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Species delimitation and systematics of the green pythons (*Morelia viridis* complex) of melanesia and Australia

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ABSTRACT

Molecular data sets and the increasing use of integrative systematics is revealing cryptic diversity in a range of taxa – particularly in remote and poorly sampled landscapes like the island of New Guinea. Green pythons (*Morelia viridis* complex) are one of the most conspicuous elements of this island's fauna, with large numbers taken from the wild to supply international demand for exotic pets. We test hypotheses about species boundaries in green pythons from across New Guinea and Australia with mitochondrial genomes, 389 nuclear exons, and comprehensive assessment of morphological variation. Strong genetic structuring of green python populations and species delimitation methods confirm the presence of two species, broadly occurring north and south of New Guinea's central mountains. Our data also support three subspecies within the northern species. Subtle but consistent morphological divergence among the putative taxa is concordant with patterns of molecular divergence. Our extensive sampling identifies several zones of hitherto unknown biogeographical significance on the island of New Guinea. We revise the taxonomy of the group, discuss the relevance of our findings in the context of Papuan biogeography and the implications of our systematic changes for the conservation management of these taxa.

1. Introduction

The failure to detect cryptic diversity in morphologically conservative but wide-ranging species underestimates genetic diversity, obscures evolutionary relationships, and acts as an impediment to proper conservation management (Colborn et al., 2001; Bickford et al., 2007). The now common application of molecular genetic techniques in systematics has revealed cryptic diversity in many taxonomic groups, confirming that evolutionary divergence is not necessarily accompanied by morphological change (Bickford et al., 2007; Metzger et al., 2010). For even the most recognizable and charismatic animal taxa, molecular genetic techniques are revealing that supposedly well-known and widespread species in fact comprise multiple deeply divergent lineages (Toussaint et al., 2015; Nater et al., 2017). Morphological conservatism despite significant molecular divergence has challenged traditional taxonomic approaches based solely on morphology, and drives the necessity for integrative approaches in unravelling evolutionary relationships (Sinclair et al., 2004; Dayrat, 2005). The challenge is compounded in situations where species inhabit remote and poorly studied regions of the world, where sparse specimen sampling can be inadequate for traditional taxonomic comparisons and evaluation of genetic relationships at the population level (Malhotra and Thorpe, 2004).

The island of New Guinea is an example of such a region. Large

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parts of New Guinea are difficult to access because of the rugged nature of the terrain. Recent exploration has resulted in the continuous discovery of new species that add to the already rich faunal diversity (Metzger et al., 2010; Oliver et al., 2013). The island's diversity is driven in part by a series of relatively recent tectonic events resulting in the rapid formation of multiple biogeographic barriers across the island, promoting extrinsic reproductive isolation (Polhemus, 2007; Toussaint et al., 2014). The rapid nature of this tectonic upheaval has resulted in high levels of cryptic diversity across all taxonomic groups that have been studied (Donnellan and Aplin, 1989; McGuigan et al., 2000; Heads, 2002; Metzger et al., 2010; Oliver et al., 2013). However, translating this new molecular information into updated taxonomic outcomes has been a slow process.

Large land masses with high topographic heterogeneity and a recent dynamic geomorphological history can promote rapid and recent speciation for many co-distributed faunal groups, resulting in readily recognised biogeographic patterns. For some Papuan taxa the potential biogeographic barriers promoting species-level divergence or demarking species boundaries are obvious. For example, New Guinea's high elevation, recently formed, central cordillera is a clear barrier to gene flow for lowland taxa, as is the geographic bottleneck at the Vogelkop Isthmus in West Papua, Indonesia, which has resulted in the accumulation of many north-south and east-west sister species pairs (Beehler, 2007; Polhemus, 2007). In other cases, however, there are deep molecular divergences between sister taxa occurring where there are no obvious barriers to gene flow (Mack and Dumbacher, 2007; Deiner et al., 2011). The relative paucity of studies in New Guinea presents a challenge for identifying broader biogeographic patterns across the island, identifying units for conservation, for testing broader hypotheses about species delimitation, and for identifying zones of sympatry and levels of introgression.

Comprehensive sampling of wide-ranging species inhabiting a variety of temperature and altitudinal gradients represent a valuable model for examining biogeographical patterns across New Guinea. Green pythons (*Morelia viridis* complex) represent such a group. Green pythons are medium-sized (< 2 m) arboreal snakes inhabiting closed forests from sea level to 2000 m throughout mainland New Guinea, many of its offshore islands, and a small area of north-eastern Australia (O'Shea, 1996; Natusch and Natusch, 2011). Green python hatchlings are either yellow or brick red and undergo a remarkable ontogenetic change in color to bright lime green (Wilson et al., 2007; Natusch and Lyons, 2012). The extraordinary colors displayed by this species has made them popular pets; green pythons have become one of the world's most common reptile species in the live animal trade, with many taken from the wild for this purpose (Lyons and Natusch, 2011; CITES Trade Database, 2019).

To the untrained eye, green pythons from all localities simply appear to be 'green snakes'. However, the species' wide altitudinal and geographic range are attributes suggestive of cryptic diversity (Donnellan and Aplin, 1989; Bickford et al., 2007). Color variations corresponding to specific collection localities have long been recognised, suggesting the species may indeed be polytypic (Maxwell, 2005; Kivit and Wiseman, 2005). Subsequent morphological analysis has revealed subtle differences in body sizes, head shapes, and color of snakes from different populations (Lyons and Natusch, 2013; Natusch and Lyons, 2012; Natusch and Lyons, 2014). Examination of mitochondrial DNA (mtDNA) from a small sample of green pythons revealed the existence of two strongly divergent clades distributed on either side of New Guinea's central mountain range (Rawlings and Donnellan, 2003). Nevertheless, vast expanses of forest form a continuous ring of suitable habitat around New Guinea's central range, with few apparent geographical and ecological isolating barriers (Mack and Dumbacher, 2007).

The ecological and phenotypic similarity of the two genetically deeply divergent clades of green pythons make these snakes excellent candidates for examining hypotheses about species limits across the island of New Guinea. Here, using morphological data combined with hundreds of independently evolving nuclear loci and complete mitochondrial genomes, we resolve the phylogenetic relationships, assess their genetic structuring and define new taxonomic boundaries using different species delimitation methods. We discuss the biogeographical implications in what is perhaps the most extensive combined genetic and morphological geographic sampling of a terrestrial taxon from New Guinea.

2. Materials and methods

2.1. Specimen sampling

Tissue samples or DNA extracts used for our molecular genetic analyses are held in the Australian Biological Tissue Collection (ABTC). For our morphological analyses we examined a total of 1647 specimens of green pythons from two sources. First, we examined green pythons in the following collections: American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); Australian National Wildlife Collection, Canberra (ANWC); British Museum of Natural History, London (BMNH); Bernice P. Bishop Museum, Honolulu (BPBM); California Academy of Sciences, San Francisco (CAS); Louisiana Museum of Natural History, Baton Rouge (LSUMZ); National Museum of Natural History, Paris (MNHN); Museum Victoria, Melbourne (MV); Museum Zoologicum Bogoriense, Bogor (MZB); Queensland Museum, Brisbane (QM); National Museum of Natural History, Washington DC (USNM); and the University of Papua, Manokwari (UPM). Secondly, we examined green pythons captured in the field either by ourselves or by local villagers (*sensu* Natusch and Natusch, 2011; Natusch and Lyons, 2014). We only included specimens in our analyses whose specific locality could be confirmed. In most cases, this meant excluding pythons held by middlemen or major collectors at transit ports. The geographic locations from which tissue and morphological samples were derived are presented in Fig. 1. Samples sizes and specimen numbers of green pythons from each locality are provided in Supplementary Material I.

2.2. Molecular analyses

2.2.1. DNA sequencing and alignment preparation

We extracted DNA using a Qiagen DNeasy Blood & Tissue kit. The data were collected at the Center for Anchored Phylogenomics (www.anchoredphylogeny.com) at Florida State University using anchored hybrid enrichment (Lemmon et al., 2012). In summary, libraries were prepared from the extracted DNA following Lemmon et al. (2012) and Prum et al. (2015), using a Beckman Coulter Xp liquid-handling robot. During this process, libraries were given single 8-bp indexes. Libraries were then pooled in groups of 16 for enrichment with AHE probes developed for amniotes by Prum et al., 2015; Ruane et al., 2015; Tucker et al., 2016 and produced Agilent Technologies as an XP SureSelect kit. The probes targeted ~400 exons, each ~1350 bp in length.

Enriched libraries were pooled and sequenced on one lane of an Illumina HiSeq 2500 PE150 at the College of Medicine Translational Laboratory at Florida State University. After demultiplexing the quality-filtered reads with no mismatches tolerated, we merged the overlapping reads following Rokyta et al. (2012) and assembled the loci following Hamilton et al. (2016), using *Anolis carolinensis* and *Calamaria pavimentata* genomes as references. We formed consensus sequences from assembly clusters containing over 250 mapped reads. We determined orthology using a neighbor-joining clustering approach (Hamilton et al., 2016) using pairwise sequence distances, and orthologues were aligned using MAFFT v7.3 (Katoh and Standley, 2013). Alignments were auto-trimmed/masked following Hamilton et al. (2016), but with MINGOODSITES = 14, MINPROPSAME = 0.4, and MISSINGALLOWED = 24. Finally, we visually inspected the auto-trimmed/masked alignments in Geneious R9 (Biomatters Ltd., Kearse et al., 2012) to

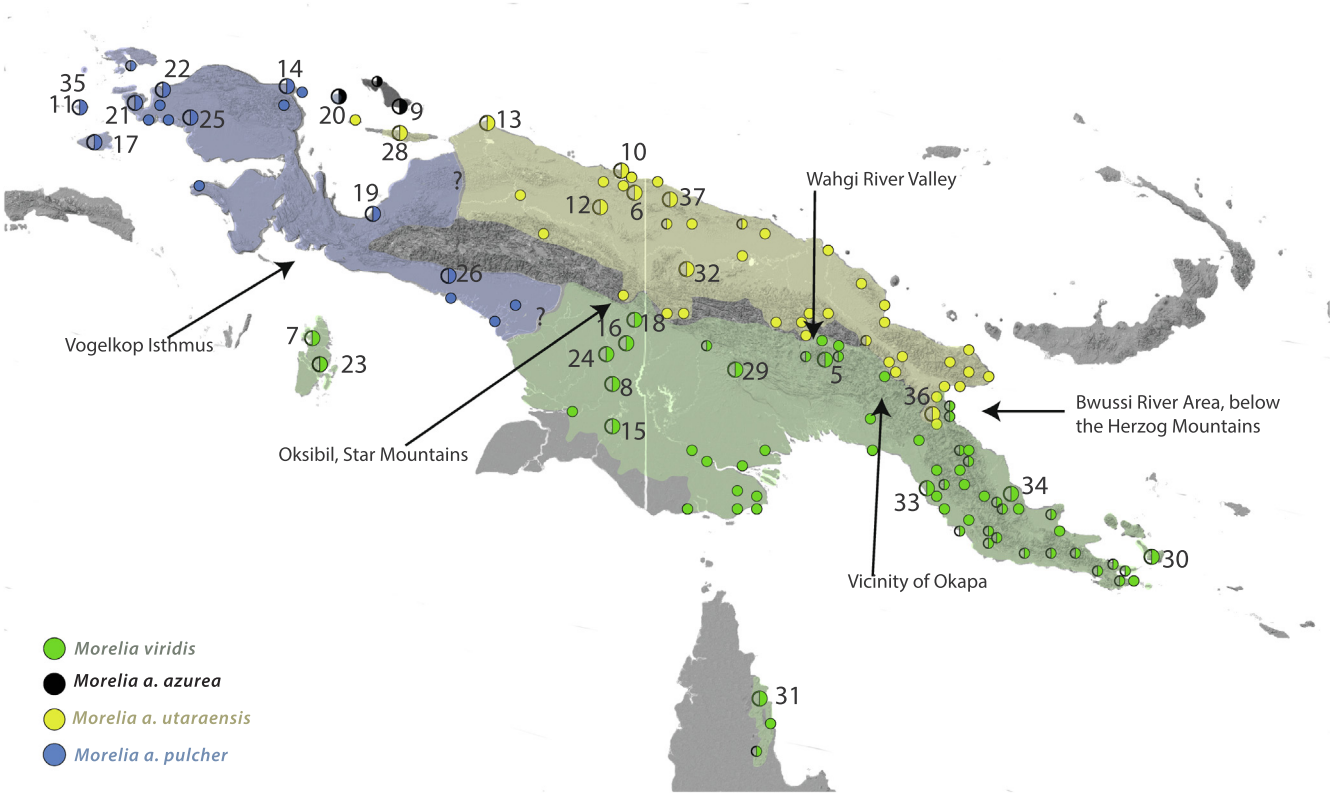

Fig. 1. Sampling localities for the taxa included in this study, according to the legend in the bottom left. Shaded areas of each color correspond to the geographic range of the different taxa based on their molecular identity. Half-filled circles depict localities for which molecular and morphological data are available while whole circles depict localities with only morphological samples. Large half-filled circles with numbering represent localities from which nDNA are available while small circles include only mtDNA. Arrows depict specific points of biogeographic significance referenced within the text. These areas do not have discrete boundaries. Arrow tips show the approximate locations under discussion.

verify that any misaligned regions were removed. The final dataset comprised 389 nuclear loci, each with an average length of 1750 bp.

We also reconstructed the mitochondrial genomes from the raw reads retrieved as by-catch from the AHE sequence captures for each sample using MITObim version 1.9 (Hahn et al., 2013). We used the mitochondrial genome of *Python regius* GenBank AB177878 as a reference (Dong and Kumazawa, 2005). We aligned the sequences using MAFFT version 7.3 and inspected the alignment by eye. We used published mitochondrial *cytochrome b* (*cytb*) sequences (Rawlings and Donnellan, 2003) and sequenced *cytb* for additional samples that were not included in the nuclear sequencing (see Table S1 in Supplementary Material for specimen information). To amplify via Polymerase Chain Reaction (PCR) and sequence *cytb* we used the primers (numbered from *Python regius* mitochondrial genome) provided in Table S2 of the Supplementary Material.

2.2.2. Alignment partition and substitution model selection

To estimate the best partitioning scheme and molecular substitution model for each partition we used PartitionFinder 2, using the Bayesian Information Criterion (BIC) to select the best fit (Lanfear et al., 2016). To make the search computationally feasible we used a relaxed clustering algorithm (Lanfear et al., 2014). The best fit divided the nuclear loci into 35 partitions and the mitochondrial genomes into nine partitions with a GTR + G substitution model for all partitions.

2.3. Phylogenetic hypotheses

We used three different approaches to reconstruct a hypothesis of the phylogenetic relationships between the *Morelia viridis* complex populations; two based on concatenation and one based on the multispecies coalescent to estimate a species tree. First, we used the concatenated alignment to reconstruct the phylogeny using a Maximum Likelihood (ML) approach with the program RAxML version 8.2 (Stamatakis, 2014). We partitioned the alignment with the scheme described above and used the *GTRGAMMA* model. We performed a rapid bootstrap analysis with 100 replicates and simultaneously searched for the highest scoring ML tree using the option "*-f a*". We initially performed these analyses on the dataset with two phased alleles, and as they proved to be monophyletic for each individual we repeated the analyses after randomly removing one allele per locus. Second, using the same alignment and partitioning scheme as above we estimated the phylogeny under a Bayesian framework with the program MrBayes version 3.2 (Ronquist et al., 2012). We ran two independent analyses with three heated and cold chains each for 40 million generations. We sampled every 1000 generation with a burnin of 20.000 million generations. As a final approach, we performed a coalescent-based analysis using Astral III (Zhang et al., 2017). We obtained individual gene trees for each locus using RAxML with the same specifications described above. Astral III also estimates branch lengths in coalescent units and branch support using multi-locus bootstrapping based on 100 bootstrap replicates from the gene trees (Seo, 2008). For all of the analyses described above, we used the outgroups *Morelia bredli*, *M. carinata* and *M. spilota* to root the trees. We also analysed the partitioned mitochondrial genome alignment with RAxML version 8.2.

2.4. Species delimitation

We used the four clades identified from the phylogenetic analyses (see Results) to test species delimitation hypotheses. First, we performed a fully Bayesian species delimitation analysis using the program BPP version 3.3 (Yang, 2015). This program uses the multispecies coalescent model to compare the posterior probabilities of different

species delimitation models (Rannala and Yang, 2013; Yang and Rannala, 2010). To avoid integrating over all possible species delimitations and increase computational efficiency, we provided the topology inferred by the phylogenetic programs as a guide tree for the analysis. We assigned the population size (θ) and the divergence time at the root of the tree (τ) a gamma prior of G(1, 10) and G(2, 2000), respectively. These priors suggest large ancestral population sizes and shallow divergence times, which makes the analysis more conservative in its species delimitation (Leaché and Fujita, 2010; de Oca et al., 2017; Yang and Rannala, 2010). We ran the reversible jump (rj) MCMC for 50,000 generations, with a burnin of 2000 and a sampling frequency of four. We performed this twice to confirm convergence between the runs.

It has been recently argued that species delimitation using the multi-species coalescent struggles to distinguish between genetically structured populations and species (Sukumaran and Knowles, 2017). For this reason, it is important to complement purely genetic analyses with other types of data, to have a more integrative approach to delimit species. We incorporated our phenotypic data (see below) in our species delimitation using the program iBPP version 2.1 (Solís-Lemus et al., 2015). This program uses the same framework as BPP (described above) but can also incorporate trait data conditioned under a Brownian Motion (BM) model of evolution. We performed two analyses using only our trait data: one using morphometric data (residuals on snout-vent length - hereafter SVL - of tail length, head length and head width) and one using meristic data (number of ventral scales, subcaudal scales, supralabials, infralabials, supralabials in contact with the eye, heat pits in supralabials and heat pits in infralabials). We additionally performed another analysis (twice) using the combined morphological and genomic data. We used the same θ and τ priors as above and ran the chain for the same length, burnin and sampling frequency. For our morphological data, we placed uniform priors for the BM control parameters ν and κ.

2.5. Population structure

Population genetic structure was assessed with the program *STRUCTURE* version 2.3 (Pritchard et al., 2000). We called all the SNPs for each locus using the pipeline *SNPCaller* (Lin et al. 2008). We used the Linkage model with correlated allele frequencies. We performed five independent runs, with K (number of genetic clusters) of one to four. Each run consisted of 1.000.000 MCMC generations with a burnin of 500.000 steps. We extracted the most likely value of K using the Evanno or ΔK method (Evanno et al., 2005) and the ln $\Pr(D|K)$ method (Pritchard et al., 2000) implemented in Clumpak (Kopelman et al., 2015), which uses DISTRUCT version 1.1 (Rosenberg, 2004) to produce the genetic structure plots.

2.6. Morphological analyses

We tested for concordance between molecular variation in green pythons and aspects of scalation, coloration, and patterning considered taxonomically important in other studies of python systematics (McDowell, 1975, Kluge, 1993). We recorded the following meristic characters: number of ventral scales; number of dorsal midbody rows; number of subcaudal scales; number of supralabial and infralabial scales; number of supralabial scales contacting the orbit; and the number of thermoreceptive pits in both the supralabial and infralabial scales. We measured SVL and included it as a covariate in our analysis of tail lengths. We restricted tail length analyses to measurements of live specimens collected in the field (*sensu* Natusch and Natusch, 2011, Natusch and Lyons, 2014). Green pythons exhibit minor sexual dimorphism in some traits (e.g., body sizes, relative head sizes), but not others e.g., tail lengths (Wilson et al., 2006, Natusch and Lyons, 2014). In many cases (for preserved specimens) it was not possible to determine the sex of specimens without destructive examination. For this reason, we tested for sexual dimorphism in scalation based on counts taken from live specimens (N = 543), which revealed no dimorphism in any of our examined measures (ANCOVA; p-values for all counts > 0.05). We thus pooled males and females for our morphological analyses.

To test whether the genetic lineages identified by our molecular analyses were distinguishable morphologically, we applied a single discriminant analyses to our meristic characters. We performed a stepwise deletion of non-significant characters until we were only left with significant effects. For our tail length comparisons, we included body size as a covariate in an analysis of covariance (ANCOVA) to adjust for absolute body size differences among individuals. Data were log-transformed for all analyses. Finally, we recorded a number of qualitative characters known to vary geographically in green pythons, including: iris coloration, juvenile morph coloration, tail coloration, and general colour and pattern. Details and results of these characters are provided in the Supplementary Material (II).

3. Results

3.1. Phylogenetic hypotheses

For the nuclear data, the ML tree inferred by RAxML, the Bayesian tree inferred by MrBayes and the species tree inferred by Astral III are concordant in showing strong support for four main clades (Figs. 2 and S5). We used these clades as initial hypotheses for our species delimitation analyses. The clades include populations from: (1) southern New Guinea, the Aru Islands and Australia; (2) the Vogelkop Peninsula in northwestern New Guinea; (3) Biak and Numfor Islands, in northern New Guinea; and (4) the remaining populations of northern New Guinea from Yapen to Wau. We will refer throughout this section to these clades as the southern New Guinea, Vogelkop, Biak and northern New Guinea clades (see Fig. 1 and the Discussion section for further detail on the exact limits of distribution for each clade). Within these clades, there is considerable uncertainty and discordance in the relationships between the populations, which may have gene flow.

Analysis of the mtDNA infers the same clades as above, but with different relationships between them and more phylogenetic structure. The nuclear DNA infers the Vogelkop clade as sister to the rest of the northern green pythons (Biak and northern New Guinea) whereas the mtDNA infers those from northern New Guinea as sister to the Vogelkop and Biak clades (Figs. 2, 3). Moreover, the mtDNA tree infers two distinct clades within the southern New Guinea clade, one with specimens from Southern Papua, east through the Western and Gulf Provinces, south of the Owen Stanley Ranges to Milne Bay, and the other from Normanby Island and on the mainland north of the Owen Stanley Ranges to 20 km south of Lae.

3.2. Species delimitation

The Bayesian multi-species coalescent species delimitation analysis of the molecular data (by BPP) showed very strong support for the four clades being separate species (posterior probability - pp = 1.0) with no support for all other hypotheses (pp = 0.0). The pp for speciation is 1.0 on every node of the tree. The species delimitation analysis ran on iBPP with morphology alone found strongest pp (0.61) for a delimitation that comprises three species: from southern New Guinea, the Vogelkop and Biak + northern New Guinea. This was followed by a delimitation that included pythons from southern New Guinea and a species containing all other clades (pp = 0.27). The node that splits southern New Guinea and the rest has the highest support (pp = 1.0), and the node that splits Vogelkop from Biak + northern New Guinea has moderate support (pp = 0.73). The node splitting Biak and northern New Guinea has very weak support (pp = 0.16). In the run with the combined genomic and morphological data, however, the results are identical to the BPP run with the genomic data only, i.e., pp = 1 of the delimitation including

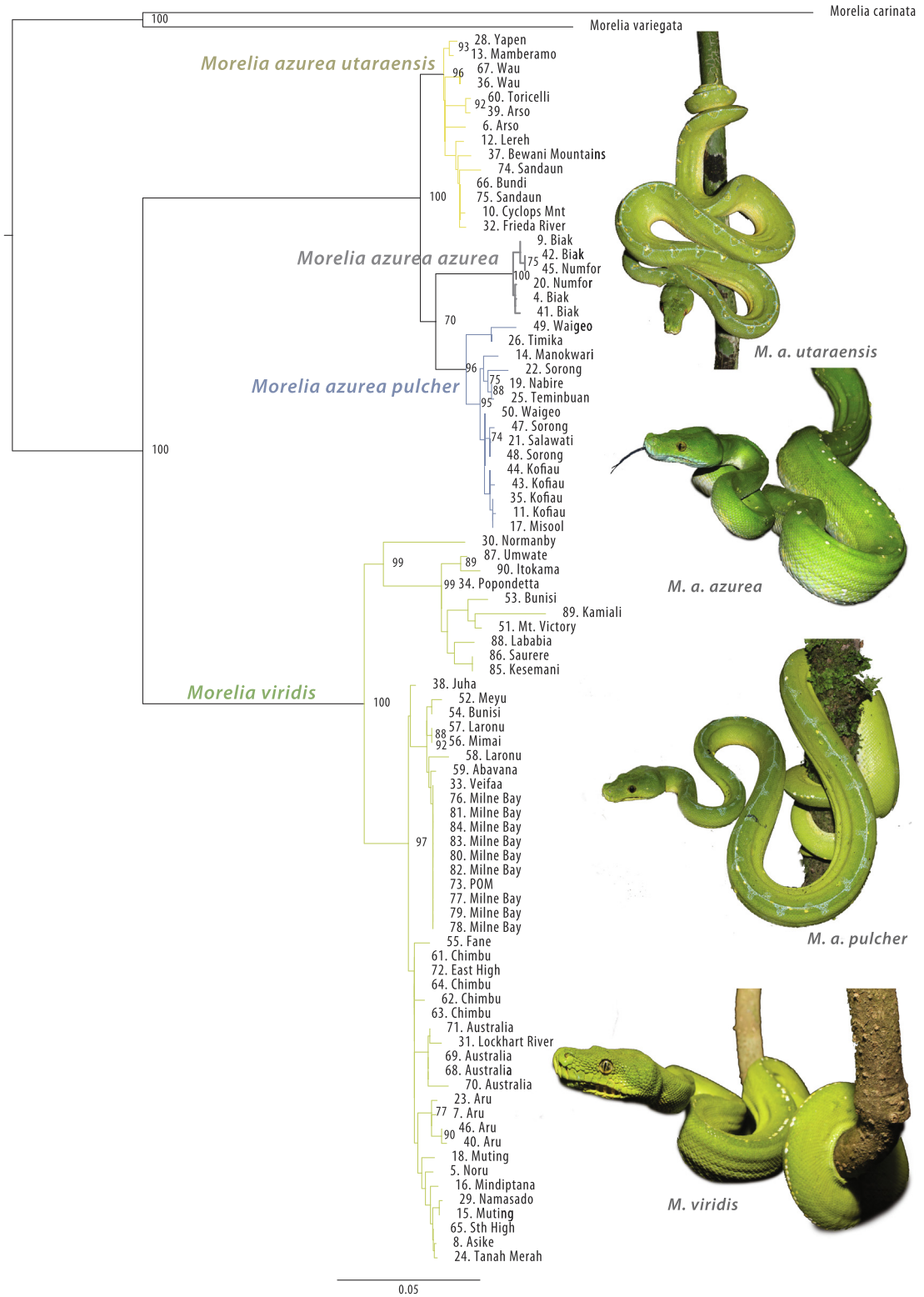

Fig. 2. Maximum Likelihood phylogeny inferred from mtDNA using RAxML. Node numbers indicate bootstrap values for supported nodes (> 70).

the four clades as species and pp = 1 for every node.

3.3. Population structure

The genetic structure analysis of the SNP data suggested that the most likely number of genetic clusters (K) is two according to the Evanno or ΔK method, and three according to the ln Pr($D|K$) method (Fig. 5). With two genetic clusters, the individuals from southern New Guinea all have a majority of alleles belonging to one cluster, while the individuals from Biak and northern New Guinea have their alleles mostly belonging to the other cluster. The individuals within the Vogelkop clade have alleles from both clusters, although they mostly belong to the same cluster as those from Biak. With three genetic clusters we observe that pulcher now forms a more unique genetic cluster, still

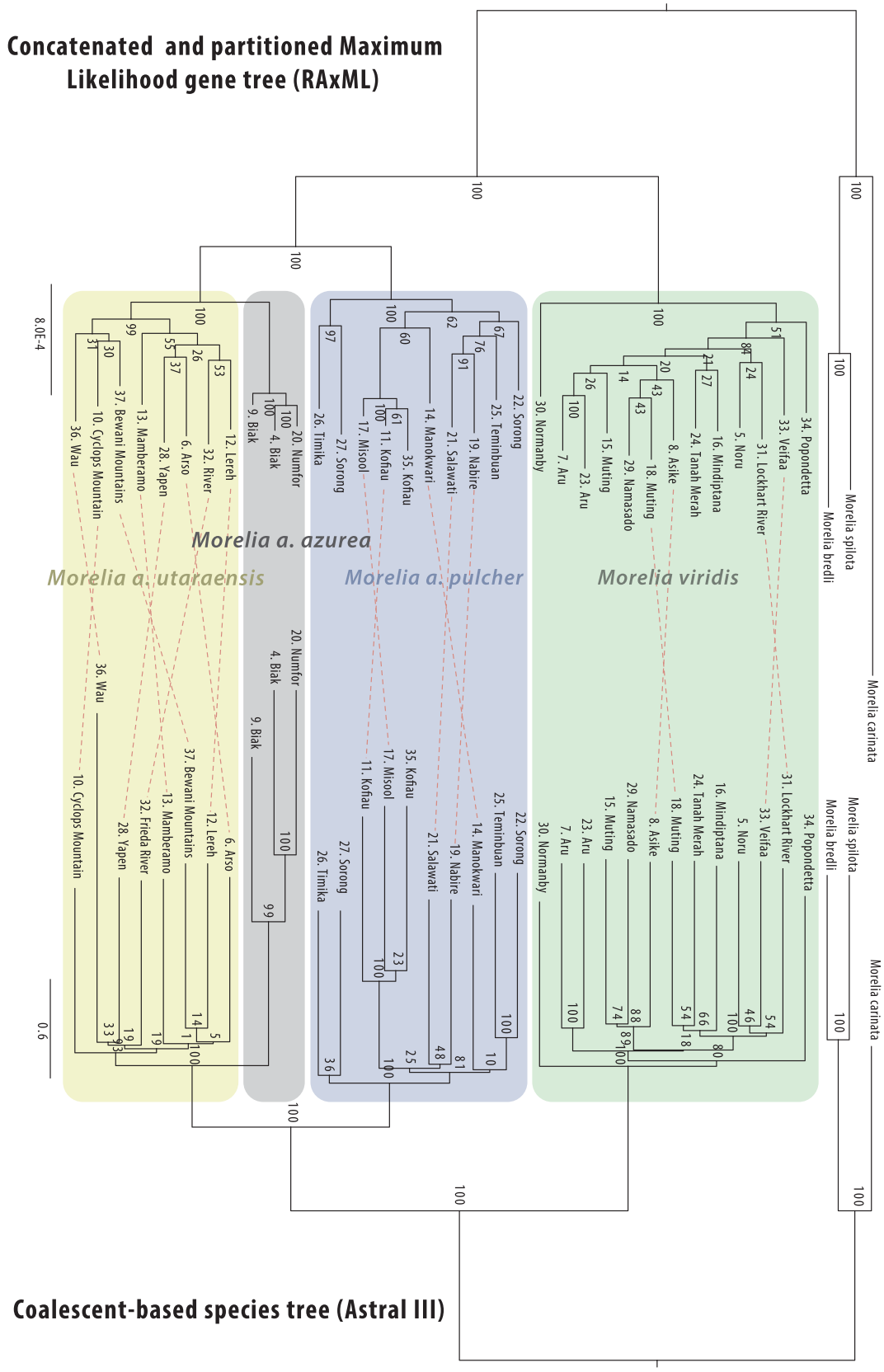

Fig. 3. Phylogenetic hypotheses inferred by RAxML and Astral III on nDNA. Branch support values correspond to bootstrap and multi-locus bootstrap respectively. Colored squares indicate clades we considered candidate species. Dashed red lines indicate discordances between the two trees.

Table 1
Summary statistics for morphological traits among green pythons. Mean ± standard errors are provided, together with the range; sample sizes are provided in parentheses. Results of statistical significance tests between characters are listed in Supplementary Material II. DMB = dorsal midbody. [2]Denotes that this includes most southern New Guinea specimens except those from Milne Bay, Oro and Morobe Provinces (Papua New Guinea), which have much longer tails and hence higher sub-caudal scale counts.

Characters	*M. a. azurea*	*M. a. utaraensis*	*M. a. pulcher*	*M. viridis*
Ventral scales	244.3 ± 0.3	233.6 ± 0.7	237.7 ± 0.5	236.6 ± 0.3
	233–252 (135)	217–252 (95)	223–251 (110)	222–257 (369)
DMB scales	57.9 ± 0.2	58.2 ± 0.3	58.2 ± 0.3	57.9 ± 0.3
	54–63 (136)	50–67 (105)	52–65 (104)	47–69 (361)
Subcaudal scales	97.1 ± 0.4	90.0 ± 0.7	94.8 ± 0.7	80 ± 0.4
	81–110 (136)	74–113 (96)	76–132 (101)	63–110 (301)
Supralabial scales	13.7 ± 0.07	13 ± 0.08	13.3 ± 0.07	13 ± 0.04
	12–15 (135)	12–15 (96)	12–15 (129)	11–15 (369)
Infralabial scales	16.4 ± 0.05	15.4 ± 0.08	15.5 ± 0.08	15.1 ± 0.04
	15–18 (134)	14–17 (96)	14–17 (128)	13–17 (352)
Suprlabials contacting orbit	2 ± 0.02	2 ± 0.03	1.7 ± 0.04	1.9 ± 0.02
	1–3 (135)	1–3 (96)	0–2 (129)	0–3 (368)
Pits in supralabials	3 ± 0.02	2.9 ± 0.04	3 ± 0.02	2.9 ± 0.02
	2–4 (135)	2–4 (96)	2–3 (129)	2–4 (368)
Pits in infralabials	6 ± 0.02	6.1 ± 0.03	6 ± 0.03	6.1 ± 0.02
	6–7 (135)	5–7 (96)	5–7 (129)	6–8 (352)
Tail shape	Long	Long	Long	[2]Short
Number of juvenile morphs	2	2	2	1
Ontogenetic color change	Delayed	Rapid	Rapid	Rapid
Vertebral patterning	Solid green, minor blues	Solid continuous blue line	Solid blue patterning	Continuous white vertebral scales or non-continuous white rosettes
Dorsal shading	Uniform green	Uniform green	Uniform green	Dark green
> 1 juvenile iris band	Yes	Yes	No	No
Temperament	Highly aggressive	Moderate	Moderate	Docile

sharing some alleles from the other clades, but Biak and northern New Guinea still share most alleles between them (Fig. 5).

3.4. Morphology

Our analysis of green python meristic characters revealed significant differences in mean trait values between the putative taxa (Table 1; Table S3 in Supplementary Material). After stepwise deletion of non-significant traits, we were left with five traits in our discriminant analysis: ventral scales, subcaudal scales, infralabial scales, supralabial scales, and supralabial scales contacting the orbit. The traits with the greatest variation (ventral and sub-caudal scales) accounted for 79% of the discrimination among lineages. Overall, discriminant analysis correctly assigned 77.5% of individuals to their respective lineage, with Biak and southern New Guinea displaying the greatest level of discrimination (Table 2). When a population (N = 47) of southern New Guinea specimens from Milne Bay, Oro and Morobe Provinces with particularly high subcaudal scale counts was excluded from the analysis, correct assignment increased to 81%, with 90% of specimens from southern New Guinea correctly assigned (Table S4 in Supplementary Material). When discriminant analysis was run on just southern New Guinea and the other clades, each group was correctly assigned 93% and 87% of the time, respectively (Table S5 in Supplementary Material).

Table 2
Results of discriminant analysis for the four green python taxa, based on counts of ventral scales, subcaudal scales, infralabial scales, supralabial scales, and supralabial scales contacting the orbit. The first column beneath the heading "taxon" corresponds to the identity of the treatment, while the subsequent columns represent the assignments.

Actual	Predicted count				
Taxon	*M. a. azurea*	*M. a. utaraensis*	*M. a. pulcher*	*M. viridis*	% correct
M. a. azurea	121	4	8	0	91%
M. a. utaraensis	3	45	10	17	60%
M. a. pulcher	20	16	39	4	50%
M. viridis	4	30	11	230	84%

Additional qualitative differences in juvenile and adult coloration and pattern were also apparent among clades, which we detail in Table 1 and in the Supplementary Material II. Overall, subtle but significant morphological differences exist between each taxon based on examination of multiple quantitative and qualitative traits. One trait is clearly diagnostic for the two main clades recognized herein (southern New Guinea and those from all other localities); i.e., the presence of only one juvenile morph (yellow) in southern New Guinea specimens.

4. Discussion

Assessing the true taxonomic diversity in cryptic lineages with little ecological differentiation remains one of the greatest challenges in systematic biology (Bickford et al., 2007; Fišer et al., 2018). The increasing accessibility of genomic data is providing important new information to help resolve cryptic diversity (Leaché et al., 2014; Lemmon et al., 2012; Ruane et al., 2015). Our study based on mitochondrial genomes, 389 nuclear exons, and a comprehensive assessment of morphological variation, with extensive sampling from across the range of green pythons, provides multiple lines of evidence for two species, *M. viridis* and *M. azurea*, and further evidence of three subspecies of *M. azurea*. The finding that *M. azurea* and *M. viridis* occur 10 km apart in some parts of their range, without evidence for introgression, strongly suggests these species are indeed reproductively isolated.

4.1. Systematic implications

Our data align closely with earlier work suggesting the existence of two species of green pythons inhabiting the island of New Guinea (Rawlings and Donnellan, 2003). However, our results go further to reveal cryptic diversity within populations of green pythons from northern New Guinea (Figs. 2, 3). As discussed by De Queiroz (2007), different species concepts agree that the primary definition of a species is a group of metapopulations that are evolving independently. The diagnosis of such separately-evolving entities is a delimitation issue for some 'cryptic' taxa where morphological differentiation from close

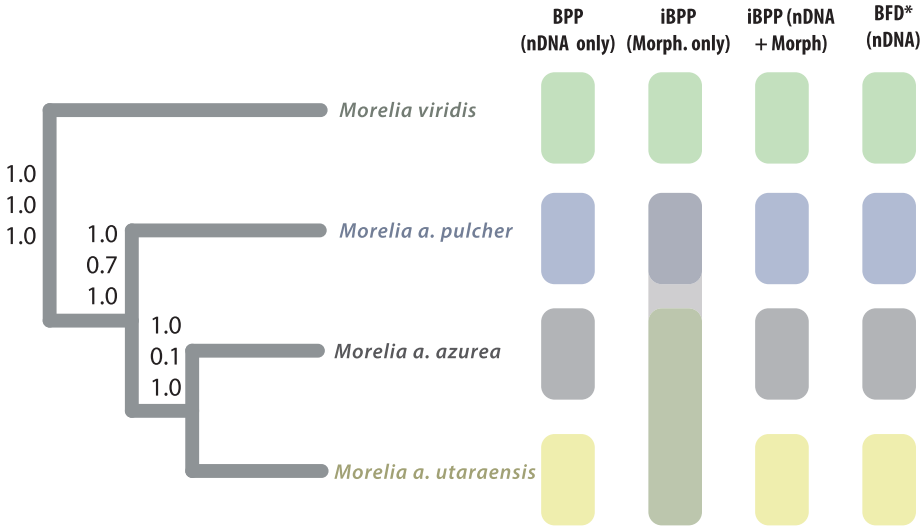

Fig. 4. Schematic of the species delimitation hypotheses inferred by BPP (using only the nuclear genomic data), iBPP (using only the morphological data) and iBPP (using both the nuclear genomic and the morphological data). For each hypothesis set as columns, separate colored squares represent support for those species as entities, whereas a brown square enclosing two of them (e.g. *M. a. pulcher* and *M. a. azurea* for the morphology only delimitation) represents only moderate support. Numbers at each node of the tree indicate the posterior probability for that node inferred by each of the analyses in the same order as presented.

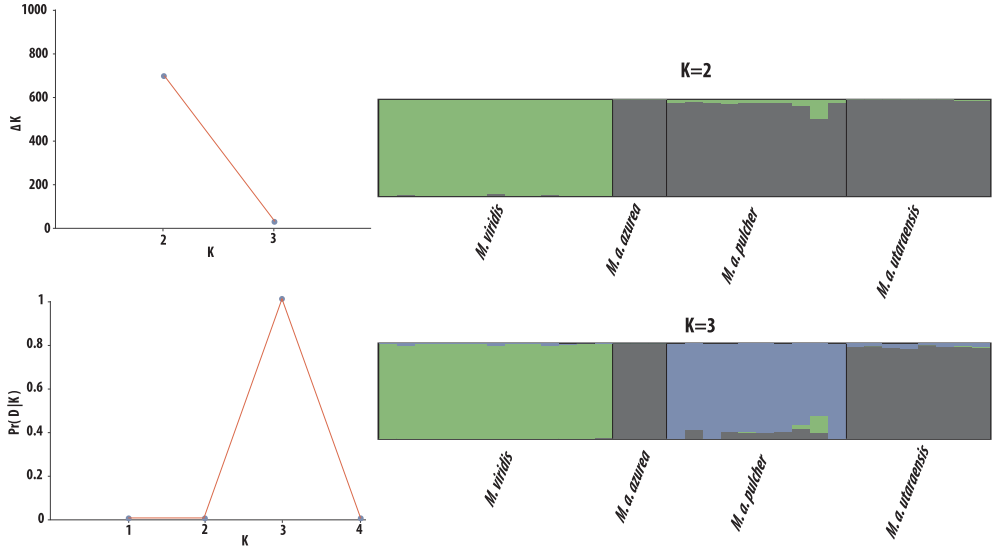

Fig. 5. Genetic Bayesian clustering of the 34 individuals based on the allelic frequencies at nuclear loci using *STRUCTURE*, identified two clusters (K) by the Evanno or ΔK method (upper panel) and three according to the ln Pr($D|K$) method (lower panel).

relatives is subtle or not apparent. We found that all putative green python taxa are morphologically similar, but the species delimitation methods used here support the recognition of at least four taxa (Fig. 4). Nonetheless, we recognise that these methods can "oversplit" taxa (Jackson et al., 2017; Leaché et al., 2018; Sukumaran and Knowles, 2017), and that some admixture is present between the northern clades (Fig. 5), so we recognise as full species only the southern taxon, *M. viridis*, and the northern taxon, *M. azurea*. To acknowledge the strong genetic structure found in the northern clade, we recognise three allopatric subspecies of *M. azurea*, which we describe below. Our action is conservative because we do not know the exact distributional limits of each taxon, so we could not test for the presence or extent of introgression between these taxa. If future studies identify genetic introgression then their sub-species status would be maintained. On the other hand, if they are found in contact and introgression is not detected then the taxa can be raised to full species status.

Our systematic arrangement is as follows: (1) the populations currently assigned to *Morelia viridis*, which occur south of the central highlands of New Guinea, north of the Owen Stanley Ranges to Lae, as well as the Aru Islands (type locality of *M. viridis*) and Cape York Peninsula, Australia. (2) The populations from Vogelkop Peninsula in northwestern New Guinea, extending east to at least Nabire (north of the central range) and the Lorentz (Unir) river (south of the central range). The name *Chondropython* (=*Morelia*) *pulcher* Sauvage 1878 is available for this clade with type locality Mansiman Island, off the coast of Manokwari, on the Vogelkop Peninsula (Sauvage, 1878). (3) The populations from Biak and Numfor Islands, in northern New Guinea. The name *Morelia azurea* Meyer 1874 is assigned to the northern lineage of green python, with type locality in Biak (Barker et al., 2015, Meyer, 1874, Schleip and O'Shea, 2010). (4) The remaining populations of northern New Guinea from Yapen to Wau form a clade sister to the *Morelia azurea* clade. There is no available name for this clade, and we give the name *utaraensis* (see below for formal description).

McDowell (1975) was unable to find broad morphological patterns in green pythons from across their geographic range. In contrast, despite green pythons being a true species complex exhibiting considerable morphological conservatism, our detailed morphological analysis has revealed subtle but consistent differences between the taxa. To the untrained eye, the only reliable trait is the presence of red juvenile morphs within *M. azurea*, which have never been recorded in populations of *M. viridis*. But when taken together, a suite of other characters (presence of a white vertebral stripe, iris banding, tail lengths and subcaudal scale numbers) can be used to differentiate these species.

The strong morphological similarity among deep genetic lineages of green pythons is common to many other cryptic taxa, and suggests morphological conservatism as a result of strong stabilizing selective

pressures common to their conserved niches (Bickford et al., 2007; Metzger et al., 2010). Remarkably, the evolutionarily distant but morphologically convergent emerald tree boa (*Corallus caninus*) exhibits the same lime green coloration, white dorsal patterning, a strongly triangulate head, near identical ecological traits, and undergoes a strikingly similar ontogenetic color change from juvenile red to adult green (Esquerré and Keogh, 2016; Henderson et al., 2009). Convergence among other distantly related forest-dwelling snakes suggests a narrow arboreal niche that must drive strong convergence towards a specific phenotype (Henderson and Binder, 1980).

Paradoxically, *M. a. azurea* exhibits a relatively large degree of morphological divergence from other green pythons within the complex (Figs. 2, 3). *Morelia a. azurea* reaches larger mean body sizes than all other green python taxa, and undergoes a delayed ontogenetic color change. They also possess prominent elongate heads with flared, enlarged, nasal plates (Maxwell, 2005). Natusch and Lyons (2012) hypothesised that this divergence from the strict body form and colour arrangement common to other green pythons is due to relaxation of ecological pressure, owing to the lower diversity of avian (i.e., visual) predators inhabiting the oceanic islands where this taxon occurs (Beehler, 2007). The faunal elements of Biak, Numfor, and Supirori all show signs of overwater colonisation, either by flying in the case of bats and birds, or serendipitous dispersal in the case of non-volant animals (Helgen and Flannery, 2004). Many species are thus endemic to these islands, likely diverging relatively quickly from their mainland conspecifics due to their inevitably small founder populations and genetic isolation (Cowie and Holland, 2006). Given this relatively marked morphological divergence, and truly allopatric distribution on oceanic islands, we recognize that green pythons from Biak, Supirori and Numfor may be on their own evolutionary trajectory and thus could warrant status as a separate species. Nevertheless, we designate green pythons from these island localities as subspecies, to avoid paraphyly of *M. azurea* (see below).

Morphological similarity is greatest between *M. a. pulcher* and *M. a. utaraensis,* yet molecular evidence clearly shows they are on independent evolutionary trajectories, not even being each other's closest relatives. We describe each taxon as subspecies rather than full species because the contact zone between these taxa remains poorly known. This zone lies somewhere in a sparsely sampled area of forest and swampland stretching 300 km from the Mamberamo River mouth to Nabire at the Vogelkop Isthmus. This region is known to act as a biogeographic barrier for several other taxa, although there are few obvious barriers to gene flow for lowland species (Murphy et al., 2007; Eldridge et al. 2018). We are thus reluctant to conclude that gene flow does not occur at a potential contact zone. Future sampling should be targeted in this area to disentangle whether these taxa should remain as subspecies, or whether all subspecies recognised herein should be elevated to full species. In contrast to the general trend of deep genetic divergence among population of green pythons, allopatric populations of *M. viridis* from the Aru Islands and Australia were nested among samples from southern mainland New Guinea (Fig. 2). This result is unsurprising given the relatively recent isolation of these populations due to Pleistocene sea level changes (Voris, 2001; Natusch and Natusch, 2011). Our study of the complex patterns of divergence among green pythons from across the island of New Guinea adds to the growing body of literature underpinning the necessity of genetic data for species delimitation in morphologically conservative groups.

4.2. Biogeography

Our widespread geographic sample of green pythons offers important insights into the biogeography of New Guinea. Several of the patterns observed in our data are well documented in the literature. For example, there is clear distinction between *M. azurea* and *M. viridis* occurring either side of the central range (Rawlings and Donnellan, 2003). The degree of divergence between these species is commensurate with the upheaval of the central range 5.8–3.5 MYA (Dumbacher and Fleischer, 2001; Rawlings and Donnellan, 2003). However, *M. azurea* and *M. viridis* do not show a perfect north–south divide. In the eastern portion of its range where elevations are < 2000 m, *M. viridis* occurs throughout the Owen Stanley Ranges north to the coast of Milne Bay, Oro and Morobe provinces (Fig. 1), a pattern that has been observed in several species (Beehler 2007). Although the Vogelkop Isthmus is a well-known barrier to gene flow (Beehler, 2007; Bruxaux et al., 2018; Eldridge et al., 2018), several other zones of contact between the putative green python taxa are significant. For example, the ranges of *M. azurea* and *M. viridis* approach each other in the vicinity of the Bwussi River near Schneider Point, approximately 20 -km south of Lae, where green pythons exhibit features typical of *M. viridis*, (which is confirmed by our mtDNA phylogeny; Fig. 2). By contrast, specimens from Lae possess all the characteristics of *M. a. utaraensis*. The area around the Bwussi River is tightly bottlenecked between the Herzog Mountains and the sea, with no obvious barriers to gene flow over this 20 -km stretch (Fig. S6). Given the elevational tolerance of green pythons, *M. viridis* is likely to penetrate high into the Herzog Mountains. Paradoxically, however, specimens from this mountain range (and from the nearby Bulolo Valley) are *M. a. utaraensis* (Fig. S6). We strongly suspect, therefore, that despite the close proximity of their ranges at these sites, *M. azurea* and *M. viridis* are reproductively isolated. Similar zones of contact occur in the Asmat region of southern Papua, the Waghi River Valley, and in the vicinity of Oksibil in the star mountains (Fig. 1; Supplementary Material). To our knowledge, this is the first record of two New Guinean taxa diverging at these zones (Beehler, 2007; see Supplementary Material for further detail). The new zones of abutting distributions identified by our data beg the question as to whether *M. azurea* and *M. viridis* occur in sympatry anywhere within their range? If the two species do occur in sympatry, we might expect sampling at specific sites to uncover both species. Although our sampling was relatively sparse, we observed a complete lack of distribution overlap between species at any of the areas where their ranges approach one another (over distances as small as 10 km). Coupled with the strong morphological and ecological similarity exhibited by both taxa, it is plausible that complete competitive exclusion occurs. Greater sampling of other taxa would establish the generality of these potential biogeographic boundaries.

4.3. Conservation implications

Our taxonomic changes have significant implications for the conservation management of green pythons. Green pythons are listed in Appendix II of the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES) and are harvested from the wild and/or bred in captivity in Indonesia for international and domestic trade (Lyons and Natusch, 2011). The addition of three taxa to the existing *M. viridis* species will necessitate Indonesia (the only range country presently exporting this species; Lyons and Natusch, 2011) and importing Parties to recognise and accurately record trade transactions for each taxon. In some cases, authorities may need to independently verify the taxon for which the trade transaction is taking place, which is complicated by the relatively few distinguishing morphological traits available for identification (at least between *M. a. pulcher* and *M. a. utaraensis*). Guidance and capacity development on the morphological distinguishing traits of each taxon should allow regulators to diagnose taxa in most situations, with resources such as the IUCN SSC Boa and Python Specialist Group being available for more demanding cases.

Of a more substantive nature is the requirement for Indonesia's CITES Scientific Authority to undertake non-detriment findings before exports of green pythons can take place (see CITES Res. Conf. 16.7). A CITES non-detriment finding is essentially an assessment of risk, to ensure wild harvesting will not jeopardize the survival of the species in the wild (Natusch et al., 2019). Our revision will necessitate non-detriment findings for harvests of all described taxa. Such an assessment

will be relatively straightforward for most taxa due to the large geographic range they occupy, coupled with low levels of offtake. However, non-detriment findings for *Morelia a. azurea* inhabiting Biak Island will necessitate greater research into the impact of trade owing to the taxon's small range and higher levels of offtake. Green python populations from Biak already have exhibited demographic changes due to trade that may be indicative of declining harvest sustainability (Lyons and Natusch, 2011). Periodic field monitoring of this population is thus warranted. In summary, however, despite trade taking place, habitat loss remains the most significant threatening process for all of these closed-forest obligate snakes (Shearman et al., 2009; Potapov et al., 2017). Any efforts to safeguard forest areas will help ensure the protection of these species.

4.4. Taxonomy

4.4.1. Taxonomic history

The green python was described originally as *Python viridis* by Hermann Schlegel in 1872, based on two specimens from the Aru Islands off the southern coast of Papua (in what is now Indonesia). In 1874, and unaware of Schlegel's description, Adolf Bernhard Meyer coined a new genus – *Chondropython* – while at the same time describing *Chrondropython azureus* based on a specimen from Biak Island from northern Papua's Cenderawasih Bay, Indonesia (Meyer, 1874). In 1878, Henri Sauvage, presumably also unaware of the description of *Python viridis* by Schlegel (1872), compared specimens collected from Mansinam Island (6 km west of present day Manokwari on the Vogelkop Peninsula, West Papua, Indonesia) to *Chondropython azureus*. Sauvage (1878) subsequently described *Chondropython pulcher* from Mansinam on the basis of fewer infralabial scales, an alternate arrangement of infralabial pits, and fewer supralabial pits. In the same year, Peters and Doria (1878) synonymised *C. pulcher* with *C. azureus* on the basis that Sauvage's (1878) diagnosis used head scales and coloration that were considered too variable in pythons to warrant specific status for *C. pulcher*. Boulenger (1893) synonymised both *C. azureus* and *C. pulcher* with *C. viridis*, based on recognition of the earlier description of *Python viridis* by Schlegel (1872). Since that time, the name "*Chondropython viridis*" has been accepted widely (Zenneck, 1898; Barbour, 1912; Sternfeld, 1913; de Rooij, 1917, Brongersma, 1933; Thomson, 1935; McDowell, 1975, McDiarmid et al., 1999). However, Meyer (1874) and Sauvage (1878) noted the similarity of *Chondropython* to *Morelia*, and Kluge (1993), in his detailed morphological analysis of pythons, found that green pythons were nested within *Morelia*. Following Kluge (1993), green pythons have been known by the name *Morelia viridis* and have been considered a single taxon.

Several authors have noted considerable geographic variation in coloration, pattern and morphology of green pythons (Maxwell, 2005, Kivit and Wiseman, 2005). Zenneck (1898) noted distinct differences in patterning of the specimens originally used by Sauvage (1878) to describe *C. pulcher*. McDowell (1975), in his comprehensive treatment of Australasian pythons, provided detailed data on scale counts of specimens in the collections of the American Museum of Natural History and the Bernice P. Bishop Museum. Despite noting significant geographic variation in scale counts, those counts did not conform to any broad geographic patterns. A molecular genetic examination of green python mitochondrial DNA suggested the existence of two distinct lineages, one present north of New Guinea's central mountain range and the other occurring in southern New Guinea and Australia, which were corroborated by a geographically limited allozyme dataset (Rawlings and Donnellan, 2003). Those authors were reluctant to establish the species status of the two identified clades using the data available to them at that time. Nevertheless, Rawlings et al. (2008) referred to green pythons from northern New Guinea as the "unnamed sibling taxon of *Morelia viridis*." Schleip and O'Shea (2010) subsequently recognised *Morelia azureus* in their checklist of living pythons, and corrected the name to *azurea* based on the accepted feminine gender of *Morelia* (Barker et al., 2015). In their review of python systematics and taxonomy, Barker et al. (2015) designated a neotype for *M. azurea* based on a specimen from Biak Island, Indonesia. However, *Morelia azurea* is yet to be recognised formally by the scientific community, due largely to the reluctance of earlier authors to elevate northern populations of green pythons to species status without further evidence, coupled with the absence of comprehensive morphological analyses (Rawlings and Donnellan, 2003).

Since Rawlings and Donnellan (2003) provided evidence for divergence between northern and southern clades of green pythons, several authors have moved to formalise naming of the northern clade as *Morelia azurea* (Schleip and O'Shea, 2010; Barker et al., 2015). However, none of these authors, or the original description of *M. azurea* by Meyer (1874), offer sufficient information to diagnose *M. azurea* from *M. viridis*. We thus provide detailed descriptions of these taxa here.

Morelia viridis

Python viridis Schlegel 1872: 54
Chondropython azureus Meyer 1874: 134
Chondropython pulcher Sauvage 1878: 37
Chondropython viridis Boulenger 1893: 90
Morelia viridis Kluge 1993

Syntypes: RMNH.RENA.4672, two specimens from the Aru Islands, Maluku, Indonesia, placed in the Naturalis Museum in Leiden, Netherlands, (Schlegel 1872).

Diagnosis: *Morelia viridis* is easily distinguished from all subspecies of *M. azurea* by the following characters: presence of a single juvenile morph (yellow vs. yellow or red in *M. azurea*); presence of a tightly knitted row of white vertebral scales along the vertebral ridge, or white 'rosettes' along the vertebral ridge in the Aru Islands population; and a dark shade of green coloration along the vertebral ridge, as opposed to uniform green in *M. azurea* (Table 1, Supplementary Material II). Most populations of *M. viridis* also possess short, stubby tails and considerably lower subcaudal scale counts vs. long, tapering tails and high subcaudal scale counts in *M. azurea* (Table 1, Supplementary Material II). The exceptions are populations from Milne Bay and the north coast of Oro and Morobe Provinces to near Lae, Papua New Guinea, which typically have long, tapering tails similar to *M. azurea*. *Morelia viridis* further differs from *M. a. azurea* and *M. a. utaraensis* in that juveniles possess a single iris band running horizontally through the eye (as opposed to a triple iris band; Table 1; Supplementary Material II). It further differs from *M. a. utaraensis* in that juveniles have a darkened tail tip and a broken pattern following the vertebral ridge vs. a light-colored tail and continuous pattern. *Morelia viridis* further differs from *M. a. azurea* by undergoing a relatively rapid color change to become uniform green in adulthood vs. delayed colour change with variable coloration).

Description: Medium body size (max SVL = 160 cm), but with some populations, like Australia, significantly smaller than others (Natusch and Lyons, 2014). Short tails are characteristic of most populations of *M. viridis*, although specimens from eastern Papua New Guinea possess long, tapering tails (Supplementary Fig. II). Background coloration uniform, darkening along the vertebral ridge and overlain by a dorsal pattern of white scales forming rosettes or a continuous vertebral line (Supplementary Material II). The ventrum is white in juveniles; the ventrum of adults can be various shades of white, yellow or blue. Neonates are born yellow and rapidly change color to green around 65 cm SVL (Natusch and Lyons, 2012). Black or dark red tail coloration is retained after the juvenile ontogenetic color change occurs, slowing fading to uniform green with increasing age. Wild specimens are typically docile.

Distribution and habitat: Inhabits rainforest, secondary regrowth and village gardens from at least Mappi in southern Papua, Indonesia, east through the Trans-fly, Gulf, Central, and Milne Bay Provinces of Papua New Guinea, south of the central highlands. Also occurs through the Owen Stanley Ranges and north through Oro and Morobe Provinces to at the least Bwussi River, near Schneider Point 20 km south of Lae.

Morelia viridis occurs to at least 2000 m and is found in several highland valleys, such as the Waghi River Valley and the vicinity of Okapa in the Eastern Highlands, PNG. It also occurs in Australia and Ferguson, Bara Bara, and Normanby Islands in the D'Entrecasteaux group.

Morelia azurea azurea

Python viridis Schlegel 1872
Chondropython azureus Meyer 1874
Chondropython pulcher Sauvage 1878
Chondropython viridis Boulenger 1893
Morelia azurea Schleip & O'Shea 2010

Neotype: UTA-R-61633, placed in the collection of the Amphibian and Reptile Diversity Research Center at the University of Texas Arlington; collected on Biak Island in 1990; died and preserved 1993 (Barker et al., 2015).

Diagnosis: *M. a. azurea* differs from *M. a. pulcher*, *M. a. utaraensis* and *M. viridis* in having a higher mean number of ventral, supralabial, infralabial, and subcaudal scales, delayed ontogenetic color change (resulting in highly variable coloration), and a longer head with prominently flared nasal scales (Natusch and Lyons, 2014; Table 1). It further differs from *M. a. utaraensis* due to its juvenile stage possessing unconnected dorsal patterning along the vertebral ridge (vs. complete vertebral pattern forming a solid line in *M. a. utaraensis*; Supplementary Material II), its lack of prominent blue dorsal pattern along the vertebral ridge in adulthood, and its uniform black tail tip (vs. a white or light red tail tip in *M. a. utaraensis*). *Morelia a. azurea* further differs from *M. a. pulcher* in having a juvenile stage that possesses a triple banded iris.

Description: *M. a. azurea* is morphologically the most distinct subspecies of *M. azurea*. Both in mass and length, *M. a. azurea* is the largest subspecies of *M. azurea*, growing to a maximum SVL of 172 cm and mean adult range of 114–133 cm (Natusch and Lyons, 2014). Tail shape is long and tapering with a black tip, eventually fading to green in late adulthood. Ontogenetic color change is delayed in this taxon, resulting in some specimens retaining yellow or reddish mottling well into adulthood (Natusch and Lyons, 2012). Adult specimens possess varying degrees of haphazardly arranged white scales on the body, ranging from none to heavily speckled. Some specimens possess faint remnants of juvenile patterning along the vertebral ridge, although most lose this colouration altogether. The ventrum is white in juveniles; adult ventrums can be various shades of white, yellow or blue. Wild specimens are typically very defensive.

Distribution and Habitat: *Morelia a. azurea* has an isolated distribution, being restricted to the oceanic islands of Biak (formerly Mysore), Numfor and Supiori in the Schouten Islands group of Cenderawasih (formerly Geelvink) Bay. They are also found on small coral islands of the Padaido group off Biak's southeast coast. They do not occur on Yapen or Mios Num (land-bridge islands) to the immediate south of Biak. *Morelia a. azurea* inhabits rainforests, secondary regrowth and village gardens.

Morelia azurea pulcher

Python viridis Schlegel 1872
Chondropython azureus Meyer 1874
Chondropython pulcher Sauvage 1878
Chondropython viridis Boulenger 1893
Morelia azurea Schleip & O'Shea 2010

Syntypes: MNHN 50875089, four specimens collected from Mansinam Island near Manokwari, Indonesia, by M. Laglaize and placed in the Muséum National d'Histoire Naturelle in Paris, France.

Diagnosis: Morphologically, *M. a. pulcher* differs only subtly from *M. azurea utaraensis* in having a higher mean number of ventral and subcaudal scales, a single iris band in juvenile specimens, and a dark tail tip (vs. a light-colored tail tip in *M. azurea utarensis*).

Description: A moderately-sized subspecies of *Morelia azurea*, growing to a maximum of 156 cm SVL and mean adult range of 116–130 cm SVL. Tail is long and tapering with a dark-colored tip, fading to uniform green in adulthood. Coloration is uniform lime green, with light blue patterning (the remnant of juvenile coloration) superimposed on the vertebral ridge. White scales are arranged haphazardly along the vertebral ridge in some specimens. Adult ventrums can be various shades of white or yellow.

Designation and description of a lectotype: To stabilise the name, we designate MNHN 5088 as the lectotype for *Morelia azurea pulcher*. The lectotype is a young animal from Mansinam Island, Indonesia. Sex unknown. Specimen is light blue in coloration owing to preservative; a small number of white scales are haphazardly arranged on the dorsal surface following the vertebral line. Ventral surface is cream. Supralabials number 13/13 with the 7th and 8th in contact with the orbit; the 7th supralabial on the left side of the head being divided. The rostral and anterior two supralabials are deeply pitted while the third carries a weekly defined pit. Infralabials number 15/15; 8–13/7–12 are deeply pitted. Midbody dorsal rows number 64; there are 233 ventral scales and 97 subcaudal scales including the tip.

Distribution and habitat: Distributed on the Vogelkop (bird's head) Peninsula of West Papua, Indonesia. The range extends to the Bomberai Peninsula through the Vogelkop Ithmus, north to at least the town of Nabire. In the south, *M. a. pulcher* is distributed between the Sudirman range and the coast, at least to the Unir (formerly Lorentz) River in the Asmat region of southern Papua. *M. azurea pulcher* also occurs on a number of offshore islands, namely Batanta, Misool, Kofiau, Gam, Gag, Salawati, Waigeo, and Mansinam.

Morelia azurea utaraensis subsp. ***nov***

Python viridis Schlegel 1872
Chondropython azureus Meyer 1874
Chondropython pulcher Sauvage 1878
Chondropython viridis Boulenger 1893
Morelia azurea Schleip & O'Shea 2010

Holotype: AMNH 62020; adult female collected by W.B. Richardson at 'Hollandia' (present day Jayapura) in Papua, Indonesia, on 9 July 1938.

Diagnosis: Morphologically, *M. a. utaraensis* differs only subtly from *M. azurea pulcher* in having a lower mean number of ventral and subcaudal scales, a triple iris band in juvenile specimens, and a light tail tip (vs. a dark-colored tail tip in *M. azurea pulcher*). *Morelia a. utaraensis* differs from *M. a. azurea* in having a lower mean number of ventral, supralabial, infralabial and subcaudal scales, a relatively rapid ontogenetic color change, a shorter head and snout, and a fully connected juvenile pattern (vs broken/unconnected patterning in *M. a. azurea*), and a light tail tip (vs dark in *M. a. azurea*)

Description: A moderately-sized subspecies of *Morelia azurea*, growing to a maximum SVL of 160 cm and mean adult range of 112–123 cm. Tail shape is long and tapering with a white, yellow, or light-red tip, fading to uniform green in adulthood. The dorsum is uniform dark or light green with a solid (complete) line of light-blue residual juvenile patterning following the vertebral ridge. White scales are arranged haphazardly along the vertebral ridge in some specimens. Adult ventrums can be various shades of white or yellow.

Description of holotype: Adult female. Total length of approximately 148.5 cm; tail is long and tapering and measures 20 cm. Supralabials number 14/15, with the 7th and 8th contacting the orbit. Infralabials number 16/16, with deep pits in scales 8–13. There are 231 ventral scales, 60 dorsal midbody rows, and 90 + tip divided subcaudal scales.

Etymology: The name *utaraensis* is derived from the Indonesian language word for "north". *Morelia azurea utaraensis* occurs in northern New Guinea, with its name meaning "from the north".

Distribution and habitat: *Morelia a. utaraensis* is distributed in eastern Papua New Guinea from Lae and the Huon Peninsula, west through northern Papua New Guinea and Papua, Indonesia, to the island of Mios Num (west of Yapen) in the west. It is separated from *M. viridis* to the south by New Guinea's central cordillera, but penetrates into several highland valleys (Bulolo, Waghi). At least one population (Oksibil, Pegunungan Regency, Indonesia) is located south of the main

dividing range. The exact western limit of its distribution on mainland New Guinea is unknown, but may include all areas to the east of the Mamberamo River (the only obvious barrier to gene flow).

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2019.106640.

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