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Discovery of an old, archipelago-wide, endemic radiation of Philippine snakes

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ABSTRACT

The extraordinarily rich land vertebrate biodiversity of the Philippines includes at least 112 species of terrestrial snakes (74% of which are endemic to the archipelago) in 41 genera (12% endemic). Endemic Philippine snake genera include *Cyclocorus* (two species), *Hemibungarus* (three species), *Hologerrhum* (two species), *Oxyrhabdium* (two species), and *Myersophis* (monotypic). Although *Hemibungarus* and *Oxyrhabdium* have been included in previous species-level phylogenies, the affinities of the other three Philippine endemic genera are completely unknown. We generated novel DNA sequences for six species from four genera and analyzed these in conjunction with data from earlier studies to infer a phylogeny for the group containing Colubridae, Elapoidea (Elapidae + Lamprophiidae), and Homalopsidae. We present a novel phylogenetic result that strongly supports the existence of an entirely endemic Philippine radiation of elapoid snakes that originated 35–25 million years ago. We provide a revised, phylogeny-based classification to accommodate the new clade, transfer *Cyclocorus*, *Hologerrhum*, and *Myersophis* to Lamprophiidae, and provide the first estimate of the evolutionary relationships among these genera and the related *Oxyrhabdium*, setting the stage for future investigation of this entirely endemic, novel Philippine elapoid radiation.

1. Introduction

The Philippine archipelago is an exceptionally biodiverse region that includes at least 112 species of land snakes from 41 genera and 11 families (Uetz et al., 2017). Endemism is high, with 74% of the species and 12% of the genera restricted to this small archipelago. Endemic Philippine snake genera include *Cyclocorus*, *Hemibungarus*, *Hologerrhum*, *Oxyrhabdium*, and *Myersophis*. The phylogenetic placement of *Hemibungarus* (False Coral Snakes) as a member of Elapidae is well-supported, but very little is known about the evolutionary history and biogeography of *Cyclocorus* (two species, each possessing two named subspecies), *Hologerrhum* (two species), *Oxyrhabdium* (two species, one of which contains two subspecies), and *Myersophis* (monotypic) (Fig. 1) (Brown et al., 2000; Castoe et al., 2007; Leviton, 1983, 1964, 1965; Phenix et al., 2011). Genetic data support *Oxyrhabdium* as a member of Elapoidea, but the position of this lineage, now considered a member of the family Lamprophiidae (Uetz et al., 2017), relative to the other elapoids has remained tenuous (Slowinski and Lawson, 2005; Lawson et al., 2005; Kelly et al., 2009; Pyron et al., 2013; Figueroa et al., 2016). DNA sequence data have never been collected for *Cyclocorus*, *Myersophis*, and *Hologerrhum*, leading earlier authors to treat them as members of the family Colubridae, Lamprophiidae, or designated *incertae sedis*, with unresolved systematic affinities (Pyron et al., 2013; Leviton, 1965, 1983; Brown et al., 2000).

A variety of taxonomic arrangements have been suggested for these genera based on phenotypic characters (Leviton, 1983; Taylor, 1922). Based on overall body plan, size, and scalation, Leviton (1983) suggested that *Myersophis* should be considered a close relative of *Oxyrhabdium*, which suggests that it also might be a member of Elapoidea. Earlier authors placed *Hologerrhum* in the subfamily Natricinae (Colubridae) and this arrangement has not been contested (Brown et al., 2000; McLeod et al., 2011; Pyron et al., 2013). However, scalation and other phenotypic characters suggest a grouping of *Hologerrhum* and *Cyclocorus* and neither genus appears to have any closer relatives in Southeast Asia (Taylor, 1922; Leviton, 1965, 1983; Brown et al., 2000).

To resolve the phylogenetic placement of the endemic Philippine genera, we sequenced widely employed mitochondrial and nuclear gene regions representing four genera and six species (*Oxyrhabdium leporinum*, *O. modestum*, *Cyclocorus lineatus*, *C. nuchalis*, *Hologerrhum philippinum*, and *Myersophis alpestris*). We analyzed these data with homologous sequences for 117 species from 108 genera spanning major clades of Colubridae, Elapsoidea, Homalopsidae, and Pareidae (see Savage (2015) for a discussion on the name Pareidae and the often misdesignated name Pareatidae) and we used Bayesian Inference (BI)

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Fig. 1. Representative taxa of the Philippine elapoid radiation, subfamily Cyclocorinae: (A) *Oxyrhabdium leporinum leporinum* (KU 322339), (B) *Oxyrhabdium leporinum visayanum*, (C) *Oxyrhabdium modestum* (Uncataloged KU specimen [RMB 19937]), (D) *Hologerrhum philippinum* (KU 330056), (E) *Cyclocorus lineatus* (KU 275744), (F) *Cyclocorus nuchalis* (KU 344159), (G) and (H) *Myersophis alpestris* (holotype, KU 203012).

and Maximum Likelihood (ML) methods to infer higher-level phylogenetic affinities of the Philippine endemics. Specifically, we evaluated the expectation that *Cyclocorus* and *Hologerrhum* form a clade within Natricinae and we asked whether improved taxon sampling (plus inclusion of *Myersophis alpestris*) could stabilize the position of *Oxyrhabdium* within Elapoidea.

2. Methods

2.1. Tissues, DNA extraction, and sequencing

We obtained ethanol-preserved liver or muscle tissue samples for 11 individuals that were collected by RMB and colleagues (including E.L. Rico, C.D. Siler, and A.C. Diesmos) during multiple Philippine field expeditions between 1991 and 2017 and deposited in the University of Kansas Biodiversity Institute. We extracted and purified genomic DNA by lysing tissues with Proteinase K and then using a Maxwell® Rapid Sample Concentrator Instrument with the Maxwell® 16 Tissue DNA Purification Kit (Promega Corporation). We performed polymerase chain reaction (PCR) to amplify ~1350 base pairs (bp) of the mitochondrial gene *Cytochrome-b* (*Cytb*) and ~580 bp of the nuclear, protein-coding gene *oocyte maturation factor mos* (*cmos*). Amplified products were visualized using gel electrophoresis on 1.5% agarose gels. Purification of PCR product, cycle sequencing, cycle sequencing cleanups, and nucleotide sequence determination were conducted with standard GeneWiz protocols®. We used Burbrink et al. (2000) and Lawson et al. (2005) primers for both amplification and sequencing of *Cytb* and *cmos*, respectively. We *de novo* assembled and edited sequences using Geneious® v6.1 and the MUSCLE plugin in Geneious to align sequences (Kearse et al., 2012; Edgar, 2004).

2.2. Taxon sampling

We collected new DNA sequence data from 11 individuals (seven previously described and one undescribed species), including: *Cyclocorus lineatus*, *C. nuchalis*, *Myersophis alpestris*, *Oxyrhabdium modestum*, *O. leporinum*, *Hologerrhum philippinum*, an unidentified sample that we call “Unnamed Leyte-Samar lineage” (KU 337269), and *Psammodynastes pulverulentus*. This study is the first to include molecular data for *Cyclocorus*, *Hologerrhum*, *Myersophis alpestris*,

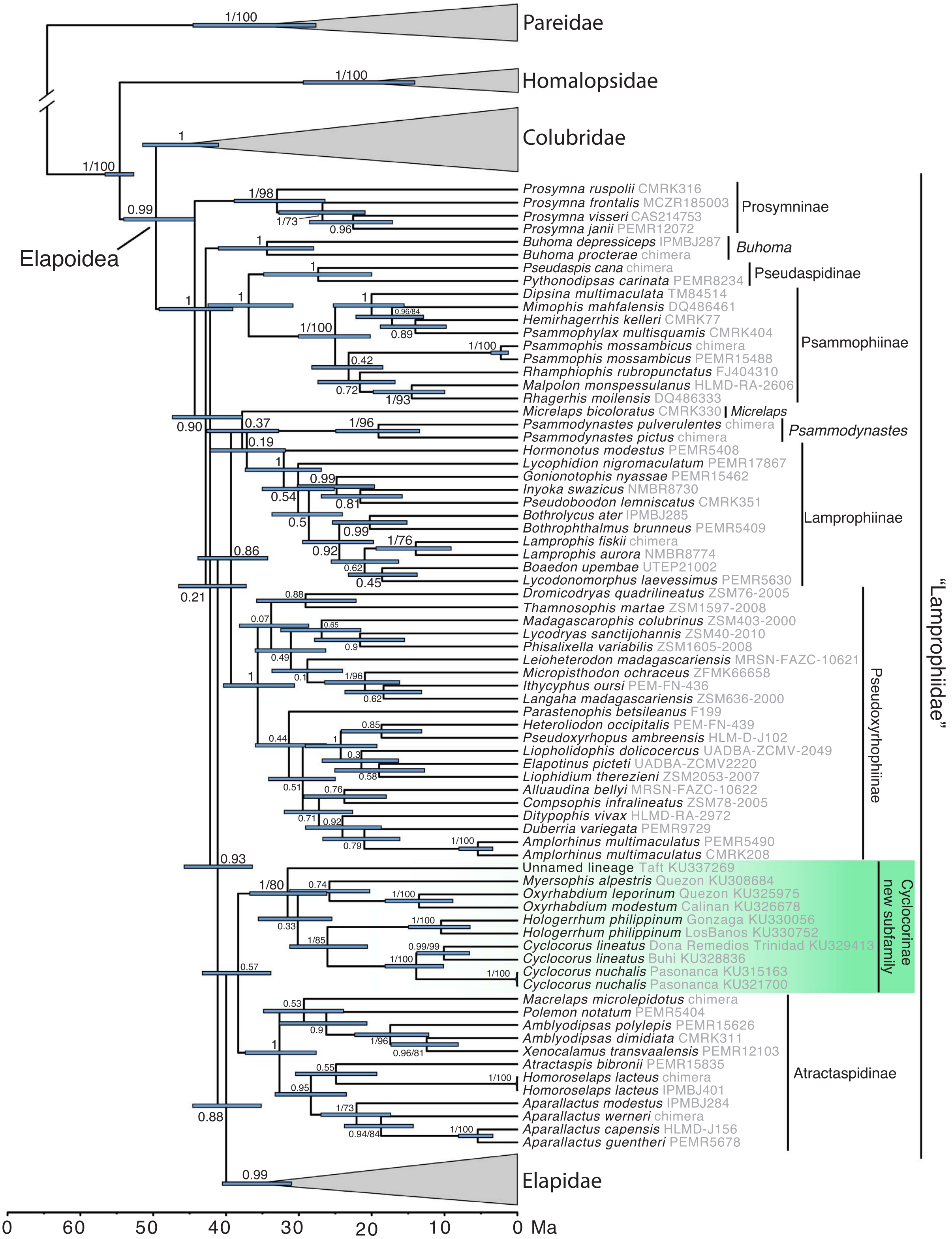

Fig. 2. Bayesian (BEAST) concatenated-gene time-tree of Elapoidea and close relatives, including members of the Philippine radiation Cyclocorinae **new subfamily**. Loci sampled: *Cytb*, *cmos*, *BDNF*, *NT3*, *RAG1*, and *RAG2*. Numbers at internal nodes indicate posterior probabilities (bootstrap support also shown for nodes with BS > 70).

Oxyrhabdium modestum, and the unidentified lineage.

We obtained additional *Cytb* sequences from GenBank for 135 individuals (128 species, 104 genera) spanning Colubridae, Elapoidea *sensu* Kelly et al. (2009), Homalopsidae, and Pareidae. All individuals are represented by homologous *Cytb* sequences and at least one individual from each sub-familial or equivalent major lineage (Figueroa et al., 2016) is represented by the nuclear gene *cmos*. Additionally, portions of the genes *Brain Derived Neurotrophic Factor* (*BDNF*), *3′-Nucleotidase* (*NT3*), *Recombination Activating 1* (*RAG1*), and *Recombination Activating 2* (*RAG2*) were included for ten, nine, six, and ten individuals, respectively, for taxa spanning all higher-level taxonomic groups. GenBank accession numbers for all DNA sequences used in this study are listed in Table S1.

2.3. Phylogenetic inference

2.3.1. Bayesian phylogenetic inference

We used BEAST v2.2.0 (Bouckaert et al., 2014) to infer a multilocus (concatenated-gene) tree under a Yule tree process and we designated *Aplopeltura boa*, *Pareas formosensis*, and *Asthenodipsas lasgalenensis* (i.e., the members of Pareidae) as outgroups by constraining pareids as monophyletic and by constraining the group containing the elapoids + colubrids + homalopsids (i.e., all non-pareids) to be monophyletic. For each gene partition, we assigned a relaxed lognormal clock. We ran BEAST twice: for the first run (i.e., first chain), we used the reversible-jump substitution model for each locus to explore multiple substitution models during phylogenetic inference, we sampled from the posterior distribution every 10,000 generations for 46.47 million generations, and we omitted the first 10% of generations as burnin. For the second BEAST chain, we used the best-fit substitution model (inferred from the first BEAST chain) for each locus, we sampled from the posterior distribution every 10,000 generations for 100 million generations, and we omitted the first 50% of generations as burnin. Additionally, for the second BEAST chain, we constrained Colubridae + Lamprophiidae + Elapidae + Homalopsidae to form a clade and we calibrated the crown node age of this clade to be 54.67 million years old (Ma) by using a normal distribution prior (mean = 54.76 Ma, SD = 33%), following the divergence-time results of Zheng and Wiens (2016). For both BEAST chains, we used Tracer v1.5 (Rambaut et al., 2014a) to assess posterior convergence (i.e., if effective sample sizes (ESS) > 250). We used TreeAnnotator v1.8.1 (Rambaut et al., 2014b) to generate a maximum clade-credibility tree with median divergence times, and FigTree v1.4.0 (Rambaut, 2012) to visualize trees. We considered posterior probabilities (PP) ⩾ 0.95 to be strong support for the monophyly of a group.

2.3.2. Maximum likelihood phylogenetic inference

We used a RAxML v8.0 (Stamatakis, 2014) to infer a multilocus ML tree. We treated each locus as a separate partition with the General Time-Reversible (GTR) + Gamma substitution model. We did not force monophyly for any groups (i.e., we did not select an outgroup *a priori*). We performed 1000 bootstraps using the rapid hill-climbing algorithm to assess heuristic support for inferred clades (Stamatakis et al., 2008). We considered bootstrap support (BS) values ⩾ 70 to be strong support for the monophyly of a group.

3. Results

3.1. Alignment and best-fit substitution models

The final alignment used for phylogenetic inference included DNA sequences for 145 individuals (1012–3897 bp per individual), including 62% of elapid and 90% of lamphrophiid genera, plus representatives from Homalopsidae, Pareidae, and from each of the subfamilies of Colubridae. The highest posterior density substitution model for each locus (estimated from the first BEAST chain) was considered the respective best-fit model and is shown in parentheses for each locus: *Cytb* (GTR), *BDNF* (Tamura-Nai 93 model [TN93]), *cmos* (Hasegawa-Kishino-Yano 85 model [HKY85]), *RAG1* (HKY85), *RAG2* (HKY85), and *NT3* (HKY85). Phylogenetic relationships are reported below for the second BEAST chain, which used the best-fit substitution models identified from the first chain.

3.2. Phylogenetic inference

Both BI and ML phylogenetic analyses recovered the groups Colubridae (PP = 1; BS = 20), Elapidae (PP = 0.99; BS = 46), Elapoidea (PP = 0.99; BS = 51), Homalopsidae (PP = 1; BS = 100), and Pareidae (PP = 1; BS = 100) as monophyletic. Our results place two lamprophiid subfamilies, Actractaspidinae and Cyclocorinae **new subfamily** (see systematic account in Section 4.2), closer to Elapidae than to other lamprophiids (pp = 0.88; BS = 2), thus making Lamprophiidae paraphyletic (Fig. 2). Surprisingly, both ML and BI analyses strongly support the existence of an endemic Philippine radiation that includes the genera *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium* (PP = 1; BS = 80). This Philippine clade is strongly supported as a member of Elapoidea, but its position relative to the other clades is not resolved. Within the Philippine elapoid clade, both ML and BI methods place *Cyclocorus* as the sister taxon to *Hologerrhum* (PP = 1, BS = 85) and place *Oxyrhabdium* as the sister taxon to *Myersophis* (PP = 0.74, BS = 66). The “Unnamed Leyte-Samar lineage” (KU 337269) is recovered as either the sister taxon to the *Oxyrhabdium* + *Mysersophis* lineage (BS = 51) or as the sister taxon to the lineage containing *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium* (PP = 0.33) (Fig. 2). Divergence-time estimation from the BEAST analysis supports initial diversification within the Philippine endemic elapoids beginning ~35 Ma (95% highest posterior density 29–41 Ma).

4. Discussion

4.1. Phylogenetic relationships

Our results support the existence of a novel clade of Philippine elapoid snakes including all but one of the archipelago’s endemic and most enigmatic genera: *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium*. The close relationship of *Cyclocorus* and *Hologorrhum* is supported by the shared presence of a scalation character not observed in any other Southeast Asian species (Leviton, 1965, 1983; Brown et al., 2000). Although *Hologerrhum* has been treated indiscriminately as a member of the subfamily Natricinae (Brown et al., 2000; Pyron et al., 2013), our results render this relationship no longer tenable (Fig. 2). Although no unambiguous phenotypic synapomorphies have been identified, genetic data strongly support the recognition of *Cyclocorus*, *Hologerrhum*, *Myersophis*, *Oxyrhabdium*, and the “Unnamed Leyte-Samar lineage” as a novel clade, albeit with unclear affinities relative to other, similarly divergent, well-supported clades (subfamilies) of Elapoidea.

Our discovery of an entirely endemic Philippine snake radiation (Figs. 2 and 3) that includes deeply divergent lineages suggests that pre-Pleistocene, *in-situ* diversification has been much more important for the development of the archipelago’s snake faunas than previously assumed (Brown et al., 2013). The Oligocene–Miocene ages of cyclocorine taxa preclude their interpretation as an exclusive product of the sea-level driven “species pump” action of the Pleistocene Aggregate Island Complex (PAIC) diversification model (Brown and Diesmos, 2009). Uncertainty in branching order among the Elapidae, Atractaspidinae, and Cyclocorinae (Fig. 2) render statistical inference of ancestral range evolution impossible given the available data, but numerous unrelated terrestrial vertebrate clades have been dated to well before the Pleistocene (e.g., lizards: *Gekko*, *Eutropis*, and *Brachymeles*; shrews: *Crocidura*; frogs: *Platymantis*, *Sanguirana*, and *Pulchrana*), suggesting early long-distance overseas colonization of Philippine paleoislands and/or paleotransport on rifting continental fragments as possible mechanisms that may have established the initial precursors of this endemic Philippine snake radiation (Barley et al., 2015; Brown et al., 2013, 2015, 2016; Esselstyn and Brown, 2009; Chan and Brown, 2017; Siler et al., 2012, 2011). Blackburn et al. (2010) proposed a Palawan Ark mechanism of vicariance-rafting for the origin of *Barbourula* and subsequent authors have favored a Palawan Ark origin for Philippine *Gekko* (Siler et al., 2012) and *Sanguirana* (Brown et al., 2016; Chan and Brown, 2017), but Cyclocorinae is not known from the Palawan PAIC, which supports a different biogeographic origin for these snakes. Despite the archipelago’s diverse terrestrial snake fauna, phylogenetic studies of Philippine snakes are notably few; as such, the biogeographic origins and whether *in-situ* cladogenesis has also been

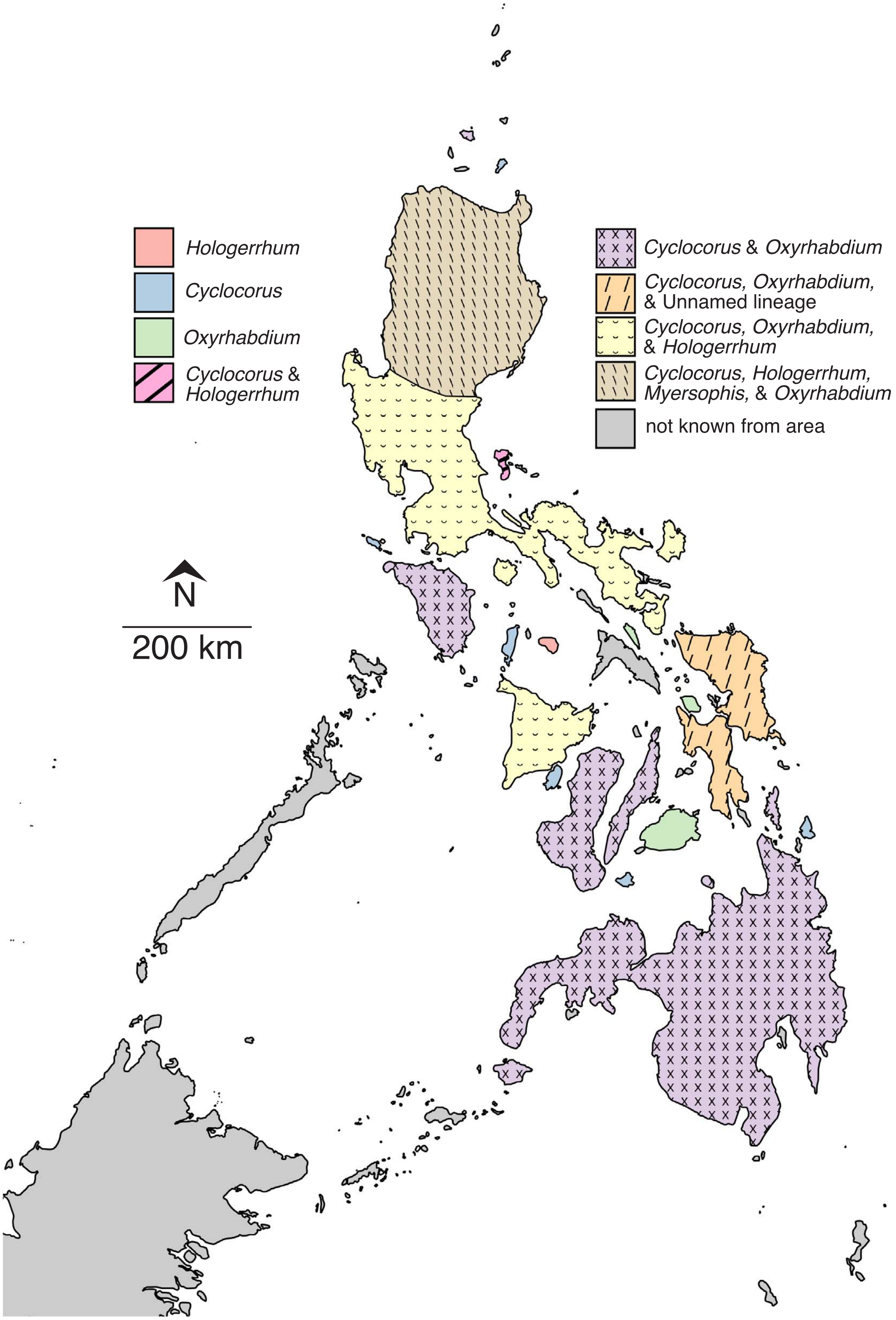

Fig. 3. Geographic distribution of Cyclocorinae **new subfamily** in the Philippines, including *Cyclocorus*, *Hologerrhum*, *Myersophis*, *Oxyrhabdium*, and the unnamed lineage.

underestimated for other Philippine snake groups is as yet unclear. These questions provide immediate opportunities for future study.

Our preferred phylogenetic estimate recovers higher-level relationships generally similar to other recent analyses (Figueroa et al., 2016; Pyron et al., 2013; Zheng and Wiens, 2016), except that our novel sampling allows for the identification of a new endemic Philippine snake radiation, comparable in age, phylogenetic distinctiveness, and phenotypic uniqueness to other subfamilies of Lamprophiidae. This entirely Philippine radiation is estimated to have originated approximately 35–25 Ma (Eocene–Miocene), is clearly geographically circumscribed, and will likely eventually be recognized as possessing an unusual biogeographic origin compared to other Philippine taxa (Jansa et al., 2006; Blackburn et al., 2010; Siler et al., 2012; Brown et al., 2016; Chan and Brown, 2017). Differences between our topology and those inferred in other recent analyses primarily include variation in early initial branching order, most likely resulting from reduced phylogenetic signal-to-noise ratio at deep nodes (fast mutation rates of mitochondrial DNA, saturation of mutations). Nevertheless, we recovered strong support for more recent nodes and relationships at these strongly supported nodes are consistent with earlier studies. As documented by Figueroa et al. (2016) and Pyron et al. (2014), Elapidae renders Lamprophiidae paraphyletic.

4.2. Systematic account

Cyclocorinae (**new subfamily**)
Type genus: Cyclocorus Duméril, Bibron, and Duméril, 1854
Type species: Lycodon lineatus Reinhardt, 1843

Diagnosis: Members of the Philippine endemic subfamily Cyclocorinae can be distinguished from many members of the Elapoidea by possession of (1) intermediate body size (250–600 mm total length, excepting the unnamed lineage represented here by the specimen KU 337269); (2) 15 or 17 smooth scale rows at midbody; (3) a single row of subcaudals (shared by members of the genera *Cyclocorus*, *Hologerrhum*, and the unnamed lineage represented by KU 337269); (4) a distinctively elongate snout, characterized by the presence of enlarged anterior chin shields and an elongate loreal scale (shared by members of *Oxyrhabdium* and *Myersophis*); (5) a small number (5–6) of supralabials (*Oxyrhabdium*, *Myersophis*, and the unnamed lineage represented by KU 337269); and (6) markedly bulging, dorsally protruding eyes (*Oxyrhabdium* and *Myersophis*).

Phylogenetic definition: Cyclocorinae refers to the clade originating in the last common ancestor of *Oxyrhabdium leporinum* (Günther, 1858), *Cyclocorus lineatus* (Reinhardt, 1843), the unnamed lineage represented by KU 337269, and all species that descend from that ancestor. It can also be conceived of as the largest crown-clade containing members of the genera *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium*, and members of the unnamed lineage represented by KU 337269.

Content: Cyclocorinae includes four endemic Philippine genera:
Genus *Cyclocorus*: *Cyclocorus lineatus lineatus*, *C. l. alcalai*, *C. nuchalis nuchalis* and *C. n. taylori*.
Genus *Hologerrhum*: *Hologerrhum philippinum* and *H. dermali*.
Genus *Oxyrhabdium*: *Oxyrhabdium leporinum leporinum*, *O. l. visayanum* and *O. modestum*.
Genus *Myersophis*: *Myersophis alpestris*.

Comment: We consider the unnamed lineage (here represented by the specimen KU 337269), which putatively shares a most recent common ancestor with the clade containing *Cyclocorus*, *Hologerrhum*, *Myersophis*, and *Oxyrhabdium*, to be a member of the subfamily Cyclocorinae.

4.3. Future directions

Future studies are required to resolve higher-level relationships within Elapoidea, with goals likely to include investigation into the paraphyly (with respect to Elapidae) of Lamprophiidae. If this set of relationships, favored by recent phylogenetic studies, is upheld, subsequent family-level classification of Elapoidea will be required. Monophyletic families could be achieved by elevating most of the current lamprophiid subfamilies (including Cyclocorinae), merging the Aparallactinae and Atractaspidinae into a single family-level group, and recognizing additional families for *Buhoma*, *Psammodynastes*, and *Micrelaps*. Alternatively, Elapidae could be conservatively expanded so that it is synonymous with our Elapoidea (Fig. 2). Both of these alternatives have advantages, but also negative consequences. The former would drastically, and possibly needlessly, increase the number of snake families (including arbitrary monotypic family-level groups), whereas the latter conceivably could upset sensibilities of apomorphy-focused researchers accustomed to historical use of the name Elapidae to refer exclusively to highly venomous snakes allied with cobras, kraits, marine snakes, and coral snakes. We make no alterations to higher-level classification here because the paraphyly of Lamprophiidae remains weakly supported and because many recent revisionary classifications based on few loci have caused instability, confusion, and arbitrary changes that have required reversal following acrimonious debate (Dubois, 1992; Inger, 1996; Frost et al., 2006; Poe et al., 2017).

Future comparative empirical studies are needed to determine whether *in-situ*, archipelago-wide evolutionary diversification has been underestimated in other Philippine snake groups (Leviton, 1964; Brown and Alcala, 1970; Brown et al., 2013). In addition to Cyclocorinae, earlier studies have found unexpectedly high *in situ* diversification for many Philippine lizard clades (Barley et al., 2015; Linkem and Brown, 2013; Siler et al., 2011, 2014; Welton et al., 2014, 2017). Furthermore, determining when—and from what geographic sources—other snake groups colonized the archipelago is necessary to complete our appreciation of the assembly and evolution of Philippine terrestrial snake faunas (Taylor, 1922; Leviton, 1964; Brown et al., 2013). The development of a comprehensive, phylogenomically time-calibrated framework for temporal diversification and accumulation of the archipelago's rich snake faunas will provide unprecedented insight into the processes associated with the production, assembly, partitioning, and geographic concentration of Philippine land vertebrate biodiversity (Brown and Diesmos, 2009; Brown et al., 2013).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.11.004.

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Table S1 *page 1*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Acanthophis antarcticus	NTM-R 17880	AF217813	—	—	—	—	—
Ahaetulla anomala	NCBS AQ185	KY769196	—	—	KY769199	—	—
Ahaetulla nasuta	[1]RAP 517; [2]FMNH 255023	[1]KC347453	—	[1]KC347377	[1]KC347415	—	[2]KX652016
Ahaetulla pulverulenta	RS-C	KC347454	—	KC347378	KC347416	—	—
Aipysurus laevis	WAM 165709	KC014389	—	—	—	—	—
Alluaudina bellyi	MRSN-FAZC 10622	AY188005	—	—	—	—	—
Amblyodipsas dimidiata	CMRK 311	DQ486346	—	—	—	—	—
Amblyodipsas polylepis	PEM-R 15626	AY612027	—	—	—	—	—
Amplorhinus multimaculatus	PEM-R 5490	AY612062	—	FJ404248	—	FJ404418	—
Amplorhinus multimaculatus	CMRK 208	DQ486340	—	DQ486164	—	—	—
Aparallactus capensis	HLMD-J 156	AY188006	—	—	—	—	—
Aparallactus guentheri	PEM-R 5678	AY235730	—	—	—	—	—
Aparallactus modestus	IPMB J284	AY612007	—	—	—	—	—
Aparallactus werneri	[3]CAS 168914; [4]FMNH 251842	[3]AF471035	[4]EU402626	[3]AF471116	—	—	[4]EU390907
Aplopeltura boa	[5]KIZ 011963; [6]MZUSP 12187	[5]JF827673	[6]FJ433984	[5]JF827696	—	—	[6]FJ434085
Aspidelaps scutatus	HLMD-J 128	AY188007	—	—	—	—	—
Aspidomorphus schlegeli	AA 16304	GQ397169	—	—	—	—	—

Table S1 *page 2*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Asthenodipsas lasgalenensis	LSUHC 10668	KC916776	—	—	—	—	—
Atractaspis bibronii	PEM-R 15835	AY612023	—	—	—	—	—
Austrelaps superbus	Voucher unknown	EU547078	—	—	—	—	—
Boaedon upembae	UTEP 21002	KM519700	—	—	—	—	—
Bothrolycus ater	IPMB J285	AY612041	—	—	—	—	—
Bothrophthalmus brunneus	PEM-R 5409	AY612056	—	—	—	—	—
Buhoma depressiceps	IPMB J287	AY612042	—	AY611951	—	FJ404422	—
Buhoma procterae	[7]IPMB J240; [8]no voucher	[7]AY612001	—	[7]AY611910	—	[8]FJ404423	—
Bungarus multicinctus	Bm9204	AJ565002	—	—	—	—	—
Calamaria pavimentata	ROM 35605	AF471081	FJ434005	AF471103	—	EF144116	FJ434106
Calamaria septentrionalis	FTB 2839	KR814699	—	KR814675	KR814735	—	—
Calamaria yunnanensis	ROM 41547	KX694891	KX694702	KX694805	KX695069	—	KX695000
Calliophis melanurus	RS 148	KC347458	—	—	—	—	—
Cerberus rynchops	CAS 206574	AF471092	—	—	—	—	—
Cerberus rynchops	HKV 32404	EF395900	—	EF395925	—	—	—
Compsophis infralineatus	ZSM 78-2005	EF203994	—	—	—	—	—
Cyclocorus lineatus	KU 328836	MG458749	—	MG458759	—	—	—
Cyclocorus lineatus	KU 329413	MG458750	—	—	—	—	—
Cyclocorus nuchalis	KU 315163	MG458753	—	MG458763	—	—	—

Table S1 *page 3*

Species	ID	Cytb	BDNF	CMOS	RAG1-M	RAG2	NT3
Cyclocorus nuchalis	KU 321700	MG458754	—	MG458764	—	—	—
Demansia psammophis	AMS 147748	GQ397172	—	—	—	—	—
Dendrelaphis bifrenalis	RAP 455	KC347470	—	KC347396	KC347434	—	—
Dendrelaphis pictus	CAS 210338	KX660456	—	KX660322	—	—	KX652009
Dendroaspis polylepis	IPMB 28651	FJ404295	—	—	—	—	—
Dipsas pratti	MHUA 14278	GQ334482	—	—	—	—	GQ334667
Dipsina multimaculata	TM 84514	DQ486357	—	—	—	—	—
Ditypophis vivax	HLMD-RA 2972	AY188013	—	—	—	—	—
Dromicodryas quadrilineatus	ZSM 76-2005	DQ979989	—	—	—	—	—
Drysdalia mastersii	ABTC 35075	GU062838	—	—	—	—	—
Duberria variegata	PEM-R 9729	FJ404306	—	—	—	—	—
Elapognathus coronatus	SAM R22966	AF217819	—	—	—	—	—
Elapotinus picteti	UADBA-ZCMV 2220	EU394724	—	—	—	—	—
Elapsoidea sundevallii	HLMD-RA 2211	AY188016	—	—	—	—	—
Emydocephalus annulatus	MG Ea3	JX423409	—	—	—	—	—
Enhydris enhydris	FMNH 250119	EF395904	—	—	—	—	—
Ephalophis greyae	WAM 157940	JX002976	—	—	—	—	—
Gonionotophis nyassae	PEM-R 15462	AY612078	—	—	—	—	—
Gonyosoma jansenii	No voucher	DQ902113	—	DQ902100	—	—	—
Gonyosoma oxycephalum	ROM 37622	KX694870	KX694725	KX694808	KX695090	—	KX695018

Table S1 *page 4*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Grayia ornata	USNM-FS 246205	KX694888	—	—	—	—	—
Grayia smythii	LSUMZ-H 9143	DQ112077	—	DQ112080	—	—	—
Grayia tholloni	CMRK 380	DQ486351	—	DQ486175	—	—	—
Hemachatus haemachatus	No Voucher	AF217821	—	—	—	—	—
Hemiaspis damelii	Voucher unknown	EU547073	—	—	—	—	—
Hemibungarus calligaster	TNHC 62483	EF137411	—	—	—	—	—
Hemirhagerrhis kelleri	CMRK 77	DQ486335	—	—	—	—	—
Heterodon platirhinos	[9]MVZ 175928; [10]ROM 42472; [11]SBH 268311; [12]YPM 13421	[9]GU112412	[10]JQ599028	[10]JQ598986	—	[11]FJ416823	[12]GU353271
Heteroliodon occipitalis	PEM-FN 439	FJ404308	—	—	—	—	—
Hologerrhum philippinum	KU 330056	MG458757	—	MG458766	—	—	—
Hologerrhum philippinum	KU 330752	MG458758	—	MG458767	—	—	—
Homoroselaps lacteus	IPMB J401	AY612026	—	—	—	—	—
Homoroselaps lacteus	[13]IPMB J157; [14]CTMZ 06841; [15]IPMB 28676	[13]AY611992	[14]JQ599029	[13]AY611901	—	[15]FJ404410	—
Hormonotus modestus	PEM-R 5408	FJ404296	—	FJ404261	—	FJ404433	—
Hydrelaps darwiniensis	MG Hyd33	KC014413	—	—	—	—	—
Hydrophis mcdowelli	ABTC 101326	JX002978	—	—	—	—	—
Inyoka swazicus	NMB-R 8730	HQ207142	—	—	—	—	—

Table S1 *page 5*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Ithycyphus oursi	PEM-FN 436	FJ404309	—	—	—	—	—
Lamprophis aurora	NMB-R 8774	HQ207143	—	—	—	—	—
Lamprophis fiskii	[16]PEM-R 5764; [17]CMRK 492	[16]DQ486354	—	[17]HQ207087	—	[16]FJ404437	—
Langaha madagascariensis	ZSM 636-2000	AY188020	—	—	—	—	—
Laticauda colubrina	Voucher unknown	KX239643	—	—	—	—	—
Leioheterodon madagascariensis	MRSN-FAZC 10621	AY188022	—	—	—	—	—
Liophidium therezieni	ZSM 2053-2007	EU394722	—	—	—	—	—
Liopholidophis dolicocercus	UADBA-ZCMV 2049	DQ979990	—	—	—	—	—
Lycodonomorphus laevissimus	PEM-R 5630	DQ486338	—	—	—	—	—
Lycodryas sanctijohannis	ZSM 40-2010	HE798436	—	—	—	—	—
Lycophidion nigromaculatum	PEM-R 17867	FJ404298	—	—	—	—	—
Macrelaps microlepidotus	[18]IPMB J142; [19]IPMB 28666	[18]AY611993	—	[18]AY611902	—	[19]FJ404412	—
Madagascarophis colubrinus	ZSM 403-2000	AY586253	—	—	—	—	—
Malpolon monspessulanus	HLMD-RA 2606	AY188029	—	—	—	—	—
Micrelaps bicoloratus	CMRK 330	DQ486349	—	DQ486173	—	—	—
Micropechis ikaheka	BPBM 18936	GQ397171	—	—	—	—	—
Micropisthodon ochraceus	ZFMK 66658	AY188030	—	—	—	—	—

Table S1 *page 6*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Micruroides euryxanthus	AMNH 128233	AF217823	—	—	—	—	—
Micrurus fulvius	Voucher unknown	JF357938	—	—	—	—	—
Mimophis mahfalensis	No Voucher	DQ486461	—	—	—	—	—
Myersophis alpestris	KU 308684	MG458752	—	MG458762	—	—	—
Naja kaouthia	[20]Voucher unknown; [21]CAS 212250; [22]CAS 206602; [23]Voucher unknown	[20]FR693728	[21]EU402654	[22]AY058938	[21]EU402857	—	[23]EU390930
Naja naja	Voucher unknown	FR693725	—	—	—	—	—
Natrix natrix	MTD-T 9270	HF680011	—	—	—	—	—
Natrix natrix	[24]Voucher unknown; [25]LSUMZ 21952; [26]Voucher unknown; [27]LSUMZ-H 05128	[24]AY487749	[25]EU402655	[26]AF544697	[25]EU402858	—	[27]KF234022
Notechis ater	SAM-R 31604	AF217836	—	—	—	—	—
Ophiophagus hannah	CAS 206601	AF217842	—	—	—	—	—
Oxyrhabdium leporinum	unknown SURC #	AF471029	—	DQ112081	—	FJ404466	—
Oxyrhabdium leporinum	KU 325975	MG458755	—	MG458765	—	—	—
Oxyrhabdium modestum	KU 326678	MG458756	—	—	—	—	—
Oxyuranus scutellatus	WW 1199	AY340787	—	—	—	—	—
Parahydrophis mertoni	MG Pm32	KC014451	—	—	—	—	—
Parastenophis betsileanus	unknown UADB #	GU994803	—	—	—	—	—
Pareas formosensis	NMNS 05631	KJ642194	—	—	—	—	—

Table S1 *page 7*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Pareas hamptoni	ROM 38104	KX694896	KX694746	KX695123	KX694789	—	KX695036
Pareas hamptoni	[28]FMNH 258687; [29]R 0721; [30]Voucher unknown	[28]AY425809	[28]EU402657	[29]JF827703	[28]EU402860	—	[30]EU390933
Phisalixella variabilis	ZSM 1605-2008	GU994789	—	—	—	—	—
Plagiopholis blakewayi	YBU 14540	KT199013	—	—	—	—	—
Plagiopholis styani	SCUM 080001W	EU496918	—	EU496916	—	—	—
Polemon notatus	PEM-R 5404	AY612030	—	—	—	—	—
Prosymna frontalis	MCZ-R 185003	KR814693	—	KR814680	—	—	—
Prosymna janii	PEM-R 12072	FJ404319	—	FJ404293	—	FJ404464	—
Prosymna ruspolii	CMRK 316	DQ486347	—	DQ486171	—	—	—
Prosymna visseri	CAS 214753	AY188033	—	AY187994	—	FJ404463	—
Psammodynastes pictus	[31]LSUHC 4093, [32]FMNH 267940	[31]KX660507	—	[32]KX660341	—	—	—
Psammodynastes pulverulentus	[33]CAS 213503; [34]KU 309922	[33]AF471031	—	[34]MG458761	—	—	—
Psammophis mossambicus	PEM-R 15488	FJ404314	—	—	—	—	—
Psammophis mossambicus	[35]CMRK 125; [36]PEM-R 15488	[35]DQ486383	—	[35]DQ486185	—	[36]FJ404393	—
Psammophylax multisquamis	CMRK 404	DQ486437	—	—	—	—	—
Pseudaspis cana	[37]IPMB J409; [38]CMRK 246; [39]PEM-R 17084	[37]AY612080	—	[38]DQ486167	—	[39]FJ404458	—

Table S1 *page 8*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Pseudechis australis	SAM-R 31703	AF217824	—	—	—	—	—
Pseudoboodon lemniscatus	CMRK 351	DQ486350	—	—	—	—	—
Pseudorabdion longiceps	ADM 0004	KX660529	—	KX660400	—	—	KX652070
Pseudorabdion oxycephalum	CMNH 5802	AF471073	—	DQ112083	—	—	—
Pseudoxenodon karlschmidti	[40]ROM 30627; [41]ROM 41033	[40]AF471080	[41]JQ599045	[40]AF471102	—	—	—
Pseudoxyrhopus ambreensis	HLMD-J 102	AY188035	—	—	—	—	—
Pythonodipsas carinata	PEM-R 8234	AY188036	—	—	—	—	—
Rhabdophis adleri	WJC 20090801	KF800931	—	—	—	—	—
Rhabdophis chrysargos	MSNG 54962	HG763866	—	—	—	—	—
Rhagerhis moilensis	HLMD (# unknown)	DQ486333	—	—	—	—	—
Rhamphiophis rubropunctatus	No voucher	FJ404310	—	—	—	—	—
Scaphiodontophis annulatus	KU 289943	GQ927323	—	—	—	—	—
Sibynophis bistrigatus	FTB 2471	KC000127	—	—	—	—	—
Sibynophis collaris	FTB 2661	KC000129	—	—	—	—	—
Sibynophis collaris	FTB 2656	KC000122	—	KC000120	KC000109	—	—
Simoselaps bertholdi	Voucher unknown	EU547062	—	—	—	—	—
Sinomicrurus japonicus	CAS 204980	AF217831	—	—	—	—	—

Table S1 *page 9*

Species	**ID**	**Cytb**	**BDNF**	**CMOS**	**RAG1-M**	**RAG2**	**NT3**
Suta suta	Voucher unknown	EU547066	—	—	—	—	—
Thamnosophis martae	ZSM 1597-2008	FJ403481	—	—	—	—	—
Toxicocalamus loriae	BPBM 19506	KT778542	—	—	—	—	—
Unnamed lineage	KU 337269	MG458751	—	MG458760	—	—	—
Walterinnesia aegyptia	No voucher	AF217838	—	—	—	—	—
Xenocalamus transvaalensis	PEM-R 12103	AY612025	—	—	—	—	—

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[a] Institutional and field tag acronyms and abbreviations used in this table include: AA: Allen Allison field tag; ABTC: Australian Biological Tissue Collection, South Australian Museum (Adelaide, Australia); ADM: Alexander D. McKelvy field tag; AMNH: American Museum of Natural History (New York City, USA); AMS: Australian Museum (Sydney, Australia); Bm: Ulrich Kuch personal tissue collection; BPBM: Bernice P. Bishop Museum (Honolulu, USA); CAS: California Academy of Sciences (Berkeley, USA); CMNH: Carnegie Museum of Natural History (Pittsburgh, USA); CMRK: Christopher M. R. Kelly field tag; FMNH: Field Museum of Natural History (Chicago, USA); FTB: Frank T. Burbrink field tag; HKV: Harold K. Voris field tag; HLMD: Hessisches Landesmuseum Darmstadt (Darmstadt; HLMD-RA for catalog numbers and HLMD-J for field tags); IPMB: Institute of Pharmacy and Molecular Biotechnology, University of Heidelberg (Germany; IPMB-J for field tags); KIZ: Kunming Institute of Zoology (China); KU: University of Kansas Natural History Museum and Biodiversity Institute (Lawrence, USA); LSUHC: World Museum of Natural History, La Sierra University (Riverside, USA); LSUMZ: Louisiana State University Museum of Natural Science (Baton Rouge, USA; LSUMZ-H for tissues); MCZ: Museum of Comparative Zoology, Harvard University (Cambridge, USA); MG: Michael Guinea field tags; MHUA: Museo de Herpetología, Universidad de Antioquia (Medellín, Colombia); MRSN: Museo Civico di Storia Naturale di Torino (Torino, Italy); MSNG: Museo Civico di Storia Naturale "Giacomo Doria" (Genova, Italy); MTD: Museum of Zoology, Senckenberg Dresden (Germany; MTD-T for tissue collection); MVZ: Museum of Vertebrate Zoology, University of California at Berkeley (USA); MZUSP: Museo de Zoologia de Universidade de São Paulo (Brazil; CTMZ for tissues); NCBS: National Institute for Biological Sciences (Bangalore, India); NMB: National Museum, Bloemfontein (South Africa); NMNS: National Museum of Natural Science (Taichung, Taiwan); NTM-R: Northern Territory Museum of Arts and Sciences (Darwin, Australia); PEM: Port Elizabeth Museum (South Africa; PEM-R for catalog numbers and PEM-FN for field tags); R: Hainan Normal University (Haikou, China); RAP: R. Alex Pyron field tags; ROM: Royal Ontario Museum (Ontario, Canada); RS: Ruchira Samaweera field tag; SAM: South African Museum (Cape Town, South Africa); SBH: S. Blair Hedges field tags; SCUM: Sichuan University Museum (Chengdu, China); SURC: Silliman University Reference Collection (Dumaguete, Philippines); TM: Ditsong National Museum of Natural History (formerly Transvaal Museum; Pretoria, South Africa); TNHC: Texas Natural History Collections, University of Texas at Austin (USA); UADB: Université d'Antananarivo, Départment de Biologie Animale (Antananarivo, Madagascar); USNM: National Museum of Natural History (Washington, D.C., USA; USNM-FS for field tags); UTEP: University of Texas at El Paso (USA); WAM: Western Australian Museum (Perth, Australia); WJC: Ji-Chao Wang field tags; WW: Wolfgang Wüster personal collection; YBU: Yibin University (Yibin, China); YPM: Yale Peabody Museum (New Haven, USA); ZFMK: Zoologisches Forschungsmuseum (Bonn, Germany); ZSM: Zoologisches Staatssammlung München (München, Germany).