



Phylogenetic partitioning of the third-largest vertebrate genus in the world, *Cyrtodactylus* Gray, 1827 (Reptilia; Squamata; Gekkonidae) and its relevance to taxonomy and conservation

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Abstract

The gekkonid genus *Cyrtodactylus* is the third most speciose vertebrate genus in the world, containing well over 300 species that collectively range from South Asia to Melanesia across some of the most diverse landscapes and imperiled habitats on the planet. A genus-wide phylogeny of the group has never been presented because researchers working on different groups were using different genetic markers to construct phylogenies that could not be integrated. We present here Maximum likelihood and Bayesian inference mitochondrial and mito-nuclear phylogenies incorporating of 310 species that include dozens of species that had never been included in a genus-wide analysis. Based on the mitochondrial phylogeny, we partition *Cyrtodactylus* into 31 well-supported monophyletic species groups which, if used as recommended herein, will increase the information content of future integrative taxonomic analyses that continue to add new species to this genus at an ever-increasing annual rate. Data presented here reiterate the outcome of several previous studies indicating that *Cyrtodactylus* comprises an unprecedented number of narrow-range endemics restricted to single mountain tops, small islands, or karst formations that still remain unprotected. This phylogeny can provide a platform for various comparative ecological studies that can be integrated with conservation management programs across the broad diversity of landscapes and habitats occupied by this genus. Additionally, these data indicate that the true number of *Cyrtodactylus* remains substantially underrepresented.

Keywords

Asia, Bent-toed Geckos, endemism, Indochina, integrative taxonomy, Melanesia, Southeast Asia species groups

Introduction

Bent-toed Geckos of the gekkonid genus *Cyrtodactylus* Gray, 1827 comprises the third most speciose vertebrate genus in the world, containing well over 300 species (Uetz et al. 2020 and see below) and ranges across some of the most diverse and imperiled landscapes on the planet from South Asia to Melanesia (Fig. 1). The ecological diversity among these primarily scansorial species is unparalleled in any other gekkotan genus, and the increasing annual rate at which new species are being described shows no signs of leveling off—demonstrating that the taxonomic diversity within this genus is still greatly underrepresented (Fig. 2). Until recently, however, a comprehensive phylogeny of *Cyrtodactylus* could not be reconstructed because researchers working on different groups from specific geographic regions were using different genetic markers to construct

small, geographically localized, phylogenies that could not be integrated with one another. This is problematic for a number of reasons. By not being able to include the necessary suite of closely related species in the construction of these small, localized phylogenies, sampling error could potentially plague their phylogenetic accuracy, manifesting itself in low nodal support values and/or misleading relationships with high nodal support (e.g. Zwickl et al. 2002; Heath et al. 2008). Additionally, incompletely sampled phylogenies potentially diminish the accuracy of the diagnoses and delimitations of new species. By not fully knowing to which species a putatively new species is related, it might not be comprehensively compared to the most relevant set of species for a complete and informative diagnosis. Hence, it may not be unequivocally demonstrated that

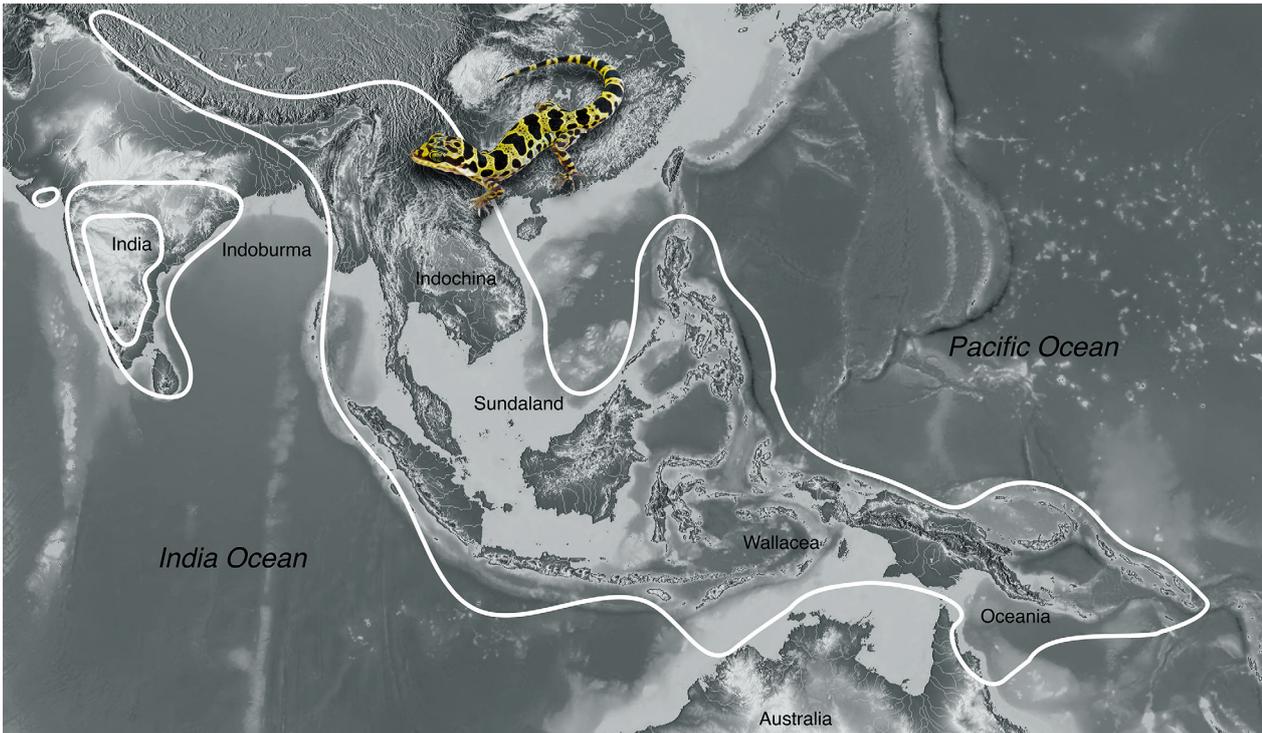


Figure 1. General distribution of the genus *Cyrtodactylus*. The species illustrated is *Cyrtodactylus myintkyawthurai* from Myanmar. Photo by L. Lee Grismer.

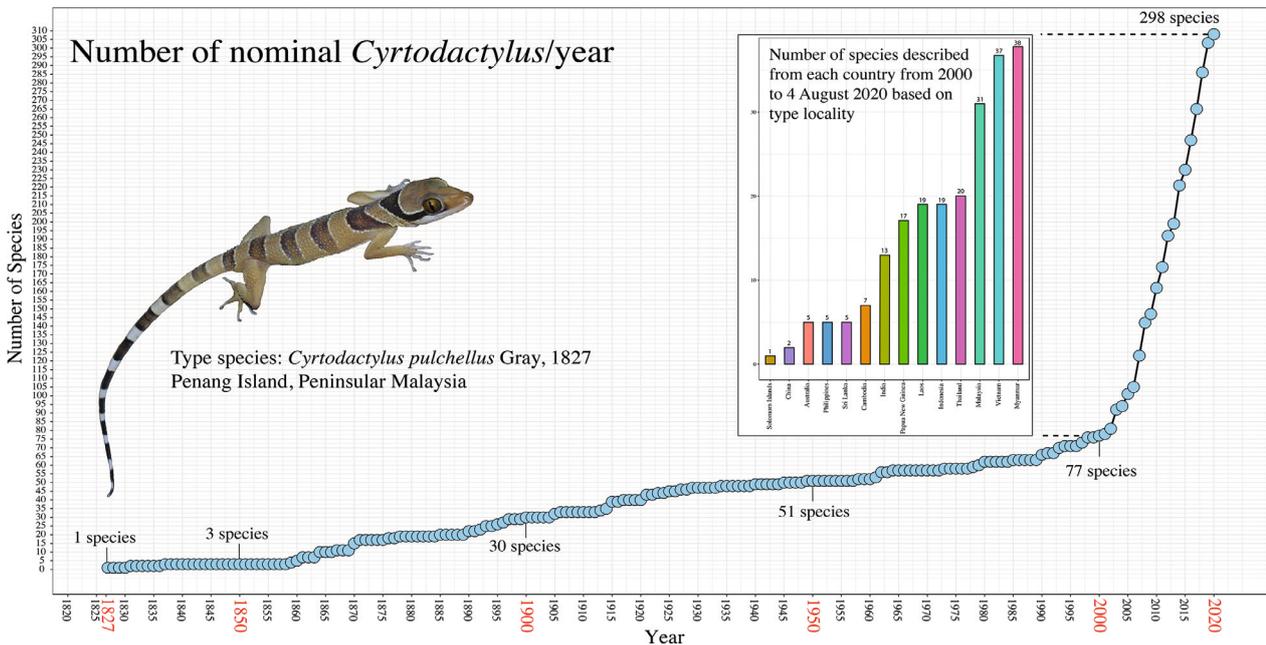


Figure 2. Number of species of *Cyrtodactylus* described per year. The trajectory of new species descriptions from 2000 to 20 September 2020, indicates that the true diversity of this genus is not yet calculable and that 48% of the newly described species during this period have come from Myanmar, Vietnam, and Malaysia.

it is phylogenetically distinct; i.e. a new species. Additionally, incompletely informed diagnoses accompanying the descriptions of new species may contain only comparisons to distantly related species that happen to occur in the same geographic area while the appropriate comparisons to closely related species may go overlooked because they are not geographically proximate or are missing from the phylogeny. Recently however,

this stumbling block was in-part removed with a mitochondrial phylogeny composed of 243 species (Grismer et al. 2020a)—123 more species than the previous largest phylogeny (O’Connell et al. 2019)—which for the first time, integrated dozens of species into a single tree that had never before been included in the same data set and taht generated the first phylogenetic data for several other species.

In a continuing effort to mitigate these methodological limitations, a phylogeny of 310 species of *Cyrtodactylus* is presented here which, for the first time, places as many species as possible into a single tree consisting of 244 nominal species (79% of described species as of 20 September 2020, Uetz et al. 2020) and 66 undescribed candidate species. This phylogeny provides sufficient evidence for the recognition of 31 well-supported monophyletic species groups. By focusing on these species groups, diagnoses and delimitations of future species descriptions will be more phylogenetically informative by limiting the number of species to which a new taxon needs to be compared to 1) only those species in a specific species group, 2) closely related species groups, and 3) geographically proximate species if necessary. Additionally, the use of these species groups will eliminate unnecessary morphological comparisons to distantly related species that have no bearing on delimiting the new species and will considerably streamline the amount of text needed in the morphological comparison sections of species descriptions.

This phylogeny can also provide a foundation for comparative ecological analyses that can inform and be integrated with conservation measures across the broad range of landscapes and habitats encompassed by this genus (Fisher and Owens 2004; McCartney-Melstad and Shaffer 2015; Shaffer et al. 2015). For example, Grismer et al. (2020a) quantitatively demonstrated that karstic landscapes are the habitats wherein the most species-rich radiations within *Cyrtodactylus* independently evolved across Indochina and Sundaland and they brought attention to the urgent need for the conservation of these species in these largely unprotected landscapes (now underway in Myanmar [Komerički et al. 2020]). Hence, the evolution and origin of large radiations and their ecological proclivities can be recovered in comparative phylogenetic analysis and be informative for conservation management programs.

Materials and methods

Mitochondrial DNA

A data set comprised of 310 described and undescribed species of *Cyrtodactylus* was assembled from GenBank (n=247) and newly sequenced material (n=63; Table 1A). A phylogeny was constructed based on 1469 base pairs of the mitochondrial gene NADH dehydrogenase subunit 2 gene and its flanking tRNAs (hereafter as ND2). *Mediodactylus russowii* and *Hemidactylus frenatus* were used as outgroups to root the tree based on Gamble et al. (2012).

For molecular phylogenetic analyses, genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using standard phenol-chloroform-proteinase K (final concentration 1 mg/ml) extraction procedures with consequent isopropanol precipitation following Hillis et al. (1996) or a SPRI magnetic

bead extraction protocol (<https://github.com/phyleticalab-protocols/blob/master/extraction-spri.md>). The ND2 gene, with parts of adjacent tRNAs, was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 1.0 µl genomic DNA (10–30 µg), 1.0 µl light strand primer L4437b (concentration 10 µM), 1.0 µl heavy strand primer H5934 (concentration 10 µM), 1.0 µl dinucleotide pairs (1.5 µM), 2.0 µl 5× buffer (1.5 µM), MgCl 10× buffer (1.5 µM), 0.1 µl Taq polymerase (5u/µl), and 6.4 µl ultra-pure H₂O. Both primers are from Macey et al. (1997) PCR reactions were executed on Bio-Rad T100 gradient thermocycler under the following conditions: initial denaturation at 95°C for 2 min, followed by a second denaturation at 95°C for 35 s, annealing at 55°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 31 cycles. All PCR products were visualized using 1.0 % agarose gel electrophoresis. Successful PCR products were sent to Evrogen (Moscow, Russia), Genetech Sri Lanka Pvt. Ltd. (Colombo, Sri Lanka), or Genewiz (South Plainfield, New Jersey, USA, First Base, Malaysia) for PCR purification, cycle sequencing, sequencing purification, and sequencing using the same primers as in the amplification step (see Grismer et al. 2020a). Sequences were analyzed from both the 3' and the 5' ends separately to confirm congruence between reads. Forward and reverse sequences were uploaded and edited in Geneious 2019.0.4 (<https://www.geneious.com>). Following sequence editing we aligned the protein-coding region and the flanking tRNAs using the MAFFT v7.017 (Katoh and Kuma, 2002) plugin under the default settings in Geneious 2019.0.4 (<https://www.geneious.com>). Mesquite v3.04 (Maddison and Maddison, 2015) was used to calculate the correct amino-acid reading frame and to confirm the lack of premature stop codons in the ND2 portion of the DNA fragment.

Nuclear DNA

Data sets using the recombination activating 1 gene (RAG1; 1050 base pairs, ~112 species), phosphocin (PDC; 395 bp, ~78 species), and matrix remodeling associated 5 (MXRA5; 839 bp, ~60 species) with varying combinations of ingroup species were assembled from GenBank (see Wood et al. 2012). Each gene was analyzed independently and together in a concatenated data set. Twenty-two species from the gekkotan families Pygopodidae, Diplodactylidae, Gekkonidae, and Sphaerodactylidae were used as outgroups to root the tree based on Wood et al. (2012).

Mito-nuclear data

A concatenated data set comprised of the mitochondrial gene ND2 plus its flanking tRNAs and the nuclear genes RAG1, PDC, and MXRA5 (3753 bp) that contained all 310 species was assembled from the above data sets. *Mediodactylus russowii* and *Hemidactylus frenatus* were used as outgroups to root the tree based on Gamble et al. (2012).

Table 1. Best-fit models for the partitions of the Maximum Likelihood analyses as determined by BIC.

Maximum likelihood Analyses	Model
ND2	
codon position 1	TVM+F+I+G4
codon position 2	TIM3+F+I+G4
codon position 3	GTR+F+ASC+G4
tRNAs	GTR+F+I+G4
RAG1	
codon position 1	HKY+F+G4
codon position 2	HKY+F+G4
codon position 3	K3Pu+F+G4
PDC	
codon position 1	TIM2e+G4
codon position 2	TPM3+F+G4
codon position 3	TIM3e+G4
MXRA5	
codon position 1	HKY+F+G4
codon position 2	TPM2u+F+I
codon position 3	HKY+F+G4
RAG1+PDC+MXRA5	
RAG1	HKY+F+G4
PDC	TNe+I+G4
MWRA5	HKY+F+G4
Mito-nuclear	
ND2	GTR+F+R8
RAG1+PDC+MXRA5	TN+F+R3
tRNAs	TVMe+R5

Phylogenetic analyses

Maximum likelihood (ML) analyses were implemented for six data sets (one mitochondrial, four nuclear, and one mito-nuclear) using the IQ-TREE webserver (Nguyen et al. 2015a; Trifinopoulos et al. 2016) preceded by the selection of substitution models using the Bayesian Information Criterion (BIC) in ModelFinder (Kalyaanamoorthy et al. 2017; Table 1). For the mito-nuclear data set, IQ-Tree version 2.1.1 using the `-m MFP+MERGE -B` command was employed using the greedy strategy (Lanfear et al. 2012) to find the best partition scheme (Table 1). One-thousand bootstrap pseudoreplicates via the ultrafast bootstrap (UFB; Hoang et al. 2018) approximation algorithm were employed, and nodes having UFB values of 95 and above were considered strongly supported (Minh et al. 2013). We considered nodes with values of 90–94 as well-supported.

Bayesian phylogenetic trees were estimated using Bayesian Evolutionary Analysis by Sampling Trees (BEAST) version 2.4.6 (Drummond et al. 2012) implemented in CIPRES (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010) for the ND2 and concatenated nuclear data sets. Input files were constructed in Bayesian Evolutionary Analysis Utility (BEAUti) version 2.4.6 using a lognormal relaxed clock with unlinked site models, linked trees and clock models, and a Yule prior and run in BEAST version 2.4.6 (Drummond et al. 2012) on CIPRES. bModelTest, implemented in BEAST,

was used to numerically integrate over the uncertainty of substitution models while simultaneously estimating phylogeny using Markov chain Monte Carlo (MCMC). MCMC chains were run for 300,000,000 generations and logged every 30,000 generations. The BEAST log file was visualized in Tracer v. 1.6.0 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) were well-above 200 for all parameters. Maximum clade credibility trees using mean heights at the nodes were generated using TreeAnnotator v.1.8.0 (Rambaut and Drummond 2013) with a burn-in of 1000 trees (10%). Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered strongly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002). We considered nodes with values of 0.90–0.94 as well-supported.

Results

Discussed below are the combined results of the six different phylogenetic analyses and the resulting three trees considered most critical to this study. The ND2 data recovered the best-resolved trees (i.e. no polytomies, having nodes with the highest nodal support values, and the least amount of missing data) and provided the topological framework on which the delineation of the 31 species groups (Table 2) are based (see **Species groups**). Descriptions and comparisons of the three trees follow.

Mitochondrial data

The ML and BEAST analyses retrieved very similar topologies, recovering 272 of the same 298 nodes (91%) and both recovering *Cyrtodactylus* as monophyletic (Fig 3). The tree was generally well- to strongly supported in both analyses, especially among the shallower nodes (i.e., those nodes within species groups). Only four of the 34 backbone nodes (i.e. nodes not designating species groups) were topologically discordant between the ML and BI analyses. The remaining 30 nodes were recovered in both analyses and of those, 26 were well- to strongly supported in one or both analyses. The 31 species groups recovered in this tree (Fig. 3) were well- to strongly supported in most cases, usually by both analyses. The exception lies within the clade of the seven Melanesian species groups (the *arcanus*, *capreoloides*, *loriae*, *louisiadensis*, *novaeguineae sermowaiensis*, and *tuberculatus* groups), which itself was recovered only in the ML analysis (UFB 92). The topology within this clade was recovered in both analyses but only the sister group relationship between the *tuberculatus* and *louisiadensis* species groups is strongly supported by both (100/1.00), though all the species groups were strongly supported as monophyletic. These results mirror those of Tallwin et al. (2018).

Table 2. Species composition of the *Cyrtodactylus* species groups used in this study and their general regional distribution.

Species group	Region	Species group	Region	Species group	Region
agamensis group		irregularis group		peguensis group	
<i>C. jarakensis</i>	Peninsular Malaysia	<i>C. bidoupimontis</i>	Vietnam	<i>C. annandalei</i>	Myanmar
<i>C. majulah</i>	Peninsular Malaysia	<i>C. bugiamapensis</i>	Vietnam	<i>C. bhupathyi</i>	India
<i>C. metropolis</i>	Peninsular Malaysia	<i>C. caovansungi</i>	Vietnam	<i>C. gubernatoris</i>	India
<i>C. pantiensis</i>	Peninsular Malaysia	<i>C. cattienensis</i>	Vietnam	<i>C. meersi</i>	Myanmar
<i>C. payacola</i>	Peninsular Malaysia	<i>C. chungii</i>	Laos, Vietnam	<i>C. myintk-yawthurai</i>	Myanmar
<i>C. psarops</i>	Sumatra	<i>C. cryptus</i>	Vietnam	<i>C. nyinyikyawi</i>	Myanmar
<i>C. rosichonarieflorum</i>	Natuna Besar Island	<i>C. cucdongensis</i>	Vietnam	<i>C. peguensis</i>	Myanmar
<i>C. semenanjungensis</i>	Peninsular Malaysia	<i>C. culaochamensis</i>	Vietnam	<i>C. pyadalinenensis</i>	Myanmar
<i>C. semicinctus</i>	Sumatra	<i>C. dati</i>	Vietnam	<i>C. pyinyaungensis</i>	Myanmar
<i>C. tiomanensis</i>	Peninsular Malaysia	<i>C. gialaiensis</i>	Vietnam	<i>C. russelli</i>	Myanmar
<i>C. cf. agamensis</i>	Sumatra	<i>C. huynhi</i>	Vietnam	<i>C. slowinskii</i>	Myanmar
sp. Sumatra GU550728	Sumatra	<i>C. kingsadai</i>	Vietnam	sp. KM255196 Arunachal Pradesh	India
sp. Sumatra KR921705	Sumatra	<i>C. phnomchiensis</i>	Cambodia	philippinicus group	
sp. Sumatra MH248914	Sumatra	<i>C. phuocbinhensis</i>	Vietnam	<i>C. agusanensis</i>	Philippines
angularis group		<i>C. pseudoquadrivirgatus</i>	Vietnam	<i>C. annulatus</i>	Philippines
<i>C. angularis</i>	Thailand	<i>C. sangi</i>	Vietnam	<i>C. aurensis</i>	Peninsular Malaysia
<i>C. bansocensis</i>	Laos	<i>C. takouensis</i>	Vietnam	<i>C. baluensis</i>	Borneo
<i>C. calamei</i>	Laos	<i>C. taynguyenensis</i>	Vietnam	<i>C. sp. Borneo HLM0313</i>	Borneo, Peninsular Malaysia
<i>C. chanhomeae</i>	Thailand	<i>C. yangbayensis</i>	Vietnam	<i>C. gubaot</i>	Philippines
<i>C. darevskii</i>	Laos	<i>C. ziegleri</i>	Vietnam	<i>C. ingeri</i>	Borneo
<i>C. hinnamnoensis</i>	Laos	<i>C. cf. cattienensis</i>	Vietnam	<i>C. jambangan</i>	Philippines
<i>C. jaegeri</i>	Laos	<i>C. cf. irregularis</i>	Vietnam	<i>C. muluensis</i>	Borneo
<i>C. jarujini</i>	Laos, Thailand	<i>C. cf. yangbayensis</i>	Vietnam	<i>C. philippinicus</i>	Philippines
<i>C. lomyenensis</i>	Laos	<i>C. cf. ziegleri</i>	Vietnam	<i>C. redimiculus</i>	Palawan
<i>C. multiporus</i>	Laos	sp. Champasak JX041341	Vietnam	<i>C. sumuroi</i>	Philippines
<i>C. nigriocularis</i>	Vietnam	sp. Kon Ka Kin HLM 0316	Vietnam	<i>C. taubatorum</i>	Philippines
<i>C. pageli</i>	Laos	sp. Kon Tum HLM 0354	Vietnam	<i>C. yoshii</i>	Borneo
<i>C. phongnhakebangensis</i>	Vietnam	sp. Kon Ka Kin HLM 0365	Vietnam	<i>C. cf. annulatus GU366085</i>	Philippines
<i>C. roesleri</i>	Laos, Vietnam	sp. Chu Mon Ray HLM 0366	Vietnam	<i>C. cf. philippinicus GU550825</i>	Philippines
<i>C. sommerladi</i>	Laos	sp. Loc Bac HLM 0367	Vietnam	<i>C. cf. pubisulcus JX440551</i>	Borneo
<i>C. soudthichaki</i>	Laos	sp. Loc Bac HLM 0368	Vietnam	<i>C. sp. Borneo MF706373</i>	Borneo
<i>C. teynieii</i>	Laos	sp. Song Thanh NAP 08781	Vietnam	pulchellus group	
sp. Nahin HLM 0349	Laos	khasiensis group		<i>C. astrum</i>	Peninsular Malaysia
sp. Lomyen HLM 0342	Laos	<i>C. aunglini</i>	Myanmar	<i>C. australotitiwangsaensis</i>	Peninsular Malaysia
sp. Nahin HLM 0353	Laos	<i>C. ayeayarwadyensis</i>	Myanmar	<i>C. bintanggrendah</i>	Peninsular Malaysia
arcanus group		<i>C. brevidactylus</i>	Myanmar	<i>C. bintangtinggi</i>	Peninsular Malaysia
<i>C. arcanus</i>	Papua New Guinea	<i>C. chrysopylos</i>	Myanmar	<i>C. dayangbuntingensis</i>	Peninsular Malaysia
<i>C. manos</i>	Papua New Guinea	<i>C. gansi</i>	India	<i>C. evanquahi</i>	Peninsular Malaysia
brevipalmatus group		<i>C. guwahatiensis</i>	India	<i>C. hidupselamanya</i>	Peninsular Malaysia

Table 2 continued.

Species group	Region	Species group	Region	Species group	Region
<i>C. brevipalmatus</i>	Thailand	<i>C. jaintiaensis</i>	India	<i>C. jelawan-gensis</i>	Peninsular Malaysia
<i>C. interdigitalis</i>	Thailand	<i>C. kazirangaensis</i>	India	<i>C. langkaw-iensis</i>	Peninsular Malaysia
<i>C. elok</i>	Peninsular Malaysia	<i>C. khasiensis</i>	India	<i>C. lekaguli</i>	Thailand
<i>C. cf. brevipalmatus</i>	Peninsular Malaysia	<i>C. myaleiktaung</i>	Myanmar	<i>C. lenggon-gensis</i>	Peninsular Malaysia
<i>C. cf. interdigitalis</i>	Laos, Thailand	<i>C. mombergi</i>	Myanmar	<i>C. macrotuber-culatus</i>	Peninsular Malaysia, Thailand
sp. Suan Phueng HLM 0372	Thailand	<i>C. montanus</i>	India	<i>C. pulchellus</i>	Peninsular Malaysia
capreoloides group		<i>C. nagalandensis</i>	India	<i>C. sharkari</i>	Peninsular Malaysia
<i>C. boreoclivus</i>	northern New Guinea	<i>C. septentrionalis</i>	India	<i>C. timur</i>	Peninsular Malaysia
<i>C. capreoloides</i>	Papua New Guinea	<i>C. tripuraenensis</i>	India	<i>C. trilatofas-ciatius</i>	Peninsular Malaysia
<i>C. medioclivus</i>	Papua New Guinea	<i>C. urbanus</i>	India	sadansinensis group	
<i>C. minor</i>	Papua New Guinea	sp. Ban Mauk HLM 0310	Myanmar	<i>C. pharbaun-gensis</i>	Myanmar
<i>C. tanim</i>	Papua New Guinea	sp. Arunachal Pradesh KM255192	India	<i>C. sadansin-ensis</i>	Myanmar
chauquangensis group		sp. Arunachal Pradesh KM255193	India	<i>C. sanpelensis</i>	Myanmar
<i>C. auribalteatus</i>	Thailand	sp. Mizoram KM255197	India	sermowaiensis group	
<i>C. bichnganae</i>	Vietnam	lateralis group		<i>C. atremus</i>	Papua New Guinea
<i>C. bobrovi</i>	Vietnam	<i>C. durio</i>	Peninsular Malaysia	<i>C. crustulus</i>	Papua New Guinea
<i>C. chauquangensis</i>	Vietnam	<i>C. lateralis</i>	Sumatra	<i>C. sermowaien-sis</i>	New Guinea
<i>C. cucphuongensis</i>	Vietnam	lawderanus group		sinyineensis group	
<i>C. doisuthep</i>	Thailand	<i>C. battalensis</i>	Pakistan	<i>C. aequalis</i>	Myanmar
<i>C. dumnuui</i>	Thailand	<i>C. chamba</i>	India	<i>C. amphipet-raeus</i>	Thailand
<i>C. erythrops</i>	Thailand	<i>C. himalayanus</i>	India	<i>C. bayinnyien-sis</i>	Myanmar
<i>C. huongsonensis</i>	Vietnam	<i>C. lawderanus</i>	India	<i>C. chaung-hanakwaensis</i>	Myanmar
<i>C. otai</i>	Vietnam	<i>C. tibetanus</i>	Tibet	<i>C. dammath-etensis</i>	Myanmar
<i>C. puhuensis</i>	Vietnam	linnwayensis group		<i>C. dattkyaiken-sis</i>	Myanmar
<i>C. soni</i>	Vietnam	<i>C. linnwayensis</i>	Myanmar	<i>C. inthanon</i>	Thailand
<i>C. sonlaensis</i>	Vietnam	<i>C. pinlaungensis</i>	Myanmar	<i>C. maelanoi</i>	Thailand
<i>C. spelaeus</i>	Laos	<i>C. shwetaungorum</i>	Myanmar	<i>C. naung-kayaingensis</i>	Myanmar
<i>C. taybacensis</i>	Vietnam	<i>C. ywanganensis</i>	Myanmar	<i>C. sinyineensis</i>	Myanmar
<i>C. vilaphongi</i>	Lao	loriae group		<i>C. taung-wineensis</i>	Myanmar
<i>C. wayakonei</i>	China, Laos	<i>C. serratus</i>	Papua New Guinea	<i>C. welpyan-ensis</i>	Myanmar
sp. Tham Pla HLM 0357	Thailand	<i>C. cf. loriae</i> Bunisi HQ401209	Papua New Guinea	sworderi group	
condorensis group		<i>C. cf. loriae</i> Fane BPBM 18650	Papua New Guinea	<i>C. guakanthan-ensis</i>	Peninsular Malaysia
<i>C. condorensis</i>	Vietnam	<i>C. cf. loriae</i> Siyomu EU268350	Papua New Guinea	<i>C. gunung-senyumensis</i>	Peninsular Malaysia

Table 2 continued.

Species group	Region	Species group	Region	Species group	Region
<i>C. eisenmanae</i>	Vietnam	<i>C. cf. loriae</i> Wau JQ820299	Papua New Guinea	<i>C. quadrivirgatus</i>	Peninsular Malaysia, Sumatra, Thailand
<i>C. grimeri</i>	Vietnam	<i>C. cf. loriae</i> Yuro AMS R115469	Papua New Guinea	<i>C. sworderi</i>	Peninsular Malaysia
<i>C. leegrimeri</i>	Peninsular Malaysia, Thailand, Vietnam	<i>C. sp. West Sepik</i> ABTC 114857	Papua New Guinea	<i>C. tebuensis</i>	Peninsular Malaysia
darmandvillei group		lousiadensis group		triedrus group	
<i>C. batucolus</i>	Peninsular Malaysia	<i>C. epiroticus</i>	Papua New Guinea	<i>C. albofasciatus</i>	India
<i>C. darmandvillei</i>	Lesser Sunda Islands, Indonesia	<i>C. klugei</i>	Papua New Guinea	<i>C. collegalensis</i>	India
<i>C. jellesmae</i>	Sulawesi	<i>C. lousiadensis</i>	Papua New Guinea	<i>C. deccanensis</i>	India
<i>C. kimberleyensis</i>	NW Australia	<i>C. murua</i>	Papua New Guinea	<i>C. fraenatus</i>	Sri Lanka
<i>C. petani</i>	Java	<i>C. robustus</i>	Papua New Guinea	<i>C. jeyporensis</i>	India
<i>C. sadleiri</i>	Christmas Island	<i>C. salomonensis</i>	Papua New Guinea	<i>C. nebulosus</i>	India
<i>C. seribuatensis</i>	Peninsular Malaysia	<i>C. tripartitus</i>	Solomon Islands	<i>C. ramboda</i>	Sri Lanka
sp. Kai Islands MF760380	Kai Islands	<i>C. sp. Mt. Pekopekowana</i> HQ401193	Papua New Guinea	<i>C. rishivalleyensis</i>	India
Timor JX440560	Timor Island	malayanus group		<i>C. soba</i>	Sri Lanka
sp. East Nussa Tenggara-KU232623	Lesser Sunda Islands, Indonesia	<i>C. cavernicolus</i>	Borneo	<i>C. speciosus</i>	India
sp. Bali Island KU232625	Lesser Sunda Islands, Indonesia	<i>C. limajalur</i>	Borneo	<i>C. srilekhae</i>	India
sp. Yamadena Island-KU232621	Lesser Sunda Islands, Indonesia	<i>C. malayanus</i>	Borneo, Peninsular Malaysia	<i>C. triedrus</i>	Sri Lanka
sp. Bali Island KU232624	Lesser Sunda Islands, Indonesia	<i>C. cf. consobrinus</i>	Borneo, Peninsular Malaysia	<i>C. varadgirii</i>	India
fasciolatus group		marmoratus group		<i>C. yakhuna</i>	Sri Lanka
<i>C. fasciolatus</i>	W Himalayas, India	<i>C. marmoratus</i>	Java	cf. <i>triedrus</i> JX440522	Sri Lanka
<i>C. cf. fasciolatus</i>	W Himalayas, India	<i>C. papuensis</i>	New Guinea	cf. <i>triedrus</i> DMSSK 181	Sri Lanka
intermedius group		<i>C. cf. papuensis</i> JX440546	Java	cf. <i>albofasciatus</i> JX440521	India
<i>C. auralensis</i>	Cambodia	<i>C. sp. HLM0371</i>	Java	cf. <i>deccanensis</i> KM878628	India
<i>C. bokorensis</i>	Cambodia	<i>C. sp. KAC 2015a</i> KR921697	Java	cf. <i>nebulosus</i> KM878621	India
<i>C. cardamomensis</i>	Cambodia	<i>C. sp. KAC 2015a</i> KR921689	Java	cf. <i>nebulosus</i> KM878620	India
<i>C. hontreensis</i>	Cambodia	<i>C. sp. KAC 2015a</i> KR921700	Sumatra	cf. <i>nebulosus</i> KM878619	India
<i>C. intermedius</i>	Thailand	<i>C. sp. KAC 2015a</i> KR921699	Sumatra	cf. <i>speciosus</i> KM878629	India
<i>C. kohrongensis</i>	Cambodia	novaeguineae group		tuberculatus group	
<i>C. laangensis</i>	Cambodia	<i>C. equestris</i>	New Guinea	<i>C. adorus</i>	Australia
<i>C. phuquocensis</i>	Vietnam	<i>C. mimikanus</i>	New Guinea	<i>C. pronarus</i>	Australia
<i>C. septimontium</i>	Vietnam	<i>C. novaeguineae</i>	Papua New Guinea	<i>C. tuberculatus</i>	Australia
<i>C. thylacodactylus</i>	Cambodia	<i>C. rex</i>	Papua New Guinea	<i>C. hoskini</i>	Australia
<i>C. cf. thylacodactylus</i>	Cambodia	<i>C. zugii</i>	New Guinea	<i>C. mcdonaldii</i>	Australia
<i>C. cf. intermedius</i> HLM 0362	Thailand	<i>C. sp. Mamberamo</i> JQ820316	New Guinea	yathepyanensis group	
<i>C. cf. intermedius</i> GU550710	Thailand	oldhami group		<i>C. linnoensis</i>	Myanmar

Table 2 continued.

Species group	Region	Species group	Region	Species group	Region
		<i>C. sp. Krabi HLM 0358</i>	Thailand		
<i>C. cf. intermedius</i> KT013117	Thailand	<i>C. lenya</i>	Myanmar	<i>C. sadanensis</i>	Myanmar
sp. Chanthaburi HLM 0360 Chanthaburi	Cambodia	<i>C. oldhami</i>	Thailand	<i>C. yathepyanensis</i>	Myanmar
		<i>C. cf. saiyok HLM 0334</i>	Thailand	<i>C. spinosus</i>	Sulawesi
sp. <i>incertae sedis</i> 2 KT013114	Cambodia	<i>C. payarhtanensis</i>	Myanmar	Orphaned species	
		<i>C. sanook</i>	Thailand	<i>C. rubidus</i>	Andaman Islands, India
		<i>C. thirakhupti</i>	Thailand	<i>C. badenensis</i>	Vietnam
		<i>C. zebraicus</i>	Thailand	<i>C. biordinis</i>	Guadalcanal, Solomon Islands
		<i>C. cf. oldhami HLM 0307</i>	Thailand	<i>C. tigroides</i>	Thailand
				<i>C. spinosus</i>	Sulawesi

Nuclear data

As in Wood et al. (2012), the phylogenies generated from the ML analyses of the RAG1, PCD, and MXRA5 data sets showed little topological discordance and, as such, were concatenated and re-run as a single data set following the methods described above. The nuclear ML and BEAST phylogenies were generally concordant throughout, but each suffered from little to no backbone support (Figs 4, 1S). The main difference between the two was that *Cyrtodactylus* was not well supported as monophyletic in the BEAST analysis (0.89)—with *C. tibetanus* being the sister species to the remaining *Cyrtodactylus*—and had no well- to strongly supported backbone nodes (Fig. 2S). The ML phylogeny had only two strongly supported backbone nodes, one of which rendered *Cyrtodactylus* paraphyletic by recovering the six species of *Hemidactylus* in that data set as nested within *Cyrtodactylus* (Fig. 2S). Of the 31 well- to strongly supported species groups recovered in the ND2 phylogeny (see below), only 22 are represented by the coverage of species used in the nuclear ML analysis. Of these, nine are recovered as polyphyletic (the *agamensis*, *darmandvillei*, *lateralis*, *lawderanus*, *malayanus*, *peguensis*, *pulchellus*, *triedrus*, *tuberculatus* species groups) and two as paraphyletic (the *irregularis* and *khasiensis* species groups). The remaining 12 species groups (*angularis*, *brevipalmatus*, *condorensis*, *intermedius*, *loriae*, *lousiadensis*, *marmoratus*, *novaeguineae*, *oldhami*, *peguensis*, *philippinicus*, and *sermowaiensis*) were recovered with the same sets of species (albeit greatly reduced in numbers due to sparser sampling in most cases) as those recovered in the ND2 trees. Only one well-supported (UFB 91) relationship among the species groups that did not involve a paraphyletic or polyphyletic group was recovered in the nuclear tree—the sister group relationship between the Melanesian species groups *sermowaiensis* and *lousiadensis*. This relationship was not recovered in the ND2 tree nor in the mito-nuclear phylogeny of Tallowin et al. (2018) and only the sister group relationship between the *tuber-*

culatus and *novaeguineae* Melanesian species groups was strongly supported (100/1.00) in the ND2 tree and in Tallowin et al. (2018).

The nuclear tree also recovered several species as paraphyletic or polyphyletic that were recovered as monophyletic in previous, more taxonomically narrower analyses (Fig. 4): *Cyrtodactylus tripuraensis* (Agarwal et al. 2014); *C. pulchellus* (Grismer et al. 2012a, 2014a; Quah et al. 2019; Wood et al. 2020a); *C. tuberculatus* (Tallowin et al. 2018); *C. albofasciatus*, *C. deccanensis*, and *C. speciosus* (Agarwal and Karanth 2015); *C. pseudoquadri-virgatus* (Luu et al. 2017); *C. pubisulcus* (Davis et al. 2019, 2020), and *C. malayanus* (Davis et al. 2020). The non-monophyly of the latter species, however, may have to do with GenBank misidentifications and not mito-nuclear mismatch (Davis et al. 2020).

Mito-nuclear data

The topology of the mito-nuclear phylogeny is overall very similar to that of the ND2 tree and very different from that of the nuclear tree (Fig. 5). Both the mito-nuclear and ND2 phylogenies recovered the exact same monophyletic species groups (although with varying support), with only five nodes showing topological discordance and six nodes showing significant nodal support differences (Fig. 3 and 5). Overall, the mito-nuclear tree did not improve the ND2 tree by increasing nodal support of deep nodes.

Topological discordances. The ND2 phylogeny recovered *Cyrtodactylus spinosus* as the unsupported sister species to the *malayanus* group (60/0.48). In the mito-nuclear tree, *C. spinosus* was the sister species to a lineage composed of the *darmandvillei*, *marmoratus*, *lateralis*, *sworderi*, *agamensis*, *malayanus*, *philippinicus*, *condorensis*, and *irregularis* groups—with a UFB support of 100—even though nuclear data for *C. spinosus* does not exist. The *condorensis* and *irregularis* groups

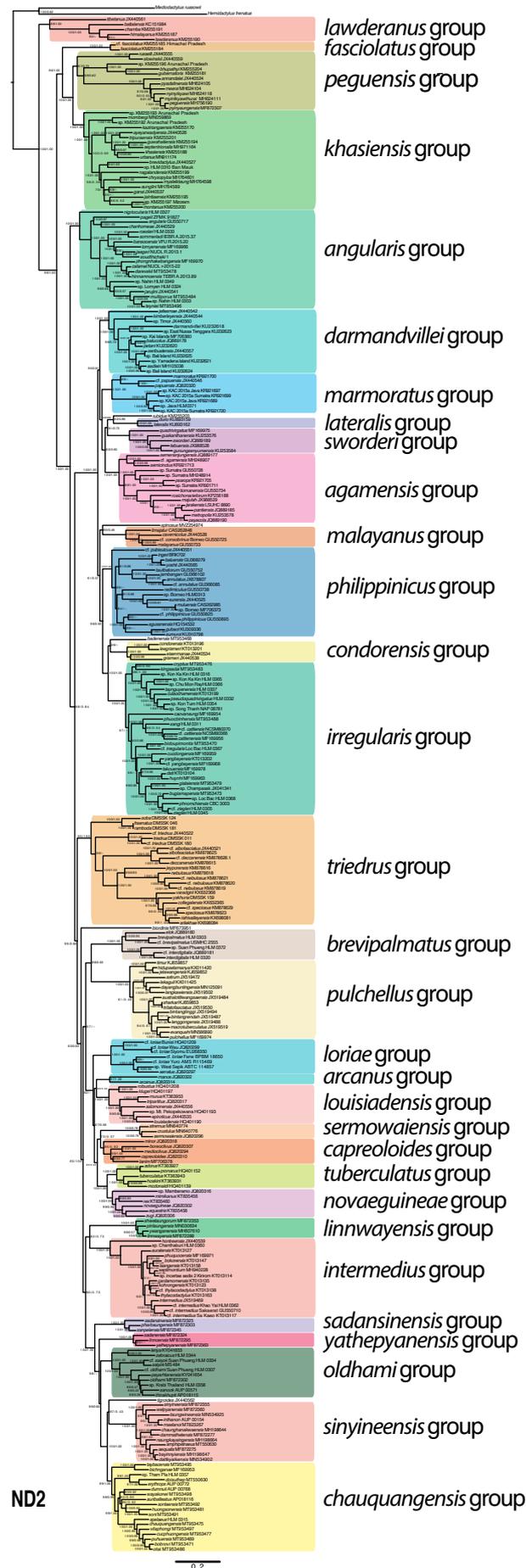


Figure 3. Majority-rule consensus trees from ML bootstrap replicates of *Cyrtodactylus*. Phylogeny based on 1469 bp of the mitochondrial gene ND2 with UFBoot and BPP support values, respectively, at the nodes.

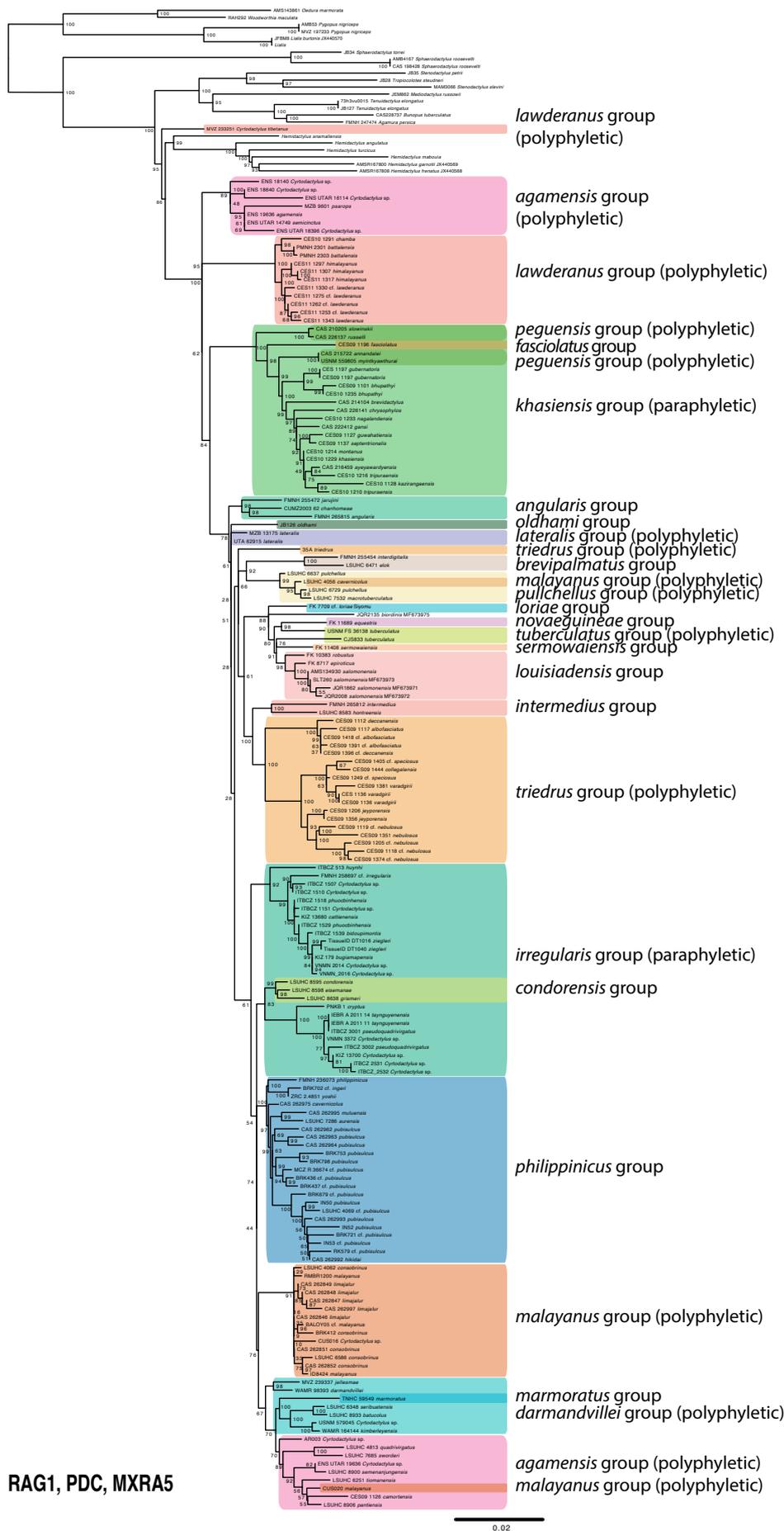


Figure 4. Majority-rule consensus trees from ML bootstrap replicates of *Cyrtodactylus*. Phylogeny based on 2284 bp of a concatenated data set from the nuclear genes RAG1, MXRA5, and PDC with UFB support values at the nodes.

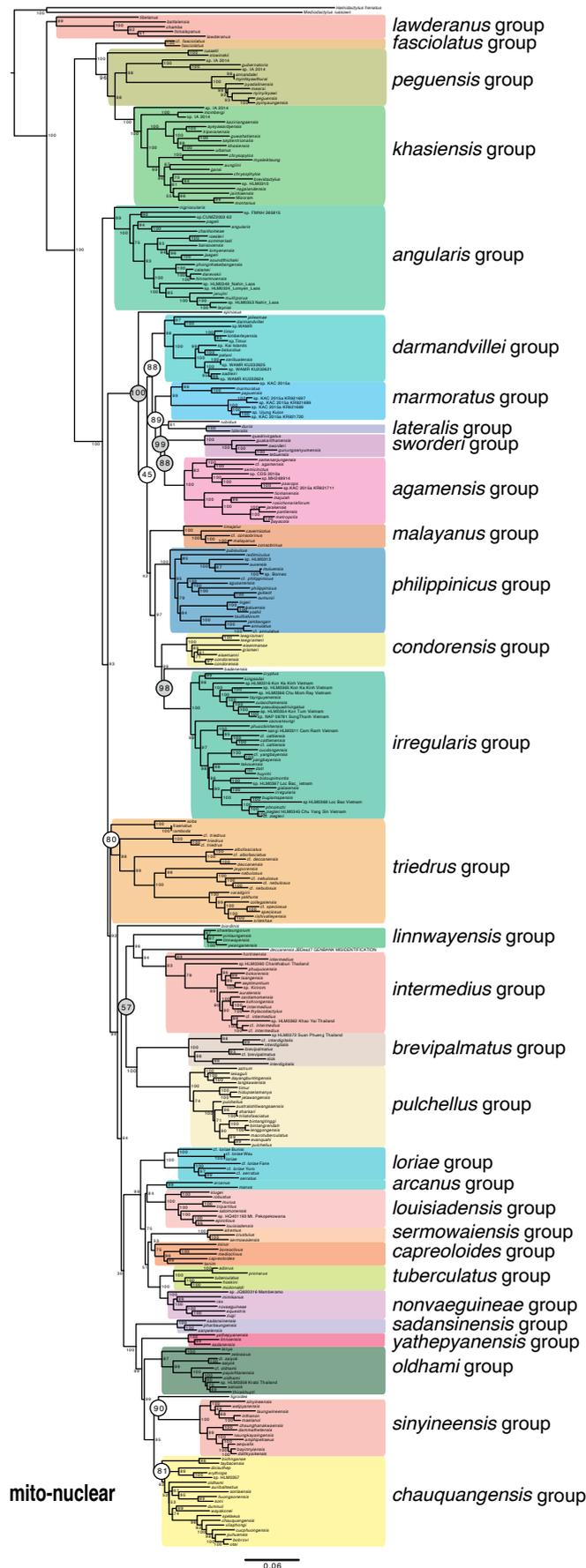


Figure 5. Majority-rule consensus trees from ML bootstrap replicates of *Cyrtodactylus*. Phylogeny based on 3752 bp of a concatenated data set from the mitochondrial gene ND2 and the nuclear genes RAG1, MXRA5, and PDC with UFB support values at the nodes. Nodes subtended with gray circles represent topological discordances with the ND2 phylogeny. Nodes subtended with white circles represent significant nodal support discordances with the ND2 phylogeny.

plus *C. badenensis* formed a strongly supported monophyletic group in both analyses. The ND2 data recovered *C. badenensis* as the strongly supported sister species to the *condorensis* group in the ML analysis (UFB 99) but as the unsupported (0.17) sister species to the *irregularis* group in the Bayesian analysis (Fig. 1S). The mito-nuclear data recovered *C. badenensis* as the strongly supported (UFB 98) sister species to the *irregularis* group, but again in the absence of nuclear data for *C. badenensis*. The *sworderi* and *lateralis* groups plus *C. rubidus* were recovered as monophyletic in the ND2 phylogeny but without support (81/0.73). In the mito-nuclear tree, however, the *sworderi* and *agamensis* groups were sister clades with better support (UFB 88) even though there are no nuclear data available for any species of the *sworderi* group. The above topological differences between the ND2 and the mito-nuclear phylogenies regarding these previous three examples, are not the result of additional nuclear data subtending and strengthening the respective nodes, but instead, result from a lack of nuclear data and a paucity of ND2 data. This leaves those lineages topologically unconstrained, allowing them to change position between the two trees when nuclear data from other species are added. If the missing nuclear data for the unconstrained species were added, they would likely change position in the tree once again.

Together, the *linnwayensis* and *intermedius* groups formed a sister clade to a lineage composed of the *sadanensis*, *yathepyanensis*, *oldhami*, *sinyleneensis*, *chauquanensis* groups plus *C. tigroides* (90/0.73) in the ND2 phylogeny. Whereas in the mito-nuclear tree, the *linnwayensis* and *intermedius* groups compose the unsupported (UFB 57) sister clade to a lineage composed of the *brevipalmatus* and *pulchellus* groups even though in the nuclear tree, the *pulchellus* group was polyphyletic with respect to the *malayanus* group, and the *condorensis* group was nested within the *irregularis* group.

Nodal support discordances. The monophyly of the *triedrus* group was strongly supported in the ND2 phylogeny (95/1.00) but was unsupported in the mito-nuclear tree (UFB 80). The *darmandvillei*, *marmoratus*, *lateralis*, *sworderi*, *agamensis*, *malayanus*, *philippinicus*, *condorensis*, *irregularis* plus *C. rubidus* clade was strongly supported (100/1.00) in the ND2 tree but unsupported (UFB 45) in the mito-nuclear tree. The *darmandvillei*, *marmoratus*, *lateralis*, *sworderi*, *agamensis* plus *C. rubidus* clade is well-supported in the ML analysis of the ND2 tree (90/0.80) but in the mito-nuclear tree, it is not well-supported (UFB 88). Similarly, the *marmoratus*, *lateralis*, *sworderi*, *agamensis* plus *C. rubidus* clade was strongly supported in the ML analysis of the ND2 tree (98/0.80) but in the mito-nuclear tree, it was not supported (UFB 89). *Cyrtodactylus tigroides* was recovered as the well-supported sister species to the *sinyleneensis* group in the mito-nuclear tree (UFB 90) but that relationship was unsupported (87/0.43) in the ND2 analysis. The *chauquanensis* group was unsupported in the mito-nuclear tree (81) but strongly supported (99/1.00) in the ND2 tree.

Species groups

The ND2 phylogeny of the 310 species used in this analysis was partitioned into 31 monophyletic species groups plus five orphaned species that could not be confidentially placed within any species group. The composition of each species group was determined by the authors most familiar with those particular suites of species and thus there is some asymmetry in the numbers of species among some groups. Additionally, the taxonomy in many of the smaller groups is more resolved than it is in some of the larger groups. As such, there is also an asymmetry in the amount of information available among groups. Consistent among all species groups however, is that each group is monophyletic and with the exception of two groups (see below), is recovered in both the ML and BEAST analyses with at least 90/0.90 nodal support. The delimitation of each group is discussed below along with any additional taxonomic, morphological, biogeographical, and ecological information deemed relevant. Species group names use the name of the earliest described species of the group.

Asian species groups

Cyrtodactylus agamensis group

The *agamaensis* group (Fig. 6) is composed of at least 10 nominal, generally allopatric species (Figs 3, 7) formerly known in part as the ‘swamp clade’ (Grismer et al. 2012b:fig. 4). Species in this group are distributed across the Thai-Malay Peninsula south of the Isthmus of Kra to Sumatra, and the Riau Archipelago of Indonesia (Grismer and Davis 2018:fig. 5). Phylogenetic relationships in the group support multiple historical interchanges of lineages between the Thai-Malay Peninsula and Sumatra, as well as adjacent island chains (Grismer and Davis 2018; O’Connell et al. 2019). The group has four potentially undescribed putative species from Sumatra—cf. *agamensis* MH248907, sp. Sumatra GU550728, sp. Sumatra MH248914, and sp. Sumatra KR921711—that are currently being examined in an integrative taxonomic framework. Ongoing molecular analyses will likely reveal additional species belonging to this group (O’Connell et al. in prep.).

Another species, *Cyrtodactylus camortensis* from the central islands of Camorta, Katchall, and Nancowry in the Nicobar Archipelago, may belong to this group. Samples were absent from the ND2 phylogeny but it is deeply nested within this group in the nuclear phylogeny (Fig. 4). However, the *agamensis* group in the nuclear phylogeny is paraphyletic so additional ND2 data are necessary to confirm its species group placement. Prior to its revision by Chandramouli (2020), this specimen was recognized as *C. adleri* in Agarwal et al. (2014).

Cyrtodactylus angularis group

Until recently, the *angularis* group (Fig. 8) contained only one species *C. angularis* (Smith 1921). It now en-

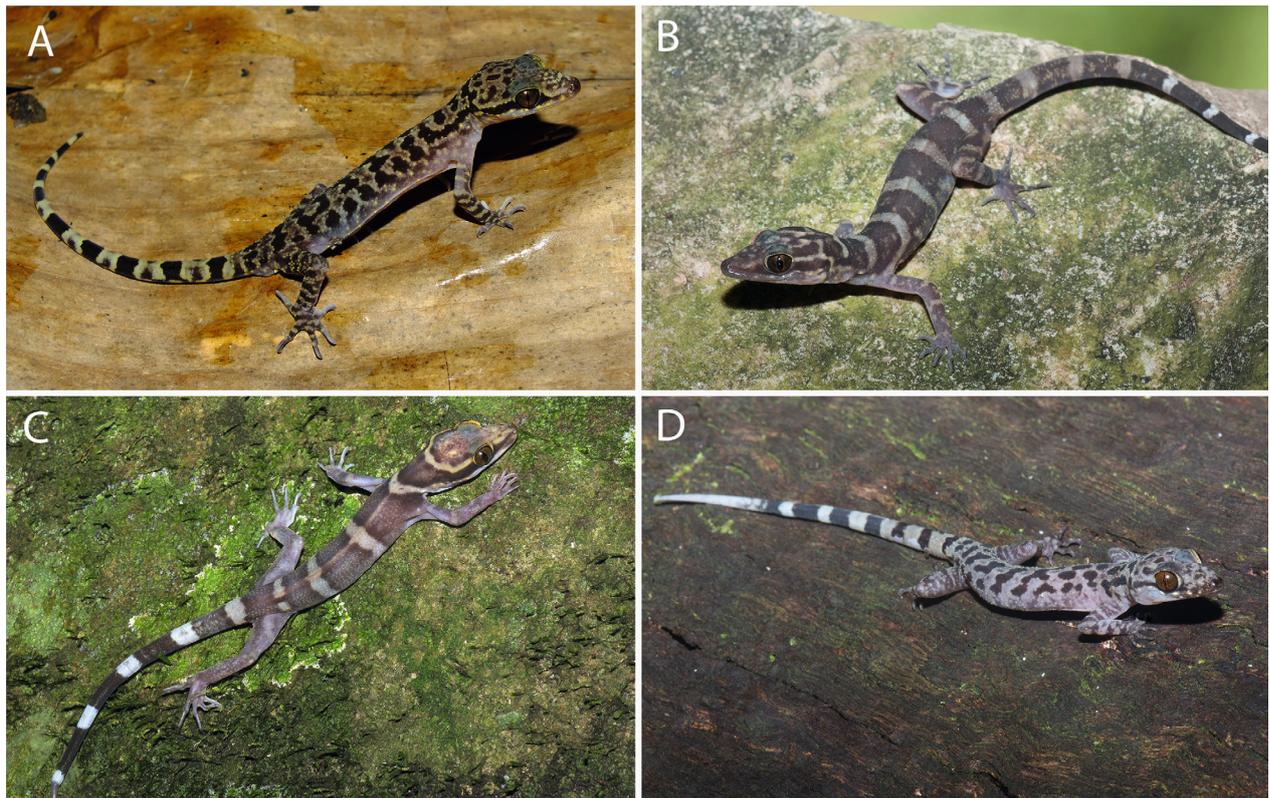


Figure 6. Examples of the *Cyrtodactylus agamensis* group. A. *C. psarops* from Sumatra, Indonesia. Photo by Eric N. Smith. B. *C. metropolis* from Selangor state, Peninsular Malaysia. Photo by L. Lee Grismer. C. *C. tiomanensis* from Tioman Island, Pahang State, Peninsular Malaysia. Photo by L. Lee Grismer. D. *C. rosichonarieforum* from Natuna Besar Island, Indonesia. Photo by L. Lee Grismer.

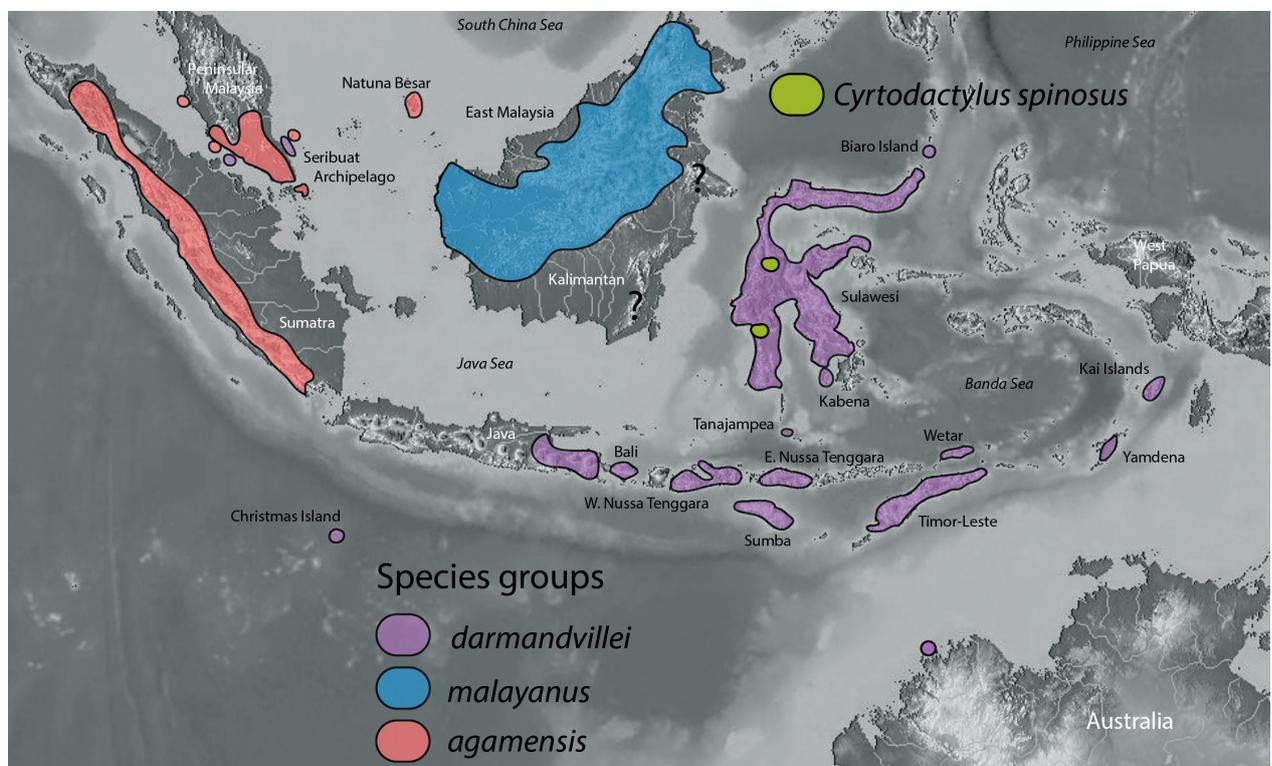


Figure 7. Distribution of the *darmandvillei*, *malayanus*, and *agamensis* species groups of *Cyrtodactylus* as delimited here.

compasses a large radiation (Fig. 3) of mostly allopatric (Fig. 9), karst-adapted species from central Vietnam, central and northern Laos, eastern and central Thailand, and

possibly southernmost China (Nazarov et al. 2014, 2018; Luu et al. 2014, 2016; Sithivong et al. 2019:figs. 6, 7). All bear a characteristic banding pattern of well-defined



Figure 8. Examples of the *Cyrtodactylus angularis* group. A. *C. sommerladi* from Khammouan Province, Laos. Photo by Vinh Quang Luu. B. *C. nigriocularis* from Tay Ninh Province, Vietnam. Photo by Nikolay A. Poyarkov. C. *C. soudthichaki* from Khammouan Province, Laos. Photo by Vinh Quang Luu. D. *C. phongnhakebangensis* (juvenile) from Quang Binh Province, Vietnam. Photo by Thomas Ziegler.

hour glass-shaped dorsal bands. The only exception is *C. nigriocularis*, which occurs much farther south in Ba Den Mountain in Tay Ninh Province, southern Vietnam, and inhabits granite boulder caves (Fig. 8B). The *angularis* group includes at least 21 nominal species, of which 17 are analyzed herein along with three other potentially new species (Fig. 3). Over 80% of the group's diversity was described within the last 15 years. In previous studies, this species group was referred to as the *C. phongnhakebangensis* group (as defined by Luu et al. 2016; see also Nazarov et al. 2018). Species not included in this analysis—*C. khammouanensis* (Nazarov et al. 2014), *C. muangfuangensis* (Sitthivong et al. 2019), *C. rufford* (Luu et al. 2016), and *C. thathomensis* (Nazarov et al. 2018) were demonstrated to belong to the *C. angularis* group in earlier integrative analyses using morphology and the mitochondrial gene CO1. The recently reported “*C. zhaoi*” from Yunnan Province of China (Zhu and Rao 2020) cannot be confidently assigned to any species group, but from the overall external morphology it resembles the species of the *angularis* group. However, it does not meet the ICZN requirements (Article 16.4.1; ICZN 2000) for being a validly described species in that there is no information on name-bearing type material given in the original publication.

Phylogenetic relationships at the deep nodes within this group were well-resolved with the ND2 data unlike those recovered by CO1 (e.g., Sitthivong et al. 2019) and

suggest *C. nigriocularis* is the sister species to all other members of this group (Fig. 3). The remaining *angularis* group species are clustered in three major subclades, one of which joins three species from eastern Thailand and northern Laos (*C. angularis*, *C. chanhomeae*, and *C. pageli*), the second joins species from the central Annamite karst area of eastern Laos and central Vietnam (*C. roesleri*, *C. sommerladi*, *C. bansocensis*, *C. lomyenensis*, *C. jaegeri* and *C. soudthichaki*), and the third consists of a widespread radiation of karst-adapted species from eastern Thailand (*C. jarujini*), Laos (*C. multiporus*, *C. teyniei*, *C. hinnamnoensis*, *C. darevskii*, and *C. calamei*), and Vietnam (*C. phongnhakebangensis*). Our analysis additionally revealed three potentially undescribed species from the latter clade (HLM 0349, HLM 0324, and HLM 0353); all from Khammouan Province, Laos. Their taxonomic assessments are currently being assessed (Poyarkov et al. in prep). Given that the karstic habitats of Laos and central Vietnam belong to one of the world's largest limestone areas—many parts of which still remain unexplored—additional field surveys coupled with integrative taxonomic studies will likely reveal new species of narrow-range endemics belonging to this group in need of protection.

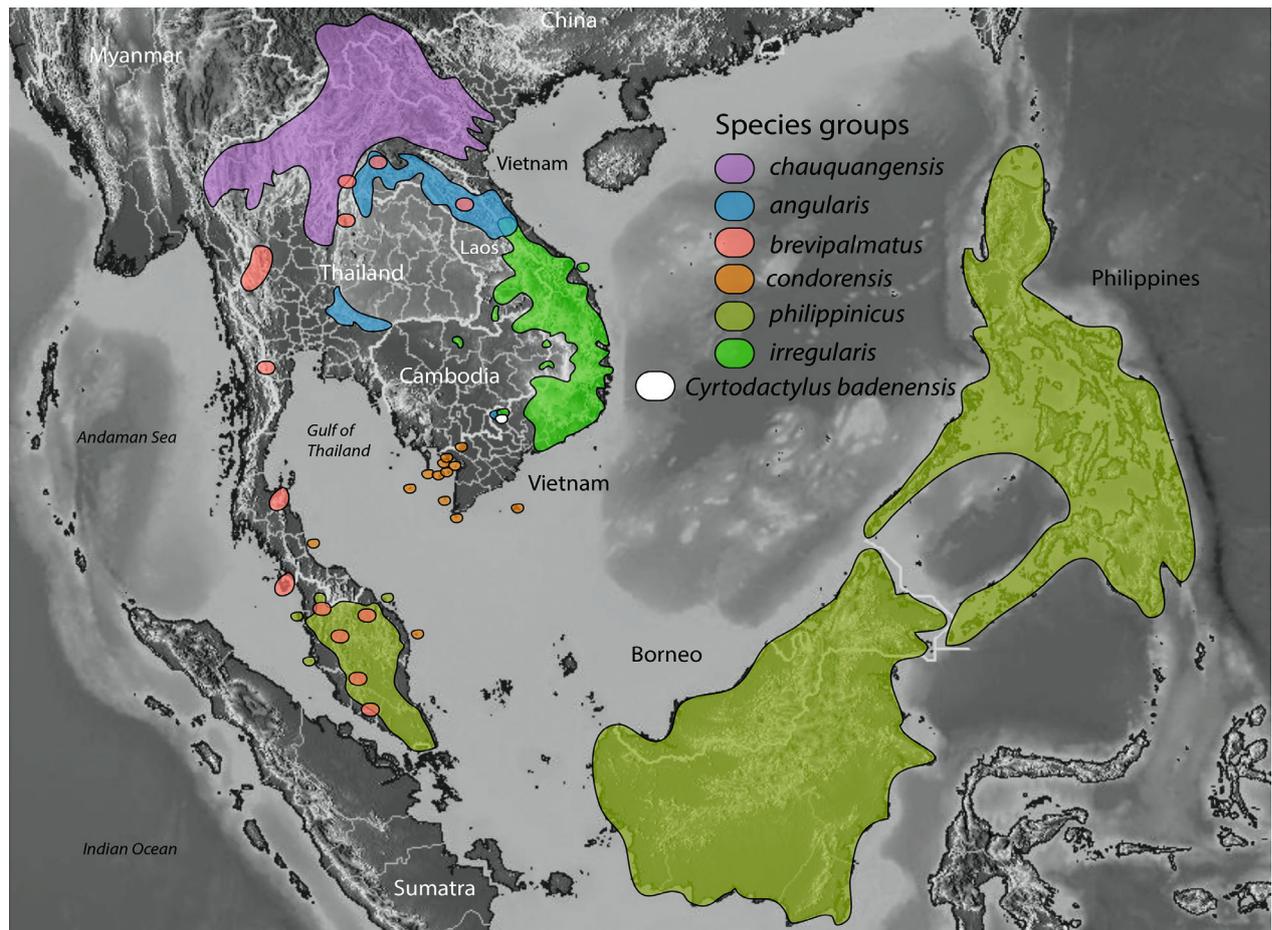


Figure 9. Distribution of the *angularis*, *brevipalmatus*, *chauquangensis*, *condorensis*, *irregularis*, and *philippinus* species groups of *Cyrtodactylus* as delimited here and *C. badenensis*.

***Cyrtodactylus brevipalmatus* group**

The *brevipalmatus* group is composed of three nominal arboreal species (Figs 3, 10) that range from central Laos through Thailand to southern Peninsular Malaysia (Smith 1930; Ulber 1993; Grismer 2008; Nazarov et al. 2018:fig. 7) (Fig. 9). Potentially new species (Fig. 3) have been reported from Langkawi Island (*C. cf. brevipalmatus* USM-HC 2555) in northern Peninsular Malaysia (Grismer et al. 2015) and central Laos (*C. cf. interdigitalis* JQ889181). A new species from southwestern Thailand (sp. Suan Phueng HLM 0372) that is sister to *C. interdigitalis* is currently being described (Grismer et al. in prep).

***Cyrtodactylus chauquangensis* group**

The *chauquangensis* group is composed of species endemic to limestone massifs in northern Indochina, ranging from northern Thailand and Laos, to northeastern Vietnam, and to Yunnan Province in southern China (Fig. 9). This group was previously referred to as the *C. wayakonei* species group (Nguyen et al. 2015b; Luu et al. 2016; Brennan et al. 2017; Pham et al. 2019; Schneider et al. 2020), and composed of generally karst-adapted species with characteristic yellowish spots and reticulations on dorsal surface of the head and body (Fig. 11). Until recently, no *Cyrtodactylus* species were known from the

highland areas of the northwestern Vietnam and northern Laos (Ngo and Chan 2011) and the first species of this group, *C. chauquangensis*, was discovered only 13 years ago (Quang et al. 2007). In the phylogeny (Fig. 3), the group is composed of 17 nominal species, plus a putative new species (HLM 0357) from northern Thailand, the description of which is in progress (Grismer et al. in prep).

Phylogenetic relationships within the *chauquangensis* group have remained stable in many analyses, but the topology recovered by this study differs from those reported by Brennan et al. (2017), Pham et al. (2019), and Schneider et al. (2020). The previous studies, based solely on CO1 and limited species coverage (Pham et al. 2019 and Schneider et al. 2020), recovered unresolved relationships at the deep nodes. In this study, the two species from northwestern Vietnam *C. bichnganae* and *C. taybacensis* form a clade that composes the sister lineage to the remainder of the group (Fig. 3). The remaining species are clustered in several clades, with the clade joining the species from northwestern Thailand (*C. erythropros*, *C. doisuthep*, and *Cyrtodactylus* sp. HLM 0357) forming a sister lineage to clades joining species from northern Thailand (*C. auribalteatus*, *C. dumnuui*), northern Laos (*C. spelaeus*, *C. vilaphongi*, *C. wayakonei*) and northwestern Vietnam (*C. sonlaensis*, *C. huongsonensis*, *C. soni*, *C. chauquangensis*, *C. cucphuongensis*, *C. puhuensis*, *C. bobrovi*, and *C. otai*). At least four species,

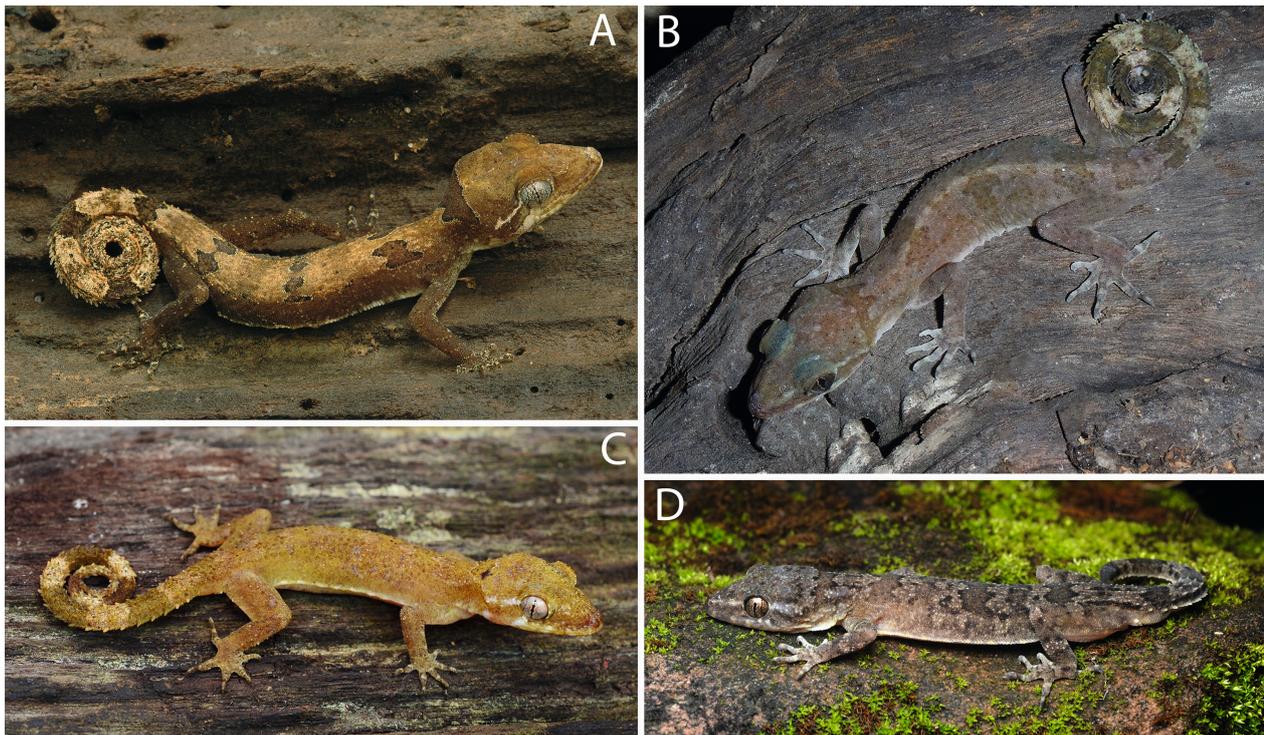


Figure 10. Examples of the *Cyrtodactylus brevipalmatus* group. A. *C. elok* from Negeri Sembilan State, Peninsular Malaysia. Photo by L. Lee Grismer. B. *C. interdigitalis* from Petchabun Province, Thailand. Photo by Montri Sumonta. C. *C. cf. brevipalmatus* from Langkawi Island, Kedah State, Peninsular Malaysia. Photo by Evan S. H. Quah. D. *C. interdigitalis* from Petchabun Province, Thailand. Photo by Nikolay A. Poyarkov.

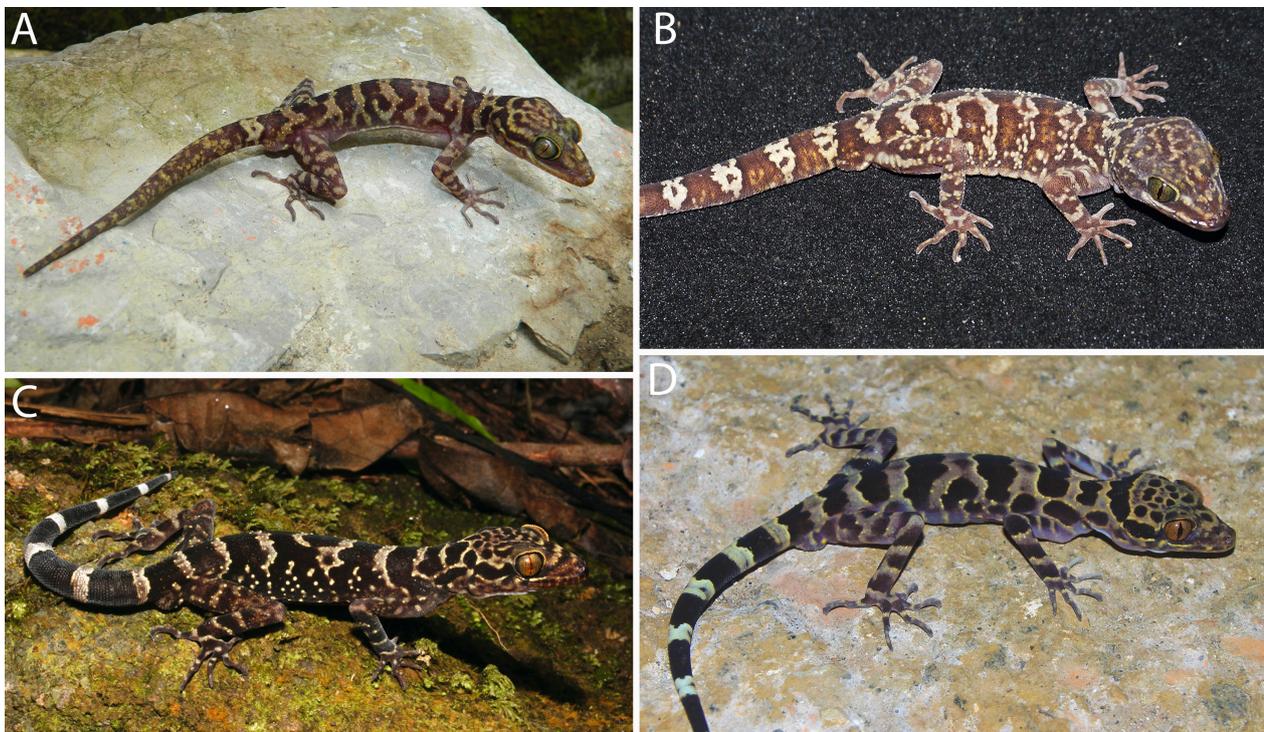


Figure 11. Examples of the *Cyrtodactylus chauquangensis* group. A. *C. soni* from Ninh Binh Province, Vietnam. Photo by Minh Duc Le. B. *C. dumnuui* from Chiang Mai Province, Thailand. Photo by Montri Sumontha. C. *C. puhuensis* from Thanh Hoa Province, Vietnam. Photo by Sang Ngoc Nguyen. D. *C. cucphuongsensis* from Ninh Binh Province, Vietnam. Photo by Vinh Quang Luu.

C. auribalteatus, *C. doisuthep*, *C. dumnuui*, and *C. erythroptus* are placed in the phylogeny here for the first time. Even though not included in our analyses, *C. martini*

from southeastern Yunnan and *C. houaphanensis* and *C. ngoiensis* from northeastern Laos, also belong to the *chauquangensis* group based on their phylogenetic rela-

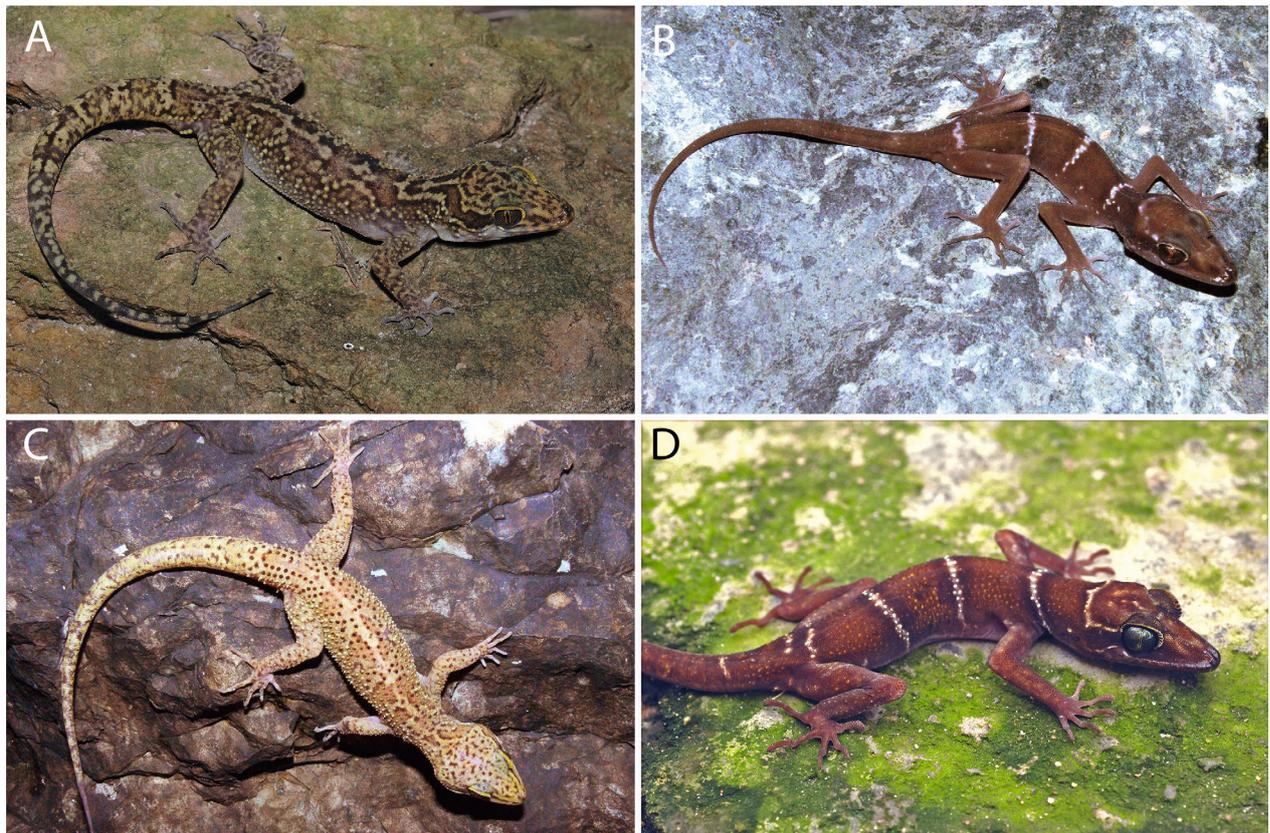


Figure 12. Examples of the *Cyrtodactylus condorensis* group. A. *C. condorensis* from Hong Chong Island, Kien Giang Province, Vietnam. Photo by L. Lee Grismer. B. *C. eisenmanae* from Hon Son Island, Kien Giang Province, Vietnam. Photo by Ngo Van Tri. C. *C. leegrimeri* from Hon Chuoi Island, Ca Mau Province, Vietnam. Photo by L. Lee Grismer. D. *C. grimeri* from An Giang Province, Vietnam. Photo by L. Lee Grismer.

tionships and morphological similarity to *C. wayakonei* from northern Laos (Nazarov et al. 2014; Pham et al. 2019; Schneider et al. 2020). Two formally undescribed *Cyrtodactylus* species were recently reported from other parts of Yunnan Province, “*C. caii*” and “*C. xiaoheijiangensis*” (Zhu and Rao 2020). However, their descriptions not meet the ICZN requirements (Article 16.4.1; ICZN 2000) for being a validly described species in that there is no information on name-bearing type material given in the original publication. Further herpetological surveys in karstic areas of southern China and northern Indochina will likely result in discovery of numerous new populations of narrow-range endemics of the *C. chauquangensis* species group in need of protection.

***Cyrtodactylus condorensis* group**

The *condorensis* group (Fig. 12) is composed of four nominal species (Fig. 3) that range from the Mekong Delta of Vietnam eastward to the Con Dao Islands and southward across several islands in the Gulf of Thailand to Tenggol and Kra islands of Peninsular Malaysia and Thailand, respectively (Chan and Norhayati 2010; Grismer and Grismer 2017; Nurngsomsri et al. 2019:fig. 7) (Fig. 9). Grismer and Grismer (2017) demonstrated this group is composed of two ecomorphologically specialized granite cave dwellers (*C. eisenmanae*, and *C. grimeri*) and two general scansorial granite forest species

(*C. condorensis* and *C. leegrimeri*). The monophyly of the group is strongly supported (100/1.00) with the exclusion of its putative sister species *C. badensis* (Fig. 3).

***Cyrtodactylus darmandvillei* group**

The *darmandvillei* group is composed of seven nominal species and at least six potentially new species (Fig. 3). Species in this group vary greatly in size (45–85mm SVL) and ecology (terrestrial to arboreal), but tend to have quite prominent and densely arranged enlarged tubercles across the body (Fig. 13) in addition to usually having contiguous femoral and precloacal pores. Based on distribution and morphology, it is likely that at least four additional species for which sequence data are unavailable also belong to this group: *C. celatus*, *C. tabora*, *C. tanahjampea*, and *C. wetarensis*. This group has one of the widest geographic distributions of any of the other species groups (Fig. 7). Its diversity is centered in Wallacea (Bali in the west, Sulawesi to the north, and the Kai Islands to the east), but geographically outlying species occur on islands off the east and west coasts of Peninsular Malaysia (*C. seribuatensis* and *C. batucolus*, respectively), Java (*C. petani*), Christmas Island (*C. sadleiri*), and Western Australia (*C. kimberleyensis*). This strikingly insular distribution indicates multiple overwater dispersals onto small islands, even though the lineage is conspicuously absent or unrecorded from

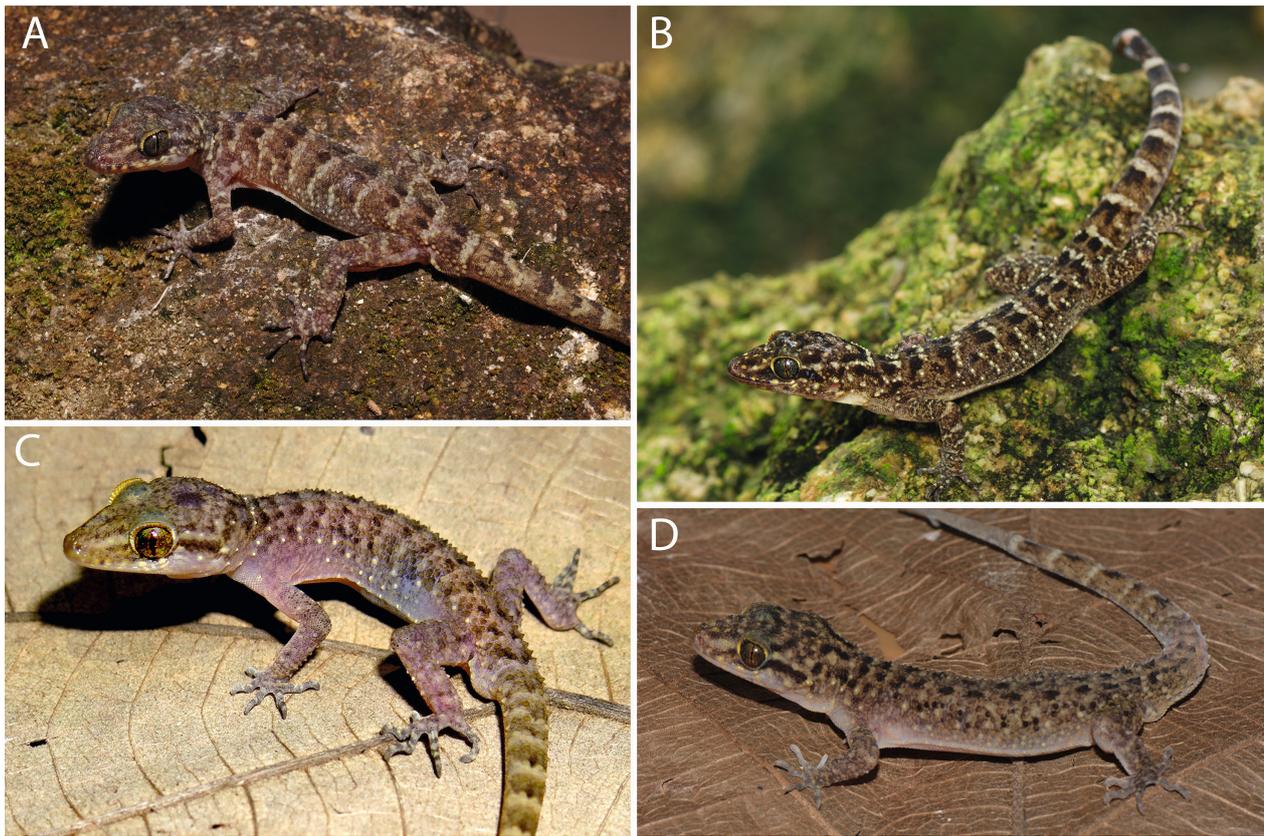


Figure 13. Examples of the *Cyrtodactylus darmandvillei* group. A. *C. seribuatensis* from Seribuat Island, Johor State, Peninsular Malaysia. Photo by L. Lee Grismer. B. *C. batuolus* from Besar Island, Johor State, Peninsular Malaysia. Photo by L. Lee Grismer. C. *C. darmandvillei* from Nusa Penida Island, Indonesia. Photo by Ruchira Somaweera. D. *C. petani* from Java, Indonesia. Photo by Awal Riyanto.

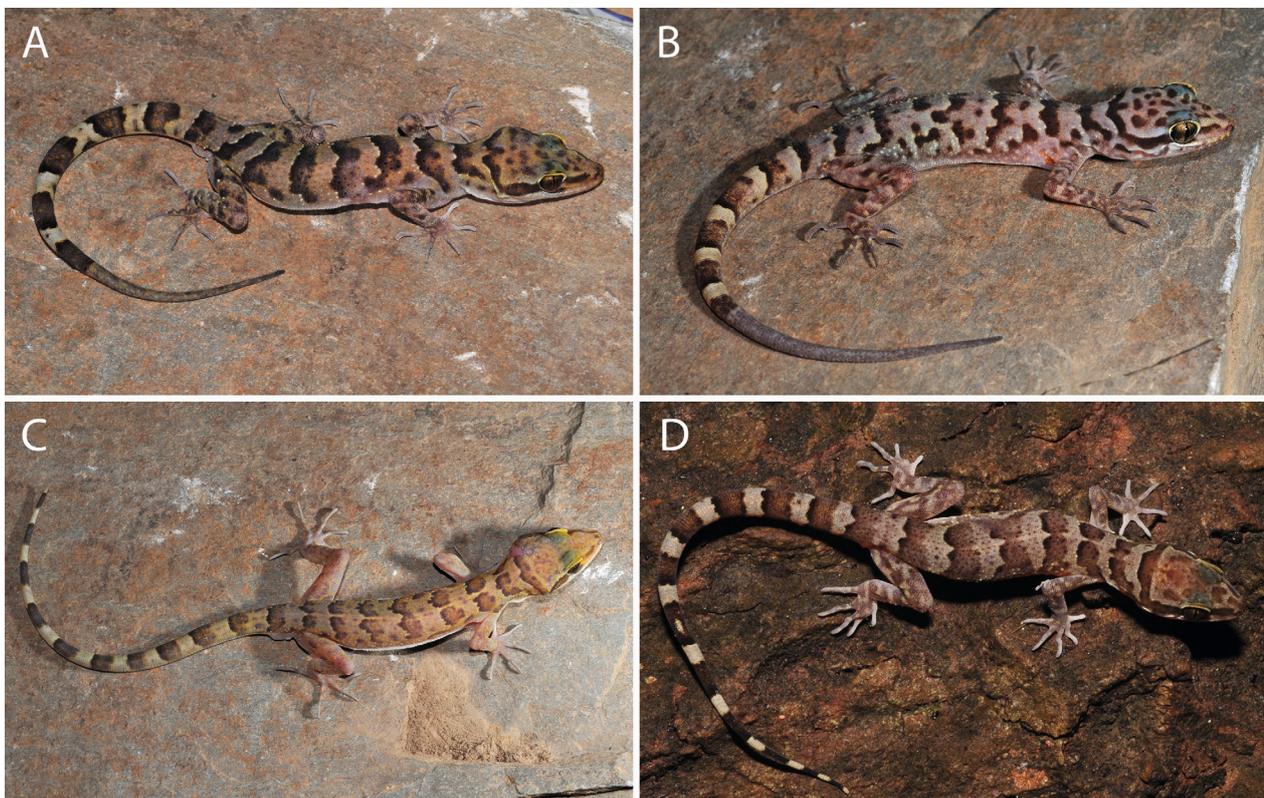


Figure 14. Examples of the *Cyrtodactylus fasciolatus* group. A. *C. fasciolatus* from Himachal Pradesh state, India. B. *C. fasciolatus* from Himachal Pradesh state, India. C. *C. fasciolatus* from Himachal Pradesh state, India. D. *C. cf. fasciolatus* from Uttarakhand state, India. Photos by Ishan Agarwal.

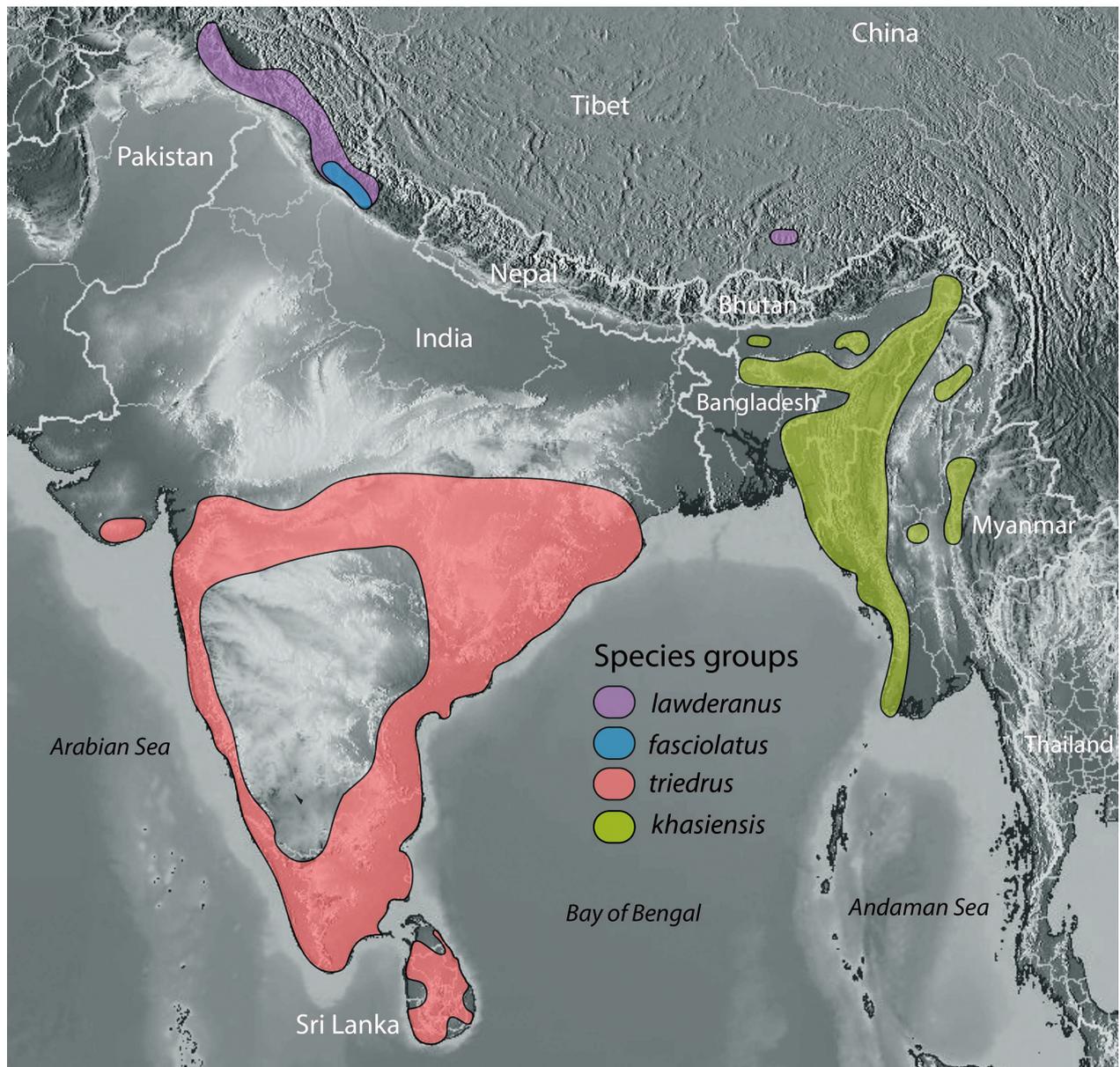


Figure 15. Distribution of the *fasciolatus*, *khasiensis*, *lawderanus*, and *triedrus* species groups of *Cyrtodactylus* as delimited here.

some of the nearby mainland areas (especially Peninsular Malaysia and New Guinea). Based on this observation, it has been hypothesized that this is an insular/disturbance specialist lineage that is good at dispersing, but struggles to persist in ‘mainland’ tropical rainforest environments (Oliver et al. 2018).

***Cyrtodactylus fasciolatus* group**

The *fasciolatus* group is composed of a single nominal species and at least one undescribed species (Figs 3, 14). This group is restricted to the Western Himalayas in India, bordering Nepal to the east (Fig. 15). It is possible this clade extends farther east into Nepal, though all sampled *Cyrtodactylus* to the west of the range of the *fasciolatus* group are members of the *lawderanus* group. Wood et al. (2012) and Agarwal et al. (2014) recovered the *fasciolatus* group as nested within a *peguensis* + *khasiensis* clade.

***Cyrtodactylus intermedius* group**

The *intermedius* group is composed of at least 10 generally allopatric and ecologically diverse nominal species (Fig. 3) that range across hilly terrain from eastern Thailand to southeastern Vietnam, including Koh Rong Island of Cambodia and Phu Quoc and Hon Tre islands of Vietnam (Murdoch et al. 2019; Grismer et al. 2020b; Fig. 16). The group’s taxonomic and ecological diversity is centered in the Cardamom Mountains of southern Cambodia and is represented by terrestrial species (*C. thylacodactylus*), granite cave species (*C. hontreensis*), karst-adapted species (*C. laangensis*), and habitat generalists (e.g. *C. kohrongensis*) (Fig. 17). The group was previously considered a single species, *C. intermedius*, until integrative taxonomic analyses demonstrated it is composed of at least 10 species (Murdoch et al. 2019; Grismer et al. 2020b). There are potentially six undescribed species—sp. HLM 0360 from Chanthaburi, Thailand, cf. *thylaco-*

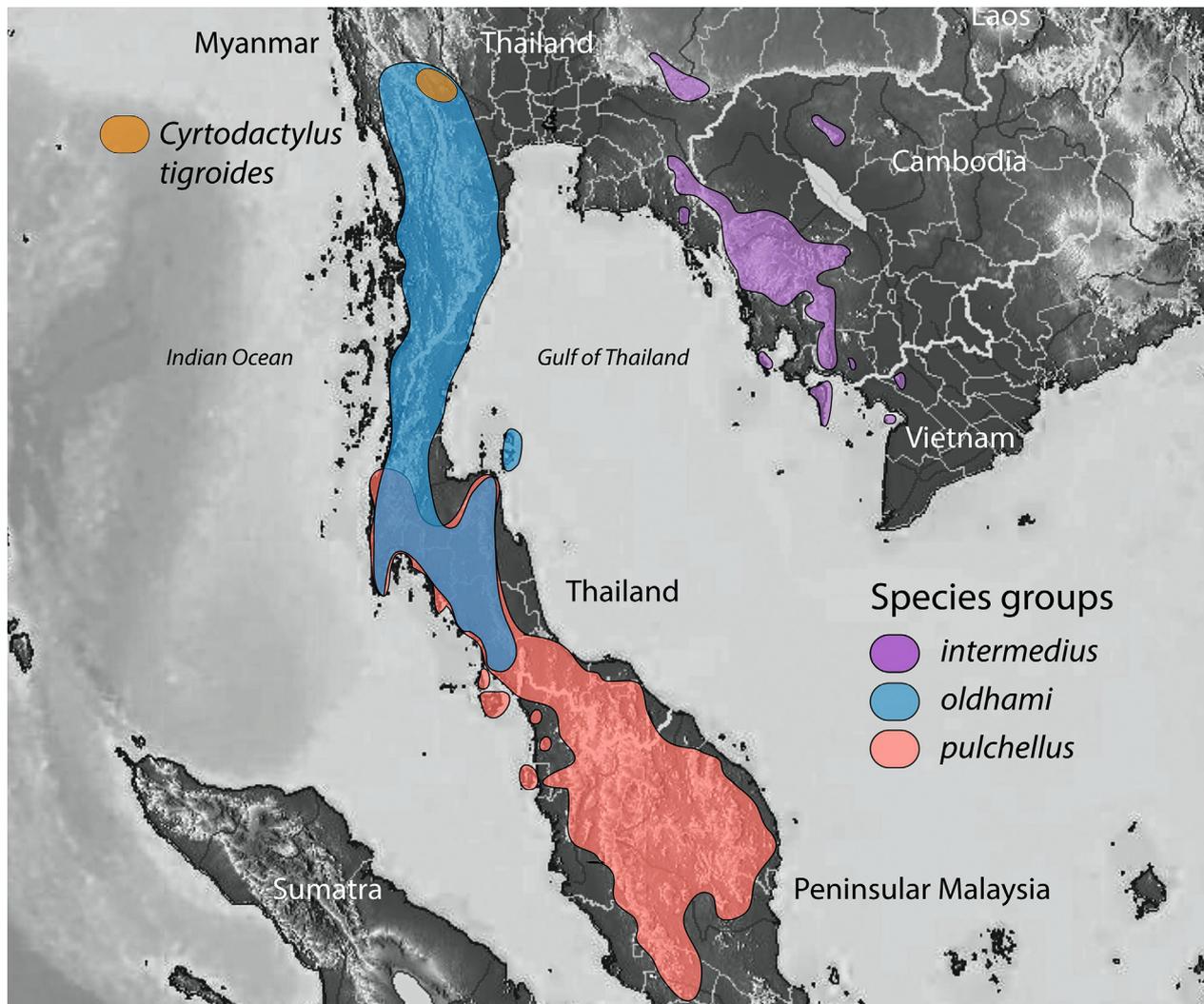


Figure 16. Distribution of the *intermedius*, *oldhami*, and *pulchellus* species groups of *Cyrtodactylus* as delimited here and *C. tigroides*.

dactylus KT013138 from O'Lakemas, Cambodia, cf. *intermedius* HLM 0362 from Khao Yai, Thailand, cf. *intermedius* GU550710 from Sakaerat, Thailand, cf. *intermedius* KT013117 from Sa Kaeo, Thailand, and sp. *incertae sedis* 2 KT013114 from Kirirom, Cambodia (Fig. 3). An additional population from the isolated mountainous region of Phnom Kulen National Park, Cambodia reported as *C. intermedius* (Geissler et al. 2019) is also a candidate for being a new species. All of these populations are currently being examined by various combinations of authors. Murdoch et al. (2019) and Grismer et al. (2020b) did not consider *C. hontreensis* from Hon Tre Island, Vietnam as part of the *intermedius* group but only as a distantly related and strongly supported sister species. It is included as part of the *intermedius* group here.

***Cyrtodactylus irregularis* group**

The *irregularis* group (Fig. 18) is the largest species group that includes at least 22 nominal, generally allopatric species, of which 20 are included in the present study, along with 11 unnamed lineages (Fig. 3). The group's distribution is centered in central and southern

Vietnam and extends to adjacent regions in easternmost Cambodia and southeast Laos (Nazarov et al. 2012; Nguyen et al. 2013; Neang et al. 2020; Ostrowski et al. 2020; Fig. 9). The group was previously considered to be a single species, *C. irregularis* (Smith 1921), until a number of studies demonstrated its unprecedented diversity with 20 new species described within the last 14 years (Nguyen et al. 2013; Neang et al. 2020; Ostrowski et al. 2020). This analysis reveals at least 11 more lineages corresponding to potentially undescribed species and taxonomic investigations on these lineages are currently underway by various authors. *Cyrtodactylus irregularis* was described by Smith (1921) from Cam Ly River's valley near Da Lat (Lam Dong Province, Vietnam). After its description, the name of *C. irregularis* was applied to all populations of *Cyrtodactylus* from the Annamites for nearly a century. There is still some uncertainty as to which lineage among the recently reported populations of the *C. irregularis* group in the Langbian Plateau corresponds to true *C. irregularis*. Nazarov et al. (2012) argued that specimens of *Cyrtodactylus* from Rung Tong Da Lat (Lac Xuan Commune) and Nui Chua Mount (environs of Da Lat) are morphologically most similar to



Figure 17. Examples of the *Cyrtodactylus intermedius* group. A. *C. auralensis* from Kampong Speu Province, Cambodia. Photo by L. Lee Grismer. B. *C. laangensis* from Kampot Province, Cambodia. Photo by Jeremy Holden. C. *C. kohrongensis* from Koh Rong Island, Koh Kong Province, Cambodia. Photo by L. Lee Grismer. D. *C. hontreensis* from Hon Tre Island, Kien Giang Province, Vietnam. Photo by L. Lee Grismer.

and located in the vicinity of the true *C. irregularis* s. str. based on Smith (1921)—an issue which is still being investigated. Thus, the use of *C. cf. irregularis* is applied here. This species is strongly supported (100/1.00) as the sister species of *C. bidoupimontis* in Nazarov et al. (2012) and here.

The absence of the enlarged subcaudals is considered to be characteristic for all *irregularis* group members except *C. caovansungi*, *C. kingsadai*, and *C. takouensis* (Orlov et al. 2007, Ngo and Bauer 2008, Ziegler et al. 2013). This diverse group occupies a wide range of habitats. Some are forest-dwelling habitat generalists typically found on the trunks of large trees, branches, tree logs, while others occur on granite boulders (*C. culaochamensis*, *C. cucdongensis*, *C. kingsadai*, *C. phuocbinhensis*, *C. takouensis*, and *C. yangbayensis*). Most *irregularis* group members inhabit montane forests of the Kon Tum–Gia Lai and Langbian Plateaus in the central and southern portions of the Annamites, also known as the Truong Son Range. A few species are distributed in lowland dipterocarp forests (e.g., *C. cattienensis*, *C. dati*, *C. huynhi*, and *C. phnomchiensis*). *Cyrtodactylus cryptus* inhabits limestone evergreen forests in Quang Binh Province in central Vietnam and Khammouane Province in central Laos and *C. culaochamensis* occurs on a small offshore island in central Vietnam (Ngo et al. 2020). However, *C. gialaiensis* occurs in the highly modified landscape of a coffee plantation in the Central Highlands of Vietnam (Luu et al. 2017), illustrating the broad range of habitats utilized by members of this group.

The monophyly of the *irregularis* group has been corroborated in previous phylogenetic analyses, although nodal support values based on CO1 are generally low (Nguyen et al. 2013; Luu et al. 2016; Ostrowski et al. 2020). A previous study using a combination of CO1 and ND2 did not provide strong nodal support for its monophyly (Brennan et al. 2017), while analyses based on ND2 alone gave mixed signals (Brennan et al. 2017; Ngo et al. 2020). In this study, the monophyly of the species group is strongly supported in both analyses (1.00/100) likely due to increased species sampling. In addition, phylogenetic relationships within the group based on CO1 were largely unresolved (Nguyen et al. 2017a; Ostrowski et al. 2020), likely due to the limited read length of this barcoding gene. In contrast, the phylogeny here based on the longer reads of ND2, is well-resolved with nearly all nodes being strongly supported by both analyses (Fig. 3).

The *irregularis* group is composed of two reciprocally monophyletic subgroups (Fig. 3) corresponding to two main centers of the group's diversity. Only the northern subgroup, however, is strongly supported in both analyses. The southern subgroup is supported only in the ML analysis (97) and encompasses species occurring on the Langbian Plateau, its foothills, and surrounding lowland dipterocarp forests in southern Vietnam and eastern Cambodia. Only two species of this subgroup (*C. gialaiensis* and *cf. irregularis*) are found in the highlands of Gia Lai Province in central Vietnam and Champasak, Laos, respectively. The northern subgroup is strongly supported

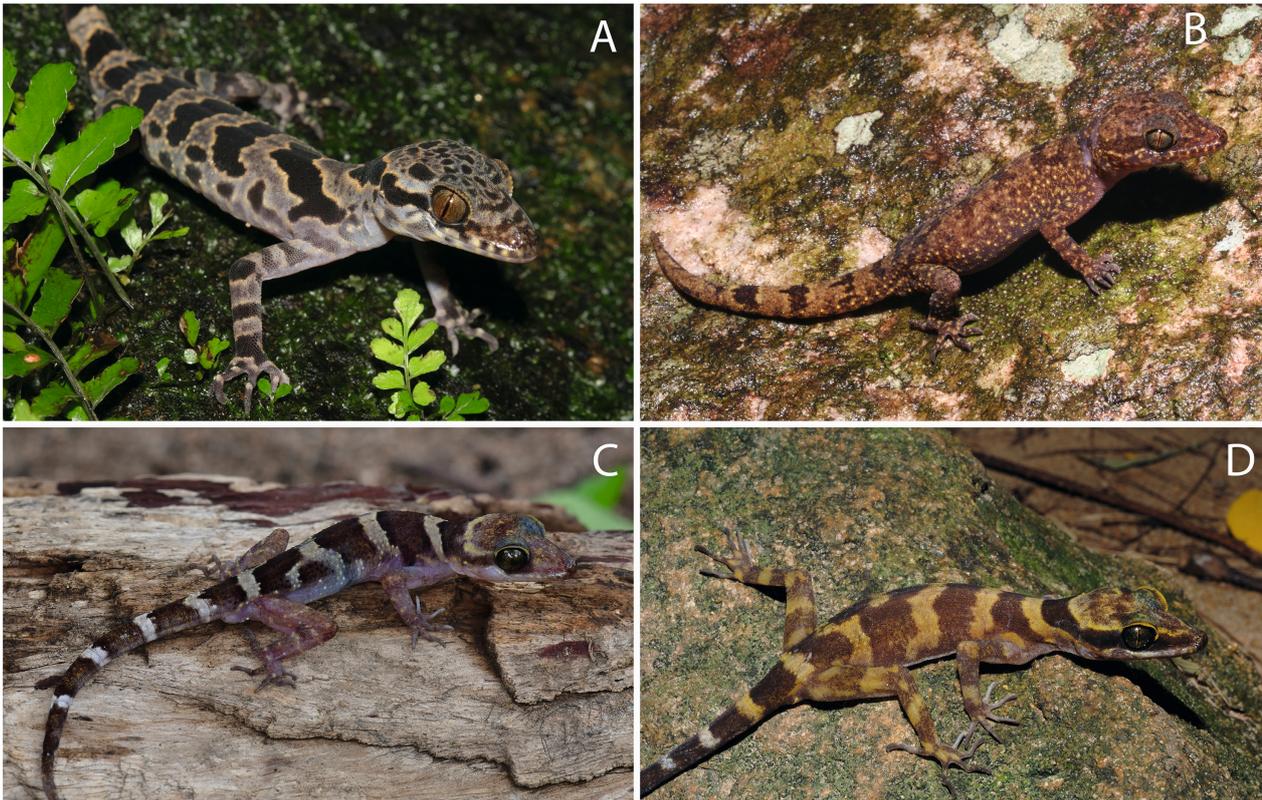


Figure 18. Examples of the *Cyrtodactylus irregularis* group. A. *C. cryptus* from Quang Binh Province, Vietnam. Photo by Thomas Ziegler. B. *C. sangi* from Ninh Thuan Province, Vietnam. Photo by Sang Ngoc Nguyen. C. *C. phnomchiensis* from Kampong Thong, Cambodia. Photo by Thy Neang. D. *C. takouensis* from Binh Thuan Province, Vietnam. Photo by L. Lee Grismer.

in both analyses (98/1.00) and primarily composed of species inhabiting Kon Tum–Gia Lai Plateau of the central Annamites, with the exception of *C. kingsadai* from Phu Yen Province of southern Vietnam, which together with *C. cryptus*, forms a lineage sister to all other members of the subgroup. Though the recently described *C. phumyensis* was not included in our analysis, it can be confidently assigned to the *irregularis* group as it was supported as a sister taxon of *C. cucdongensis* in Ostrowski et al. (2020). The phylogenetic placement of *C. buchardi* (David et al. 2004) from southern Laos has not been determined, but based on the absence of enlarged subcaudal scales and its color pattern, it has been hypothesized to belong in the *irregularis* group (Nazarov et al. 2018). This hypothesis is strengthened by the finding that the *irregularis* group is the only species group in proximity to the range of *C. buchardi* in southern Laos (Fig. 9).

According to these data, species diversity within the *irregularis* group remains underestimated. Most species are narrow-range endemics and a number of cryptic lineages have been revealed within the wide-ranging species such as *C. cattienensis* (Geissler et al. 2009; Pauwels et al. 2018), the *C. ziegleri* – *C. bugiamapensis* complex (Nazarov et al. 2008, 2012; Neang et al. 2020), and *C. pseudoquadrivirgatus* (Nguyen et al. 2017a) that require further integrative taxonomic assessment. Five unnamed populations representing putative new species are reported here from the highlands of central Vietnam in Gia Lai (HLM 0316, HLM 0365, and HLM 0366), Kon Tum (HLM 0354) and Quang Nam (ZMMU NAP-08781)

provinces; two of them (HLM 0316 and HLM 0365) are sympatric in Kon Ka Kinh National Park. This study also revealed two unnamed mitochondrial lineages from Lam Dong Province of southern Vietnam (HLM 0367 and HLM 0368). Additional undescribed species of the *irregularis* group were reported in a number of recent studies (e.g., Nguyen et al. 2013, 2017a; Pauwels et al. 2018; Neang et al. 2020). All of these populations are currently being examined by various combinations of authors.

Several taxonomic issues within the group warrant clarifications. The status of *Cyrtodactylus thuongae* (Phung et al. 2014) is in need of verification, as it was regarded as a junior synonym of *C. dati* by Ngo et al. (2017). The phylogenetic position of *C. badenensis* is still unclear. It was supported as a member of the group in previous studies (Brennan et al. 2017; Nguyen et al. 2017a; Ostrowski et al. 2020) using CO1. In this study, however, it is recovered as the sister species to the *condorensis* group in the ML analysis (99) but was not recovered as such in the BEAST analysis. Finally, *C. grismeri* was assigned to both *C. irregularis* and *C. condorensis* groups in the bar-coding tree of Brennan et al. (2017) but was placed in the *C. condorensis* group by Grismer and Grismer (2017) and here with strong support (100/1.00).

***Cyrtodactylus khasiensis* group**

The *khasiensis* group is composed of 16 nominal species and at least four undescribed species (Fig. 3) that collectively range from northeastern India and Bangladesh east-

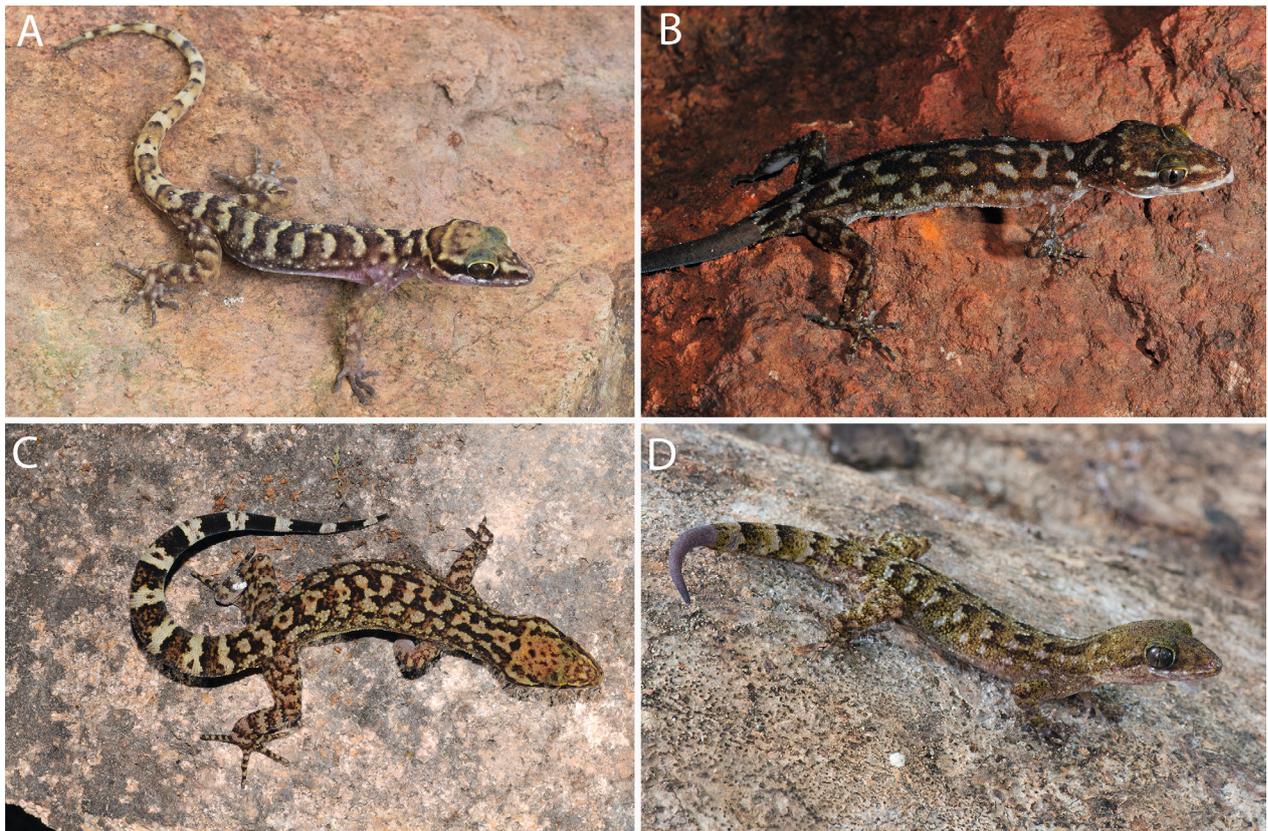


Figure 19. Examples of the *Cyrtodactylus khasiensis* group. A. *C. chrysopylos* from Shan State, Myanmar. Photo by L. Lee Grismer. B. *C. montanus* from Tripura state, India. Photo by Ishan Agarwal. C. *C. nagalandensis* from Nagaland state, India. Photo by Ishan Agarwal. D. *C. mombergi* from Kachin State, Myanmar. Photo by L. Lee Grismer.

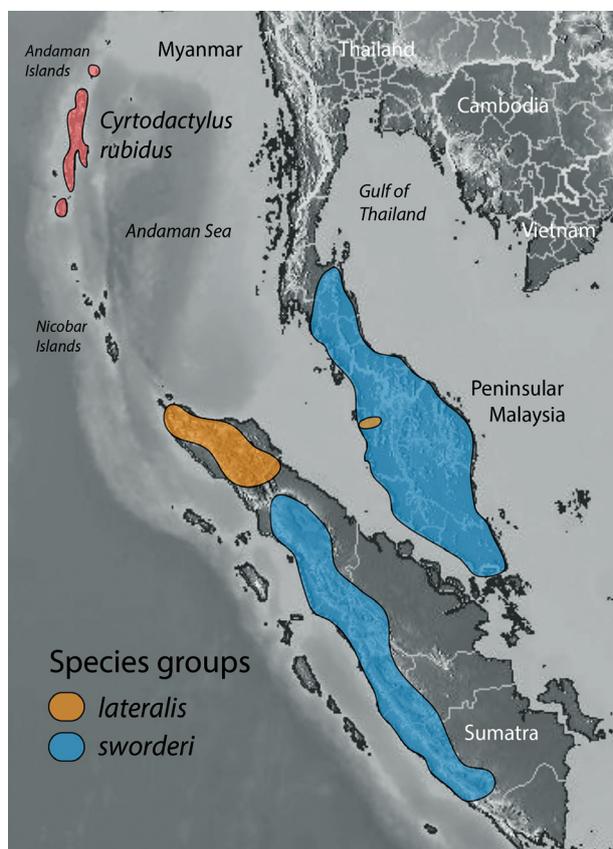


Figure 20. Distribution of the *lateralis* and *sworderi* species groups of *Cyrtodactylus* and *C. rubidus* as delimited here.

ward to the western edge of the Salween Basin in Myanmar (Fig. 15). Most are morphologically generalized species (Fig. 19) with the exception of *C. brevidactylus* which is highly terrestrial. The monophyly of the group is strongly supported in both analyses (100/1.00) and the phylogeny indicates it is composed of four sublineages—two each in Arunachal Pradesh/Myanmar and northeast India/Myanmar (Fig. 3). The undescribed species *Cyrtodactylus* sp. KM255193 from eastern Arunachal Pradesh forms one lineage; *C. mombergi* from Myanmar and *Cyrtodactylus* sp. KM255192 from eastern Arunachal Pradesh comprise the other Arunachal Pradesh/Myanmar lineage; *C. ayeyarwadyensis*, *C. guwahatiensis*, *C. kazi-rangaensis*, *C. khasiensis*, *C. septentrionalis*, *C. tripuraensis*, and *C. urbanus* constitute the first northeast India/Myanmar clade, with its distribution chiefly in India; and *C. aunghini*, *C. brevidactylus*, *C. chrysopylos*, *C. gansi*, *C. jaintiaensis*, *C. montanus*, *C. myaleiktaung*, and *C. nagalandensis* form the second northeast India/Myanmar clade, which includes the majority of the Myanmar species in the *C. khasiensis* group. The two northeast India/Myanmar clades are well supported sister clades (100/0.96) and are largely distributed south of the Brahmaputra River in northeast India and west of the Salween Basin in Myanmar. Based on the average elevations at which the constituent species are distributed, Agarwal et al. (2014) referred to the predominantly Indian clade as the lowland clade and the other as the mountain clade.

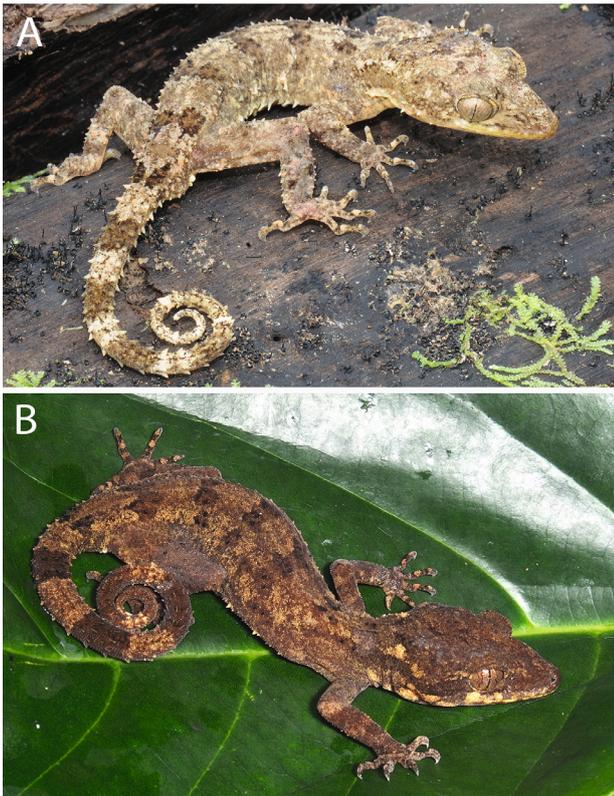


Figure 21. Examples of the *Cyrtodactylus lateralis* group. A. *C. durio* from Kedah State, Peninsular Malaysia. Photo by L. Lee Grismer. B. *C. lateralis* from Sumatra, Indonesia. Photo by Eric N. Smith.

Cyrtodactylus lateralis group

The *lateralis* group is a small clade with two species—*C. durio* from Peninsular Malaysia and *C. lateralis* from Sumatra. (Figs. 3, 20). *Cyrtodactylus rubidus* from the Andaman Islands was recovered as the sister species of this group, but this relationship was only well-supported in the ML analysis (92/0.86), and thus it was excluded although it is likely the relationship is correct. *Cyrtodactylus durio* and *C. lateralis* are highly arboreal (Grismer et al. 2010, Harvey et al. 2016) and bear morphological adaptations for arboreality such as a prehensile tail carried coiled (Fig. 21) in an elevated position. *Cyrtodactylus rubidus* also appears to have a prehensile tail which is often carried in the same manner.

Cyrtodactylus lawderanus group

The *lawderanus* group (Fig. 22) comprises five nominal species (Fig. 3) that collectively extend from the Western Himalayas in Pakistan eastward through India up to at least the border of Nepal, with a least one species disjunctly distributed on the Tibetan Plateau (Figs. 15). The monophyly of the group is strongly supported (99/1.00) in both ND2 analyses with a basal split separating *C. tibetanus* on the Tibetan Plateau from a strongly supported (100/1.00) western Himalayan clade which includes *C. battalensis*, *C. chamba*, *C. himalayanus*, and *C. lawderanus*. *Cyrtodactylus lawderanus* is likely to range into

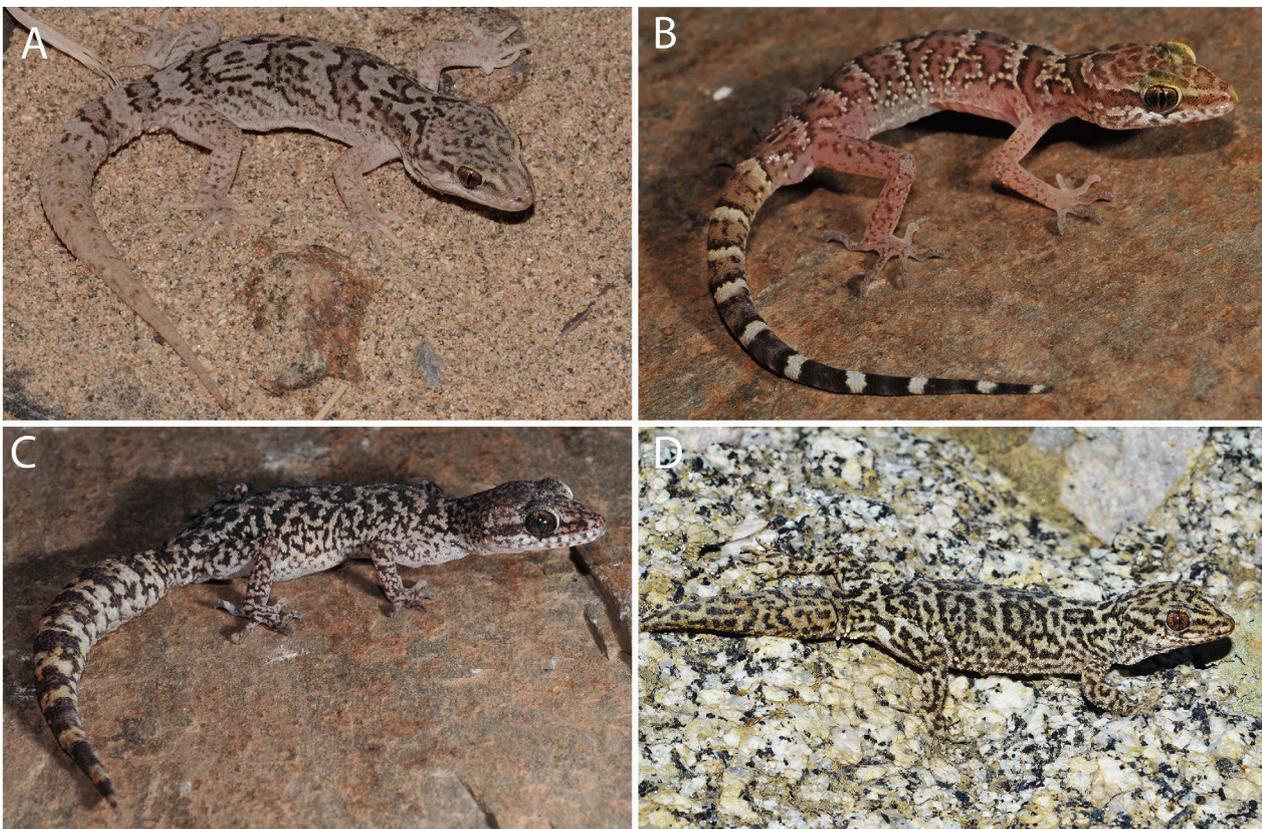


Figure 22. Examples of the *Cyrtodactylus lawderanus* group. A. *C. tibetanus* from Tibet, China. Photo by Kai Wang. B. *C. chamba* from Himachal Pradesh state, India. Photo by Ishan Agarwal. C. *C. lawderanus* from Uttarakhand state, India. Photo by Ishan Agarwal. D. *C. zhaormi* from Nyemo, Tibet, China. Photo by Baolin Zhang.

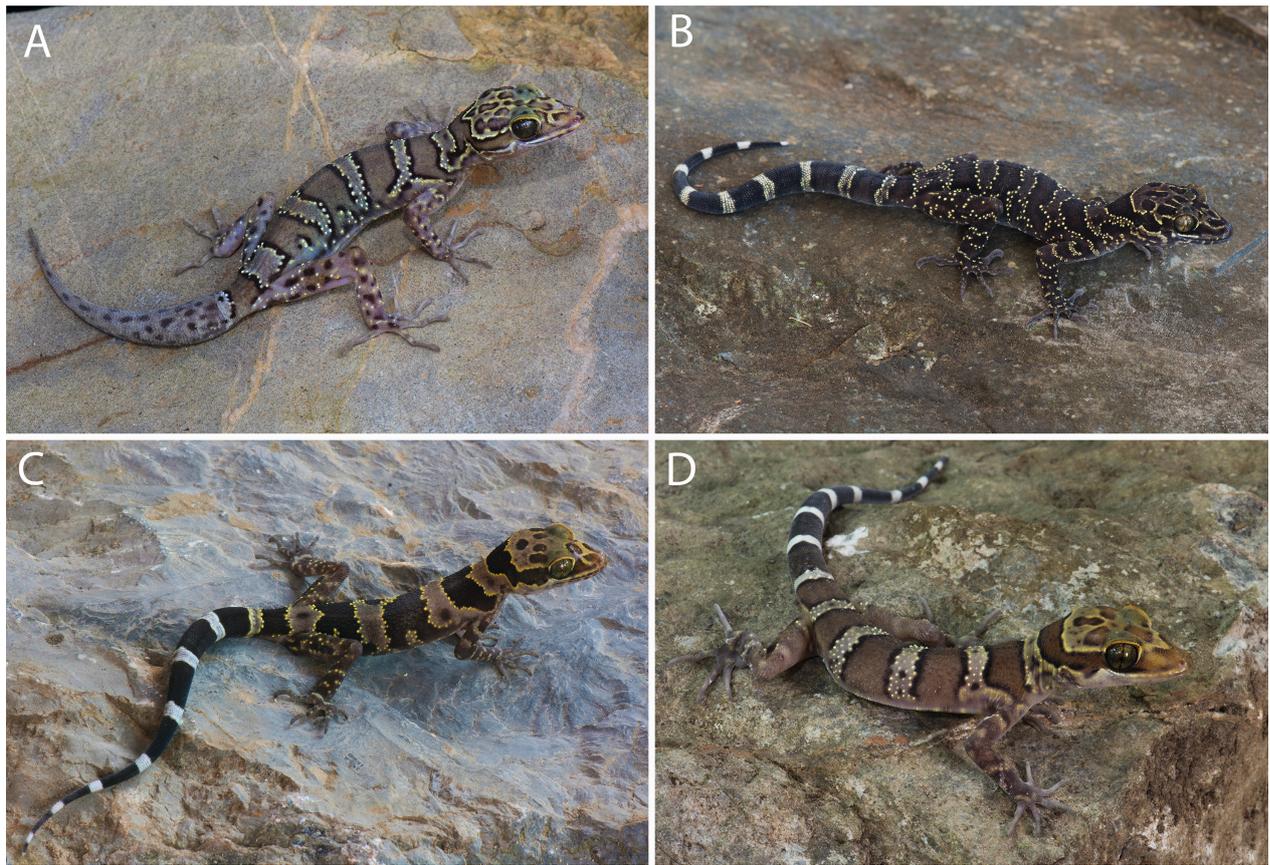


Figure 23. Examples of the *Cyrtodactylus linnwayensis* group. A. *C. linnwayensis* from Shan State, Myanmar. B. *C. pinlaungensis* from Shan State, Myanmar. C. *C. ywanganensis* from Shan State, Myanmar. D. *C. shwetaungorum* from Mandalay Region, Myanmar. Photos by L. Lee Grismer.

western Nepal. Some of the unsampled species here from the Tibetan Plateau (e.g. *C. zhaermi*) are allied to *C. tibetanus* (Che et al. 2020). In data sets with relatively limited species coverage (Wood et al. 2012, 70 species; Bauer et al. 2013, eight species; Agarwal et al. 2014, 58 species) using essentially the same sequence data (492 base pairs of ND2 and 382 base pairs of RAG1), *C. tibetanus* was recovered—with varying degrees of nodal support—as the sister species to all other *Cyrtodactylus*. However, when just the nuclear data (RAG1) of Wood et al. (2012) was re-run in Grismer et al. (2020a), *Cyrtodactylus* was recovered as paraphyletic as it does in the nuclear tree here—even with the additional species coverage. The monophyly of *Cyrtodactylus* in the multigene data sets of Wood et al. (2012), Bauer et al. (2013), and Agarwal et al. (2014) is the result of ND2 not the nuclear data and this result remains so even with the vastly expanded species coverage (310 species) here that continues to recover *Cyrtodactylus* as monophyletic but places *C. tibetanus* within the *lawderanus* group. The fluctuating phylogenetic placement of *C. tibetanus* is likely due to the uninformative nature of the short gene reads along with the lack of sequence data from other Himalayan species. In a separate mito-nuclear analysis using ND2, RAG1, and PDC and 68 species including *C. zhaermi* and a potentially undescribed species (*C. tibetanus* 1), Jing (2020) demonstrated that the latter two and *C. tibetanus* formed a monophyletic group that is the sister group

to all other *Cyrtodactylus*. That hypothesis is being tested further with an expanded data set composed of 346 species (Grismer et al. in prep.) and if supported, will require the construction of an additional species group—the *tibetanus* group.

Khan (2003) erected the genus *Siwaligekko* to accommodate western Himalayan taxa bearing intermediate morphology between *Cyrtodactylus* and Palearctic naked-toed geckos (see Bauer et al. 2013). Its type species, *C. battalensis*, makes that name available for this morphologically distinctive clade if subgenera or new genera are ever proposed.

***Cyrtodactylus linnwayensis* group**

The *linnwayensis* group is composed of four relatively large (adult SVL > 100 mm), robust, tuberculate, allopatric, karst-adapted species (Figs. 3, 23) endemic to the western section of the Shan Plateau of the Mandalay Division and Shan State, Myanmar (Grismer et al. 2018a,b, 2019; Fig. 24). Relationships within this group have remained stable in all previous phylogenetic analyses. Given the extensive amount of unexplored karstic habitat across the vast Shan Plateau and the geographic distance between some of these species in this group (~ 90 km), we believe the species composition of the *linnwayensis* group is considerably underestimated. We have seen pictures of undescribed species of *Cyrtodactylus* from

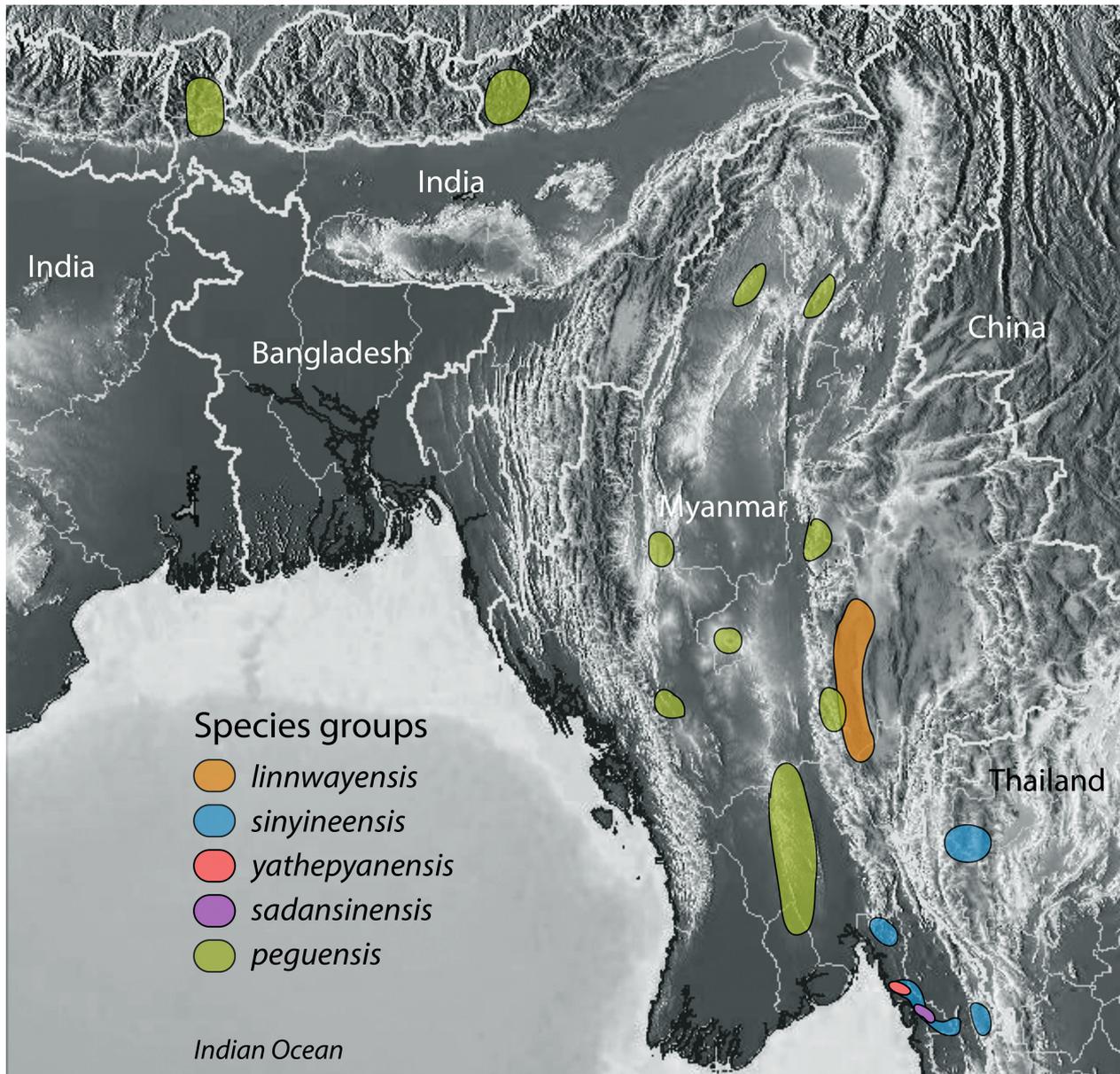


Figure 24. Distribution of the *linnwayensis*, *peguensis*, *sadansinensis*, *sinyineensis*, and *yathepyanensis* species groups of *Cyrtodactylus* as delimited here.

various caves throughout the Shan Plateau that resemble *linnwayensis* group species and expeditions are planned to survey these areas.

***Cyrtodactylus malayanus* group**

The *malayanus* group maybe endemic to Borneo (see below) and composed of at least three nominal species and at least one potentially new species (Figs. 3, 7). Although its monophyly is well-supported (100/1.00), its relationships to other species groups are not. In a previous analysis (Davis et al. 2019, 2020), some species of the *malayanus* group as constituted herein were nested within what is considered here as the well-supported (100/1.00) *philippinicus* group. However, the taxonomy of those phylogenies had a number of species (*C. pubisulcus*, *C. cavernicolus*, *C. yoshii*, *C. malayanus*, and *C. consobrinus*) occurring in multiple places throughout the tree

rendering them polyphyletic and making comparisons with this tree not possible. Current research (Grismer et al. in progress) indicates that one of the species, *C. consobrinus* which also ranges throughout Peninsular Malaysia (Grismer 2011) is a species complex (Fig. 25) and members of this complex belong in both the *malayanus* and *philippinicus* groups.

***Cyrtodactylus marmoratus* group**

The *marmoratus* group (Fig. 26) is composed of at least three nominal species (two of which are analyzed here) and six potentially undescribed species (O'Connell et al. 2019; Riyanto et al. 2015) that range from New Guinea westward across the Lesser Sundas and Java, to parts of southern and western Sumatra (Figs. 3, 27). The group contains several undescribed species from Java and Sumatra (KR921697, KR921699, KR921689, KR921720,



Figure 25. Examples of the *Cyrtodactylus malayanus* group. A. *C. malayanus* from Sabah State, East Malaysia. Photo by Ruchira Somaweera. B. *C. cf. consobrinus* from Johor State, Peninsular Malaysia. Photo by L. Lee Grismer. C. *C. consobrinus* from the type locality in Sarawak State, East Malaysia. Photo by L. Lee Grismer. D. *C. cf. consobrinus* from Sarawak State, East Malaysia. Photo by Nikolay A. Poyarkov. E. *C. cf. consobrinus* from Pahang State, Peninsular Malaysia. Photo by L. Lee Grismer. F. *C. cf. consobrinus* from Perak State, Peninsular Malaysia. Photo by Evan S. H. Quah.

and HLM 0371) and ongoing research is describing many of these (Riyanto in prep). However, it is certain that additional species remain undiscovered across the myriad islands between Java and New Guinea.

***Cyrtodactylus oldhami* group**

The *oldhami* group contains seven nominal species and three potentially new species represented here (Fig. 3, 28). It is essentially endemic to the Thai-Malay Peninsula of southern Thailand and Myanmar with only *C. sai yok* reaching Sai Yok, Kanchanaburi Province just north of the Peninsula (Panitvong et al. 2014; Fig. 16). The tax-

onomy of *C. oldhami* is problematic in that this species is polyphyletic in the tree and preliminary investigations of a large series show considerable variation in color pattern throughout its range, including a number of islands off the west coast of Thailand. This species was previously only known from south of the Isthmus of Kra but a specimen in this analysis (*C. cf. oldhami* HLM 0307) comes from considerably farther north at Suan Phueng, Ratchaburi Province at the northern end of the Thai-Malay Peninsula. Similarly, the taxonomy of *C. zebraicus* is also in a state of flux and current investigations from populations throughout its range south of the Isthmus of Kra and adjacent east coast islands have revealed considerable mor-

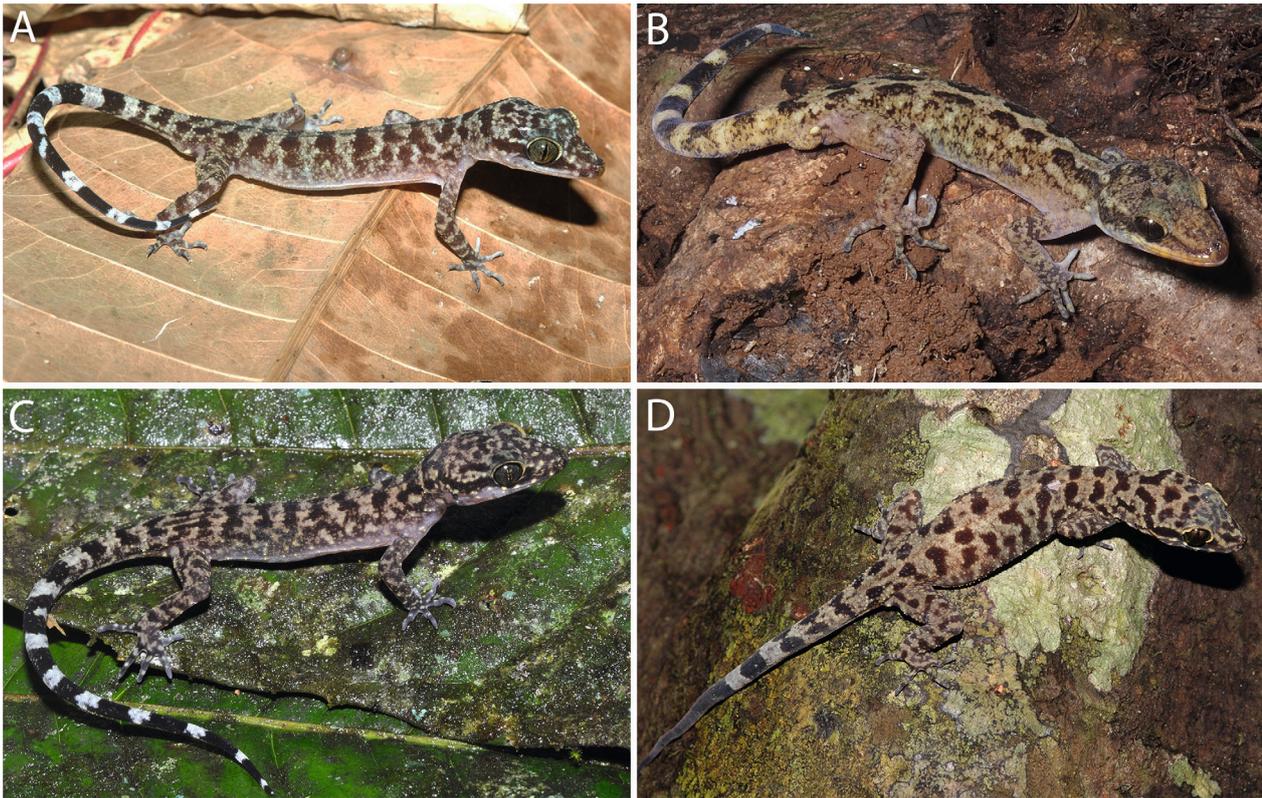


Figure 26. Examples of the *Cyrtodactylus marmoratus* group. A. *C. papuensis* from the Western Province, Papua New Guinea. Photo by Stephen Richards. B. *C. marmoratus* from Java. Photo by Eric M. Smith. C. *C. papuensis* from the Timika Province, Papua New Guinea. Photo by Stephen Richards. D. *C. cf. papuensis* from Papua Province, Indonesia. Photo by Stephen Richards.

phological variation (Grismer et al. in prep.). Reports of *C. zebraicus* from northern Peninsular Malaysia remain unconfirmed (see Grismer 2011).

***Cyrtodactylus peguensis* group**

The *peguensis* group (Fig. 29) is composed of 11 nominal species and at least one undescribed species (Fig. 3) and extends from the eastern Himalayas of India bordering Bhutan and Nepal, eastward to Myanmar across the Ayeyarwady Basin to the western edge of the Shan Plateau (Fig. 24). Although the monophyly of the group was recovered in both analyses, only in the ML analysis was it strongly supported (97/0.73), and as such deviates from the criteria used to construct the other species groups except the *sermowaineis* species group (see below). The other option would have been to combine the *fasciolatus*, *peguensis*, and *khasiensis* groups into one group (Fig. 3) but we elected to emphasize the independence of these three clades. The group is composed of two Burmese lineages and one Indian lineage. *Cyrtodactylus russelli* and *C. slowinskii* compose the northern Burmese lineage and *C. annandalei*, *C. pyadalimensis*, *C. meersi*, *C. nyinyikyawi*, *C. myintkyawthurai*, *C. pyinyaungensis*, and *C. peguensis* compose the southern Ayeyarwady Basin lineage. *Cyrtodactylus bhupathyi*, *C. gubernatoris* and an undescribed species from western Arunachal Pradesh form the Indian or Eastern Himalayan lineage and compose the sister lineage to the southern Burmese lineage (Fig. 3).

***Cyrtodactylus philippinicus* group**

The *philippinicus* group is composed of at least 17 nominal species (13 included here) and at least five undescribed species (Fig. 3) that are predominantly distributed across the Philippine Archipelago (nine species) and Borneo (six species), with an additional species occurring on the Thai-Malay Peninsula, and another on Pulau Aur off the southeast coast of Peninsular Malaysia (Fig. 7). Of the 17 recognized species comprising this group, the majority are single island (or geological platform) endemics—the exceptions being *C. consobrinus* (Borneo, Thai-Malay Peninsula, and Singapore), and three Philippine species (*C. annulatus*, *C. jambangan*, and *C. philippinicus*) that are widely distributed across various insular components of that archipelago (Siler et al. 2010, Welton et al. 2009, 2010). To date, none of these species are known to occur in sympatry, and species occurring on the same island (e.g. Borneo or Mindanao) are endemic to single mountains (*C. baluensis* on Mt. Kinabalu, Borneo Island) or unique geological components of aggregate islands (*C. agusanensis* on eastern Mindanao Island). While it remains a possibility that widespread species in this group are indeed just that, additional survey efforts and closer examination of allopatric populations of such species continue to document previously unrealized taxonomic diversity. Indeed, a number of populations currently ascribed to *C. philippinicus* are currently under investigation, and likely warrant specific designation (Wood and Welton, in prep; R. Brown pers. comm.). Similarly, the

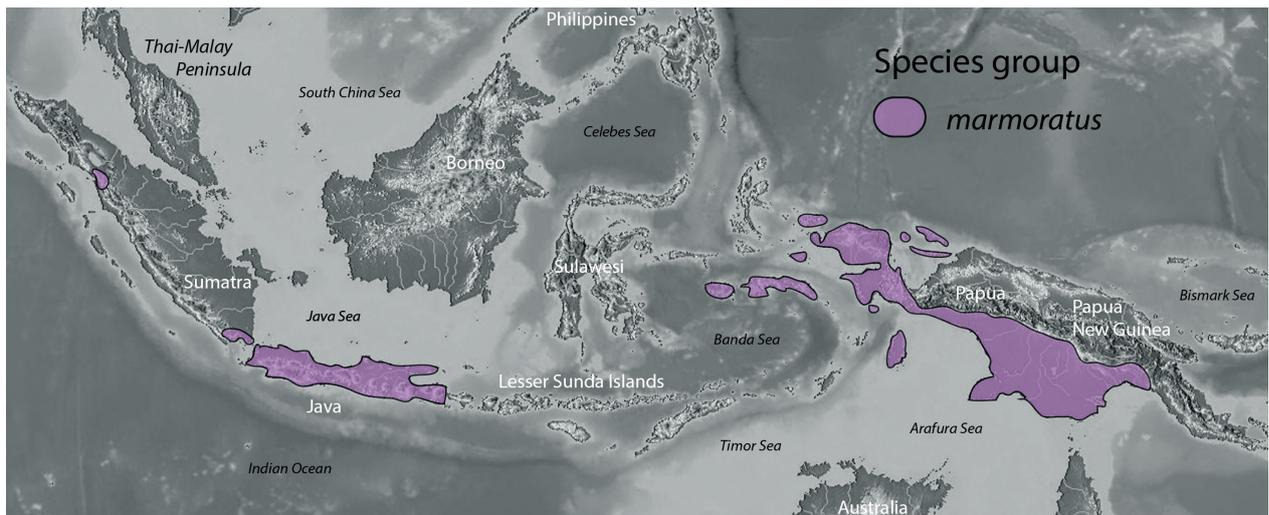


Figure 27. Distribution of the *marmoratus* species group of *Cyrtodactylus* as delimited here.

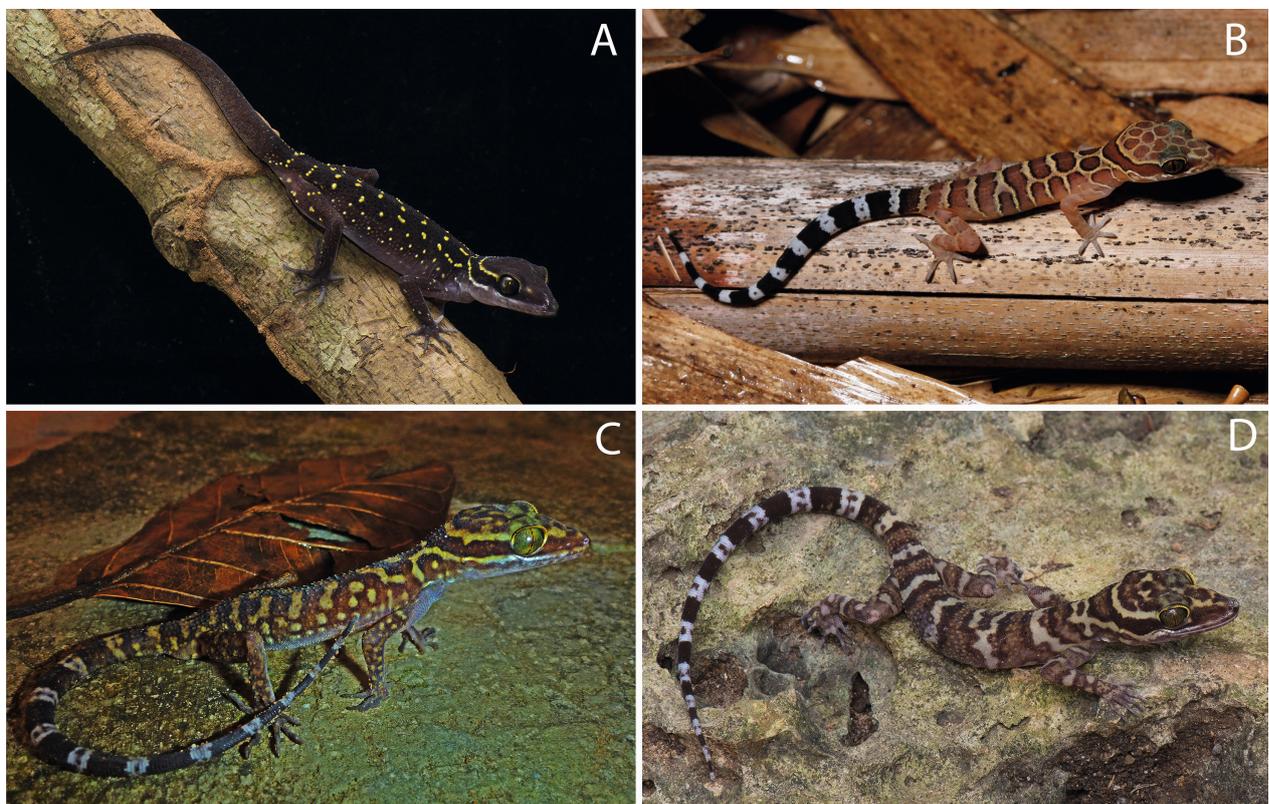


Figure 28. Examples of the *Cyrtodactylus oldhami* group. A. *C. oldhami* from Phuket Island, Thailand. Photo by L. Lee Grismer. B. *C. zebraicus* from Krabi Province, Thailand. Photo by Parinya Pawangkhanant. C. *C. sanook* from Chumphon Province, Thailand. Photo by Montri Sumontha. D. *C. thirakhupti* from Surat Thani Province, Thailand. Photo by L. Lee Grismer.

widespread *C. consobrinus* is currently being scrutinized for novel taxonomic diversity across its range (Grismer et al. in prep).

Phylogenetically, the *philippinicus* group comprises three major well-supported mitochondrial lineages, the combination of which is inferred as sister to the basally divergent *Cyrtodactylus pubisulcus* (Fig. 3). These three clades correspond to 1) a Bornean radiation (*C. baluensis*, *C. ingeri*, and *C. yoshii*) sister to at least three southern Philippine taxa (*C. annulatus*, *C. jambangan*, and *C. tautbatorum*); 2) a single Philippine taxon (*C. red-*

imiculus) sister to at least three Sundaic species (*C. consobrinus*, *C. aurensis*, and *C. muluensis*); and 3) an exclusively Philippine clade (*C. agusanensis*, *C. gubaot*, *C. mamanwa* (not in this study), *C. philippinicus*, and *C. sumuroi*). Worth noting, is that the topology inferred here differs from those recovered in previous studies that included multiple members of the group (Brennan et al. 2017; Davis et al. 2020; Nielsen and Oliver 2017; Siler et al. 2010; Welton et al. 2010a,b; Wood et al. 2012), likely due to increased taxon sampling and the loci utilized. Though the relationships between Philippine and

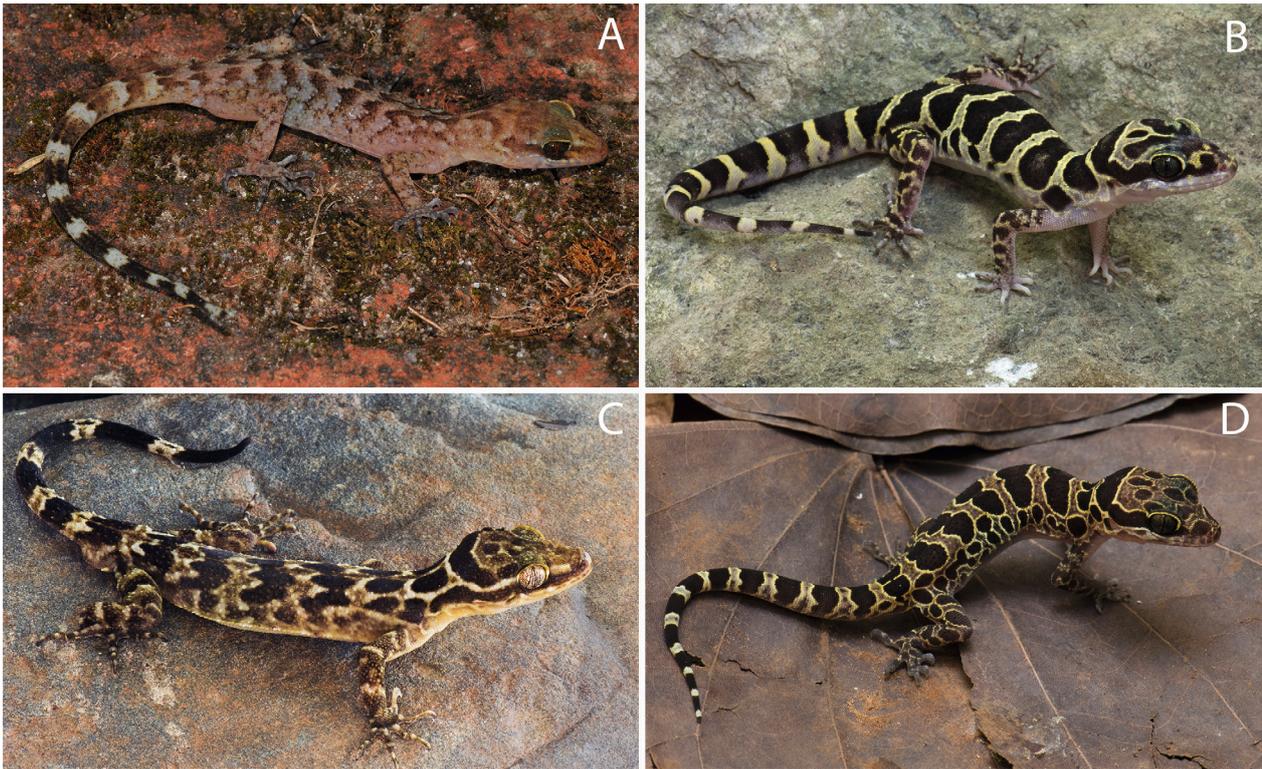


Figure 29. Examples of the *Cyrtodactylus peguensis* group. A. *C. bhupathyi* from West Bengal state, India. Photo by Ishan Agarwal. B. *C. pyinyaungensis* from Mandalay region, Myanmar. Photo by L. Lee Grismer. C. *C. russelli* from Kachin State, Myanmar. Photo by L. Lee Grismer. D. *C. peguensis* from Bago Region, Myanmar. Photo by L. Lee Grismer.

Sundaic taxa is unsurprising, the topology inferred from mitochondrial data indicates multiple dispersal events between the two faunal regions, yielding the Philippine assemblage of species paraphyletic. The topological patterns recovered here highlight the importance of Palawan Island (Philippines) in the biogeographical history of the *philippinicus* group. Both major lineages comprising Philippine and Sundaic taxa include one of the two species of *Cyrtodactylus* that are endemic to Palawan (*C. redimiculus* or *C. tautbatorum*). In combination with the geographical position of Palawan being nestled between Borneo and the remainder of the Philippine Archipelago, it is perhaps unsurprising that this island would serve as a stepping-stone in the evolution and historical biogeography of this group.

Phenotypically, the *philippinicus* group might be considered relatively unremarkable, with the majority of species exhibiting cryptic coloration consisting of brown and tan earth tones—some species exhibit dark transverse bands on the trunk while others have spots or longitudinal stripes overlain on a lighter ground color (Fig. 30). Exceptional species in this group include *C. consobrinus*, which often exhibits a nearly black ground color overlain with well-defined, thin yellow-gold transverse bands and *C. jambangan*, which has yellow-gold supraocular scales and canthal stripes.

Taxonomic work on this group has predominantly been focused in the Philippine Archipelago, where more than half of the recognized species have been described since the turn of the century. These works have been the result of a combination of renewed scrutiny of supposed

widespread species, coupled with more comprehensive sampling across a number of species' ranges stemming from contemporary field surveys. As noted above, it is without doubt that additional species from this group will be described in the coming years, serving to increase our knowledge about the evolution and diversification of not only *Cyrtodactylus*, but the faunal communities to which these species belong.

Cyrtodactylus pulchellus group

The *pulchellus* group is endemic to the southern one-half of the Thai-Malay Peninsula of Thailand and Peninsular Malaysia, ranging from the Isthmus of Kra to southern Peninsular Malaysia (Fig. 16). The group was previously considered a single species, *C. pulchellus*, until integrative taxonomic analyses demonstrated that it is a monophyletic lineage composed of at least 17 nominal species (Grismer et al. 2012a, 2014a; Sumontha et al. 2012; Quah et al. 2019; Wood et al. 2020a) of which 16 are presented here (Figs. 3, 31). The phylogenetic relationships of *C. phuketensis* from Phuket Island, Thailand have not been determined but it has been hypothesized based on morphology and color pattern, that it is closest to *C. macroreticulatus* (Sumontha et al. 2012) if not synonymous. In Grismer et al. (2012a, 2014a, 2016b), Quah et al. (2019), and Wood et al. (2020a), the karst clade—most recently composed of *C. astrum*, *C. dayangbuntingensis*, *C. langkawiensis*, and *C. lekaguli*—was recovered as the sister lineage to a clade containing the remaining species. In this analysis, the karst clade is nested within

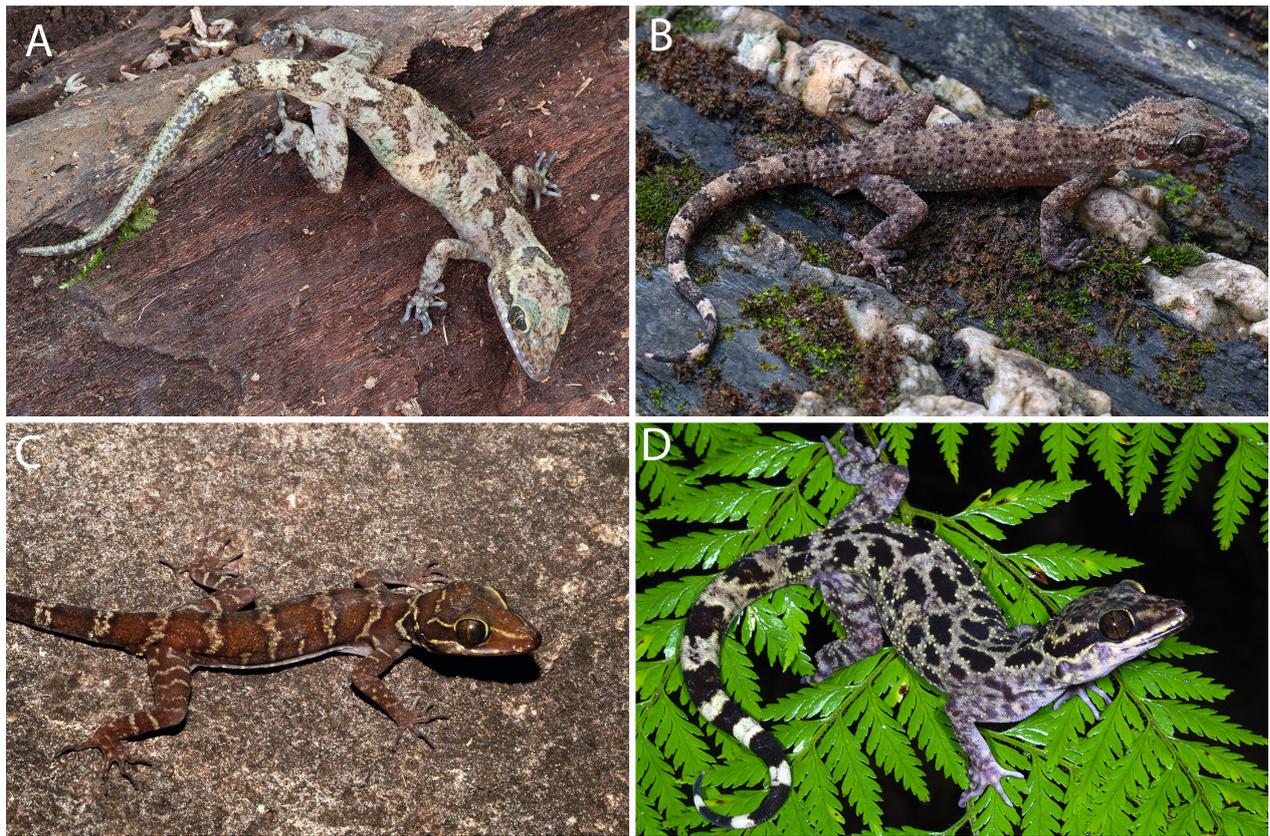


Figure 30. Examples of the *Cyrtodactylus philippinicus* group. A. *C. annulatus* from Samar Island, Philippines. Photo by Cameron D. Siler. B. *Cyrtodactylus* sp. nov. from Lubang Island, Philippines. Photo by Cameron D. Siler. C. *C. aurensis* from Aur Island, Johor State, Peninsular Malaysia. Photo by L. Lee Grismer. D. *C. baluensis* from Sabah, East Malaysia. Photo by Steve Wilson.

the group but with poor support (61/0.49). Additionally, *C. sharkari* from a lowland karstic region does not appear to be genetically distinct from *C. trilatofasciatus* from an upland granite habitat. A genomic data set for this group is currently being constructed (Wood et al. in prep.). As new populations from unexplored karstic regions are discovered, the number of species in this group will increase substantially (Wood et al. in prep).

***Cyrtodactylus sadansinensis* group**

The *sadansinensis* group is composed of three nominal allopatric karst-adapted species endemic to small limestone hills in the Salween Basin of southern Myanmar (Grismer et al. 2018b; Fig. 32). This group is the strongly supported (100/1.00) sister lineage to a large clade composed of the *yathepyanensis*, *oldhami*, *sinyineensis*, *chauquangensis* groups, and *C. tigroides* that collectively range from western Myanmar, through southern China, Thailand, Laos, and northeastern Vietnam (Figs. 3, 24). More species are expected to be discovered in this group when the vast number of small, isolated, karstic hills in the Salween Basin are surveyed.

***Cyrtodactylus sinyineensis* group**

The *sinyineensis* group (sec. Grismer et al. 2018b) ranges from the uplands of northwestern Thailand to the lowland

karstic archipelagos of the Salween Basin in southeastern Myanmar (Grismer et al. 2018b, 2020c) and is composed of 12 nominal species (Figs 3, 24, 33). The group is divisible into two strongly supported clades (Chomdej et al. 2020; Fig. 3). Clade 1 (100/1.00) is composed of three species (*C. sinyineensis*, *C. taungwineensis*, and *C. welpyanensis*) from the Salween Basin and two species (*C. inthanon* and *C. maelanoi*) from upland regions of the Thanon Thong Chai mountain range in northwestern Thailand (Grismer et al. 2020c). Clade 2 (98/1.00) is composed of five species (*C. bayinnyiensis*, *C. dattkyaikensis*, *C. naungkayaingensis*, *C. chaunghanakwaensis*, and *C. dammathetensis*) from the Salween Basin and two species from upland regions fringing the northern (*C. aequalis*) and western (*C. amphipetraeus*) margins of the Salween Basin (Figs. 3, 24). All species in this group are narrow-range endemics (Grismer et al. 2018b, 2020d; Chomdej et al. 2020) and more species belonging to this group are expected to be discovered when the vast number of small, isolated, karstic hills in the Salween Basin and the many unsurveyed mountain tops in western Thailand are explored.

***Cyrtodactylus sworderi* group**

The *sworderi* group is composed of five species endemic to the Thai-Malay Peninsula south of the Isthmus of Kra of southern Thailand (Figs. 3, 20). One species, *C. quadrivirgatus* is a habitat generalist that ranges as far north



Figure 31. Examples of the *Cyrtodactylus pulchellus* group. A. *C. dayangbuntingensis* from Tuba Island, Kedah State, Peninsular Malaysia. Photo by Evan S. H. Quah. B. *C. trilatofasciatus* from Pahang State, Peninsular Malaysia. Photo by L. Lee Grismer. C. *C. evanquahi* from Kedah State, Peninsular Malaysia. Photo by Evan S. H. Quah. D. *C. bintangrendah* from Perak State, Peninsular Malaysia. Photo by Evan S. H. Quah.

as the Isthmus of Kra and as far south as Singapore and Sumatra (Grismer 2011). The remaining four species (Fig. 34) are endemic to Peninsular Malaysia. *Cyrtodactylus guakanthanensis* and *C. gunungsenyumensis* are karst-adapted species (Grismer et al. 2014b, 2016a), *C. tebuensis* is an upland habitat generalist (Grismer et al. 2013) and *C. sworderi* is restricted to lowland swampy areas (Grismer 2011).

***Cyrtodactylus triedrus* group**

The *triedrus* group is composed of 17 nominal species of which 14 are presented here, along with eight undescribed species (Figs. 3, 35). This group is endemic to India and Sri Lanka (Fig. 15) and composed of two major clades (Fig. 3). The well-supported (100/1.00) *fraenatus* clade is endemic to Sri Lanka, and currently hypothesized to contain six nominal species (de Silva and Ukuwela 2020). The first revision of this clade was done by Batuwita and Bahir (2005) where they split the single, widely distributed *C. fraenatus* (Günther 1864) into six species including five new species, showing that they comprise an endemic radiation of several morphologically differentiated species. Based on morphology, color pattern, and distribution, we hypothesize that the Sri Lankan endemics *C. cracens*, *C. edwardtaylori*, and *C. subsolanus* will also belong to this group. However, the genetic similarity between *C. ramboda* and *C. fraenatus* suggests further

revision of these species may be necessary even though Batuwita and Bahir (2005) presented morphological differences separating them. Previously, the distribution of *Cyrtodactylus* in Sri Lanka was restricted to the wet zone, but recently two undescribed species were found near the northern and eastern borders in the dry zone (DWC 2008, see Karunaratna et al. 2019). The *fraenatus* clade species are large (adult SVL 100–125 mm) scansorial species found on the bark of large tall trees, on large granite boulders, within granite caves, and on abandoned wattle and daub houses (Somaweera and Somaweera 2009).

The *triedrus* clade is composed of the remaining 11 nominal species and at least eight undescribed species, and is endemic to peninsular India and Sri Lanka (Agarwal and Karanth 2015). The group is recovered as monophyletic in the ML analysis with strong support (96), while the BEAST analysis recovers a Sri Lankan lineage composed of *C. triedrus* and two *C. cf. triedrus* as sister to the *C. fraenatus* clade with low/moderate support (0.86). *Cyrtodactylus triedrus* and two closely related undescribed species are endemic to Sri Lanka, while the Indian radiation of the *triedrus* clade includes the northern Western Ghats *C. albofasciatus* and *C. deccanensis* lineages that include two undescribed species, the northern Eastern Ghats *C. jeyporensis* and the *C. nebulosus* lineages that includes three undescribed species, and the largely south Indian *C. collegalensis* lineage that includes *C. collegalensis*, *C. rishivalleyensis*, *C. speciosus*, *C. sri-*



Figure 32. Examples of the *Cyrtodactylus sadansinensis* group. A. *C. sanpelensis* from Mon State, Myanmar. B. *C. pharbaungensis* from Mon State, Myanmar. C. *C. sadansinensis* from Mon State, Myanmar. Photos by L. Lee Grismer.

lekhae, *C. varadgirii*, the Sri Lankan *C. yakhuna*, and one undescribed species. Historical records of *C. collegalensis* from Sri Lanka likely represent additional unnamed lineages of the *C. collegalensis* lineage. All members of the *triedrus* clade are largely ground-dwelling in habit and range in size from 50–80 mm SVL; while members of the *fraenatus* clade are scansorial and are 100–125 mm SVL. Members of the Indian species lack precloacal pores which occur in males of *C. triedrus* and species in the *fraenatus* clade (Batuwita and Bahir 2005; SK pers. obs.). Precloacal and femoral pores are also absent from Sri Lankan *C. cf. collegalensis* and *C. yakhuna*. The name *Geckoella* (type species *C. triedrus*) has been applied to the ground-dwelling members of the *triedrus* group (e.g. Kluge 1993; Agarwal and Karanth 2015), though the monophyly of *Geckoella* is recovered only in the ML analyses.

***Cyrtodactylus yathepyanensis* group**

The *yathepyanensis* group is composed of three nominal, narrow-range, allopatric, karst-adapted species (Fig. 36) found on small limestone hills in the northern Salween

Basin of southern Myanmar (Grismer et al. 2018b; Figs. 3, 24). All three species are moderately sized (SVL 60–78 mm) gracile species with irregularly shaped dorsal bands (Grismer et al. 2018b). More species belonging to this group are expected to be discovered when the vast number of small, isolated, karstic hills in the Salween Basin are surveyed.

Melanesian *Cyrtodactylus* species groups

Three major clades of *Cyrtodactylus* are present in Melanesia and northeastern Australia, apparently representing three separate invasions of Melanesia (Fig. 3). *Cyrtodactylus papuensis* is part of the widespread *marmoratus* group, which is considered above. *Cyrtodactylus biordinis* appears to have no close living relatives and colonized Melanesia before the remaining species (Tallowin et al. 2018). The remaining 30+ species form a well-supported ML (92) and Bayesian clades (0.98; Tallowin et al. 2018) that have radiated throughout the region. Below we divide this clade into seven species groups—the *arcanus*



Figure 33. Examples of the *Cyrtodactylus sinyineensis* group. A. *C. aequalis* from Mon State, Myanmar. Photo by L. Lee Grismer. B. *C. naungkayaingensis* from Kayin State, Myanmar. Photo by L. Lee Grismer. C. *C. taungwineensis* from Kayin State, Myanmar. Photo by L. Lee Grismer. D. *C. amphipetraeus* from Tak Province, Thailand. Photo by Nikolay A. Poyarkov.



Figure 34. Examples of the *Cyrtodactylus sworderi* group. A. *C. guakanthanensis* from Perak State, Peninsular. B. *C. sworderi* from Johor State, Peninsular Malaysia. C. *C. tebuensis* from Terengganu State, Peninsular Malaysia. D. *C. quadrivirgatus* from Pahang State, Peninsular Malaysia. Photos by L. Lee Grismer.

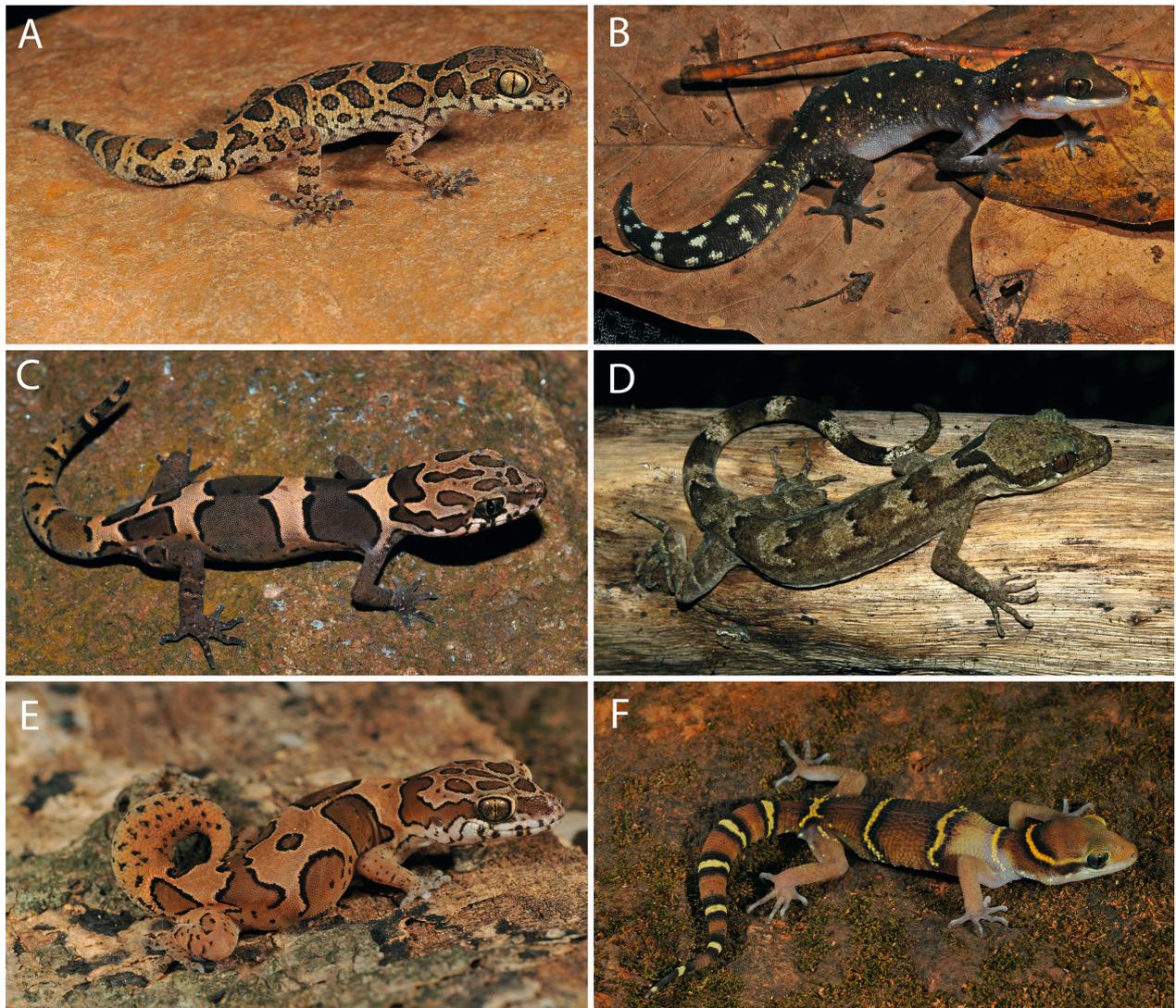


Figure 35. Examples of the *Cyrtodactylus triedrurus* group. A. *C. jeyporensis* from Andhra Pradesh state, India. Photo by Ishan Agarwal. B. *C. triedrurus* from Central Province, Sri Lanka. Photo by Ishan Agarwal. C. *C. cf. speciosus* from Tamil Nadu state, India. Photo by Ishan Agarwal. D. *C. fraenatus* from Central Province, Sri Lanka. Photo by Suranjan Karunarathna. E. *C. srilekhae* from Karnataka state, India. Photo by Ishan Agarwal. F. *C. deccanensis* from Maharashtra state, India. Photo by Ishan Agarwal.

group, *capreoloides* group, *loriae* group, *lousiadensis* group, *novaeguineae* group, *sermowaiensis* group, and *tuberculatus* group—on account of their divergent morphologies and ecologies, which we presume to have arisen as a result of a rapid radiation following initial colonization of Melanesia. Rapid early diversification of the main Melanesian *Cyrtodactylus* radiation is also suggested by the poor resolution of basal relationships and short branch lengths among the seven species groups (see also Tallowin et al. 2018). Three of the species groups include independently evolved gigantic species (SVL > 150 mm) (Oliver et al. 2014), and these are highly arboreal and typically found on the trunks of large trees. The other groups are smaller and morphologically divergent from these groups, and one of them includes at least one karst-adapted species. *Cyrtodactylus deveiti* is a moderately sized *Cyrtodactylus* from Halmahera Island, Indonesia (Brongersma 1948), has a robust build, color pattern consisting of large indistinct blotches, and a high number of femoral and precloacal pores (18–23).

These characters suggest it is likely allied to taxa in the Melanesian radiation of *Cyrtodactylus* rather than other species in the Maluku region; however, molecular phylogenetic analyses are required to refute or confirm this hypothesis.

***Cyrtodactylus arcanus* group**

The *arcanus* group is composed of two recently recognized and poorly known species from hill and lower-montane forests along the Central Cordillera in Papua New Guinea (Figs. 3, 37). *Cyrtodactylus arcanus* and *C. manos* are known, respectively, from two male and one female voucher specimens but appear to share small-to-moderate size and a complex dorsal pattern of numerous (6–11) transverse blotches or bands (Oliver et al. 2012, 2019). *Cyrtodactylus manos* (Fig. 38) is only known from lower-montane forests on the karst basement in Southern Highlands Province, on the southern versant of New Guinea. *Cyrtodactylus arcanus* is known from at



Figure 36. Examples of the *Cyrtodactylus yathepianensis* group. A. *C. linnoensis* from Kayin State, Myamar. B. *C. sadanensis* from Kayin State, Myanmar. C. *C. yathepianensis* from Kayin State, Myanmar. Photos by L. Lee Grismer.

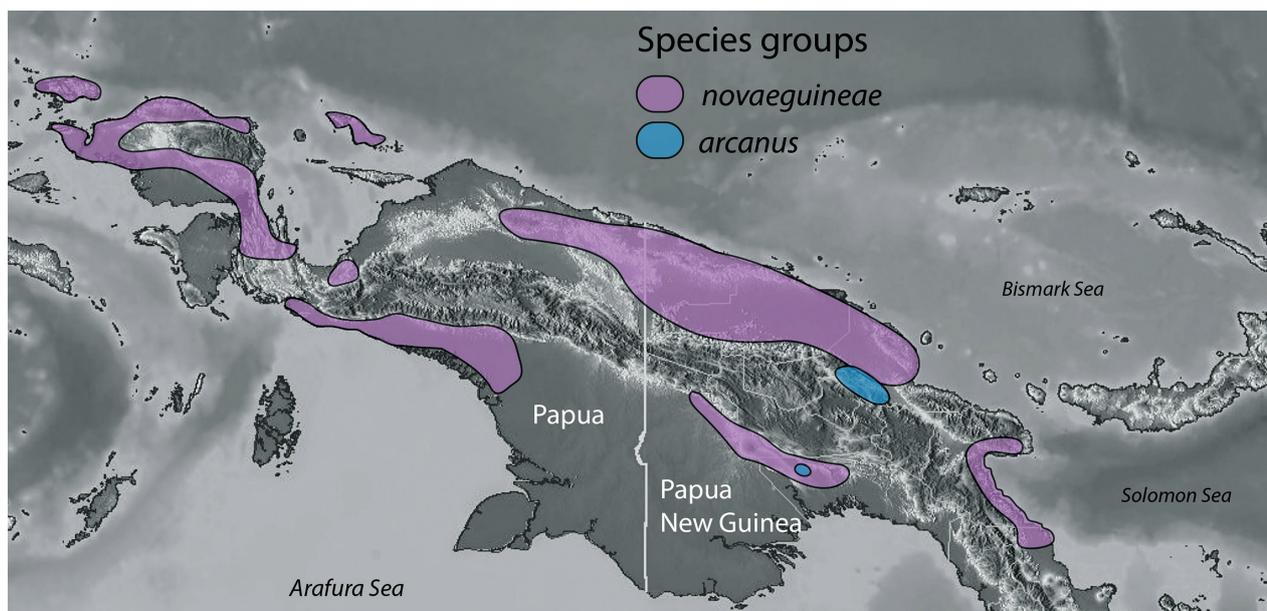


Figure 37. Distribution of the *arcanus* and *novaeguineae* species groups of *Cyrtodactylus* as delimited here.

least two sites on the northern versant in New Guinea in Madang and Jiwaka Provinces. At both sites, however, specimens were brought in by locals; thus, as far as we are aware, this species has never been seen or captured

in situ by herpetologists (Oliver et al. 2012, Oliver and Switak 2019). This species group provides an example of a divergent lineage of *Cyrtodactylus* that is composed entirely of species described in the last ten years.



Figure 38. Example of the *Cyrtodactylus arcanus* group: *C. mannos* from Southern Highlands Province, Papua New Guinea. Photo by Stephen Richards.

***Cyrtodactylus capreoloides* group**

The *capreoloides* group comprises three species occurring in hill and lower-montane forests on the southern versant of the Central Cordillera extending from Gulf Province into West Papua (*C. capreoloides*, *C. medioclivus* and *C. tanim*), one species from the Huon Peninsula (*C. minor*), and one species from the northern coastal ranges of Papua New Guinea and West Papua (*C. boreoclivus*) (Fig. 39). Species in this group are morphologically heterogeneous in size, coloration and tail scalation (Fig. 40), although males always appear to have a tripartite pore arrangement (Oliver et al. 2012; Oliver and Richards 2012; Nielsen and Oliver 2017). *Cyrtodactylus tanim* is currently the only known *Cyrtodactylus* from New Guinea that shows evidence of morphological specializations associated with living in karst microhabitats (Nielsen and Oliver 2017). Tallowin et al. (2018) placed *C. minor* in a monophyletic species group on the basis of its biogeographic and phylogenetic divergence from other members of the *capreoloides* species group. Contrary to this, it is placed here within an expanded *capreoloides* group based on the increasing support for the node subtending *C. minor* and other members of the *capreoloides* group and to minimize the number of recognized orphaned species. This species group provides another example of a divergent lineage of *Cyrtodactylus* composed largely of species recently documented. The nominate taxon was described in 2007 (Rösler et al. 2007), with three additional species described only in the ensuing decade. A small number of specimens that are also likely members of this species group from the Central Cordillera in West Papua (e.g., around Wamena) are held in museums (P. Oliver, pers. obs.); however, the taxonomic affiliations of these specimens have not yet been properly investigated.

***Cyrtodactylus loriae* group**

The *loriae* group is currently known to be distributed along the lower and middle elevations of the mountainous spine of Papua New Guinea, including the Central

Highlands and the Owen Stanley Mts. of the Papuan Peninsula (Fig. 39). An outlier population from the Cape Nelson Peninsula is unrepresented in our phylogeny but also belongs to this species group. This group is characterized by moderately large to large size (~ 120–160 mm SVL; Fig. 41) and the enlarged femoral/precloacal scales are arrayed in a single long, shallow chevron (Kraus 2008). This group is poorly studied taxonomically and represents a complex of species, most of which remain to be described. Taxonomic clarification in the group is hindered by a lack of additional specimens from the type locality (Moroka, Papua New Guinea). Our sample includes populations from 130–240 km on either side of the type locality, and it is impossible at present to know if either represents true *C. loriae*, although the population from Fane is the closest to the type locality. Hence, our decision has been to refer to our several, admittedly divergent samples as “cf. *loriae*”. The sister population of *C. serratus* referred to as “sp. West Sepik ABTC 114857” is clearly an undescribed species found on the opposite side of the Central Cordillera from true *C. serratus* (Kraus 2007). On the basis of meeting the morphological definition of this group, *C. derongo*, which is known only from the type locality (Brown and Parker 1973) and is not included in our analysis, may be another member of this species group. However, the characters defining this group (Kraus 2008) may be plesiomorphic within the main Melanesian clade of *Cyrtodactylus*, so they may not accurately reflect historical relationships for *C. derongo*. The *C. loriae* group was previously retrieved as monophyletic by Tallowin et al. (2018) as well (Fig. 3).

***Cyrtodactylus louisidensis* group**

The *louisidensis* group is endemic to the eastern versant of the Papuan Peninsula of New Guinea, the Huon Peninsula of that same island, offshore islands of southeastern New Guinea, and the Solomon Islands (Fig. 39). It includes seven nominal species (Fig. 3) and is defined by its unique combination of moderately large to large size (~ 90–160 mm SVL), a single row of enlarged subcaudals, high numbers (> 35) of precloacal/femoral pores, and only 4–7 dark bands on the body (Kraus 2008; Fig. 42). All members are highly arboreal. Several species within this group were previously identified as the single wide-ranging species, *C. louisidensis* (including populations in Queensland, Australia, cf. Bauer and Henle, 1994). However, Rösler et al. (2007), designated the populations in the Solomon Islands as a distinct species; Kraus (2008) designated populations on New Guinea, Misima Island, Rossel Island, and the D’Entrecasteaux Islands as separate species; and Tallowin et al. (2018) obtained phylogenetic results making clear that the Queensland populations represent members of a separate (*tuberculatus*) species group—a finding repeated here. The phylogenetic results of Tallowin et al. (2018), as well as those here, suggest that at least one additional species from Mt. Pekopekowanana may need to be recognized within the group, but that population is currently represented by only a single specimen, so the issue remains unsettled.

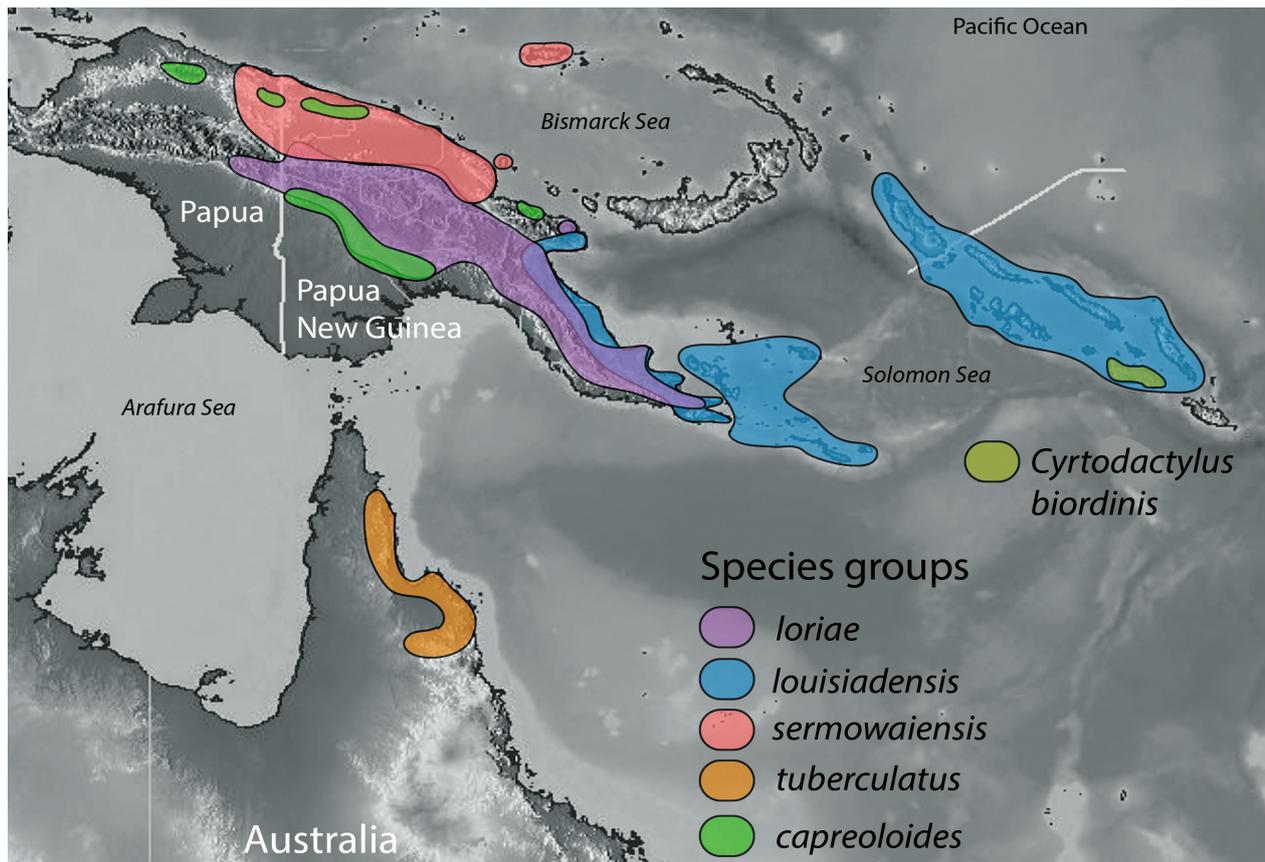


Figure 39. Distribution of the *capreoloides*, *loriae*, *louisiadensis*, *sermowaiensis*, and *tuberculatus* species groups of *Cyrtodactylus* as delimited here and *C. biordinis*.

Within this group, relationships obtained here are identical to those found by Tallowin et al. (2018).

***Cyrtodactylus novaeguineae* group**

The *novaeguineae* group comprises a phenotypically highly heterogeneous group of six recognized species (of which five are represented in the phylogeny) and at least one unrecognized species (Fig. 3) that is widespread across most of lowland New Guinea, with the exception of most of the Papuan Peninsula (Fig. 37). This group comprises two phenotypically divergent clusters of species that do not share obvious morphological characters linking them. One cluster consists of a clade of four recognized species (four included in the tree: *C. novaeguineae*, *C. equestris*, *C. rex*, and *C. zugi*) of large to very large species (120–170 mm SVL), with a relatively small number of dark transverse bands or blotches (< 4) and extensive tuberculation on the throat and beneath the lateral folds (Fig. 43). *Cyrtodactylus irianjayaensis* (not yet sequenced) is grouped within this clade based on its shared large size, elements of color pattern, and throat and ventral tuberculation (Oliver et al. 2008). The second phenotypic cluster within this species group is a paraphyletic grade of much smaller species that share a much higher number of narrow dorsal bands (>7) and widened subcaudal scales. This comprises one recognized species that we have sequenced, one additional undescribed species also sequenced, and likely also *C. aaroni* from north-

western New Guinea, which is morphologically similar to and parapatric with the aforementioned unrecognized species. A further lingering issue with this species group is that samples currently ascribed to *C. novaeguineae* occur across a wide range of southern New Guinea and show extensive phenotypic variation (Oliver et al. 2016); however, genetic data are only available for samples from eastern New Guinea. These eastern specimens occur nearly 1000 km from the type locality of this species in Triton Bay, raising the possibility that true *C. novaeguineae* is not included in the tree presented here.

***Cyrtodactylus sermowaiensis* group**

The *sermowaiensis* group consists of three species (Fig. 3), one of which, *C. atremus*, is morphologically divergent from the other two in its larger size, dorsal pattern, and habits (Fig. 44). The nominate species is distributed across much of the lower elevations of the northern versant of New Guinea, *C. atremus* is endemic to Karkar Island (Kraus and Weijola 2019), and *C. crustulus* is endemic to Manus Island (Oliver et al. 2020; Fig. 39). This group is unique among trans-Wallacean *Cyrtodactylus* in lacking enlarged femoral scales and in males lacking femoral/preloacal pores. The relationships recovered here within this group are identical to those previously obtained by Tallowin et al. (2018) and Oliver et al. (2020). The group is hypothesized to have arisen on the former islands of the South Caroline Arc (Tallowin et al. 2018; Kraus and



Figure 40. Examples of the *Cyrtodactylus capreoloides* group. A. *C. medioclivus* from Southern Highlands Province, Papua New Guinea. Photo by Stephen Richards. B. *C. tanim* from Western Province, Papua New Guinea. Photo by Paul M. Oliver. C. *C. capreoloides* from Southern Highlands Province, Papua New Guinea. Photo by Stephen Richards.

Weijola 2019; Oliver et al. 2020), although the ancestors of *C. atremus* and *C. crustulus* clearly colonized Karkar and Manus islands, respectively, via trans-oceanic dispersal, due to the recent geological origins of those islands (Kraus and Weijola, 2019; Oliver et al. 2020).

***Cyrtodactylus tuberculatus* group**

The *tuberculatus* group comprises five allopatric species occurring along the eastern portion of the Cape York Peninsula, in far northeastern Australia (Figs 3, 39). Species in this group are moderately large to large (~100–130 mm SVL), have numerous femoral and precloacal pores (29–64), and typically five brown bands on the body (Shea et al. 2011; Fig. 45). The nominate species had long been included in the synonymy of *C. louisidensis* (Bauer and Henle 1994), but was later reinstated as a valid species, along with several newly named relatives (Shea et al. 2011). The phylogenetic results of Tallowin et al. (2018) made clear that *C. tuberculatus* and its Australian

relatives were not, in fact, closely related to the *C. louisidensis* group, a finding duplicated here. The *tuberculatus* group is the only lineage of the Melanesian *Cyrtodactylus* radiation restricted to saxicoline habitats, which have likely functioned as evolutionary refugia from expanding arid conditions in northern Australia (Wilmer and Couper 2015). The absence of *Cyrtodactylus* in the savannahs of both northern Australia and southern New Guinea provides further evidence that these habitats are unacceptable for this genus.

Cyrtodactylus deveti

This moderately sized *Cyrtodactylus* from Halmahera Island, Indonesia (Brongersma 1948) has a robust build, color pattern consisting of large indistinct blotches, and a high number of femoral and precloacal pores (18–23). These characters suggest it is likely allied to taxa in the Melanesian radiation of *Cyrtodactylus* rather than other species in the Maluku region; however, molecular phy-



Figure 41. Examples of the *Cyrtodactylus loriae* group. A. *C. serratus* from Gulf Province, Papua New Guinea. Photo by Stephen Richards. B. *C. serratus* from Western Province, Papua New Guinea. Photo by Stephen Richards. C. *C. cf. loriae* Fane from Central Province, Papua New Guinea. Photo by Fred Kraus. D. *C. cf. loriae* Bunisi from Milne Bay Province, Papua New Guinea. Photo by Fred Kraus.

logenetic analyses are required to refute or confirm this hypothesis.

Orphaned species

The following five species (Fig. 46) could not be unequivocally placed within a species group because 1) they showed no close relationship to a specific species group (*Cyrtodactylus biordinis*), 2) their sister relationship to a specific species group was not well- or strongly supported by both analyses (*C. rubidus* and *C. badenensis*), or 3) their sister relationship to a specific species was not well- to strongly supported in either analysis (*C. spinosus* and *C. tigroides*). As such, they are treated here as orphaned species (Fig. 3) pending further analyses.

Cyrtodactylus badenensis

Cyrtodactylus badenensis is a highly specialized granite cave-dwelling species known only from a small area in the Ba Den Mountain, Tay Ninh Province of southern Vietnam (Nguyen et al. 2006; Fig. 9). It was not considered a member of the *condorensis* group because it was only supported as the group's sister taxon in the ML analysis (Fig. 3). In order to avoid recognizing a species

group supported by only one analysis, *C. badenensis* is placed outside the *condorensis* group.

Cyrtodactylus biordinis

Cyrtodactylus biordinis is endemic to Guadalcanal Island in the Solomon Islands (Fig. 39) and seems to be unique in the genus in males having two rows of femoral pores (Brown and McCoy 1980). This species was retrieved as distantly related to all other Melanesian and Australian *Cyrtodactylus* in the phylogenetic reconstruction of Oliver et al. (2018) and Tallowin et al. (2018). Results here confirm and extend that finding by placing *C. biordinis* as sister to a large clade of Melanesian and Asian species groups (Fig. 3); however, Tallowin et al. (2018) placed *C. biordinis* sister only to the remaining Melanesian species with higher support values than its placement here as sister to both Melanesian and Asian species. The ancestor of *C. biordinis* clearly crossed Wallace's Line long before the ancestor of all other trans-Wallacean species. It may be the only, relictual survivor of this invasion, or it may be that additional relatives remain to be discovered in the Solomon Islands or New Guinea.



Figure 42. Examples of the *Cyrtodactylus lousiadensis* group. A. *C. epiroticus* from Morobe Province, Papua New Guinea. Photo by Fred Kraus. B. *C. murua* from Milne Bay Province, Papua New Guinea. Photo by Fred Kraus. C. *C. salomonensis* from Guadalcanal, Solomon Islands. Photo by Steve Wilson. D. *C. robustus* from Rossel Island, Milne Bay Province, Papua New Guinea. Photo by Fred Kraus.

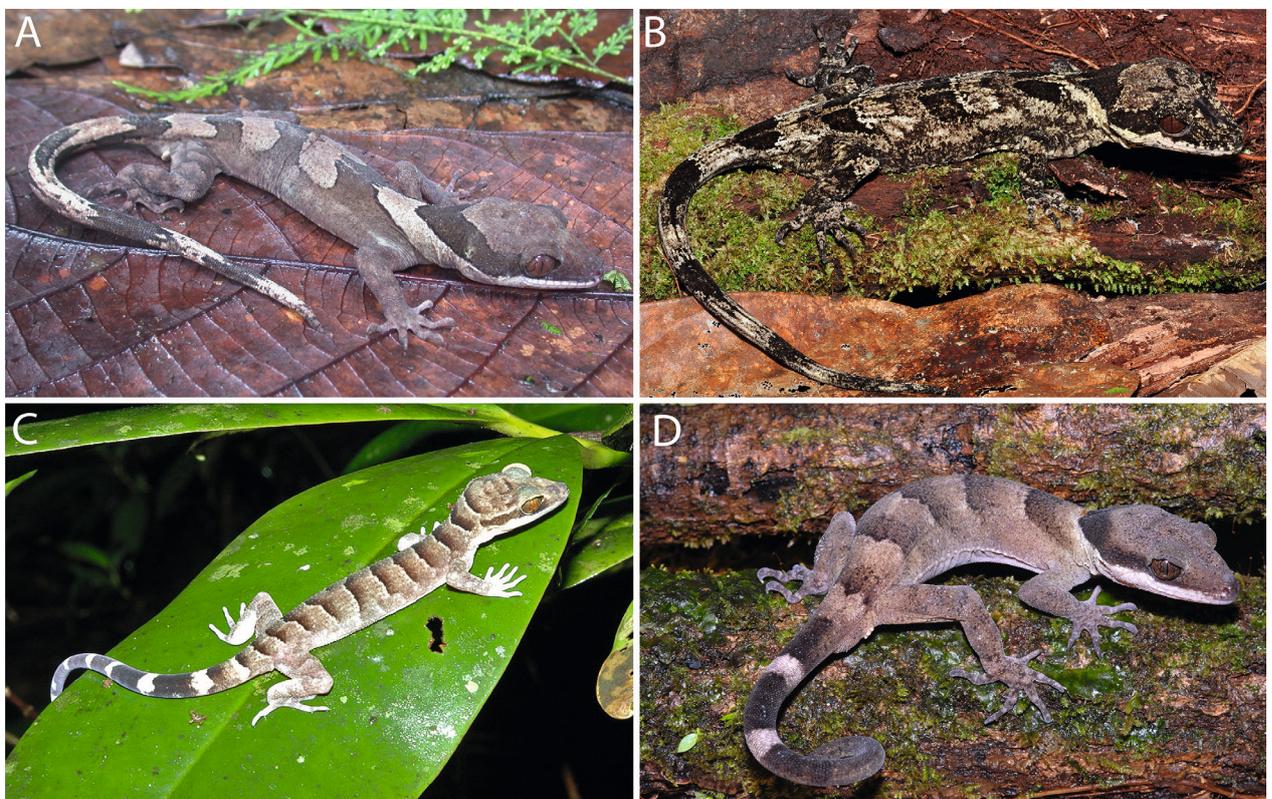


Figure 43. Examples of the *Cyrtodactylus novaeguineae* group. A. *C. equestris* from West Sepik Province, Papua New Guinea. Photo by Fred Kraus. B. *C. rex* from East Sepik Province, Papua New Guinea. Photo by Stephen Richards. C. *C. mimikanus* from Papua Province, Indonesia. Photo by Stephen Richards. D. *C. novaeguineae* from Gulf Province, Papua New Guinea. Photo by Stephen Richards.

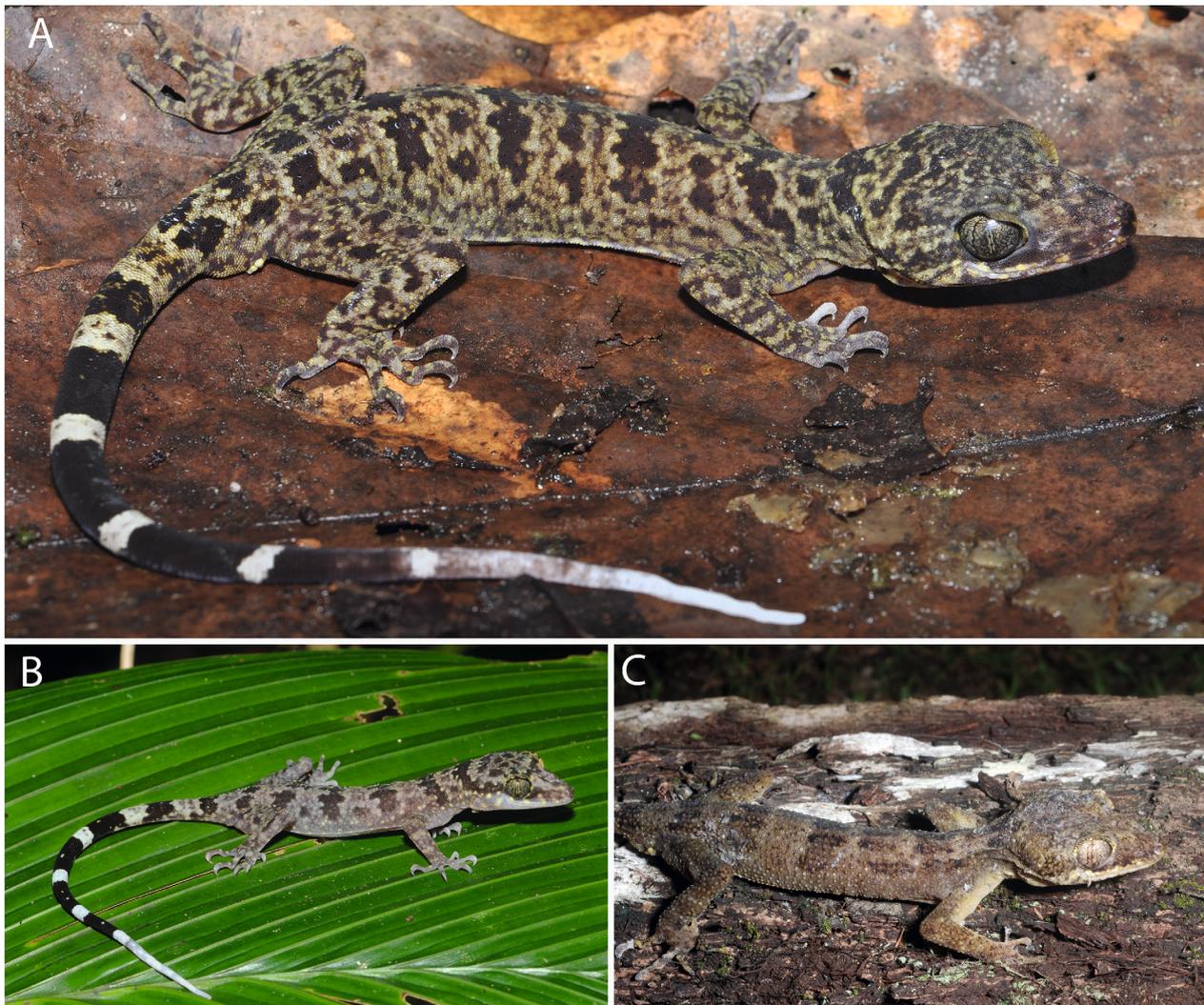


Figure 44. Examples of the *Cyrtodactylus sermowaiensis* group. A. *C. sermowaiensis* from East Sepik Province, Papua New Guinea. Photo by Stephen Richards. B. *C. crustulus* from Manus Island, Manus Province, Papua New Guinea. Photo by Stephen Richards. C. *C. atremus* from Karkar Island, Madang Province, Papua New Guinea. Photo by Fred Kraus.

Cyrtodactylus tigroides

Cyrtodactylus tigroides occurs in a narrow region of western Thailand (Fig. 16) in the karstic habitat of the Sai Yok District near the border of Myanmar (Bauer et al. 2003). Grismer et al. (2018b) recovered *C. tigroides* as the strongly supported sister species of the *C. sinyineensis* group in both the Bayesian and ML analyses. It is recovered here, however as a weakly supported sister species (87/0.43) to the *C. sinyineensis* group (Fig. 3). Based on this, we elect not to include it as part of the *C. sinyineensis* group and leave it orphaned.

Cyrtodactylus spinosus

Cyrtodactylus spinosus is an arboreal species endemic to Sulawesi, Indonesia and known only from the type locality at Lore Lindu National Park, Kecamatan Kulawi, Kabupaten Donggala, Sulawesi Tengah Province and Torompupu Mountain at Desa Limboro, Kecamatan Bana-wa, Tengah, Kabupaten Donggala and Ulu Saddang, Kecamatan Lembang, Kabupaten Pinrang, Sulawesi Selatan

Province (Fig. 7). Although *C. spinosus* was recovered as the well-supported sister species of the *C. malayanus* group in Grismer et al. (2020a), the expanded data set here recover it as poorly supported (60/0.48) and as such, is not considered a part of that group (Fig. 3).

Cyrtodactylus rubidus

Cyrtodactylus rubidus is endemic to, and widespread throughout the Andaman Islands (Chandramouli 2020; Fig. 20). Both analyses recovered it as the sister species to the *lateralis* group of Peninsular Malaysia and Sumatra (Fig. 3) but it was only well-supported in the ML analysis (92/0.86). As such, it was not considered a member of the *lateralis* group even though this makes good biogeographic sense and that it has a body stature and presumably prehensile tail as do *C. durio* and *C. lateralis* of the *lateralis* group (Fig. 21). Chandramouli (in litt, 2020) indicated this species is scansorial and found on forest vegetation and man-made structures. Increased sampling may add stronger support to its current phylogenetic position.

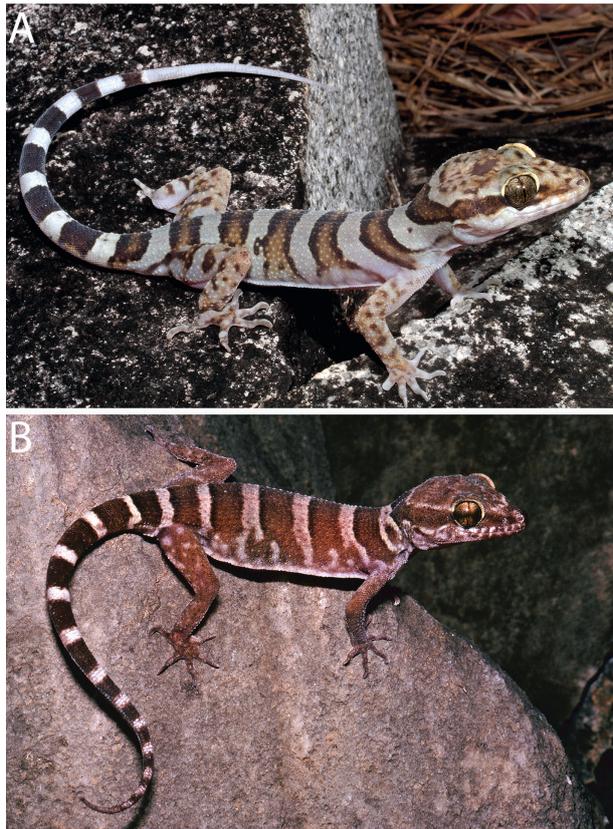


Figure 45. Examples of the *Cyrtodactylus tuberculatus* group. A. *C. tuberculatus* from Queensland State, Australia. B. *C. mcdonaldi* from Queensland State, Australia. Photos by Steve Wilson.

Discussion

As noted above, future integrative taxonomic analyses will benefit substantially from this phylogeny and its partitioning into species groups by serving to focus new species diagnoses and molecular phylogenetic analyses to comparisons with only the relevant, closely related species. It is hoped this analysis will encourage taxonomists to recognize the importance of integrating—when possible—molecular phylogenies with their species descriptions (see Padial et al. 2010; Pante et al. 2015; Streicher and Meik 2018) and using the appropriate genetic markers (in this case at least ND2) so as to increase the accuracy and information content of their proposed classifications. This will also continue to expand and increase the utility of this ever-branching phylogeny.

Comparisons of previous genus-wide phylogenies

Wood et al. (2012) constructed a concatenated tree using ND2, RAG1, PDC, and MXRA5 containing 71 species and Agarwal et al. (2014) followed with a tree generated from ND2, RAG1 and PDC. Agarwal et al. (2014) added additional South Asian species (described and undescribed) to a significantly pruned tree of Wood et al.

(2012), totaling 58 species with which it showed modest topological congruence. Brennan et al. (2017) published a barcoding analysis using CO1 and a limited number of ND2 sequences and 90 species but that inference lacked deep nodal support and was phylogenetically uninformative at that level. Grismer et al. (2020a) published a much larger ND2 tree with 243 species, which is nearly 100% consistent with the ND2 tree here, but their analysis was focused on the evolution of habitat preference.

Below, we compare the congruence of the phylogenies of Wood et al. (2012) and Agarwal et al. (2014) to the ND2 and mito-nuclear trees generated here (Fig. 3) in relation to the species groups designated here. Wood et al. (2012) designated 13 clades that are remarkably consistent with the species groups designated here. Their clade B is equivalent to the lineage composed of the *fasciolatus*, *peguensis*, and *khasiensis* groups and to clade C in Agarwal et al. (2014). Clade C of Wood et al. (2012) is equivalent to the *angularis* group, which is not represented in Agarwal et al. (2014). Clade D of Wood et al. (2012) is equivalent to the *triedrus* group, which is equivalent to the unsupported clade K in Agarwal et al. (2014) and the unsupported *triedrus* group in the mito-nuclear tree here. Clade E in Wood et al. (2012) is equivalent to the *intermedius* group, which also was recovered in Agarwal et al. (2014) but unnamed. Clade F in Wood et al. (2012) is equivalent to the *brevipalmatus* group, also recovered in Agarwal et al. (2014) but unnamed. Clade G in Wood et al. (2012) is equivalent to the *pulchellus* group, also recovered in Agarwal et al. (2014) but unnamed. Clade H in Wood et al. (2012), which includes *C. tigroides*, is equivalent to the *oldhami* group, and was also recovered in Agarwal et al. (2014) but unnamed. Here, however, *C. tigroides* is recovered as an orphaned species not recovered within any species group in the ND2 tree but eligible to be included in the *sinyineensis* group in the mito-nuclear tree here. Clade I in Wood et al. (2012) is equivalent to the Melanesian clade here and in Tallowin et al. (2018) and was recovered in Agarwal et al. (2014) but unnamed. Clade J in Wood et al. (2012) is equivalent to the lineage composed of the *darmandvillei*, *marmoratus*, *lateralis*, *sworderi*, and *agamensis* groups plus *C. rubidus* and was recovered in Agarwal et al. (2014) as clade J. Clade K in Wood et al. (2012) is in part, consistent with the *malayanus* group except for its inclusion of *C. irregularis*, which is recovered here as part of the distantly related *irregularis* group. However, the inclusion of *C. irregularis* in Wood et al.'s clade K, is supported only in their maximum-parsimony analysis. This clade was not represented in Agarwal et al. (2014). Clade L in Wood et al. (2012) is equivalent to the *condorensis* group and represented in Agarwal et al. (2014) but unnamed. Clade M in Wood et al. (2012) is equivalent to the *philippinicus* group, but represented by one species in Agarwal et al. (2014) with ambiguous relationships. The only clades retrieved by Wood et al. (2012) and Agarwal et al. (2014), but not supported in the ND2 and mito-nuclear trees here, are their clades A, which recover *C. tibetanus* as the strongly supported sister species to the rest of *Cyrtodactylus*. *Cyrtodactylus tibetanus* is strongly supported

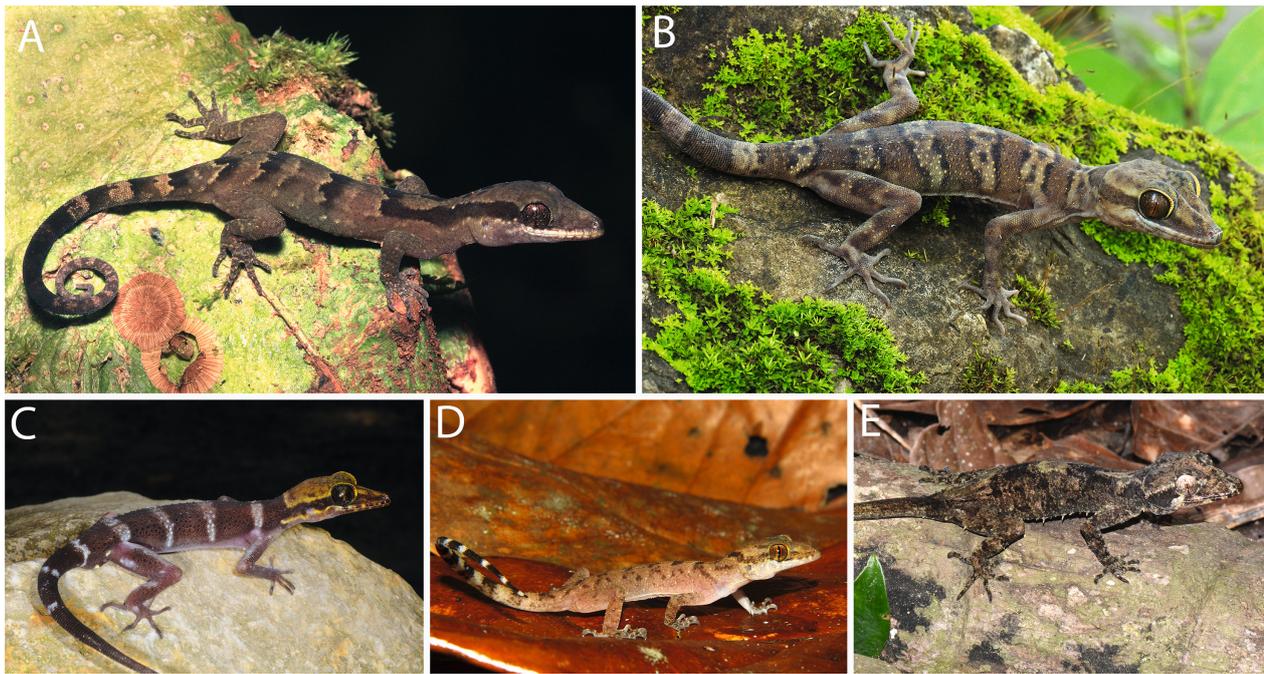


Figure 46. Orphaned species in the phylogeny of *Cyrtodactylus*. A. *C. biordinis* from Guadalcanal Island, Solomon Islands. Photo by Scott L. Travers. B. *C. tigroides* from Kanchanaburi Province, Thailand. Photo by L. Lee Grismer. C. *C. badenensis* from Tay Ninh Province, Vietnam. Photo by Nikolay A. Poyarkov. D. *C. rubidus* from Little Andaman, Andaman Islands, India. Photo by S. Harikrishnan. E. *C. spinosus* from Sulawesi, Indonesia. Photo by Awal Riyanto.

in the ND2 (99/1.00) and mito-nuclear (UFB 99) trees as being the sister species to the remaining species in the *lawderanus* group (but see above).

The consistency between Wood et al. (2012) and the ND2 and mito-nuclear trees here is largely the result of the ND2 data. Wilmer and Couper (2015) and Grismer et al. (2020a) constructed concatenated nuclear trees from the data of Wood et al. (2012) and noted that they were little more than large polytomies that did not change the support or increase the resolution at any of the deep nodes. Nor did the nuclear and ND2 trees consistently converge on the same relationships among the shallower nodes in Wood et al. (2012) or here. Although the vastly increased species sampling here resulted in close concordance of the ND2 and mito-nuclear trees, this too is largely the result of the 100% complete species sampling (310) of the ND2 dataset, with only 10.8% missing sequence data, whereas as in the mito-nuclear tree, only 112 species were represented by nuclear data resulting in 56.9% missing sequence data with 64% of those species missing those data. This is not to say that the nuclear data are uninformative. To the contrary, their weak backbone support subtending very short branch lengths (Fig. 3B) is evidence of clades that may have radiated so rapidly throughout the evolution of this genus that their relationships could not be recovered by these relatively more slowly evolving nuclear genes.

Conservation

As measures to conserve landscapes and species are urgently progressing in this era of biodiversity crisis and

climate change (Dawson et al. 2011; Sgro et al. 2011; Luque et al. 2018; Nunez et al. 2019; Tittensor et al. 2019), it is becoming clear that phylogenetic principles have been emerging as a cornerstone of such endeavors (Erwin, 1991; Vane-Wright et al. 1991; Williams et al. 1991; Vázquez and Gittleman 1998; Moritz et al. 2000; Forest et al. 2007; Harvey et al. 2011; Sgro et al. 2011; Rolland et al. 2012; Winter et al. 2012; Shaffer et al. 2015; Beaumont and Wang 2019; Fay et al. 2019; Holderegger et al. 2019). Successful conservation programs not only turn on the simple understanding of what species exist (i.e., taxonomy) and how they are distributed across a landscape (Mace 2004), but they are becoming more informed by robust evolutionary analyses. Well-supported phylogenies can provide an evolutionary platform for a wide range of comparative ecological analyses that can be integrated with conservation measures (Fisher and Owens 2004; McCartney-Melstad and Shaffer 2015; Shaffer et al. 2015). This enables researchers to identify species-rich landscapes and habitats with current and historically high rates of speciation and genetic diversity and target them for protection. Phylogenies of large, widely ranging, ecologically diverse lineages that extend across a broad range of environments, such as *Cyrtodactylus*, are particularly useful in this regard. They not only help to inform researchers as to which regions and habitats have high degrees of endemism, but they indicate where clades have independently radiated across certain landscapes (Vane-Wright et al. 1991; Nee and May 1997; Moritz et al. 2000), thus identifying those regions as centers of speciation that should bear higher conservation priority (Sgro et al. 2011; McCartney-Melstad and Schaffer 2015; Shaffer et al. 2015; Grismer et al. 2020a).

This is especially true for the species groups of *Cyrtodactylus* that contain an unprecedented number of isolated, and in many cases, narrow-range endemics. Species and populations such as these cannot readily disperse when conditions become unfavorable because they are often confined to small, ecologically restrictive or discontinuous habitats (Harvey et al. 2011). Thus, management plans should aim to protect landscapes and habitats where the evolutionary potential of these small populations can also be conserved (Sgro et al. 2011). Robust phylogenies within the species groups will help serve that purpose. Such phylogenies have already underscored the importance of karstic landscapes as not only regions of refuge and narrow-range endemism in *Cyrtodactylus*, but as foci of speciation for the largest independent radiations in the genus—the *angularis* group and the lineage comprising the *linnwayensis*, *intermedius*, *sadansinensis*, *yathepyanensis*, *oldhami*, *sinyineensis*, and *chauquangensis* groups (Grismer et al. 2020a). And in Myanmar, this has resulted in the formal protection of these landscapes and all the species inhabited by them across the taxonomic spectrum (Komerički et al. 2020). The identification of diverse phylogenetic radiations bearing high degrees of narrow-range endemism from other regions and habitats are now more recoverable and will continue to be so as more species are added to the tree.

Nota bene

Some authors may question the utility or even validity of the species groups delineated herein because the groups are not and sometimes cannot be diagnosed (as opposed to defined) with morphological characters—synapomorphic or otherwise. The remarkable range of interspecific variation within—and convergence among—the species in most species groups precludes these groups from *any* morphological diagnosis. However, these monophyletic lineages (i.e., species groups) exist because of the phylogenetic relationships among them and the species they contain. The ability or inability to diagnose these species groups using morphology regardless of the practical implications, is irrelevant—that is to say the reality of their existence (i.e., their monophyly) stands independent of any diagnosis or absence thereof. The conflation of these ontological and epistemological principles has long confounded systematists (Frost and Hillis 1990; Frost and Kluge 1994; Hillis 2019).

Taxonomic vandalism

Taxonomic vandalism—the malicious dismantling of scientific classifications—has become the opiate of the unskilled and unsophisticated. The partitioning of *Cyrtodactylus* into informal species groups renders it vulnerable to this brand of self-glorifying, counter-intellectual malevolence (see Kaiser et al. 2013; Kaiser 2014; Wood et al. 2020b). Until the appropriate plenary action is taken by the International Code of Zoological Nomenclature

(ICZN) to formally invalidate nomenclatural acts derived from such taxonomic malpractice, we recommend, if necessary, ignoring the principle of priority by simply rejecting these unethical machinations. Because no new data are used in the construction of these vacuous classifications, none are necessary to deconstruct them.

We elected not to recognize these species groups as distinct genera or subgenera because of the potential limited utility of a Sanger data set—mito-nuclear or otherwise. The informal designation of these species groups represents robust testable hypotheses based on the data at hand. Had we constructed a formal taxonomy of these species groups, the potential re-sorting of species into different groups following a phylogenomic analysis (now in progress) could be a source of taxonomic instability. The option of designating these species groups as formal taxonomic categories will be revisited following the implementation of a phylogenomic analysis.

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Appendix 1

Table A1. GenBank accession numbers for ND2, vouchers, and locality data of the newly sequenced species used in this analysis. GenBank accession numbers of previously sequenced species, follow their names in Figure 3. Institutional acronyms follow Sabaj-Perez (2014). Non-standard acronyms are AUP = Agricultural University of Phayao, Phayao, Thailand; CBC = Center for Biodiversity, Conservation, Royal University of Phnom Penh, Cambodia; HLM = Herpetology Lab, Moscow State University (tissue samples); and NAP = Nikolay A. Poyarkov, Moscow State University.

Species groups of <i>Cyrtodactylus</i> and vouchers	Locality	GenBank Acc. No.
khasiensis group		
<i>Cyrtodactylus</i> sp. HLM 0310	Ban Mauk, Sagaing, Myanmar	MW713970
angularis group		
<i>C. bansocensis</i> VFU R.2015.20	Ban Soc Village, Bualapha District, Khammouane Province, Laos	MT953469
<i>C. soudthichaki</i> VFU R.2015.18	Phou Hin Poun NPA, Khammouane Province, Laos	KX077905
<i>C. calamei</i> NUOL r-2015-22	Tham Nok Aen region, Thong Xam Village, Hin Nam No NPA, Khammouane Province, Laos	KX064043
<i>C. darevskii</i> ZMMU R-13981-2	Boulapha, Na Home, Khammouan, Laos	MT953478
<i>C. hinnamnoensis</i> TEBR A.2013.89	Hang Toi region, Noong Ma Village, Hin Nam No NPA, Khammouane Province, Laos	KX064045
<i>Cyrtodactylus</i> sp. HLM 0349	Nahin, Khammouan, Laos	MW713944
<i>Cyrtodactylus</i> sp. HLM 0324	Lomyen, Laos	MW713943
<i>C. multiporus</i> ZMMU R13985-1	Nahin, Khammouan, Laos	MT953484
<i>C. sommerladi</i> IEBR A.2015.37	Hang Toi region, Noong Ma Village, Hin Nam No NPA, Khammouane Province, Laos	MT953490
<i>Cyrtodactylus</i> sp. HLM 0353	Kon Tum Province, Vietnam	MW713946
<i>C. teynieii</i> KM2012.14	Khammouane Province, Laos	MT953496
marmoratus group		
<i>Cyrtodactylus</i> sp. HLM 0371	Indonesia, Java, Ujung Kulon	MW713945
philippinicus group		
<i>C. sp.</i> Borneo HLM 0313	Borneo	MW713957
philippinicus irregularis group		
<i>C. cryptus</i> HNN 89.14	Hin Nam No NPA, Khammouane Province, Laos	KX064038
<i>C. kingsadai</i> IEBR A.2013.3	Dai Lanh Cape, Tuy Hoa District, Phu Yen Province, Vietnam	MT953483
<i>Cyrtodactylus</i> sp. HLM 0316	Kon Ka Kinh, Gia Lai, Vietnam	MW713951
<i>Cyrtodactylus</i> sp. HLM 0365	Kon Ka Kinh, Gia Lai, Vietnam	MW713950
<i>Cyrtodactylus</i> sp. HLM 0366	Chu Mom Ray, Kon Tum Province, Vietnam	MW713954
<i>Cyrtodactylus</i> sp. HLM 0354	Kon Tum Province, Vietnam	MW713955
<i>Cyrtodactylus</i> sp. NAP 08781	Song Thanh, Quang Nam Province, Vietnam	MW713949
<i>C. phuocbinhensis</i> KH-Res041	Ninh Thuan, Vietnam	MT953488
<i>C. bidoupimontis</i> VNMN 03375	Nha Trang, Khanh Hoa Province, Vietnam	MT953470

Table A1 continued.

Species groups of <i>Cyrtodactylus</i> and vouchers	Locality	GenBank Acc. No.
<i>C. gialaiensis</i> VNUF R.2017.1	Chu Se District, Gia Lai Province, Central Highlands, Vietnam	MG460299
<i>C. bugiamapensis</i> IEBR A.2011.3B	Bu Gia Map NP, Binh Phuoc Province, Vietnam	MT953473
triedrus group		
<i>C. soba</i> DMSSK 124	Knuckles Forest, Matale District, Sri Lanka	MW713938
<i>C. fraenatus</i> DMSSK 046	Gannoruwa Forest, Kandy District, Sri Lanka	MW713940
<i>C. ramboda</i> DMSSK 181	Ramboda Forest, Nuwara Eliya District, Sri Lanka	MW713939
<i>C. triedrus</i> DMSSK 011	Dunumadalawa Forest, Kandy District, Sri Lanka	MW713937
<i>C. cf. triedrus</i> DMSSK 180	Knuckles Forest, Matale District, Sri Lanka	MW713941
<i>C. yakhuna</i> DMSSK 159	Giritale Forest, Polonnaruwa District, Sri Lanka	MW713942
brevipalmatus group		
<i>C. cf. brevipalmatus</i> USMHC 2555	Langkawi Island, Kedah state, Malaysia	MT468899
<i>C. brevipalmatus</i> HLM 0303	Khao Ram Mt., Nakon Si Thammarat, Thailand	MW713959
<i>Cyrtodactylus</i> sp. HLM 0372	Suan Phueng, Ratchaburi, Thailand	MW713960
loriae group		
<i>C. cf. loriae</i> BPBM 18650	Fane, Central Province, Papua New Guinea	MW713976
<i>C. cf. loriae</i> AMS R115469	Yuro, Chimbu Province, Papua New Guinea	MW713975
<i>Cyrtodactylus</i> sp. ABTC 114857	West Sepik Province, Papua Ne Guinea	MW713977
intermedius group		
<i>Cyrtodactylus</i> sp. HLM 0360	Chanthaburi Province, Thailand	MW713966
<i>C. cf. intemedius</i> HLM 0362	Khao Yai, Nakhon Ratchasima Province, Thailand	MW713965
irregularis group		
<i>Cyrtodactylus</i> sp. Kon Ka Kinh HLM 0316	Kon Ka Kinh N.P., Gia Lai, Vietnam	MW713951
<i>Cyrtodactylus</i> sp. Kon Ka Kinh HLM 0365	Kon Ka Kinh N.P., Gia Lai, Vietnam	MW713950
<i>Cyrtodactylus</i> sp. Chu Mom Ray HLM 0366	Chu Mom Ray N.P., Kon Tum, Vietnam	MW713954
<i>C. taynguyenensis</i> HLM 0337	Mang Canh, Kon Tum, Vietnam	MW713953
<i>Cyrtodactylus</i> sp. Kon Tum HLM 0354	Kon Plong, Kon Tum, Vietnam	MW713955
<i>Cyrtodactylus</i> sp. Song Thanh NAP 08781	Song Thanh N.P., Quang Nam, Vietnam	MW713949
<i>C. sangi</i> HLM 0311	Cam Ranh, Khanh Hoa, Vietnam	MW713956
<i>C. cf. irregularis</i> Loc Bac HLM 0367	Loc Bac, Lam Dong, Vietnam	MW713952
<i>Cyrtodactylus</i> sp. Loc Bac HLM 0368	Loc Bac, Lam Dong, Vietnam	MW713978
<i>C. cf. zieglerei</i> HLM 0305	Yok Don, Dak Lak, Vietnam	MW713963
<i>C. zieglerei</i> HLM 0345	Chu Yang Sin N.P., Dak Lak, Vietnam	MW713968
<i>C. cattienensis</i> UNS 0389	Ta Kou N.P. Bin Thuan, Vietnam	MF169956
<i>C. cf. cattienensis</i> NCSM 80366	Ta Kou N.P. Bin Thuan, Vietnam	MW713947
<i>C. cf. cattienensis</i> NCSM 80370	Phan Son Commune, Binh Thuan, Vietnam	MW713948
<i>C. phnomchiensis</i> CBC 3003	Prey Lang Wildlife Sanctuary, Phom Chi, Kampong Thom, Cambodia	MT066405
oldhami group		
<i>C. zebraicus</i> HLM 0344	Krabi, Mueang Krabi, Thailand	MW713971
<i>C. cf. saiyok</i> HLM 0334	Suan Phueng, Ratchaburi Province, Thailand	MW713964
<i>C. saiyok</i> MS 484	Ratchaburi Province, Thailand	MW713974
<i>C. cf. oldhami</i> HLM 0307	Suan Phueng, Ratchaburi Province, Thailand	MW713967
<i>Cyrtodactylus</i> sp. HLM 0358	Krabi, Trang Province, Thailand	MW713969
<i>C. sanook</i> AUP 00571	Ninh Thuan Province, Vietnam	MW713973
sinyineensis group		
<i>C. inthanon</i> AUP 00154	Doi Inthanon, Thailand	MT550625
chauquangensis group		
<i>C. taybacensis</i> IEBR4379	Ca Nang Village, Ca Nang Commune, Son La Province, Vietnam	MT953495
<i>Cyrtodactylus</i> sp. HLM 0357	Moe Cham Pae, Mae Hong Son, Thailand	MW713961
<i>C. erythropros</i> AUP 00772	Moe Cham Pae, Mae Hong Son, Thailand	MW713958
<i>C. dumnuui</i> AUP 00768	Chiang Dao, Chiang Mai, Thailand	MW713972
<i>C. wayakonei</i> ZFMK 91016	Kao Rao Cave, Ban Nam Eng, Vieng Phoukha District, Luang Nam Tha, Laos	MT953498
<i>C. sonlaensis</i> IEBR A.2017.1	Muong Bang Commune, Phu Yen District, Son La Province, Vietnam	MT953492
<i>C. huongsonensis</i> IEBR A.2011.3A	Huong Son, My Duc District, Ha Noi, Vietnam	MT953481

Table A1 continued.

Species groups of <i>Cyrtodactylus</i> and vouchers	Locality	GenBank Acc. No.
<i>C. soni</i> IEBR R.2016.4	Da Han Village, Gia Hoa Commune, Van Long Wetland Nature Reserve, Gia Vien District, Ninh Binh Province, Vietnam	MT953491
<i>C. spelaeus</i> HLM 0315	Kasi, Vientiane, Laos	MW713962
<i>C. chauquangensis</i> NA2016.1	Quy Hop District, Nghe An Province, Vietnam	MT953475
<i>C. vilaphongi</i> IEBR A.2013.103	Luang Prahang District, Luang Prahang Province, Laos	MT953497
<i>C. cucphuongensis</i> CP 17.02	Cuc Phuong NP, Ninh Binh Province, Vietnam	MT953475
<i>C. puhuensis</i> ND 01.15	Pu Hu, Thanh Hoa Province, Vietnam	MT953489
<i>C. bobrovi</i> IEBR A.2015.29	Ngoc Lau Commune, Ngoc Son – Ngo Luong NR, Lac Son District, Hoa Binh Province, Vietnam	MT953471
<i>C. otai</i> TBU 2017.2	Na Bai Village, Chieng Yen Commune, Xuan Nha NR, Van Ho District, Son La Province, Vietnam	MT953486