled a single individual of each. The remaining species in clade B are each strongly supported as monophyletic. Both BI and ML analyses recovered a clade containing *Boiga ceylonensis*, *B. beddomei* and *B. quincunciata* (UFboot = 89; PP = 0.66); the ML analysis recovered *B. beddomei* sister to *B. quincunciata* (UFboot = 48), whereas the BI analysis recovered *B. beddomei* sister to *B. ceylonensis* (PP = 0.47). The following clades were recovered as sequential outgroups to the *B. ochracea* + *B. multomaculata* clade: (1) *B. trigonata*, (2) the clade containing *B. beddomei*, *B. ceylonensis* and *B. quincunciata*, (3) *B. barnesii* and (4) *B. jaspidea*.

Within clade C, the *cynodon* and *dendrophila* species groups are inferred to be sequential outgroups of the clade containing *B. philippina* and *B. nigriceps* (Fig. 2). The BI analysis recovers a clade containing the *drapiezii* and *irregularis* species groups (PP = 0.44), which are together recovered as sister to the clade containing *B. philippina*, *B. nigriceps* and the *cynodon* and *dendrophila* species groups. In contrast, the ML analysis recovers the *drapiezii* and *irregularis* species groups to be sequential outgroups of the clade containing *B. philippina*, *B. nigriceps* and the *dendrophila* and *cynodon* species groups. Both ML and BI analyses recover *B. bourreti* to be sister to the clade containing all other members of clade C (Fig. 2).

Within each species group, most relationships are strongly supported (Fig. 2). Specifically, the *drapiezii* species group includes *Boiga angulata* (Peters, 1861), *B. schultzei* Taylor, 1923 and *B. bengkuluensis* Orlov *et al.*, 2003 as sequential outgroups to *B. drapiezii* (Boie, 1827) (Fig. 2). The *cynodon* species group includes *B. cynodon* and *B. forsteni* (Duméril *et al.*, 1854) as sequential outgroups to the clade containing *B. guangxiensis* Wen, 1998 and *B. siamensis* Nutaphand, 1971 (UFboot = 94; PP = 0.93). Within the *irregularis* species group, Sulawesi populations of *B. irregularis* [*sensu* Uetz *et al.*, 2019; hereafter called *B. flavescens* (Duméril *et al.* 1854)] are deeply genetically diverged from all other *B. irregularis* populations (UFboot = 88; PP = 1; Fig. 2). Within the *dendrophila* group, *B. cyanea* is sister to the clade containing *B. dendrophila* and *B. tanahjampeana* Orlov & Ryabov, 2002 (UFboot = 100; PP = 1). Additionally, the sister relationship between *B. dendrophila melanota* and *B. tanahjampeana* is strongly supported (UFboot = 100; PP = 1), which makes *B. dendrophila* paraphyletic; the *B. d. dendrophila* + *B. d. gemmicincta* clade is sister to *B. d. occidentalis* + *B. d. annectens*, which are together recovered as the sister-group to the clade containing *B. d. levitoni* and *B. d. divergens* (Fig. 2); and *B. d. gemmicincta* is shown to be paraphyletic with respect to *B. d. dendrophila* (UFboot = 100; PP = 1; Fig. 2).

BIOGEOGRAPHIC RANGE EVOLUTION

Under each of the alternative biogeographic models (i.e. DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE or BAYAREALIKE+J), model fit is highest when dispersal direction is unconstrained and dispersal rates are proportional to faunal similarity (Table 1). Furthermore, model schemes with dispersal rates proportional to faunal similarity and dispersal direction either unconstrained (N = 6 model schemes) or constrained (DEC, BAYAREALIKE and DIVALIKE biogeographic models) were significantly better than expected by chance ($P < 0.05$, permutation tests), whereas all other model schemes (N = 27 model schemes) were not (Table 1; Supporting Information, Figs S1–5). Model schemes with dispersal direction unconstrained and dispersal rates proportional to faunal similarity
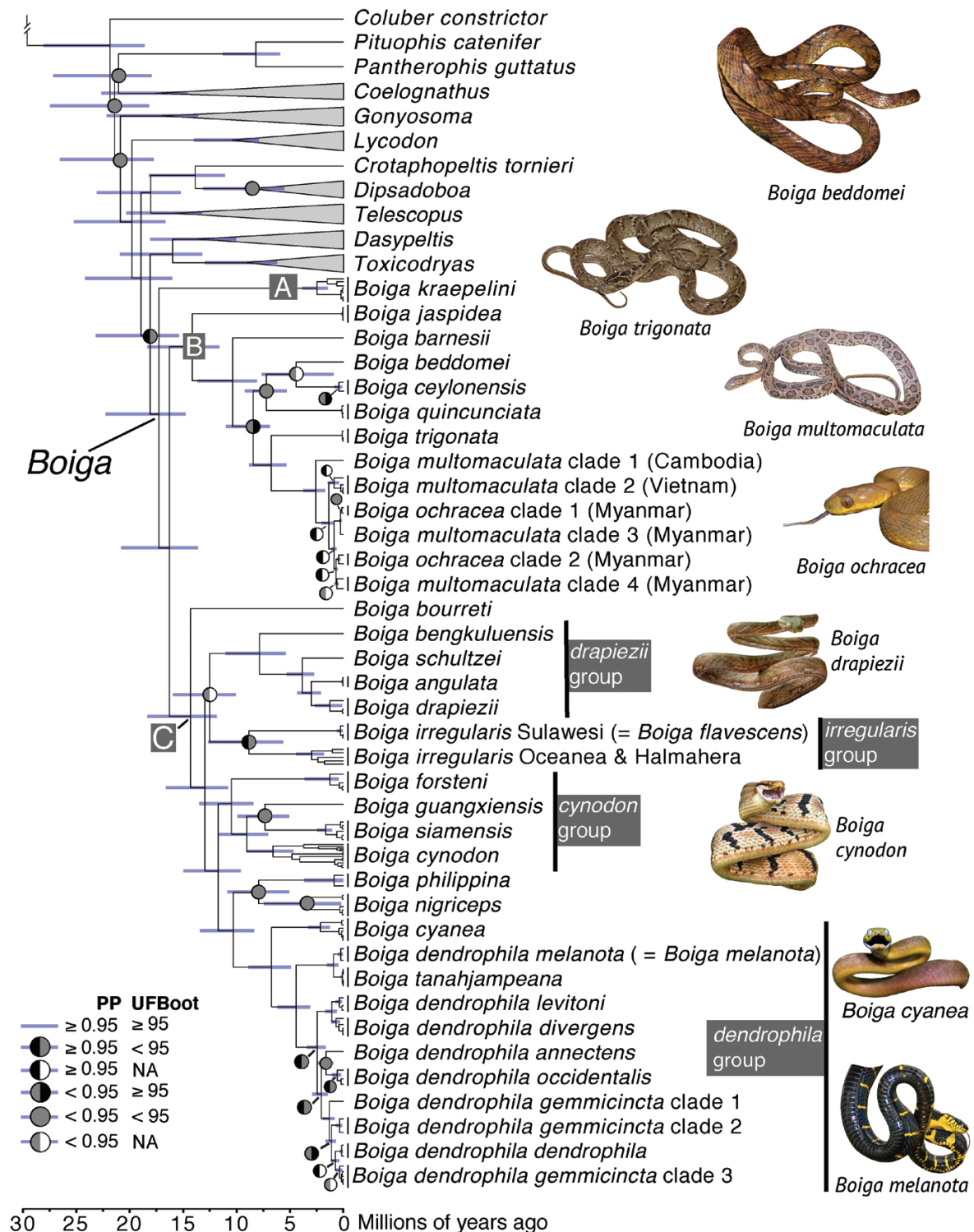
Figure 2. Bayesian inference (BI) time-tree of *Boiga*. Horizontal bars centred at internal nodes indicate 95% highest posterior density for clade age. Circles indicate posterior probability (PP) and ultrafast bootstrap support (UFBoot) for clades that were not highly supported by BI and/or ML analyses (PP < 0.95 and/or UFBoot < 95); nodes without circles indicate clades that were highly supported in both BI and ML analyses (PP ≥ 0.95 and UFBoot ≥ 95). Photos: Ishan Agarwal (*Boiga beddomei*, *B. trigonata* and *B. ochracea*), Kin Onn Chan (*Boiga melanota*, *B. drapiezii*, *B. cynodon* and *B. cyanea*) and Perry L. Wood, Jr (*Boiga multomaculata*).

Table 1. Alternative model schemes considered for BioGeoBEARS analyses. Dispersal direction either unconstrained (all dispersal rates nonzero) or constrained (dispersal rates zero for island to continent dispersal); nonzero dispersal rates either equal, randomly generated or equal to a measure of faunal similarity. *P* is the permutation test *P*-value, *P* < 0.05 means that < 5% of models in the null distribution have an AIC score less than the AIC of the alternative model; rows are sorted by biogeographic model and then by increasing AIC
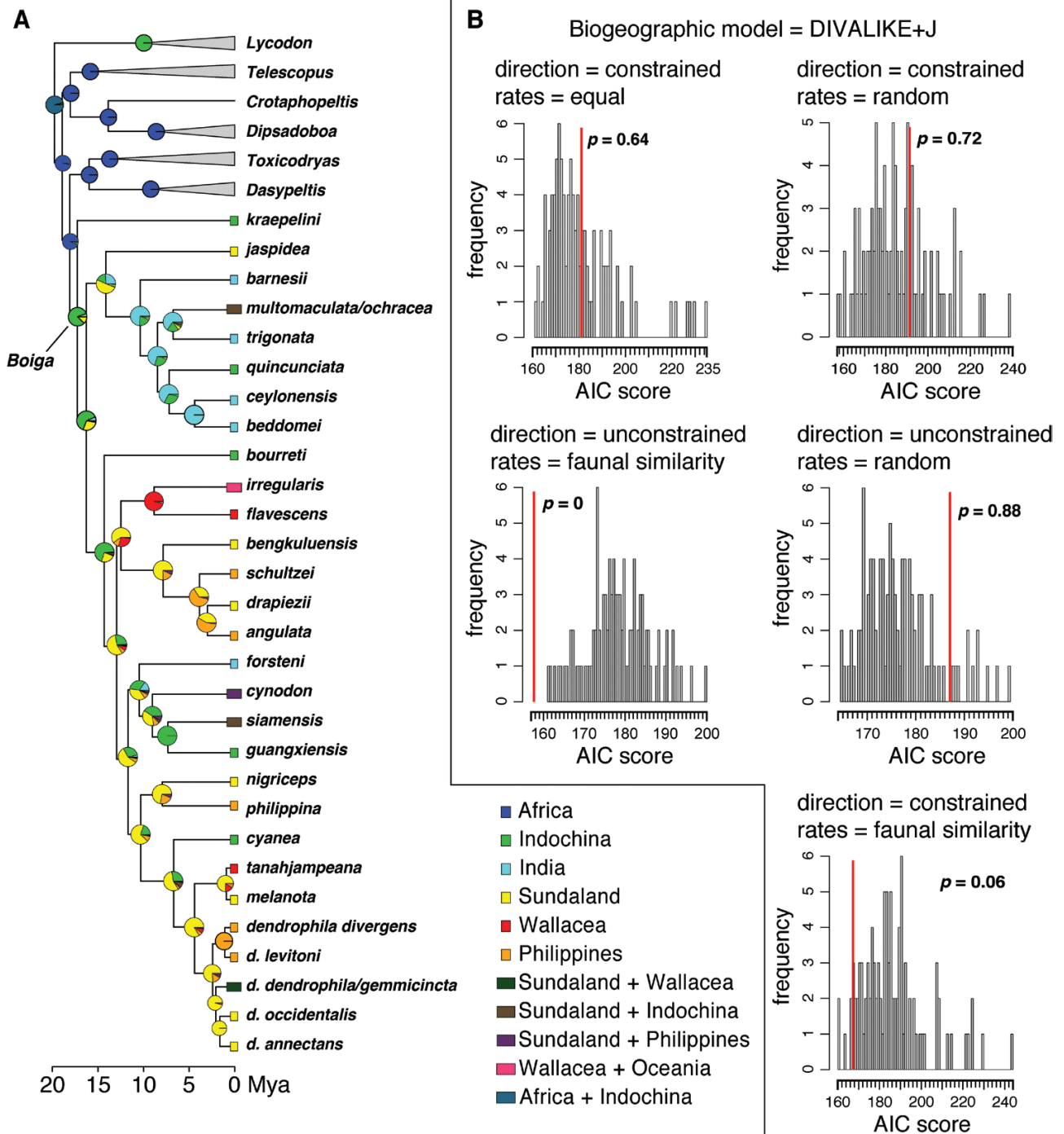
Biogeographic model	Dispersal direction	Dispersal rates	AIC	*P*	Model
BAYAREALIKE	unconstrained	faunal similarity	232.1	0.01	M5
BAYAREALIKE	constrained	faunal similarity	235.02	0.04	M5
BAYAREALIKE	unconstrained	equal	245.37	—	M5
BAYAREALIKE	constrained	equal	249.36	0.5	M5
BAYAREALIKE	unconstrained	random	252.37	0.75	M5
BAYAREALIKE	constrained	random	254.22	0.48	M5
BAYAREALIKE+J	unconstrained	faunal similarity	163.48	0	M6
BAYAREALIKE+J	constrained	faunal similarity	173.84	0.08	M6
BAYAREALIKE+J	unconstrained	equal	178.05	—	M6
BAYAREALIKE+J	constrained	equal	186.07	0.64	M6
BAYAREALIKE+J	unconstrained	random	191.59	0.87	M6
BAYAREALIKE+J	constrained	random	196.09	0.72	M6
DEC	unconstrained	faunal similarity	198.51	0.01	M1
DEC	constrained	faunal similarity	203.13	0.04	M1
DEC	unconstrained	equal	213.07	—	M1
DEC	constrained	equal	218.58	0.52	M1
DEC	unconstrained	random	222.33	0.82	M1
DEC	constrained	random	223.98	0.53	M1
DEC+J	unconstrained	faunal similarity	158.01	0.01	M2
DEC+J	constrained	faunal similarity	166.11	0.05	M2
DEC+J	unconstrained	equal	173.65	—	M2
DEC+J	constrained	equal	179.45	0.61	M2
DEC+J	unconstrained	random	186.65	0.88	M2
DEC+J	constrained	random	188.12	0.64	M2
DIVALIKE	unconstrained	faunal similarity	197.16	0.01	M3
DIVALIKE	constrained	faunal similarity	203.31	0.04	M3
DIVALIKE	unconstrained	equal	212.5	—	M3
DIVALIKE	constrained	equal	218.59	0.52	M3
DIVALIKE	unconstrained	random	226.69	0.88	M3
DIVALIKE	constrained	random	228.04	0.58	M3
DIVALIKE+J	unconstrained	faunal similarity	157.68	0	M4
DIVALIKE+J	constrained	faunal similarity	167.25	0.06	M4
DIVALIKE+J	unconstrained	equal	173.35	—	M4
DIVALIKE+J	constrained	equal	181.2	0.64	M4
DIVALIKE+J	unconstrained	random	187.04	0.88	M4
DIVALIKE+J	constrained	random	191.25	0.72	M4

support either Indochina (DEC, DEC+J, DIVALIKE, DIVALIKE+J and BAYAREALIKE+J models) or Indochina + Africa (BAYAREALIKE model) as the most likely range for the most recent common ancestor of *Boiga*, with subsequent dispersal events of *Boiga* from Indochina to Sundaland and from Sundaland to India (except under BAYAREALIKE), Wallacea and the Philippines (Fig. 3). Additionally, biogeographic analyses support dispersal from Wallacea to Oceania, from India to Indochina and from the Philippines back to Sundaland (Fig. 3).

DISCUSSION

BIOGEOGRAPHY

Island archipelagos tend to be thought of as dead-end roads in terms of colonization, because reverse-dispersal to continents appears to be rare (Bellemain & Ricklefs, 2008). Our results support the prediction of the diversity-invasibility theory that island colonization by mainland-derived lineages occurs more frequently than mainland colonization by island-derived lineages to continent colonization (Elton, 1958), and agree

Figure 3. A, BioGeoBEARS geographic range evolution of *Boiga* under the highest supported model scheme (biogeographic model = DIVALIKE+J, dispersal direction = unconstrained and dispersal rates = faunal similarity). Pie charts at internal nodes indicate the posterior estimate of ancestral geographic distributions and rectangles at tips indicate modern geographic distributions. B, model scheme AIC score (red bar) and corresponding null distribution of AIC scores (grey bars) for each of the five model schemes with biogeographic model = DIVALIKE+J (dispersal rate multipliers either: all equal, random or proportional to faunal similarity; dispersal direction either: constrained or unconstrained). Null AIC distributions and *P*-values are from permutation tests of dispersal rate multipliers; $P < 0.05$ indicates significantly better model fit under the alternative model scheme compared to permutation set of model schemes; see Supporting Information, Figures S1–5 for results under the other biogeographic models.

with earlier phylogenetic studies that found reverse-dispersal to be rare for other animal groups (Bellemain & Ricklefs, 2008; Siler *et al.*, 2010; Welton *et al.*, 2014, 2017; Mezzasalma *et al.*, 2017; Tavares *et al.*, 2018). For example, earlier phylogenetic studies have shown that multiple reptile, amphibian and mammal groups have apparently never reverse-colonized continental Asia or Australasia from the Philippines (Esselstyn & Oliveros, 2010; Siler *et al.*, 2011, 2012; Brown & Siler, 2014; Siler *et al.*, 2014; Welton *et al.*, 2017; Weinell & Brown, 2018).

Although reverse-colonization appears to be rare, we present strong, statistical evidence of reverse-colonization of South-East Asia from the Philippines, and of Australasia from Wallacea, by multiple lineages of *Boiga*. Earlier studies have demonstrated reverse-colonization of Central and South America by one or more lineages of snakes, lizards, frogs and bats (Nicholson *et al.*, 2005; Heinicke *et al.*, 2007; Figueroa *et al.*, 2016; Tavares *et al.*, 2018), of Africa from Madagascar at least once by a group of lizards (Mezzasalma *et al.*, 2017), of Indomalaya from the Philippines at least six times by various lizard groups (Brown *et al.*, 2000; Honda *et al.*, 2006; Siler *et al.*, 2010; Grismer *et al.*, 2013; Welton *et al.*, 2014; Barley *et al.*, 2015) and of Australasia from Wallacea or Oceania at least once by lizards and birds (Filardi & Moyle, 2005; Linkem *et al.*, 2013). In cases where reverse-colonization was followed by diversification (e.g. *Anolis* Daudin, 1802 and *Eleutherodactylus* Duméril & Bibron, 1841), colonization has had a clear effect on regional species pools, namely by the addition of species (Nicholson *et al.*, 2005; Heinicke *et al.*, 2007), but little is known about how reverse-colonization events might also have affected regional species pools through ecological interactions, such as competition or predation.

PHYLOGENETIC RELATIONSHIPS

Most recent molecular phylogenetic studies have recovered *Boiga* to be paraphyletic with respect to the African genera *Crotaphopeltis*, *Dasypeltis*, *Dipsadoboa*, *Telescopus* and *Toxicodryas* (Pyron *et al.*, 2013; Zheng & Wiens, 2016), although Figueroa *et al.* (2016) recovered monophyly for *Boiga*, and Šmíd *et al.* (2019) recovered this genus as either monophyletic (BI topology) or paraphyletic (ML topology). These earlier studies each sampled a small set of loci for one individual per species of 10–16 *Boiga* species, suggesting that low phylogenetic information in earlier datasets may explain the conflicting phylogenetic results. Our results are consistent with the phylogeny of Figueroa *et al.* (2016) and the Bayesian phylogeny of Šmíd *et al.* (2019), which support a monophyletic *Boiga*, although some species-level relationships

in the present analysis differ from the Figueroa *et al.* (2016) topology. In particular, Figueroa *et al.* (2016) found strong support for a sister-relationship between *B. kraepelini* and *B. jaspidea*, whereas we recover *B. kraepelini* as the sister-lineage to all other *Boiga* and *B. jaspidea* as the sister-group to the clade containing *B. barnesi*, *B. quincunciata*, *B. beddomei*, *B. ceylonensis*, *B. trigonata* and *B. multomaculata/ochracea* (Fig. 2).

Earlier authors have never suggested that *Boiga multomaculata* and *B. ochracea* are the same species, presumably because their colour patterns are strikingly different, although our genetic data do not support their distinction (Manthey & Grossmann, 1997; Kästle *et al.*, 2013; Stuebing *et al.*, 2014). *Boiga multomaculata* is known from both Sundaland and Indochina (type locality: Java) and has a dorsal body colour pattern that is grey or light brown with darker spots or blotches (Manthey & Grossmann, 1997; Stuebing *et al.*, 2014), whereas *B. ochracea* is restricted to western Indochina (type locality: Pegu, Myanmar) and has a uniform reddish-brown colour pattern (Kästle *et al.*, 2013). Our limited geographic sampling of *B. multomaculata* (relative its large geographic range) makes it impossible, at present, to differentiate whether *B. multomaculata* and *B. ochracea* are a single, polychromatic species, or if multiple geographically circumscribed species exist, although both have been observed in sympatry in Myanmar (Lee Grismer & Mark Herr, personal communication).

The brown tree snake, *Boiga irregularis*, is infamous for its devastating invasion of Guam, but the taxonomy of the group has been complicated (Rodda & Savidge, 2007; Bauer & Günther, 2013). Recent authors have treated the name *Boiga flavescens* as a synonym of *Boiga irregularis*. Duméril *et al.* (1854) and De Rooij (1917) reported colour pattern and scalation differences between *B. flavescens* and *B. irregularis*, and De Rooij (1917) and De Haas (1950) included Sulawesi within the distribution of both of these species. Subsequently, In den Bosch (1985) treated *B. flavescens* as a synonym of *B. irregularis* and concluded that colour pattern and scalation characters cannot distinguish these taxa, and later authors have followed In den Bosch's (1985) taxonomy (De Lang & Vogel, 2005; Uetz *et al.*, 2019). However, our phylogenetic results strongly support the presence of two, deeply genetically diverged lineages on opposite sides of Weber's Line (Figs 1, 3), and we treat these geographically and genetically cohesive lineages as distinct species; *Boiga flavescens* includes all individuals belonging to the Sulawesi-endemic lineage [type locality 'Macassar, Celebes' (= Makassar, Sulawesi)] and *B. irregularis* includes all individuals from populations other than Sulawesi. Recognition of *B. flavescens* should not cause confusion for conservation research and management of invasive

B. irregularis in Guam, which are derived from one or more source *B. irregularis* populations in north-eastern New Guinea (Richmond *et al.*, 2014).

Boiga tanahjampeana is a large, phenotypically distinct species endemic to Sulawesi (Stuebing *et al.*, 2014), and our results support the monophyly of this species. Although *B. tanahjampeana* renders *B. dendrophila* paraphyletic (Fig. 2), we prefer to maintain the species-level status of *B. tanahjampeana*, an action that requires elevating *B. dendrophila melanota* (Boulenger, 1896) to the taxonomic rank of species (as *Boiga melanota*) to preserve the monophyly of *Boiga dendrophila*. As such, we recognize only the following *B. dendrophila* subspecies: *Boiga dendrophila annectens* (Boulenger, 1896), *B. d. dendrophila* (Boie, 1827), *B. d. divergens* Taylor, 1922, *B. d. gemmicincta* (Duméril *et al.*, 1854), *B. d. latifasciata* (Boulenger, 1896), *B. d. Levitoni* Gaulke *et al.*, 2005, *B. d. multicincta* (Boulenger, 1896) and *B. d. occidentalis* (Brongersma, 1934). *Boiga melanota* can be distinguished from *B. tanahjampeana* and each of the *B. dendrophila* subspecies by having the following combination of characters: 11–12 (rarely ten) infralabial scales; adults have 21–46 thin, yellow dorsal bands on the body that usually do not meet middorsally; gular scales yellow, without black tips or edges; ventral scales without yellow midventral spots (Vogel, 2000; Gaulke *et al.*, 2005; Vogel & Chanhome, 2006). The morphological distinctiveness and monophyly of *B. d. annectens*, *B. d. divergens*, *B. d. levitoni* and *B. d. occidentalis* suggest that these subspecies will likely eventually be recognized as full species (Leviton, 1970; David & Vogel, 1996; Gaulke *et al.*, 2005; Gaulke, 2011; Stuebing *et al.*, 2014). In contrast, *B. d. dendrophila* renders *B. d. gemmicincta* paraphyletic, a finding that conflicts with the marked colour pattern differences between these two subspecies (De Lang & Vogel, 2005; De Lang, 2017). More widespread genetic sampling of these two subspecies on Sulawesi is necessary before making taxonomic changes in the *B. d. dendrophila* + *B. d. gemmicincta* clade. We were unable to include a samples of *B. d. multicincta* or *B. d. latifasciata* in this study, which leaves their phylogenetic position relative to *B. melanota*, *B. tanahjampeana* and the other *B. dendrophila* subspecies unclear. Therefore, we suggest that a more comprehensive phylogenetic systematic study of the *Boiga dendrophila* group is necessary before making additional taxonomic changes.

FUTURE DIRECTIONS

Our phylogeny includes ~ 69% of described *Boiga* species, which greatly expands upon the taxon sampling of all earlier studies. Among the species that we were unable to include in our analyses, the majority

(*N* = 7 species) are from India and Sri Lanka, including *Boiga dightoni* (Boulenger, 1894), *B. flaviviridis* Vogel & Ganesh, 2013, *B. gocool* (Gray, 1834), *B. multifasciata* (Blyth, 1861), *B. nuchalis* (Günther, 1875), *B. thackerayi* Giri, Giri *et al.*, 2019 and *B. westermanni* (Reinhardt, 1863). Smith (1943) suggested that *B. gocool* is closely related to *B. trigonata*. Wall (1909) and Vogel & Ganesh (2013) note that *B. nuchalis* and *B. flaviviridis* are morphologically similar to both *B. ceylonensis* and *B. beddomei*, which suggests that these species may be closely related. Molecular and morphological data reported by Giri *et al.*, (2019) support a close relationship between *B. thackerayi* and either *B. beddomei* or *B. ceylonensis*, and a phylogenetic study by Mohan *et al.* (2018) supports a sister-relationship between *B. westermanni* (formerly *Elachistodon westermanni*) and the Indian clade that includes all descendants of the most recent common ancestor of *B. barnessei* and *B. beddomei*. If future phylogenetic studies confirm close relationships between Indian species unsampled in the current study to those that were sampled, then the effect of missing Indian taxa on our biogeographic results should be minimal.

We were also unable to include genetic samples of four species with distributions outside of the Indian subcontinent: *Boiga andamanensis* (Wall, 1909), *B. hoeseli* Ramadhan *et al.*, 2010, *B. saengsomi* Nutaphand, 1985 and *B. wallachi* Das, 1998, and their inclusion in future biogeographic studies will likely reveal additional colonization events in this group. *Boiga hoeseli* is known from the Nusa Tenggara Islands (biogeographically within Wallacea) and closely resembles *B. cynodon* in both colour pattern and morphology (Ramadhan *et al.*, 2010). A close relationship between *B. hoeseli* and *B. cynodon*, if confirmed, would suggest an additional colonization either to or from Wallacea, and to or from either Sundaland or the Philippines. *Boiga saengsomi* is only known from southern Thailand within the transition zone between Sundaland and Indochina, and has been hypothesized to be a close relative of *B. cyanea* (Nutphand *et al.*, 1991), an Indochinese species. Future biogeographic studies that include *B. saensomi* should run analyses multiple times with alternative settings defining the geographic distribution of this species. Furthermore, future research is needed to determine the biogeographic origins of *B. andamanensis* and *B. wallachi*, which are known from the Andaman and Nicobar Islands, respectively. *Boiga andamanensis* has previously been treated as a subspecies of *B. ceylonensis*, and a close relationship between these two species would support colonization of the Andaman Islands from the Indian subcontinent, in contrast to birds, which likely dispersed from Indochina (Ripley & Beehler, 1989). It is clear that future studies will be needed to determine the phylogenetic affinities

of *Boiga* for which phylogenetic affinities remain unknown, and the inclusion of these taxa into future biogeographic studies will likely reveal additional instances of oceanic dispersal.

The novel phylogeny of *Boiga* presented here suggests that several species and subspecies groups will require future systematic studies to update the species-level taxonomy of the genus, particularly within the *Boiga multomaculata* + *B. ochracea* group and the subspecies of *B. dendrophila*. Genetic data sampled in the present study suggest that *B. multomaculata* and *B. ochracea* are conspecific, and future genetic sampling should minimally also include *B. multomaculata* sampled from one or more Sundaland localities. Our phylogenetic results support our elevation of *B. dendrophila melanota* to full species (*B. melanota*) and are consistent with the future elevation of *B. d. annectens*, *B. d. levitoni*, *B. d. divergens* and *B. d. occidentalis* to full species. Future systematic studies of *B. dendrophila* should include samples of *B. d. latifasciata* and *B. d. multicincta*, which were unsampled in the present study. Paraphyly of *B. d. gemmicincta* with respect to *B. d. dendrophila* recovered in this study is consistent with the presence of multiple, independent evolutionary lineages within *B. d. gemmicincta*, although future studies are needed to rule out other potential causes of paraphyly, including low phylogenetic information in the current dataset, incomplete lineage sorting or gene flow.

Our robust phylogeny of *Boiga*, and the fact that these snakes are highly vagile, will likely make these snakes a powerful system for studying how changes in natural selection following colonization of new areas (e.g. ecological release from parasites) affect character evolution. Phylogenomic analyses of genomic or transcriptome-scale data, which were outside the scope of this analysis, provide compelling opportunities for future studies.

CONCLUSIONS

Biogeographic studies of taxonomic groups such as *Boiga*, which span continental and island archipelago systems, provide an opportunity to understand the dynamics of how these distinct geographic systems jointly influence the diversification process (Filardi & Moyle, 2005; Grismer *et al.*, 2013; Welton *et al.*, 2014; Barley *et al.*, 2015; Andersen *et al.*, 2018), although species-level phylogenetic relationships and the biogeographic history of this group have been poorly understood. Our phylogenetic study greatly expands upon the species-level sampling within *Boiga* and supports (1) the hypothesis that *Boiga* is monophyletic, (2) taxonomic revisions of some widespread species previously distinguished on the basis of colour pattern

differences and (3) an Indochinese origin of the genus. Additionally, we present strong, statistical evidence of reverse-colonization of South-East Asia from the Philippines, and of Australasia from Wallacea, by multiple lineages within *Boiga*, although our biogeographic results are consistent with earlier studies that found colonization of continents from island archipelagos appears to be rare, relative to colonization of the islands by continental fauna.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Figure S1. AIC scores of alternative model scheme (dispersal rate multipliers = all equal if nonzero, dispersal direction = constrained; indicated by red bars) and corresponding null distribution (grey bars) generated during permutation tests of dispersal rate multipliers, for the following biogeographic models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J. $P < 0.05$ indicates model fit is significantly better under the alternative model scheme compared to permutation model schemes.

Figure S2. AIC scores of alternative model scheme (dispersal rate multipliers = random, dispersal direction = unconstrained; indicated by purple bars) and corresponding null distribution (grey bars) generated during permutation tests of dispersal rate multipliers, for the following biogeographic models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J. $P < 0.05$ indicates model fit is significantly better under the alternative model scheme compared to permutation model schemes.

Figure S3. AIC scores of alternative model scheme (dispersal rate multipliers = random, dispersal direction = constrained; indicated by green bars) and corresponding null distribution (grey bars) generated during permutation tests of dispersal rate multipliers, for the following biogeographic models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J. $P < 0.05$ indicates model fit is significantly better under the alternative model scheme compared to permutation model schemes.

Figure S4. AIC scores of alternative model scheme (dispersal rate multipliers = proportional to faunal similarity between regions, dispersal direction = unconstrained; indicated by blue bars) and corresponding null distribution (grey bars) generated during permutation tests of dispersal rate multipliers, for the following biogeographic models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J. $P < 0.05$ indicates model fit is significantly better under the alternative model scheme compared to permutation model schemes.

Figure S5. AIC scores of alternative model scheme (dispersal rate multipliers = proportional to faunal similarity between regions, dispersal direction = constrained; indicated by orange bars) and corresponding null distribution (grey bars) generated during permutation tests of dispersal rate multipliers, for the following biogeographic models: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE and BAYAREALIKE+J. $P < 0.05$ indicates model fit is significantly better under the alternative model scheme compared to permutation model schemes.

Table S1. Individuals sampled in this study. GenBank accession codes in bold indicate new sequences generated for this study. For chimeric individuals, superscripts match GenBank accession numbers of DNA sequences to a particular voucher specimen or tissue; dashes indicate missing data. Acronyms associated with tissues or specimens in this study include: ANM (acronym unknown); BCY (*Boiga cynodon* cataloged at the Snake Farm, Queen Saovabha Memorial Institute, The Thai Red Cross Society, Bangkok Thailand); CAS (California Academy of Sciences); CIB (Chengdu Institute of Biology, the Chinese Academy of Sciences); FMNH (Field Museum of Natural History); HKV (Harold K. Voris field series); KU (University of Kansas Biodiversity Institute); LSUHC (La Sierra University Herpetological Collections); LSUMZ (Louisiana Museum of Natural History); MCZ (Museum of

Comparative Zoology); MVZ (Museum of Vertebrate Zoology); OD (acronym unknown); PNMH or PNM (National Museum of the Philippines); RAP (R. Alexander Pyron field series); SH (N. Helfenberger tissue collection); TNHC (Texas Natural History Collections, University of Texas at Austin); UF (Florida Museum of Natural History); ZISP (Zoological Institute, Russian Academy of Sciences, St. Petersburg); RS (Ruchira Somaweera field series); YPM (Peabody Museum of Natural History, Yale University).

Table S2. Polymerase chain reaction (PCR) and sequencing (Seq.) primers used in this study.